

## MODELLING POPULATION DYNAMICS OF GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*): A POPULATION VIABILITY ANALYSIS

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The effects of pond isolation, drought, habitat fragmentation and dispersal on populations of crested newts (*Triturus cristatus*) were investigated using stochastic models constructed from existing life history data. The models predict that small isolated populations have a higher risk of extinction than large isolated populations. However, even large populations had a relatively high extinction risk over a fifty year period if they remained isolated. Pond desiccation affects metamorphic success and recruitment, and the risk of extinction decreased with decreasing frequency of regional droughts. In a subdivided population, increasing dispersal between subpopulations decreased the extinction risk of the metapopulation as a whole. However, even in the absence of dispersal, a subdivided population had a lower overall extinction risk than a single isolated population of the same size. Environmental stochasticity may therefore result in asynchronous dynamics within subpopulations, which leads to the risk of extinction being spread across the subpopulations. Although population viability analysis has the potential to provide an objective assessment of population management decisions, it has not yet been a component of conservation planning for the crested newt in Britain.

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

### INTRODUCTION

In a thought-provoking review of species conservation programmes, Caughley (1994) argued that there are two fundamental approaches to addressing species conservation problems. These two approaches are enshrined within what he termed the 'Declining Population Paradigm' (DPP) and 'Small Population Paradigm' (SPP). In sum, the DPP is concerned with identifying those factors that have led to population declines, and the attempts to neutralize them. This approach to addressing conservation problems is firmly rooted in empirical field biology, and there are many case-studies of the application of this approach to amphibian conservation problems (e.g. Richards, *et al.* 1993; Kuzmin, 1994; Pounds & Crump, 1994; Fisher & Shaffer, 1996; Denton *et al.*, 1997). In contrast, the SPP is concerned with risk of extinction as a result of genetic and demographic stochasticity within populations that are already small. The main tools used in this approach to conservation problems are predictive models, which aim to utilize genetic, demographic and environmental information on the species concerned to make predictions about the long-term viability of the population. 'Population Viability Analysis' (or 'PVA') is a modelling process concerned with assessing the risk of extinction of a population (Boyce, 1992), and can be employed using the principles of the SPP. Caughley (1994) concluded that the DPP is short of theory, and the SPP is short of practice, and neither can therefore be totally effective if used to address conservation problems on their own.

In recent years there have been major advances in the sophistication of predictive modelling. Although widely used to assess extinction risks in mammal and bird conservation programmes (e.g. Soulé, 1987), population modelling has rarely been applied to herpetological conservation problems, or to species conservation programmes in Britain in general. As far as British amphibians are concerned, the only previous modelling study is that by Halley *et al.* (1996) on the common toad (*Bufo bufo*) and crested newt (*Triturus cristatus*). These authors predicted that crested newt populations will persist even in small ponds, providing they are close to a source of immigrants. Whether or not an initially unoccupied pond was used at all after 20 generations depended upon immigration rates. On the other hand, there are now several studies that have assembled data on the population biology of crested newts (e.g. Bell, 1979; Hagström, 1979; Verrell & Halliday, 1985; Arntzen & Teunis, 1993; Miaud, 1991; Miaud *et al.*, 1993; Cooke, 1995; Baker, 1999). In general, these studies have shown that the population dynamics of the crested newt are characterized by year-to-year fluctuations in adult population sizes, due to variable recruitment as a result of environmental variability. In addition, dispersal between ponds may play an important role in buffering extinction in local populations, and a metapopulation structure may therefore be important in maintaining crested newts within a wider landscape (Miaud *et al.*, 1993; Griffiths, 1997).

In this paper we construct a simple model of crested newt population dynamics utilizing demographic data obtained from the literature and from a metapopulation in Kent. We then use the model to predict the effects of progressive population subdivision, and newt dispersal between ponds, on population persistence.

## MATERIALS AND METHODS

## THE MODELS

We used RAMAS Metapop version 3.0 (Akçakaya, 1998) to carry out several population viability analyses. The analyses used available 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 period.

## AGE STRUCTURE, SURVIVAL AND FECUNDITY

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).

Oldham (1994) constructed a survivorship curve for crested newts by combining data from the study by Arntzen & Teunis (1993) with new information from Leicestershire. This 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 for adults, and allows survival to fall to zero in some years).

As the model included post-metamorphic age classes only, '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.

The life-table produced from these data 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 from a Poisson distribution described by the mean of fecundity  $\times$  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 detailed 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 (Akçakaya, 1998).

