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Population modelling of Great Crested Newts (*Triturus cristatus*)

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Summary

Population Viability Analysis (PVA) provides a tool for assessing the risk of extinction in threatened species, but has rarely been applied to amphibian populations. Using existing life history data, we constructed several stochastic models to predict the effects of (1) progressive subdivision of crested newt habitat; and (2) different levels of juvenile dispersal between ponds, on the persistence of crested newt populations over a fifty year period. The models predict that small isolated populations have a higher risk of extinction than large isolated populations. In a subdivided population, increasing dispersal between subpopulations decreased the extinction risk of the metapopulation as a whole. Although the extinction risk of an individual isolated population is relatively high, the collective extinction risk of a group of such populations is lower than that of a single population with the same overall population size, even in the absence of dispersal. This appears to be a result of the asynchronous population dynamics that are generated in a group of isolated populations. A subdivided population may therefore persist for longer than a single population because it is unlikely that all the subpopulations will go extinct at the same time.

Key words: *Triturus cristatus*, population viability analysis, metapopulation, modelling.

Populationsmodellierung am Kammolch (*Triturus cristatus*)

Zusammenfassung

Die Populations-Gefährdungsanalyse (PVA) ist ein Werkzeug zur Abschätzung der Aussterbewahrscheinlichkeit gefährdeter Arten, wurde jedoch bislang kaum bei Amphibienpopulationen angewendet. Unter Nutzung von Beobachtungsdaten wurden verschiedene stochastische Populationsmodelle entwickelt, um die Effekte (1) einer zunehmenden Verinselung von Kammolchhabitaten und (2) verschiedene Intensitäten der Ausbreitung von Jungtieren auf Kammolchpopulationen über einen Zeitraum von 50 Jahren vorherzusagen.

Die Ergebnisse zeigen, dass kleine isolierte Populationen ein höheres Aussterberisiko besitzen als große isolierte Populationen. Zunehmender Individuenaustausch zwischen Teilpopulationen verringert die Aussterbewahrscheinlichkeit der gesamten Metapopulation. Obwohl das Aussterberisiko einer isolierten Population relativ hoch ist, ist das gemeinsame Aussterberisiko einer Gruppe solcher Populationen niedriger als das einer Einzelpopulation mit der gleichen Individuenzahl, auch wenn ein Individuenaustausch vernachlässigt wird. Dies scheint aus der asynchronen Populationsdynamik zu resultieren, die sich in einer Gruppe isolierter Populationen herausbildet. Eine untergliederte Population kann deshalb länger überleben als eine Einzelpopulation, weil es unwahrscheinlich ist, dass alle Teilpopulationen gleichzeitig aussterben.

Schlagwörter: *Triturus cristatus*, Populations-Gefährdungsanalyse, Metapopulation, Modellierung.

Introduction

Since LEVINS (1970) proposed his classical model of metapopulation dynamics, metapopulation ideas have provided a conceptually appealing framework for the management of wildlife populations in fragmented habitats. In reality, few - if any - populations are evenly distributed, and distinguishing between a patchily distributed population and a functioning metapopulation that is characterized by extinction-colonization dynamics, is logistically difficult. Amphibians are potentially attractive candidates for metapopulation studies, as they have highly patchy distribution patterns based on seasonal breeding aggregations at temporary ponds. This may result in a 'shifting' distribution, whereby extinction occurs as a result of habitat succession and dispersal enables colonization and recolonization of ponds (STACEY et al. 1997). Despite the superficial applicability of metapopulation processes to amphibians, only three species, the red-spotted newt, *Notophthalmus viridescens* (GILL 1978), the pool frog, *Rana lessonae* (SJÖGREN 1988, 1991; SJÖGREN-GULVE 1994), and the natterjack toad, *Bufo calamita* (SINCH 1992), have been the subject of long-term studies of metapopulation dynamics. The function of metapopulation processes is expected to vary according to the life history and the mobility of the species concerned (MIAUD et al. 1993).

Spatial models have become an important tool in exploring metapopulation processes. In particular, 'Population Viability Analysis' (or PVA) is a stochastic modelling process concerned with assessing the risk of extinction of a population, or a group of populations (BOYCE 1992). Rather than using fixed input parameters as in deterministic models, stochastic models can simulate the inherent variability of ecological systems by drawing input parameters from statistical distributions described by means and variances. This means that multiple (i.e. usually 100-1000) simulations of the growth of a population can be made, and the risk of extinction simply calculated as the proportion of simulated populations that went extinct over a certain time frame (say, 10-100 years). There is now a wide range of software packages that can be used to conduct PVA analyses (e.g., see LINDENMAYER et al. 1995, BROOK et al. 1999). Although widely used as a tool to assess the viability of bird and mammal populations (e.g. SOULÉ 1987), PVA has rarely been applied to amphibian species. This may be partly due to the inherent difficulty in obtaining the necessary demographic data that is required to construct such models for amphibians. However, as there are an increasing number of studies that have assembled data on the population biology of *Triturus cristatus* (e.g. BELL 1979, HAGSTRÖM 1979, VERRELL & HALLIDAY 1985, ARNTZEN & TEUNIS 1993, MIAUD 1991, MIAUD et al. 1993, COOKE 1995, BAKER 1999), the construction of reliable predictive models is becoming feasible for this species.

