

# A population matrix model and population viability analysis to predict the fate of endangered species in highly managed water systems

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## Keywords

*Ambystoma mexicanum*; axolotl; carp; declining amphibians; restoration; tilapia; Xochimilco.

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## Abstract

Matrix models and population viability analysis (PVA) have become useful tools to understand population attributes and dynamics. Demography analysis gives valuable information for the management of threatened species, and can be used to create action plans for their conservation. PVA is particularly useful in those species with small population sizes difficult to sample. By calculating the individual fate of each member of the population, PVA simulates temporal population changes and estimates extinction risk over a time period. Here we use these models to analyse the population of axolotl *Ambystoma mexicanum*, which has decreased more than six times within only 5 years. Its natural environment (the Xochimilco aquatic system within Mexico City) has deteriorated significantly in the last decades. The matrix analysis showed large oscillations in the axolotl population growth rate (damping behaviour), which could explain the fast density reduction in only few generations. Younger ages (eggs and larvae) showed the highest sensitivity and elasticity values, suggesting that the lack of food sources such as zooplankton or the increased predation by exotic carp and tilapia are capable to reduce axolotl density. PVA shows low extinction probabilities using laboratory data for younger ages. However, a small reduction in egg or larvae survival rate is capable to increase extinction probabilities to 100% in 20 years. Based on these results, we found that the best strategy to restore the axolotl population is to increase the survival rate of eggs and larvae by restoring the habitat, eradicating introduced fish and improving water quality, rather than implementing a reintroduction programme.

## Introduction

Amphibian declines are now a major concern for many ecologists, policy makers and conservation agencies (Biek *et al.*, 2001). A broad analysis suggests that the possible causes of the decline are related to anthropogenic actions such as habitat destruction, disease, species introduction, exploitation or global warming (Beebee & Griffiths 2005; Pounds *et al.*, 2006). However, the apparent decline of some amphibian species could also be the result of high population fluctuations related to their population attributes (Alford, Dixon & Pechmann, 2001). In these cases, the analysis of these attributes is imperative in order to elucidate the fate of an endangered population in an intensively managed system, by knowing which age classes are more vulnerable to modifications, and consequently, to identify major threats for a particular population.

Matrix models have become a useful tool to understand population attributes and dynamics (Caughley, 1994). The

information obtained from a matrix analysis helps to elucidate the relationship between population structure and changes in population size over time. Also, simulations based on matrix models create scenarios of the population behaviour under different environmental conditions (Smith & Trout, 1994). Therefore, matrix models are useful to evaluate population conditions and to understand the effect of particular threats on different age classes. This tool also helps to estimate the effectiveness of different strategies employed to restore endangered populations based on the increment of survival rates by habitat transformation and the increment of population number by individual translocation or artificial breeding (Hunter, 1996).

Ideally, the construction of a matrix needs data obtained from large populations. However, the population sizes of threatened amphibians are frequently small. Thus, other approaches such as random population variation can be more useful (Heppel, Caswell & Crowder, 2000). Random population variation can affect the vital rates of natural

populations and demographic projections using stochastic models may be very different from those obtained from deterministic ones (Boyce *et al.*, 2006). Basic matrix models are deterministic, that is the mathematical properties are fixed and do not change unless the vital rates are modified. Randomness can have a small role in such models only when vital rates are evaluated (Caswell, 2001). This is not the case for populations with a few individuals, in which random catastrophic events can extinguish a healthy but small population (similarly to the way that an allele can be fixed or eliminated by genetic drift). A technique developed for studying small population dynamics is population viability analysis (PVA), which simulates temporal population changes and estimates extinction risk over a finite time period by calculating the individual fates of each member of the population at different growth periods (Boyce, 1992; Morris, *et al.*, 2002).

Amphibian demographic research using these methods has suggested direct measures for their conservation (Marsh, 2001; Green, 2002; Conroy & Brook, 2003; Schmidt, Feldmann & Schaub, 2004). Therefore, this type of analysis has become crucial for species with low population sizes, small distribution ranges and multiple threats as a result of living in highly altered systems.