## MODEL PARAMETERS

All of the models used the same age structure and Leslie matrix described above. The effects of pond isolation, catastrophe (drought), and population subdivision on extinction risk were modelled as follows:

*Isolated populations.* Models were constructed for isolated populations with starting population sizes ( $N_0$ ) of 10, 50, 100 and 200 newts. The carrying capacities for crested newt populations are unknown, but as populations have been observed to fluctuate by an order of 15 or more (e.g. Arntzen & Teunis, 1993; Cooke, 1995), carrying capacities ( $K$ ) were set at  $K=20 N_0$ .

*Drought.* Pond desiccation in the summer will result in few – if any – crested newt larvae surviving to metamorphosis. Drought was therefore modelled as causing total mortality of eggs and larvae in all ponds during drought years, which subsequently led to zero recruitment of first-time breeders 2-3 years later. The impact of a drought occurring every 1, 2, 3 or 4 years on population viability was compared using isolated ponds with  $N_0=10, 50, 100$  and 200 newts, and  $K=20 N_0$ .

*Fragmentation and dispersal.* The effects of habitat fragmentation were modelled by comparing the persistence of a metapopulation under increasing degrees of

TABLE 1. Predicted extinction risks of isolated crested newt populations that differ in population size.  $K$ , carrying capacity;  $N_0$ , starting population size;  $N_{50}$ , mean population size  $\pm$  SD of extant populations ( $n=1000$  simulations) after 50 years;  $K=20 N_0$ .

	Population parameters		Extinction risk	
	$K$	$N_0$		$N_{50}$
	200	10	100 $\pm$ 86.3	0.275
	1000	50	607 $\pm$ 395.6	0.087
	2000	100	1207 $\pm$ 778.6	0.049
	4000	200	2496 $\pm$ 1542.0	0.025

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 each of the models, the metapopulation carrying capacity ( $K=1000$ ) and starting population size ( $N_0=500$ ) was the same, with both parameters divided equally between the patches (e.g. a metapopulation of two ponds each had  $K=500$  and  $N_0=250$ ). Dispersal of amphibians between ponds can 'rescue' declining or extinct populations (e.g. Gill, 1978; Sjögren, 1991), and may therefore be important for metapopulation persistence in crested newts. Although adult newts sometimes move between ponds (e.g. Miaud *et al.* 1993; Williams, 2000), most dispersal probably occurs during the immature stages. We therefore modelled dispersal as the movement of 1-2 year-olds between ponds. Dispersal rates were modelled as 0%, 1% or 10% of 1-2 year-olds, and dispersal was assumed to occur between all ponds within the metapopulation. Fragmentation and dispersal models all incorporated the effects of a drought that eliminated recruitment on average once every three years.

RESULTS

ISOLATED POND MODEL

In isolated populations, the risk of extinction steadily declined as population size and carrying capacity increased. However, even in the absence of catastrophes or other major environmental changes, populations that can sometimes reach sizes of 100-200 individuals still have a 27% chance of disappearing over a 50 yr period, as a result of demographic and environmental stochasticity (Table 1). Predicted population sizes varied between 0 and  $K$ , resulting in

large standard deviations in estimated population size, which is consistent with real populations. According to the model, an isolated population needs to be able to support at least 1000 newts if the extinction risk is to fall below 10%.

TABLE 2. Predicted extinction risks of isolated crested newt populations that differ in population size and suffer different frequencies of drought. Interpretation as Table 1;  $K=20 N_0$ . Drought is assumed to eliminate recruitment in the year in which it occurs.

Population parameters		Frequency of drought	Extinction risk
$N_0$	$N_{50}$		
10	0	Every year	1.000
10	5±24.5	Every 2 yrs	0.911
10	19±47.5	Every 3 yrs	0.745
10	34±64.2	Every 4 yrs	0.654
50	0	Every year	1.000
50	27±120.9	Every 2 yrs	0.811
50	133±272.1	Every 3 yrs	0.533
50	231±351.5	Every 4 yrs	0.402
100	0	Every year	1.000
100	68±286.6	Every 2 yrs	0.746
100	278±554.4	Every 3 yrs	0.453
100	484±707.9	Every 4 yrs	0.335
200	0	Every year	1.000
200	134±558.9	Every 2 yrs	0.714
200	572±1140.0	Every 3 yrs	0.453
200	1052±1469.0	Every 4 yrs	0.305

TABLE 3. Predicted extinction risks of crested newt populations that are subdivided into 1, 2, 5 or 10 subpopulations, with different rates of juvenile dispersal (0, 1% or 10%) between subpopulations.  $N_0$ , starting population size of *each* subpopulation;  $N_{50}$ , average overall metapopulation size (±SD) after 50 yrs ( $n=1000$  simulations); drought occurs in all ponds on average once every three years and eliminates recruitment to the metapopulation in that year. See Table 4 for a comparison with single (i.e. isolated) populations with the same values of  $K$  and  $N_0$ .

