



**Analysis of Matrix Models as Tools
for Amphibian Conservation**

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GAKO HITZAK: Sentikortasun analisiak, populazio dinamikak, Amphibians, *Rana temporaria*, *Salamandra lanzai*.

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LABURPENA

Anfibioen gainbehera eta beren populazioen desagerpenari buruz burutu diren ikerketa gehienak, beherakada horien sorburuak indentifikatu eta tamaina neurtzeko programetara zuzenduta daude. Populazio-ereduak ornodun ugarien kontserbazioan orohar erabiltzen badira ere, anfibioekin oraindik oso gutxitan erabiliak izan dira.

Artikulu honetan, bi anfibio populazioaren hazkunde-tasa estimatzeko bi eredu kuantitatiboren erabilera azaltzen da. Lehenengo espeziea baso-igel gorria (*Rana temporaria*) da. European espezie oso arrunta da, eta ingurune ezberdinetako eremuak, latitude zein altitude baxuetatik altuetara, kolonizatzen ditu. Beste espeziea Lanzako arrabioa (*Salamandra lanzai*) da eta hori, berriz, Alpeetako eremu zehatz batean baino ez da aurkitzen. Parametro demografikoak eta biziraupen-tasak nahiko ongi dokumentaturik daude eta sentikortasun-analisen erabilera duela gutxi argitaratu zen bi espezie horientzat: populazioaren hazkundera eragin handien duten parametroak identifikatzeko, adinaren egituraren eredu bat eraiki zen. Ikerketa horietan erdietsiriko emaitza nagusiak aurkeztu eta alderatzen dira eta espezie bakoitzaren kontserbazio-lerroak proposatzeko erabiltzen dira.

SUMMARY

Most research on amphibian decline or losses of populations has focused on programmes to identify the magnitude and range extent of declines in numerous species. Population models are widely used in biological conservation of many vertebrates, but remain very scarce in Amphibians.

In this paper, I exposed the use of quantitative models to estimate the population growth rate in two amphibian species. The first species is the Common frog (*Rana temporaria*). It is widespread in Europe and colonizes various environments, from low to high latitude and altitude. The other species is the Lanza's salamander (*Salamandra lanzai*), which on the contrary is restricted to a very narrow distribution range in the Alps. The vital rates and demographic parameters have been relatively well documented and the application of sensitivity analysis has been recently published in these two species: an age-structured model was built to identify the parameters that mostly influence the population growth rate. The main results obtained in these studies are presented and compared, and used to propose guidelines for conservation in each species.

RÉSUMÉ

La plupart des études sur le déclin des amphibiens ou la disparition de populations se sont concentrées sur l'identification de l'amplitude et de l'étendue de ces phénomènes chez de nombreuses espèces. Les modèles de dynamique des populations sont couramment utilisés en biologie de la conservation de nombreux vertébrés, mais encore rarement pour les Amphibiens.

Dans cet article, je décris l'utilisation de ces modèles quantitatifs pour estimer la croissance des populations de deux espèces d'Amphibiens. La première espèce est la Grenouille rousse *Rana temporaria*. C'est une espèce commune en Europe, colonisant une gamme d'environnement étendue, de la plaine à l'étage alpin. L'autre espèce est la Salamandre de Lanza *Salamandra lanzai*, qui, au contraire, est très localisée dans les Alpes. Les paramètres démographiques et taux de survie sont relativement bien connus, et des analyses de sensibilité ont récemment été publiées chez ces deux espèces, à partir de la construction de modèles structurés en âge, pour identifier les paramètres les plus influents sur la croissance des populations. Les résultats principaux de ces études sont décrits et comparés, et utilisés pour proposer des directives d'actions de conservation pour chacune des espèces.

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INTRODUCTION

Conservation biologists use mathematical tools to analyse population viability mainly in two overlapping goals: estimating population extinction times or probabilities and targeting the best ways to improve population growth (MILLS *et al.*, 1999). The most effective and popular tools for this latter goal is the analysis of matrix population models (CASWELL, 2000a), and especially the calculation of age- or stage-specific sensitivities or elasticities indicating factors (e.g. demographic parameters) that most affect population growth.