An example of this type of species is the Mexican axolotl *Ambystoma mexicanum*, a neotenic salamander endemic to the Mexican High Plateau. Its current distribution comprises only two water bodies: Xochimilco and Chalco. Both systems used to be unified in a vast wetland that covered the basin now occupied by Mexico City and were fed by ground water that reached surface levels in the rainy season (Alcocer-Durand & Escobar-Briones, 1992).

From the first indigenous settlements to the present day, most of the wetland has been reclaimed and destroyed, isolating Xochimilco and Chalco from one another. Now, urban areas surround the remnants of both systems that have modified hydrological dynamics and deteriorated water quality. The water is no longer coming from water springs but from water treatment plants (Solís *et al.*, 2006). Finally, there have been at least 10 fish species introduced (L. Zambrano, pers. obs.). For many years, Chalco was completely desiccated, losing most of its native diversity. All these environmental changes are detrimental to native species, and consequently the axolotl has recently been moved to 'Critically Endangered' under the IUCN Red List. Despite these conditions, the axolotl has been able to survive within Xochimilco with a population density below  $0.006 \text{ org m}^{-2}$  (Graue, 1998). Because there was no census in nature before the mentioned research it is not known if these low densities represent a recent reduction. As it is an important organism for culture and for biological diversity, it is necessary to elucidate the extinction risk of the axolotl as well as the best paths for its conservation within its intensively managed native system.

Here, we construct a matrix model of *A. mexicanum* using data from field samples and from animals raised in experimental tanks placed within the remaining wetland of the Xochimilco area. We analysed the condition in each life

stage of the axolotl population and performed a PVA to get the probabilities of extinction of the axolotl within Xochimilco.

## Materials and methods

Research was conducted in Xochimilco in the southern portion of Mexico City, a water body based on a seasonal wetland beside a perennial water system formed by 182 km canal web (1 m depth on average). Canal size varies from 3 to 100 m wide and up to 3 km long. Within the canal systems, Xochimilco has urban sections, agricultural and cattle areas (Solís *et al.*, 2006). The body of water is typical of a tropical high mountain system (2200 m a.s.l.) with large changes in water temperature during the day (from 11 to 20 °C, L. Zambrano, pers. obs.) and marked seasonality, rainy from June to October and dry from November to May, capable of modifying water quantity and quality.

## Sampling

Axolotls were sampled from 8 AM to 1 PM for three seasons in a 2-year period: January–April 2002 (collecting once a week), September–November 2002 (collecting once a week), and March–November 2003 (collecting every other week). In each sampling season, 62 channels and eight lakes were covered. This resulted in 50 collecting sessions over the 2-year period. Each channel was treated as a transect, with a sampling point established every 200 m. At each point one throw of a traditional 'throw-net' or 'atarraya', 5.8 m diameter and 1/2 in. mesh size, was used. Axolotl density was calculated as the number of animals captured per area sampled within the throw net, which covered  $26.4 \text{ m}^2$  on each throw. Each axolotl collected was weighed (g), measured for total length (TL; mm) and released at the point of capture.

## Matrix model construction

Demographic analysis stems from the calculation of vital rates (i.e. fecundity and survival for each age category). In species with cryptic life histories, such as the axolotl, the calculation of vital rates by direct observation is problematic and data must be obtained from different sources such as laboratory studies or previously published works.

Axolotl fecundity ( $F_{ij}$ ) was estimated using data from the mean oviposition value of 14 females in laboratory conditions. Size-specific fecundity was estimated using a regression of the number of eggs produced versus female size.

To obtain the survival rate of hatchlings in the first year we followed 14 females lay for 12 months. Egg lays were placed in experimental tanks within a rustic laboratory without walls and windows within Xochimilco behind one of the channels. Conditions and food source were emulated by constant water tank replacement with water from the system. Survival rate was measured as the mean proportion of axolotls that reach 1 year of age from the total of organisms hatched.

An estimate of the survival rate of axolotls ( $p_{ij}$ ) older than 1 year was obtained from free-living animals in Xochimilco. First, every organism was classified into a particular age category ( $a_{ij}$ ) by measuring its TL (mm). The age of every size was calculated with a length-age (Bertalanffy, 1960) growth model adjusted with data obtained from the average of 25 axolotls that were measured every 2 days from hatchlings to 7 months old in the tanks in Xochimilco. The growth curve was tested with two sets of seven axolotls each. One set comprised animals that were cultivated in controlled conditions of both temperature ( $= 21^\circ\text{C}$ ) and food (*Daphnia* every 3 days). The survival probabilities of each individual of one age category ( $j$ ) to the next one ( $j+1$ ) was estimated with the rate  $N(j+1)/N(j)$ . This is only valid under the assumption that the size structure in natural conditions is stable.

