

Estimating viability and sensitivity of the great crested newt *Triturus cristatus* at a regional scale

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Viability and sensitivity of the great crested newt *Triturus cristatus* were simulated under different scenarios with a demographically and spatially structured stochastic model in an area of 144 km² in southeastern Sweden. Eighteen ponds were monitored using drift fences with pitfall traps, funnel traps, visual observation and netting during the spring and summer of 2004. Estimated adult population sizes ranged between 0 and 620 individuals and the mean (\pm SD) local population size was 297 \pm 233 individuals. Due to uncertainty of the data, the model was simulated with parameter ranges to estimate upper and lower bounds of viability. Estimated quasi-extinction risk (the risk of each population in the study area falling below 10 females) within a 50-year period ranged from 100% to 0%, with a “best” estimate of 19.2%. The parameter most sensitive for the model outcome was fecundity, followed by juvenile survival, adult survival and transition from juvenile to adult. When these parameters were set at their lower bound, the quasi-extinction risk increased to 80–100%, while simulating these parameters at their higher bound inferred no or nearly no risk of quasi-extinction. This highlights the importance of focusing conservation efforts and research on the early life cycle stages. Management measures such as restoration of ponds and increased pond density decreased the risk for the great crested newt to end up quasi-extinct in the study area after 50 years. The results may have implications on management measures of great crested newts throughout its distribution area.

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Among European amphibians, the great crested newt *Triturus cristatus* takes a special position in the amount of attention it has received in conservation work (Gent and Bray 1994, Langton et al. 2001). The species is distributed over most of northern and central Europe (Gasc et al. 1997, Arntzen 2003), but is reported to have declined rapidly during the last century (Beebee 1994, 1997, Edgar and Bird 2006). The great crested newt is currently listed in the category least concern (LC) in the global redlist

(Arntzen et al. 2004). It is protected under the convention on the conservation of European wildlife, annex II (strictly protected fauna species) (Council of Europe 1979) and under EUs habitat directive, in which it is protected through the Natura 2000 framework (Cederberg and Löfroth 2000).

To increase the knowledge of population dynamics and extinction risks in the great crested newt, several population viability analyses (PVA) have been performed (Halley

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et al. 1996, Griffiths and Williams 2000, Etienne et al. 2003, Griffiths 2004, Sohlman Wiessing 2004). PVAs aspire to model future population dynamics of a species with applications in conservation planning and management (Akçakaya and Sjögren-Gulve 2000, Beissinger 2002). PVAs have received much criticism for being nothing but “games played with guesses” (Caughley 1994), with unreliable estimates of extinction risks (Ludwig 1998, Fieberg and Ellner 2000). Since data from a PVA commonly are uncertain (Caughley 1994), the results of a PVA should be interpreted with caution, which is especially important for absolute extinction risks on longer terms (Akçakaya and Sjögren-Gulve 2000, Fieberg and Ellner 2000). However, PVAs can be useful for making risk assessments between different alternative scenarios (Hanski and Simberloff 1997), and PVA predictions have been shown to be surprisingly accurate (Brook et al. 2000). Furthermore, data uncertainties can be incorporated by using ranges of parameters (Akçakaya and Sjögren-Gulve 2000) to build best-case and worst-case scenario models (Akçakaya and Raphael 1998). Data uncertainties can also be analysed through a sensitivity analysis to identify important assumptions and parameters to guide further fieldwork (Akçakaya and Sjögren-Gulve 2000, Mills and Lindberg 2002), something that has been missing in amphibian decline research (Biek et al. 2002). So far PVAs of the great crested newt have not incorporated data uncertainties by building best-case and worst-case models, or applying de-

mographically and spatially structured models to real populations at a regional scale. Sensitivity analyses have not been implemented either, with one exception (Sohlman Wiessing 2004).

In this study we estimate viability and sensitivity of great crested newt populations at a regional scale by using a demographically and spatially structured model. We simulate different management scenarios and determine which parameters are most sensitive for the model outcome. Data uncertainties are incorporated by simulating the model with parameter ranges to estimate upper and lower bounds of viability. We also discuss implications from our results for the conservation of the species.