Although widely used in mammals and birds (e.g. Caswell, 2000b), population modelling has rarely been used for herpetological conservation problems (GRIFFITH & WILLIAMS, 2000). One explanation could be the lack of demographic data in numerous species. However, an increasing number of population studies provide information on e.g. age, survival or fecundity in several amphibian species and relatively limited demographic information can still be used with generalized quantitative models (BIEK *et al.*, 2002)

In this paper, I am presenting the use of sensitivity analysis to address conservation biology problems in two amphibian species. The first example is the Common frog *Rana temporaria*. This Anuran exhibits a "classical" life cycle with the succession of an aquatic phase (with two stages: egg and tadpole) and a terrestrial phase (with two stages: juvenile and adult). It is a widespread species in Europe, able to colonize low to high latitude and altitude environments. The application of a sensitivity analysis in the Common frog was carried out by Biek *et al.* (2002). The second example is the Salamander of Lanza *Salamandra lanzai*. This Urodela presents a relatively simplified life cycle because it is entirely terrestrial and viviparous. The distribution range of this species is particularly reduced, limited to some mountain slopes in the Southwest Alps. A quantitative model of this species population dynamics was proposed in Andreone *et al.* (in press). The comparison of these two contrasted species will cover characteristics of numerous other amphibian species.

METHODS

The main goal is to identify the demographic parameter and transition rates of the life cycle that most contributed to the population dynamics (e.g. to the increase or decrease in the number of individuals). The first step is to build the life cycle on a time-discrete stage structured basis (e.g. by age, sex,

reproductive status). Secondly, a constant matrix that includes the mean value of demographic rates is built. The matrix analysis yields the deterministic population growth rate λ ($\lambda = 1$ when the population is stationary), population structure, and elasticities. The change of λ due to a given proportional change in a specific stage defines the elasticity of each stage of the vital cycle. Computer software such as ULM (LEGENDRE & CLOBERT, 1995) allows the handling of these time-discrete stage-structured population models.

Matrices and demographic parameter estimates:

Biek *et al.* (2002) constructed a female-based, post-birth pulse lefkovitch matrix with annual projection intervals representing a population with three stages: prejuvenile (embryo, larva, and overwintering metamorph), juvenile, and reproductive adults. The matrix for this life history is shown in figure. 1a. Vital rates, reproductive parameters and transition probabilities were obtained from literature: Embryo survival was 0.92, larval survival was 0.06, metamorph survival was 0.34, juvenile survival was 0.33 and adult survival was 0.43 (embryo, larval, and metamorph survival together encompass the first year of life). Transition probabilities were probabilities to pass from juvenile to juvenile (0.25) and from juvenile to adult (0.08). The probability of laying was 1.0 (all mature female lay eggs), the clutch size was 650 eggs and age at maturity was 3 years old (vital rates and transition probabilities were for female only and all are annual). The fecundity of 650 eggs results of a mean clutch size divided by two (assuming a 1:1 sex-ratio) in order to represent female embryos only.

Andreone *et al.* (in press) constructed a vital cycle including both sexes for the Salamander of Lanza (fig. 1b). Parameters were obtained from literature: Newborn and juvenile annual survival are virtually unknown. It was therefore considered as constant with a mean value of 0.80. Minimum and maximum values of 0.70 and 0.90 were used in simulation for this parameter. An equal production of male and female in each litter (1:1 sex-ratio at birth) was assumed. Age at maturity influenced the transition rate from juvenile to adult stage. Mean age at maturity was 6-8 year old in males and 8 years old in females. Adult survival was 0.98 (without inter sexual difference). The mean litter size was 2.2 young. The mean duration of gestation is 3.5 years. The reproductive system used was monogamy (i.e. one male is the father of all the newborn in one litter).