### Projection matrix

Population dynamics were simulated with

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

where  $\mathbf{n}_{(t)}$  is the vector of proportions for each age category at time ( $t$ ) and  $\mathbf{A}$  is the Leslie matrix, containing transition probabilities from one age category to the other ( $p_{ij}$ ) and fecundity values of each category ( $F_{ij}$ ). Each element of  $\mathbf{A}$  is represented as  $a_{ij}$ .

Population asymptotic properties can be obtained with

$$\mathbf{A} \times \mathbf{n}^* = \lambda \times \mathbf{n}^* \quad (2)$$

where  $\mathbf{n}^*$  is the population's stable proportion vector and  $\lambda$  is the growth rate. At  $\lambda < 1$  the population decreases,  $\lambda > 1$  the population increases and  $\lambda = 1$  the population does not change. The power method was used to obtain  $\lambda$  and  $\mathbf{n}^*$  (Caswell, 2001).

### Sensitivity and elasticity analysis

Matrix sensitivity and elasticity were also explored to indicate how changes in variables such as the survival rate in each class affects the obtained matrix demographic indices (Caswell, 2001).  $\mathbf{A}$  values are directly related to the population dynamics and to  $\lambda$ , so any change in  $a_{ij}$  is reflected in demographic vital rates. The sensitivity of a matrix relates changes in  $a_{ij}$  to variations in the growth rate. Each matrix value is associated with a sensitivity value:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i \cdot w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (3)$$

where  $s_{ij}$  is the sensitivity of element  $a_{ij}$ ,  $v_i$  is the  $i$ th element of the reproductive value vector (left dominant eigenvector),  $w_j$  is the stable proportion of age class  $j$  and  $\langle \mathbf{w}, \mathbf{v} \rangle$  is the scalar product of both vectors. A higher influence of  $a_{ij}$  on growth rates means higher  $s_{ij}$  values.

Values of  $p_{ij}$  lie between 0 and 1, while values of  $F_{ij}$  only have zero as a lower limit. The relation of  $\log(a_{ij})$  to changes in  $\log(\lambda)$  is the matrix elasticity, in which entries are proportions and can be summed to add one (de Kroon

*et al.*, 1986). Elasticity values ( $e_{ij}$ ) show the proportional effect of a fluctuation in  $a_{ij}$  on the growth rate:

$$e_{ij} = \frac{a_{ij}}{\lambda} \times \frac{\partial \lambda}{\partial a_{ij}} \quad (4)$$

### Bootstrap resampling methods

Statistics for the growth rate and elasticities were obtained by choosing at random an element  $a_{ij}$  of  $\mathbf{A}$  and modifying its value in a range from 0 to 10% (also chosen randomly) in order to get a new matrix  $\mathbf{A1}$ , from which  $\lambda$  and elasticities were recalculated. This process was repeated 1000 times to get the average values, standard errors and confidence intervals. Intensive resampling methods are a good option for analysing data with unknown statistical distributions (Dixon & Pechmann, 2005).

### Environmental restoration and organism reintroduction simulations

The effect of environmental modification on the axolotl survival rate was simulated by modifying the transition values of eggs to 1-year individuals ( $a_{21}$ ) and of 1-year to 2-year individuals ( $a_{32}$ ). The original value ( $a_{21} = 0.0015$ ) was modified upwards three times with an increment of 0.0003 and four times downwards, by the same value each time. The other transition ( $a_{32} = 0.7972$ ) was increased four times and decreased five times by the amount of 0.03 each time.

Reintroduction of individuals into the population was simulated with  $\mathbf{A} \times \mathbf{H} \times \mathbf{n}_{(t)} = \mathbf{n}_{(t+1)}$ , a formula originally proposed for harvesting (Caswell, 2001). In its original form  $\mathbf{H}$  (the harvest matrix) has values from 0 to 1 in the diagonal, which show the percentage of extraction in each age category, and zeros in the other entries. Diagonal values higher than one simulate reintroduction rather than harvesting. Reintroduction rates of eggs and 1-year individuals were simulated simultaneously. Percentages of reintroduction from the total population explored for each category were 2, 4, 6, 8 and 10%.