In this paper we provide a summary of the predictions made by models that were constructed to simulate (1) habitat fragmentation and population subdivision; and (2) juvenile dispersal between subpopulations. A more extensive breakdown of the data is provided by Griffiths & Williams (2000).

Materials and Methods

The Models

Population Viability Analyses were performed using RAMAS Metapop version 3.0 (AKCAKAYA 1998), which is particularly well suited for modelling spatially structured populations. The analyses used existing data on population size, demography, spatial structure and environmental variability to calculate population trajectories over a 50 yr period. The analyses used a stochastic simulation, calculating 1000 estimates of projected population size for each year. From these 1000 estimates the number of populations going extinct within 50 yrs was used to derive the risk of extinction over this time frame.

Population Characteristics

Age structure. The basis of the models is a Leslie matrix of age-specific survival and fecundity schedules. The models used an age structure based on those derived from skeletochronological analyses of two *T. cristatus* populations in France (FRANCILLON-VIEILLOT et al. 1990, MIAUD et al. 1993). We also incorporated further skeletochronological data from three populations in Kent (WILLIAMS 1999). The percentage of individuals in each age class was calculated for each population, and then averaged across the five populations (i.e. two populations from France, three populations from England) to give an aggregated age structure. There were very few individuals in any of these populations over 12 years old, so these were pooled into the final age class (i.e. >12 yrs).

Survival. Data on annual survival was obtained from the survivorship curve constructed by OLDHAM (1994). This curve combined data from the study by ARNTZEN & TEUNIS (1993) with new information from Leicestershire. It assumed that crested newts breed for the first time at 2 or 3 years, and then breed every year until death. From this survivorship curve, annual adult survival was estimated at around 0.68, and juvenile survival at 0.2. However, published estimates of adult annual survival vary from around 0.31 to 1.0 (BAKER 1999), and juvenile survival is more variable than adult survival (ARNTZEN & TEUNIS 1993). Standard deviations of 0.3 were therefore attached to the survival estimates for each age class (as juvenile survival is lower than adults, the SD of 0.3 provides a higher coefficient of variation for juveniles than adults, and allows survival to fall to zero in some years).

Fecundity. The Leslie matrix included post-metamorphic age classes only, so 'fecundity' was modelled as the number of new individuals produced per individual within each age class (i.e. 'recruitment'). Published estimates of fecundity range from 189-220 (see citations by ARNTZEN & TEUNIS 1993). Assuming a 1:1 sex ratio, and taking account of the 50 % egg abortion, 95 % egg/larval mortality and 80 % juvenile mortality - based on data provided by ARNTZEN & TEUNIS (1993) and OLDHAM (1994) - this translates to about five new recruits per adult, with an estimated standard deviation of 0.2.

Demographic and Environmental Stochasticity. The life-table produced from the data summarised above yields a net reproductive rate (R_0) of close to 1.0 (ARNTZEN & TEUNIS 1993). This means that in the absence of catastrophes or environmental, demographic and genetic stochasticity, the population will be stable over time. Demographic stochasticity was modelled by drawing the number of survivors each year from a binomial distribution described by survival rate and population size; and by drawing the number of recruits

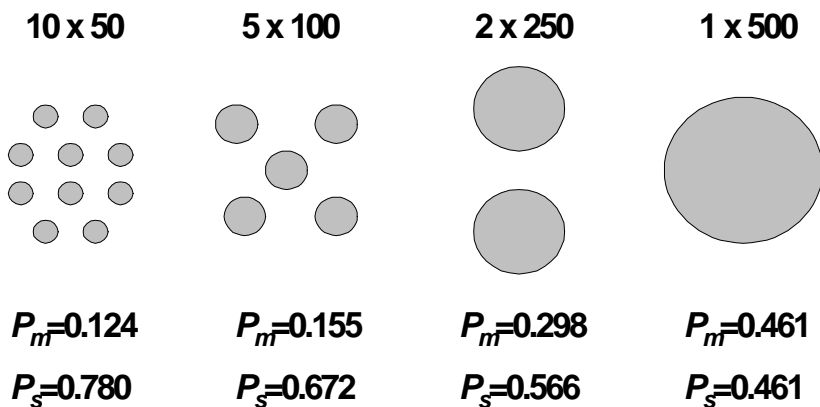


Fig. 1: Comparison of extinction risk in subdivided populations. P_m = probability that the metapopulation will go extinct within 50 yrs; P_s = probability of a single subpopulation going extinct within 50 yrs. Overall starting population size (N_0) = 500 in all cases; K = 1000.