No. subpopulations	Population parameters		$N_{50}$	Dispersal rate	Extinction risk of metapopulation
	K of each subpopulation	$N_0$			
1	1000	500	157±289.1	0	0.461
2	500	250	143±203.3	0	0.298
5	200	100	123±136.6	0	0.155
10	100	50	94±94.6	0	0.124
2	500	250	194±250.8	0.01	0.237
5	200	100	258±218.7	0.01	0.035
10	100	50	317±223.6	0.01	0.007
2	500	250	294±321.7	0.1	0.136
5	200	100	485±304.1	0.1	0.004
10	100	50	588±312.7	0.1	0.001

TABLE 4. Predicted extinction risks in single populations, with other population parameters as in Table 3.

Population parameters				Extinction risk
No. subpops.	K of each subpop.	$N_0$	$N_{50}$	
1	1000	500	157±289.1	0.461
1	500	250	69±139.0	0.566
1	200	100	24±53.1	0.672
1	100	50	10±25.1	0.780

#### DROUGHT MODEL

Recruitment increases with decreasing frequency of drought, and this was reflected in a decreased risk of extinction as drought frequency declined (Table 2). As expected, no population is viable with recruitment failure every year, and under this scenario the probability of extinction is therefore  $P=1.0$ . However, even when drought occurred only once every four years, the risk of extinction was still at least 30% even in the very largest populations modelled. In this scenario, around half of all the populations with  $K=200$  went extinct within 25 years. As in the isolated pond model, predicted population sizes over the 50 year period varied widely between 0 and  $K$ .

#### FRAGMENTATION AND DISPERSAL MODEL

Isolated populations with no dispersal have a relatively high risk of extinction. Although larger isolated populations will persist for longer than small isolated populations (Table 1), the risk of extinction is reduced when individuals are distributed across several patches, even in the absence of dispersal (Table 3). Although the risk of extinction of a small population is therefore high, collectively the risk of extinction of a group of small populations is lower than an equivalent sized population occupying a single patch (Tables 3, 4). As the rate of dispersal of 1-2 year-old newts between ponds increases, the extinction risk of the newt metapopulation as a whole decreases. Indeed, with a metapopulation spread across 10 or more patches and a dispersal rate of 10% of immatures between all ponds, the risk of extinction over 50 yrs is less than 0.1% (Table 3).

### DISCUSSION

#### MODEL JUSTIFICATION

How well do the models presented reflect reality? This question can only be answered by using the models to generate hypotheses that can be tested with field data over fifty years. The age-structure and survival-fecundity schedule used were certainly realistic as they were based on well-founded field data sets. Although these parameters may therefore be regarded as fairly

'typical' of crested newt populations, it is unlikely that real populations will have identical initial age-structures and survival-fecundity schedules as assumed here. However, incorporating environmental and demographic stochasticity into the models ensured that population structures did not remain identical for the duration of the simulations. What is certain is that the models were simplistic, and did not incorporate the full range of environmental parameters that may influence crested newt population dynamics. In a real metapopulation, for example, there are many other catastrophes (e.g. fish introduction, disease outbreaks, pollution incidents etc.) that may impact upon the population. Equally, there may be more subtle environmental changes that result in progressive fragmentation and increasing isolation of ponds that were once connected. The models also did not take into account genetic stochasticity; this can result in detrimental affects within small populations, leading to increased risk of extinctions (e.g. Hedrick, 1996). As well as being simplistic then, the models presented here may be over-optimistic.

#### METAPOPULATION DYNAMICS

The models predict that even relatively large crested newt populations may not be viable in the long term if they are completely isolated. Indeed, the likelihood of extinction within a 50 yr period may actually be rather higher than predicted, as the isolated pond model assumed recruitment every year and no catastrophes or environmental degradation – something that would appear to be rare in real populations. Although a long life-span, repeated breeding, and high fecundity may be adaptations to catastrophic loss of reproductive effort in some years (Griffiths, 1997), even relatively infrequent droughts that eliminate recruitment one year in four result in a marked increase in extinction risk compared to models with recruitment every year. However, pond desiccation can have positive effects on crested newt populations by eliminating predators, such as fish and aquatic invertebrates. The interaction between the positive and negative affects of pond desiccation is therefore worthy of further theoretical exploration and empirical testing.