### PVA

We performed a PVA to quantify the extinction probability of axolotls in Xochimilco. Contrary to basic demographic models that simulate temporal population changes through the application of  $a_{ij}$  to the size of each age category, PVA models are based on stochastic demography, which relies on the application of  $a_{ij}$  to each individual of the population. That is, population size at  $(t+1)$  is the result of evaluating the probability  $P$  that each individual will survive to the next time unit, and  $1-P$  is the individual probability of death. Because both survival and fecundity rates are considered as probabilistic processes for each individual, the population dynamics results are different from traditional projection analysis. These new assumptions allow for the possibility

of a small population to become extinct by pure chance alone.

Intensity of fecundity events ( $F_{ij}$ ), the proportion of reproductive individuals in each age category and  $p_{ij}$  were used as parameters to build a multinomial cumulative distribution. This summarizes the probability of occurrence of the possible fates for each individual in each age category. Two types of distributions were constructed. The first distribution is made from the sum of all the fates ( $p_{ij}$ ) corresponding to an age category, including death. The value of each  $p_{ij}$  in the sum is equivalent to the probability of occurrence of that fate. The particular fate of an individual is obtained with the location of a random number along the cumulative distribution. If an individual survives, then its reproductive effort is simulated with the second cumulative distribution, which is the sum of the probabilities of occurrence of reproductive events of different magnitude ( $F_{ij}$ ), including no reproduction. The fate of an individual is obtained as described above.

Based on these distributions, random numbers were used to simulate the individual fate of each member of the population (Caswell, 2001). Yearly extinction probabilities were calculated for 50 year periods under three scenarios: reduction in half of the survival rate values of every category, an overall reduction in half in fecundity values of every category, or reduction in half of both values of every category. The extinction probabilities over time were calculated by the average of the proportions of 50 model iterations.

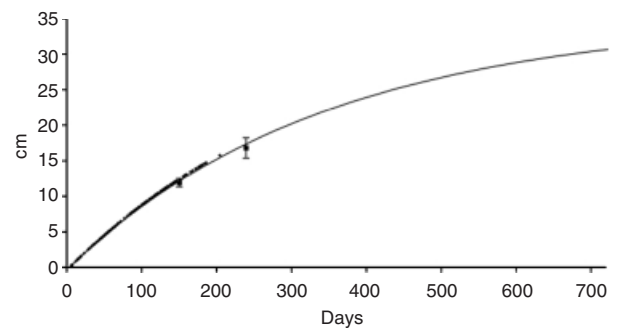
## Results

The axolotl population density was measured as  $0.0012 \text{ org m}^{-2}$ , almost six times lower than previous sampling results using the same technique (Graue, 1998). Based on the von Bertalanffy growth curve, axolotls have a fast increase in size during the first year, achieving up to 20 cm of TL. Within the second year the axolotl grows close to 10 cm, and the growth rate gets smaller from the third year. The axolotl maximum size ( $L_{\infty}$ ) was determined to be 39.5 cm (Fig. 1). Sizes of all axolotls from the populations in controlled conditions fit properly within the matrix categories. Based on this analysis axolotls collected in Xochimilco seem to be no older than 3 years ( $< 33.5$  cm). Thus, the matrix model was built only for the first 3 years.

## Matrix model

The matrix model showed high mortality during the first year and a large egg production in the second and third years.

$$A = \begin{pmatrix} 0 & 0 & 760.52 & 1000 \\ 0.0015 & 0 & 0 & 0 \\ 0 & 0.7972 & 0 & 0 \\ 0 & 0 & 0.0526 & 0 \end{pmatrix}$$



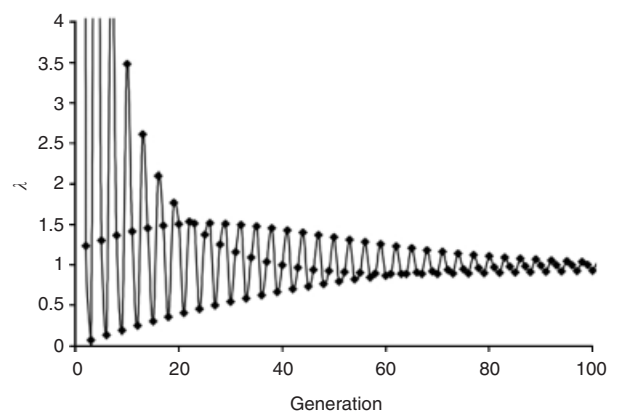
**Figure 1** Von Bertalanffy adjustment model for the size-age relationship of *Ambystoma mexicanum*. Dots are original data and squares are the averages with standard error of the two different experimental populations.