Vergleich des Aussterberisikos in geteilten Populationen. P_m = Wahrscheinlichkeit, dass die Metapopulation innerhalb von 50 Jahren ausstirbt. P_s = Wahrscheinlichkeit, dass eine Einzelne Teilpopulation innerhalb von 50 Jahren ausstirbt. Anfangspopulationsgröße in allen Fällen (N_0) = 500; K = 1000.

from a Poisson distribution described by the mean of fecundity x population size. Environmental stochasticity was modelled by drawing values randomly from lognormal distributions described by the fecundity and survival values and their associated standard deviations described above. The effects of stochasticity on fecundity, survival and carrying capacity were assumed to be correlated, and the extinction threshold for each population was set to one remaining newt. Density-dependent population growth was simulated using a ceiling model (AKCAKAYA 1998).

Catastrophes. There are a number of factors that can result in catastrophic mortality of *T. cristatus* eggs and larvae, such as fungal infections of eggs and predator introductions. However, one of the commonest factors that will reduce or eliminate recruitment is pond desiccation during years of low rainfall. All simulations therefore incorporated the effects of a drought once every three years that eliminated recruitment (i.e. survival of eggs and larvae reduced to zero).

Habitat Fragmentation and Juvenile Dispersal. All of the models used the same age structure and Leslie matrix described above. The effects of population subdivision were modelled by comparing the persistence of a population under increasing degrees of subdivision (i.e. 1, 2, 5 and 10 ponds). The total number of newts was therefore kept constant but was divided among different numbers of smaller patches. In all of the models, the metapopulation carrying capacity ($K=1000$) and starting population size ($N_0=500$) were the same, with both parameters divided equally between the patches (e.g. a metapopulation of two ponds each had $K=500$ and $N_0=250$).

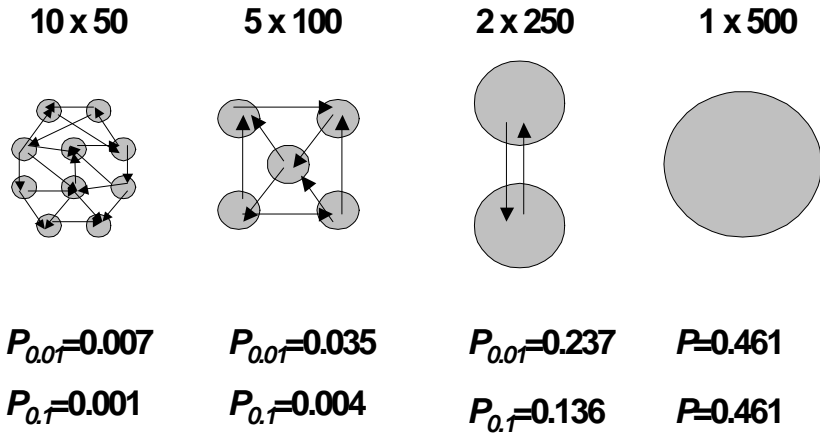


Fig. 2: Comparison of extinction risk in subdivided populations linked by dispersal. $P_{0.1}$ = probability of extinction of metapopulation within 50 yrs when 0,1 of all juveniles disperse between ponds; $P_{0.01}$ = probability of extinction of metapopulation within 50 yrs when 0,01 of all juveniles disperse between ponds. Dispersal was modelled as the movement of 1-2 yr olds between all populations. Other parameters are the same as Fig. 1.

Vergleich der Aussterberate in geteilten Populationen, die miteinander vernetzt sind. $P_{0.1}$ = Wahrscheinlichkeit des Aussterbens der Metapopulation innerhalb von 50 Jahren, wenn sich 10 % der Jungtiere zwischen den Gewässern austauschen; $P_{0.01}$ = Wahrscheinlichkeit des Aussterbens der Metapopulation innerhalb von 50 Jahren, wenn sich 1 % der Jungtiere zwischen den Gewässern austauschen. Der Individuenaustausch wurde als Wanderung von 1 - 2 Jahre alten Tieren zwischen allen Populationen modelliert. Die anderen Parameter sind gleich Fig. 1.

Assuming that most dispersal between ponds occurs during the juvenile phase, dispersal was modelled as the movement of 1-2 yr olds between populations. Dispersal rates were modelled as 0 %, 1 % or 10 % of 1-2 yr olds, and dispersal was assumed to occur between all ponds within the metapopulation.