Halley *et al.* (1996) modelled extinction risk in crested newts in terms of carrying capacities and distances between ponds. They predicted that relatively small populations could persist providing that they are close to (i.e. <0.75 km) sources of immigrants, while large populations could persist at greater distances (i.e. <1.5 km from a source). In the current study, inter-pond distances were implicitly reflected by the dispersal rates, although there are other factors, such as the landscape structure between ponds, that will also affect these parameters. Halley *et al.* (1996) tested different hypotheses to those tested here, and used different input and output parameters. However, 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 in the long-term.

The classical Levins (1970) model of metapopulation dynamics assumes that there is no variation in habitat quality between patches that support different subpopulations. This was simulated in the dispersal models used here; however, in nature habitat patches – including crested newt ponds – vary in quality. Likewise, in nature dispersal rate between ponds will not be the same for all populations. 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). The models presented here suggest that a threshold dispersal rate of around 1% of first time breeders needs to be reached if the system is to act as a functional metapopulation. However, dispersal rates higher than this may be required if the populations are small and/or the habitat varies in quality. Equally, large subpopulations that suffer fewer catastrophes may function as a metapopulation with a lower dispersal rate. In the latter case, the subpopulations may behave functionally as isolated populations, with dispersal playing no significant role in influencing population persistence.

In nature, habitat fragmentation invariably leads to (1) decreased habitat, and (2) increased isolation of the remaining patches. Both of these effects can lead to extinction independently of each other, but in practice, are difficult to distinguish. The fragmentation and dispersal models presented here illustrate the effects of isolation without an overall decrease in habitat. In that increasing fragmentation leads to a decreased risk of extinction, the results contradict traditional island biogeography theory (MacArthur & Wilson, 1967). Indeed, in terms of whether newts are best conserved in 'single large' rather than 'several small' habitat patches (e.g. see Simberloff & Abele, 1976, 1982; Wilcox & Murphy, 1985), the models tend to support the latter theory. Providing that the dynamics of individual subpopulations are asynchronous and regulated by environmental factors that are not correlated, 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 (e.g. Den Boer, 1981; Verboom *et al.*, 1993). Factors such as drought are likely to be regional rather than local in their effects, and in the models used here drought was modelled as affecting all ponds every three years in a correlated fashion. In nature, a combination of regional factors that will affect all subpopulations (e.g. drought, severe winters) and local factors that will affect individual subpopulations asynchronously (e.g. fish introductions, egg infections) are both likely to impact on crested newt metapopulation dynamics. The likelihood of a subdivided population persisting for longer than an isolated

population depends upon the relative importance of synchronous and asynchronous impacts. The current models therefore suggest that environmental stochasticity will generate sufficient asynchronicity in subpopulation dynamics to allow longer persistence of a subdivided population.

Interestingly, a similar analysis on the brushtail possum by Lindenmayer & Lacy (1995) reached the opposite conclusion. The models produced by these authors predicted that increasing subdivision of populations invariably had negative effects, irrespective of dispersal rates between populations. However, above a certain population threshold, dispersal of possums resulted in reduced extinction risk.

As Boyce (1992) points out, one of the major strengths of population viability analysis lies in its potential to provide an objective assessment of management options for species and habitats. For example, translocations can also be conveniently modelled, as it is possible to simulate the effects of both removals and introductions. Likewise, modelling can be used to explore the implications of creating a new pond within an existing metapopulation. However, the reliability of any population viability analysis depends very much on the demographic and environmental parameters upon which it is constructed. For many threatened species, there is insufficient population data to make population viability analysis a worthwhile exercise, and Halley *et al.* (1996) point out that it is currently not easy to obtain all the parameters needed to construct models of amphibian population dynamics. However, if research data on the population biology of the crested newt continues to accumulate, it will be possible to construct more reliable models. The simulations described here are therefore a useful starting point for the development of more complex models, that through progressive testing and refinement, should become a central part of great crested newt conservation planning. When that stage is reached, herpetological conservation in Britain will have gone some way towards achieving Caughley's (1994) goal of an integrated conservation strategy, in which theory and practice complement each other, rather than operating independently in parallel universes.

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