Finite growth rate has high oscillations, or damping behaviour, during many generations (Fig. 2), but once the population is stable it shows a slow depletion ( $\lambda_{\text{average}} = 0.9922 \pm \text{SE } 0.0137$ ). Estimates of survival up to the first year from experimental tanks and field observations clearly show mortality should be higher than these results in nature (c.  $\lambda = 0.70$ ). Therefore, the original matrix value of  $p_{21} = 0.0015$  was systematically modified in order to obtain the growth rate under natural conditions. These simulations indicate that  $P$  value could be three times lower ( $p_{21} = 0.0005$ ).

The sensitivity matrix suggests that  $p_{21}$  has the highest influence on growth rate. Transitions in the following years are the second most influential transitions.

$$S = \begin{pmatrix} 0 & 0 & 0.0004 & 2.38 \times 10^{-5} \\ 185.25 & 0 & 0 & 0 \\ 0 & 0.4156 & 0 & 0 \\ 0 & 0 & 0.4601 & 0 \end{pmatrix}$$

Elasticity analysis also suggests that survival in the first two stages has the highest influence on the proportional



**Figure 2** Variation of the growth rate ( $\lambda$ ) of the *Ambystoma mexicanum* population across generations from iterations of the base population matrix.

variation in growth rate, followed by fecundity in the second year (i.e. age at first reproduction).

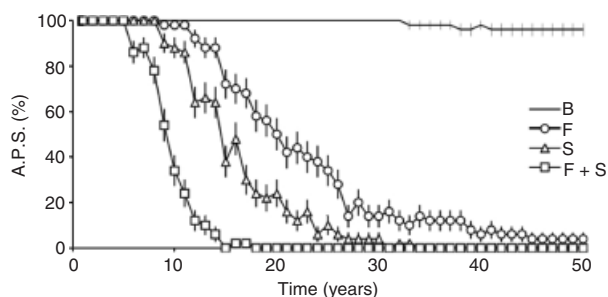
$$e = \begin{pmatrix} 0 & 0 & 0.2965 & 0.0275 \\ 0.3241 & 0 & 0 & 0 \\ 0 & 0.3242 & 0 & 0 \\ 0 & 0 & 0.0275 & 0 \end{pmatrix}$$

## Population viability

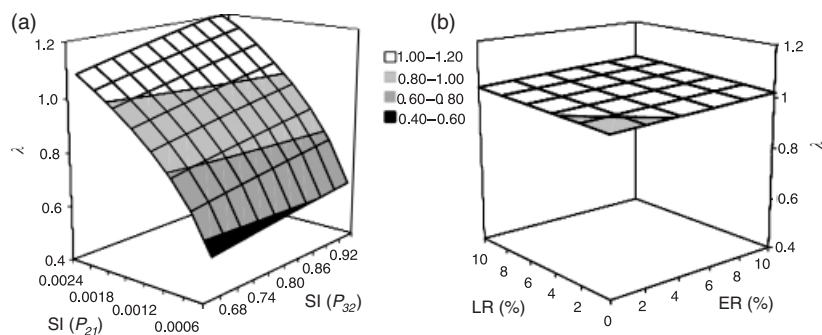
The prediction of the population extinction probability from the matrix model with the original laboratory and field sample data is low. However, a slight decrease in the survival rate or fecundity increases the possibility of extinction (Fig. 3). A small reduction in the survival rate increases the possibility of extinction within 20 years by 70%, while a decrease in fecundity only increases the possibility of extinction by 30%. The probability of extinction is close to 100% in a 50-year period.