Results

Single, isolated populations with no dispersal have a relatively high risk of extinction, and the risk of extinction increases with decreasing population size (Fig. 1). Even a relatively large population with a starting population size of 500 and a carrying capacity of 1000 has just over a 50% chance of surviving for fifty years. A ten-fold decrease in population size results in a near doubling of the risk of extinction in isolated populations. Collectively, however, a group of small isolated populations has a lower extinction risk than one large population of the same overall size. Despite the fact that the subdivided populations were initiated with identical population structures, stochasticity resulted in a slightly different population trajectory in each subpopulation. The population dynamics of small isolated populations therefore seem to be independent of each other, such that it is unlikely that they will all go extinct at the same time.

Dispersal of juveniles between ponds results in a reduction in extinction risk in all cases (Fig. 2). Indeed, the risk of extinction of the metapopulation declines with increasing dispersal between patches. For example, in a group of 10 small populations each with a starting population size of 50, and 10 % of juveniles dispersing between ponds, the extinction risk is close to zero.

Discussion

The models presented here are clearly simplistic, and do not incorporate all of the factors that impinge on the population sizes of *T. cristatus*. For example, there are many other stochastic processes that will undoubtedly operate in nature, including the presence of fish and other competitors/predators; and changes in the aquatic and terrestrial habitat that are likely to occur over a fifty year period. Equally, the quality of patches (i.e. ponds) will vary in both time and space. Dispersal rate will depend on the distances between subpopulations, the habitat structure in between, and perhaps the density of the donor and recipient populations (e.g. HANSSON 1991, FAHRIG & MERRIAM 1994). Although the models suggest that increasing juvenile dispersal by constructing corridors between ponds may be a positive conservation measure, increased connectance between subpopulations can have negative affects. Corridors can, for example, provide conduits for disease transmission and/or colonization by predators. The models also did not take into account genetic stochasticity, which can result in detrimental affects within small populations leading to increased risk of extinctions (e.g. HEDRICK 1996). It is possible to incorporate the effects of all of these factors in a PVA, providing the effect concerned is quantifiable. Future modelling exercises can therefore incorporate information on such variables as the data become available.

A functional metapopulation relies on a degree of independence between the constituent subpopulations. If the dynamics of the subpopulations are correlated, then they will tend to operate as a single large population, and there will be a risk that all populations will decline - and even go extinct - at the same time. Asynchrony between subpopulations within a metapopulation can therefore ensure that sources of colonizers will always compensate for extinctions elsewhere within the system. The importance of such asynchrony was highlighted by the models presented here, as subdivided populations persisted for longer than single populations of the same overall size, even in the absence of dispersal. What is more surprising is that this pattern emerged despite the populations being subjected to a correlated catastrophe - in this case a drought that eliminated recruitment every three years. This catastrophe was modelled as affecting all populations in the same way, as the effects of drought are regional rather than local. However, as DEN BOER (1981) and VERBOOM et al. (1993) point out, it is quite possible for a subdivided population to persist for longer than a single population of equivalent size, due to the spreading of risk between patches. It therefore appears that demographic and environmental stochasticity can generate sufficient asynchronicity between otherwise similar *T. cristatus* populations to at least partly offset correlated affects.

HALLEY et al. (1996) used a stochastic model of extinction risk that incorporated immigration rates of *T. cristatus* and proximity to a source pond. They predicted that relatively small

populations of *T. cristatus* could persist providing that they are close to (i.e. <0.75 km) sources of immigrants, and that large populations could persist at greater distances (i.e. <1.5 km of a source). In the current study, inter-pond distances were implicitly reflected in the dispersal rates, although there are other factors - such as the landscape structure between ponds - that will also affect these parameters. Although HALLEY et al. (1996) used a different type of model to that used here, their finding that even large populations (i.e. ponds with >100 females located at > 3 km from a source) have a less than 5% chance of surviving 20 generations is broadly in line with our prediction that large isolated ponds have low viability.

AS NORTH & JEFFERS (1990) point out, it has proved difficult to convince decision-makers that mathematical models have a role to play in practical conservation. Advice from modellers may be accepted providing it conforms to the preconceptions of the decision-maker, but is likely to be abandoned if the predictions have some unexpected or unfortunate consequence (NORTH & JEFFERS 1990). As far as *T. cristatus* is concerned, models have the potential to provide an objective assessment of management options. Moreover, as data continues to accumulate on the ecology of *T. cristatus*, a continual process of testing and refinement should enable models to become more sophisticated and the resulting assessments to become more realistic and relevant. Population modelling is certainly no panacea for conservation, but it is a tool that cannot afford to be left out from the conservationist's armoury.

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239-247](#)