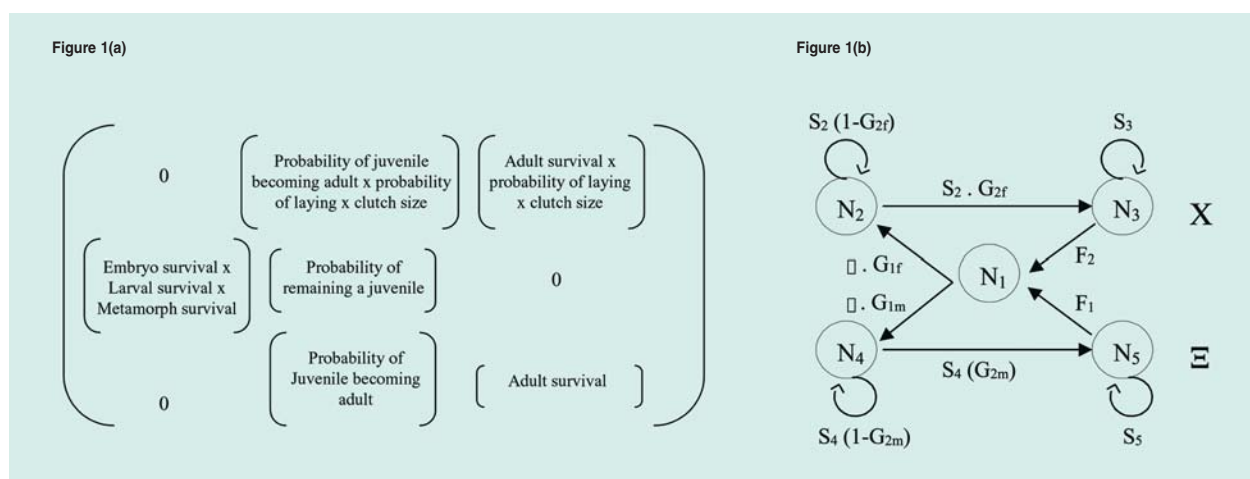


Figure 1(a). Female-based post-birth lefkovich matrice with annual projection intervals representing a population with a life history consisting of three stages: prejuvenile (embryo, larvae, overwintering metamorph), juvenile and reproductive female. This matrix was proposed for the Common frog *Rana temporaria* by Biek *et al.* (2002).

Figure 1(b). Life cycle graph proposed by Andreone *et al.* (in press) for the Salamander of Lanza *Salamandra lanzai*. There are five age-classes (N1 to N5). Each life history parameters and transitions from one age-class to another are described in Methods (adapted from ANDREONE *et al.*, in press).

RESULTS

Life cycle and age-structured model

In the Common frog, Biek *et al.* (2002) defined three age classes (N1 to N3) with specific probability of surviving. The cycle (and estimates of each parameter) was based upon an annual time scale. N1 was the prejuvenile stage (including embryo, larva, and overwintering metamorph), N2 the juvenile stage and N3 the reproductive female stage. The specific survival rate of N1 was embryo survival x larval survival x metamorph survival. During the juvenile life, individuals survive as juvenile (with a probability of remaining a juvenile), or pass onto the following age-stage, e.g. adult. The time spent as a juvenile depends on age at maturity. The specific survival of N3 was female annual survival. Annual contribution to reproduction (and then N1) was female survival x probability of laying x clutch size.

In the Salamander of Lanza, Andreone *et al.* (in press) defined five age classes (N1 to N5) with specific survival. This cycle (and estimates of each parameter) is also based upon an annual time scale. N1 was the newborn stage, N2 the 1-year-old female juvenile stage and N4 the 1-year-old male juvenile stage. The transition rate from N1 to N2 was the product of the sex ratio at birth and the probability of surviving from one year (as newborn) to the following (as 1 year old female juvenile). The transition rate from N1 to N3 was rather similar. During the juvenile life, individuals survive as juve-

niles (with a survival probability of S4 and S2 in juvenile males and females respectively), or pass onto the following age-stage, e.g. adult. The time spent as a juvenile can differ between sexes. This leads to two transition rates, i.e. [S2. (1 - G2f)] staying and surviving as a juvenile or [S2. G2f] passing from juvenile to adult stage. Because age at maturity is high (more than 1 year), G2f on an annual scale is 1/age at maturity per year. S3 and S5 refer to annual adult survival in each sex. F transition rates refer to reproductive parameters, e.g., fecundity (annual number of newborn) and gestation duration. F2 and F1 were the female and male annual contribution to the following stage (e.g., newborn). The gestation period exceeds one year so the female contribution equals $[n/d \cdot \emptyset \cdot 1/d]$ where n was the number of newborn, d gestation was the duration in year and \emptyset was the newborn sex-ratio. The male's contribution to newborn production depends on the reproductive system. During the reproductive season, each male can fecund the complete litter of only one female (monogamy), or of several females (polyandry), or only part of the litter (polygyny). This information is included in the global life cycle of *S. lanzai* because F2 will vary according to the reproductive system of these salamanders.

Simulation and elasticity analysis

In *Rana temporaria*, elasticity analyses were conducted (CASWELL, 2000). Moreover, Biek *et al.* (2002) used life-stage simulation analysis to

estimate the amount of variation in λ explained by the variation in each vital rate (MILLS & LINDBERG, 2002). This approach - based on calculation of λ at stable distribution from replicates - considers the degree of variation (e.g. standard deviation, SD) of each vital rate and reproductive parameter. The results showed that changes in vital rates did not have equal effects on λ . The greatest proportional change in λ results from a change in adult and juvenile survival rates. For life-stage simulation analysis, the most variable vital rate (SD) best explained overall variation in λ , and larval survival had by far the highest value in *Rana temporaria*.

In *Salamandra lanzai*, the first simulation (using ULM software), conducted with the mean parameters, leads to a population growth rate (λ) of 1.03. This result shows that this population was close to stability and that the proposed value of unknown parameters (juvenile survival) was biologically realistic. The asymptotic population age structure was 40% in juvenile (newborn + juvenile of both sexes), and 30% for each adult stages (males and females). The elasticity of a population's growth rate (λ) to a change in demographic parameters (transition rates) is defined as the proportional change in growth rate given a proportional, infinitesimal change in a transition rate, while all other elements remain constant (MILLS *et al.*, 1998). These elasticities were computed for $\lambda = 1$ (e.g., stable population of *S. lanzai*). The annual male survival was the demographic parameter that mostly influenced the growth rate, followed by the juvenile and female survival. The transition rate related to reproduction (e.g., fecundity) contributed clearly less to the population growth rate than adult and juvenile survival parameters.