## Species management

According to the sensitivity matrix, simulation of better conditions for oviposition and refuge for eggs and juveniles, reflected by an increased survival rate in stages  $P_{21}$  and  $P_{32}$ , showed a rise in population growth rate (Fig. 4a). In fact,



**Figure 3** Extinction probabilities of the *Ambystoma mexicanum* population in 50 years for different demographic models. A.P.S. (%) = Percentage of average population survival. B, basic matrix model; F, reduction in fecundity values; S, reduction in survival probabilities; F+S, reduction in fecundity values and survival probabilities. Vertical lines show standard errors.



**Figure 4** Variation of the growth rate ( $\lambda$ ) of the *Ambystoma mexicanum* population simulating to scenarios: (a) increasing survival rate in the transition from eggs to larvae and larvae to adults, and (b) reintroduction of eggs and 1 year individuals. SI ( $P_{21}$ ) = survival increment at transition 21. SI ( $P_{32}$ ) = survival increment at transition 32. LR (%) = percentage of larval reintroduction and ER (%) = percentage of eggs reintroduction.

just a small increase in the egg survival rate of 3% produces an increase in  $\lambda$  values higher than 1. A matrix simulation of the introduction of axolotls raised in captivity up to the first year also produces an increase in the growth rate. To achieve  $\lambda$  values higher than 1, it is necessarily to introduce more than 8% of the total eggs or juveniles existing within the system (Fig. 4b).

## Discussion

### Population and matrix model

The population size seems to be very small and is composed mainly of 1-year-old individuals. This suggests that predator pressure by introduced carp, tilapia, aquatic birds, snakes and fishing keeps the population size low as in other systems with ambystomids (Hoffman, Larson & Samora, 2004; Reid, 2005; Rubbo, Shea & Kiesecker, 2006). It is also possible that there is not enough suitable habitat for axolotls to survive longer. A short-term survey in 2005 suggested that the abundance might be even lower ( $0.0001 \text{ m}^{-2}$ ) than that reported here. Nevertheless, the abundance of young individuals indicates that the population is successfully recruiting, which is an essential process if the population is to recover.

The matrix model produced a highly oscillatory behaviour, which could be explained by massive reproductive events from few classes. Some years, most of the classes have reproduction activities, leading to a big increase in the growth rate, but the next year most of the organisms are not capable of reproducing and the growth rate is reduced to almost zero. High oscillations in the growth rate could explain the changes in axolotl density in different years. After more than 100 generations, the growth rate stabilizes at a value slightly lower than unity. Therefore, a simplistic analysis of the matrix growth rate values suggests a population of axolotls that are not on the edge of extinction even though densities have been drastically reduced. However, fecundity values were obtained from laboratory conditions, so it is possible that they could be lower in field conditions.

Nevertheless, the axolotl population faces a modified environment, so the demography is unlikely to be the same as that occurring under less restrictive conditions, such as an environment without predators and with a suitable habitat.

For example, the population age structure could be shifted due to predators (Rubbo *et al.*, 2006). Indeed, the maximum age achieved in the lab can be as much as five times higher than that in field conditions. Reproductive categories and egg production in different age classes would also vary, yielding different demographics in different habitats.

As expected, sensitivity and elasticity analyses showed that the growth rate is mainly influenced in early life stages due to high egg and juvenile mortality. The next most important processes are survival to ages two and three. However, it is surprising that the survival rate affects the growth rate more than reproduction pulses.

## PVA

In spite of the apparently bad condition of the axolotl populations, the population viability analysis suggests low extinction probabilities. This is possibly related to the axolotl's great reproductive capacity, which can help a small axolotl population to recover in few generations once the conditions are more favourable to its survival. However, the early stage of the matrix that has the highest sensitivity values was built from experimental tanks where eggs and larvae were free from predators that normally exist in the channels, such as fish or insects. Under normal conditions, it is probable that the survival rate with natural predators such as native fish or insects would be similar to that registered in the experimental tanks. However, exotic tilapia is a proven predator of axolotl larvae in experimental tanks (L. Zambrano unpubl. data). Over the last decade this fish population has exploded within the channels (Valiente Riveros, 2006), and tilapia is now considered a pest, with government programmes designed to reduce its presence in Xochimilco (Zambrano, Reynoso & Herrera, 2003). Therefore, it is highly possible that the survival rate of axolotls in early stages has been reduced in recent years, in which case extinction probabilities increase from 0 to 100% in 20–50 years.

## Population recovery strategies

Numerical simulations show that both reintroduction and environmental modification can stimulate population growth rates to reach values higher than unity. The choice of the best strategy depends on costs and technical feasibility. For example, the matrix model shows that a 3% change of  $P_{21}$  makes  $\lambda$  values higher than unity. To increase the survival rate, the modification of the environment should be related to spatial heterogeneity (Perkins & Hunter, 2006). Although most ambystomids leave their eggs without any parental care (Bruce, 2003), axolotls need a plant structure for egg laying (L. Zambrano, pers. obs.), and many salamander females have a preference for a particular structure or plant specie for egg laying (Thompson, Gates & Taylor, 1980). Preference could be related to an increase in the survival rate of the offspring due to protection and food availability. Therefore, it is possible to increase the survival rate of early axolotl stages by increasing

macrophyte coverage of particular species. This hypothesis must be tested both in the laboratory and in the field.

Reintroduction of eggs and 1-year individuals grown in aquariums also causes  $\lambda$  to grow. Although this strategy may be technically and economically feasible, it must be regularly applied for many years, as it does not intrinsically help the population to grow, as it results in a subsidized population. Further issues associated with reintroduction are related to genetic problems and potential diseases brought to the natural populations from reproductive colonies (Swanson, Peters & Kyle, 2006; Tweed *et al.*, 2006), which could lead to more damage than benefit to the axolotl population in Xochimilco. If this strategy is implemented, diseases and genetic variability must be seriously considered.

From our results we suggest that the species recovery plan should involve habitat management and restoration before any other measure such as reintroduction. The two most important threats axolotls face are related to first stages: habitat transformation, including a drastic modification of riparian habitat due to urbanization, and a population explosion of introduced fish (tilapia *Oreochromis niloticus*), which are predators of axolotl larvae (L. Zambrano unpubl. data). Therefore, to ensure the conservation of this population in the channels of Xochimilco, it is necessary to restore the system considering both threats so as to ensure survival in early stages.

## PVA for endangered species

PVA is an important tool for the management of endangered species and information generated by these models must be considered for conservation policies. These models can be used to predict the fate of a species in short and middle term, but can also help to implement conservation actions on a particular species. These models can be improved with more data, but most endangered organisms such as the axolotl have few and scattered populations, making it difficult to obtain the ideal amount data. The best way to fill the gaps generated by these small populations is by using the available literature, knowing the biology of the species and transforming this information in numbers. It is important to create different scenarios modifying those variables that can be more sensitive in the matrix. Then, it would be possible to test these scenarios experimentally or in the field. This can be a good way to create conservation policies for an endangered organism such as the axolotl.