DISCUSSION

As highlighted by Biek *et al.* (2002) in their comparative analysis of three anuran species, the key results of these analysis was that the elasticity of λ was highest for juvenile or adult survival in all three species studied. A similar result was obtained in two populations of *S. lanzai* differing in altitude and life-history traits such as age at maturity, fecundity and duration of gestation (ANDREONE *et al.*, in press). For example, Biek *et al.* (2002) reported that the 15% reduction in juvenile and adult survival results in an approximately 19% decline in λ . In

comparison, reduction in embryo survival results in a 16% decline in λ .

Both studies highlighted that when λ has a high elasticity to one or more vital rates - juvenile and adult survival in both species - relatively large effects on λ result from small variations of these rates. On the other hand, an equivalent variation in λ can also be caused by a large variation in a rate of low elasticity (e.g. embryo survival, fecundity, etc.). Finally, cumulative effects - e.g. simultaneous variation of several vital rates with low elasticities - can also lead to large variations in λ .

The knowledge of this relative importance of vital rates in amphibian population dynamics is of course a main guideline for conservation. Preventing perturbations in post-metamorphic vital rates is clearly a priority in e.g. *Rana temporaria*, and other species with similar life-history traits. This also argues to continue research effort for good quantitative estimations of the life-history traits (mean, highest and lowest values).

In *Salamandra lanzai*, the sensitivity analysis was used to classify problems in term of risk (ANDREONE *et al.*; in press). The first one concerns the small distribution range of the species. The second main problem concerns the loss or alteration of the habitat. The analysis highlights the importance of adult survival on population dynamics and every factor, which could decrease this parameter, is a threat for *S. lanzai*. According to current information, the main habitats where this salamander lives are not yet severely endangered or disturbed by anthropogenic actions. One population is now included within a regional park, a measure which should guarantee (at least in theory) a greater conservation effect. However, in some periods of the year (i.e. July and August) car traffic is particularly intense, being the main threat to these Amphibians (ANDREONE *et al.*, 2002). The managers of this regional park should propose traffic regulation (hours of traffic, position of parking, etc.) in order to minimize the risk of *S. lanzai* mortality.

In conclusion, Biek *et al.* (2002) found a welcome final sentence: "Application of sensitivity analysis and other quantitative models can help prioritise research and management efforts and thereby improve the prospects for conserving the world's amphibian diversity"

REFERENCES

- ANDREONE F., MIAUD C., BERGÒ P., BOVERO S., DOGLIO S., GUYÉTANT R., RIBÉRON A. & STOCCO P.
2002 Research and conservation activity on *Salamandra lanzai* in Italy and France (Urodela, Salamandridae). Atti del terzo Convegnoio Salvaguardia Anfibilg, Lugano, 23-24 giugno 2000: 9-19.
- ANDREONE F., C. MIAUD, P. BERGO, S. DOGLIO, P. STOCCO, A. RIBÉRON, P. GAUTIER
Living at the top: testing the effects of life history traits upon the conservation of *Salamandra lanzai*. Ital. J. Zool. in press.
- BIEK R., W. C. FUNK, B. A. MAXELL & L. S. MILLS
2002 What is missing in Amphibian decline research: Insights from Ecological Sensitivity Analysis. Conserv. Biol. 16: 728-734.
- CASWELL H.
2000a Matrix population models: construction, analysis, and interpretation. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
- CASWELL H.
2000b Prospective and retrospective perturbation analysis: their roles in conservation biology. Ecology 81: 619-627.
- GRIFFITHS R.A. & C. WILLIAMS
2000 Modelling population dynamics of great crested newts (*Triturus cristatus*): a population viability analysis. Herpetol. J. 10: 157-163.
- LEGENDRE S. & J. CLOBERT
1995 ULM : Unified Life Models, a software for conservation and evolutionary biologists. J. appl. Stat. 22: 817-834.
- MILLS L.S., D.F. DOAK & M.J. WISDOM
1999 Reliability of conservation actions based on elasticity analysis of matrix models. Conserv. Biol. 13(4) : 815-829.
- MILLS L.S. & M. LINDBERG
2002 Sensitivity analysis to evaluate the consequences of conservation actions. Pp 338-366, S.R. Beissinger & D.R. McCulloch (Eds). Population viability analysis. University of Chicago Press, Chicago.

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