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## References

- Alcocer-Durand, J. & Escobar-Briones, E.G. (1992). The aquatic biota of the now exticnt lacustrine complex of the Mexico Basin. *Freshwater Forum* **2**, 1–13.
- Alford, R.A., Dixon, P.M. & Pechmann, J.H.K. (2001). Global amphibian population declines. *Nature* **412**, 499–500.
- Beebee, T.J.C. & Griffiths, R.A. (2005). The amphibian decline crisis: a watershed for conservation biology? *Biol. Conserv.* **125**, 271–285.
- Bertalanffy, v.L. (1960). Principles and theory of growth. In *Fundamental aspects of normal and malignant growth*: 137–259. Nowinski, W. (Ed.). Amsterdam: Elsevier.
- Biek, R., Funk, W.C., Maxell, B.A. & Mills, L.S. (2001). What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conserv. Biol.* **16**, 728–734.
- Boyce, M.S., Haridas, C.V., Lee, C.T. & the NCEAS Stochastics Demographic Working Group. (2006). Demography in an increasingly variable world. *Trends Ecol. Evol.* **21**, 141–148.
- Boyce, M.S. (1992). Population viability analysis. *Ann. Rev. Ecol. Syst.* **23**, 481–506.
- Bruce, R.C. (2003). Life histories. In *Reproductive biology and phylogeny of Urodela*: 477–526. Sever, D.M. (Ed.). Plymouth, UK: Science Publishers.
- Caswell, H. (2001). *Matrix population models. Construction, analysis and interpretation*. Chicago: Sinauer.
- Caughley, G. (1994). Directions in conservation biology. *J. Anim. Ecol.* **63**, 215–244.
- Conroy, S.D.S. & Brook, B.W. (2003). Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia. *Popul. Ecol.* **45**, 105–114.
- Dixon, P.M. & Pechmann, J.H.K. (2005). A statistical test to show negligible trend. *Ecology* **86**, 1751–1756.
- Graue, W.V. (1998). Estudio genético y demográfico de la poblacion del amfibio *Ambystoma mexicanum* (Caudata: Ambystomidae) del Lago de Xochimilco. Instituto de Ciencias del Mar y Limnología. UNAM, Mexico.
- Green, D.M. (2002). The ecology of extinction: population fluctuation and decline in amphibians. *Biol. Conserv.* **111**, 331–343.
- Heppel, S., Caswell, H. & Crowder, L. (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* **81**, 654–665.
- Hoffman, R.L., Larson, G.L. & Samora, B. (2004). Responses of *Ambystoma gracile* to the removal of introduced nonnative fish from a Mountain Lake. *J. Herpetol.* **38**, 578–585.
- Hunter, M.L. (1996). *Fundamentals of conservation biology*. Chicago: Blackwell Science.
- de Kroon, H., Plaiser, A., van Groendendael, J. & Caswell, H. (1986). Elasticity: the relative contribution of demography parameters to population growth. *Ecology* **67**, 1427–1431.
- Marsh, D.M. (2001). Fluctuations in amphibian populations: a meta-analysis. *Biol. Conserv.* **101**, 327–335.
- Morris, W., Bloch, P., Hudgens, B., Moyle, L. & Stinchcombe, J. (2002). Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecol. Appl.* **12**, 708–712.
- Perkins, D.W. & Hunter, M.L. (2006). Effects of riparian timber management on amphibians in Maine. *J. Wildl. Mgmt.* **70**, 657–660.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167.
- Reid, I.S. (2005). Amphibian, fish stocking, and habitat relationships in Siskiyoumountain Wilderness Lakes, California and Oregon. *Northw. Nat.* **86**, 25–33.
- Rubbo, M.J., Shea, K. & Kiesecker, J.M. (2006). The influence of multi-stage predation on population growth and the distribution of the pond-breeding salamander, *Ambystoma jeffersonianum*. *Can. J. Zool.* **84**, 449–458.
- Schmidt, B.R., Feldmann, R. & Schaub, M. (2004). Demographic processes underlying population growth and decline in *Salamandra salamandra*. *Conserv. Biol.* **19**, 1149–1156.
- Smith, G. & Trout, R. (1994). Using Leslie matrices to determine wild rabbit population growth and the potential for control. *J. Appl. Ecol.* **31**, 223–230.
- Solís, C., Sandoval, J., Pérez-Vega, H. & Mazari-Hiriart, M. (2006). Irrigation water quality in southern Mexico City based on bacterial and heavy metal analyses. *Nucl. Instr. Methods Phys. Res.* **249**, 592–595.
- Swanson, B.J., Peters, L.R. & Kyle, C.J. (2006). Demographic and genetic evaluation of an american marten reintroduction. *J. Mammal.* **87**, 272–280.
- Thompson, E.L., Gates, J.E. & Taylor, G.J. (1980). Distribution and breeding habitat selection of the Jefferson salamander, *Ambystoma jeffersonianum*, in Maryland. *J. Herpetol.* **14**, 113–120.
- Tweed, E.J., Foster, J.T., Woodworth, B.L., Monahan, W.B., Kellerman, J.L. & Lieberman, A. (2006). Breeding biology and success of a reintroduced population of the critically endangered puaiohi (*Myadestes palmeri*). *Auk* **123**, 753–763.
- Valiente Riveros, E. (2006). Efecto de las especies introducidas en Xochimilco para la rehabilitación del hábitat del ajolote (*Ambysoma mexicanum*). Posgrado en Ciencias Biológicas, UNAM. Mexico DF.
- Zambrano, L., Reynoso, V.H. & Herrera, L.G. (2003). Abundancia y estructura poblacional del axolotl (*Ambystoma mexicanum*) en los sistemas dulceacuícolas de Xochimilco y Chalco, CONABIO. Mexico DF.