Material and methods

Study area

The study area constitute 144 km² located about 30–40 km south of the city Linköping in southeastern Sweden (58°09'N, 15°18'E – 58°03'N, 15°30'E) (Fig. 1) on the edge of the southern Swedish highlands. The area consists of hilly coniferous woodland with large numbers of smaller lakes and wetlands. Cultivated land is concentrated to built-up areas and is rich in pastures and meadows.

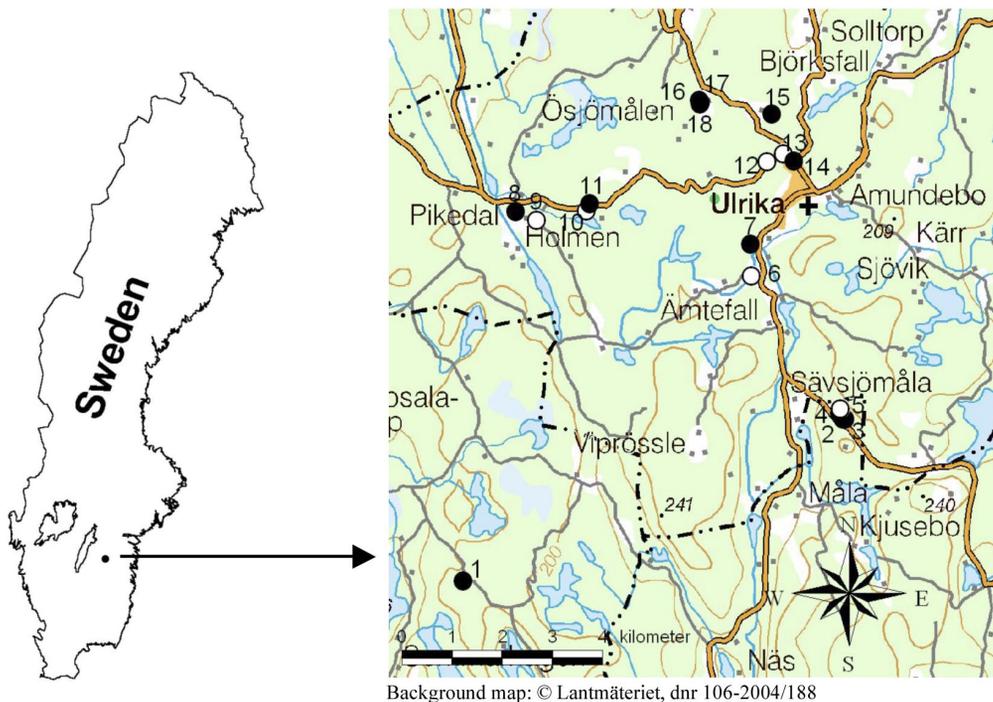


Fig. 1. The study area in southeast Sweden showing the relative positions of monitored ponds. Black circles indicate breeding ponds included in the model, while white circles indicate monitored ponds that were excluded from the model because reproduction of the great crested newt was not verified.

The study area was surveyed for great crested newts in 2003, and the species was found in 14 ponds (Karlsson 2003). These ponds, including four additional ponds, were monitored during the spring and summer of 2004 to estimate population sizes and ascertain reproduction (below). The characteristics of the ponds are described in Table 1.

Population monitoring and population size estimates

Population sizes were estimated by three methods; drift fence with pitfall traps, funnel traps and visual observation (Malmgren et al. 2005). Pond no. 7 was completely encircled by a drift fence with pitfall traps from April 4 to May 17 in 2004. The pond was partly covered by ice when the drift fence was erected, and ice melting took place during the first days of the study period. The fence was constructed of 'milk box' cardboard material fixed by poles, and had a height of about 50 cm above and 10 cm below ground. The fence was slightly sloped outwards from the pond and had overhanging lips both inwards and outwards the pond to prevent newts from climbing over the fence. The pitfalls were made up of 10-litre plastic buckets

buried with the rim at level with the ground close to the fence. The traps were filled with water to a depth of 5–10 cm to protect the newts from dehydration and from predators. Stones were placed in the traps as counterweights against upwelling water, and for providing cover for the newts and as resorts for trapped terrestrial animals. The traps (n=21) were placed at a distance of about 10 m from each other both outside (n=11) and inside (n=10) the fence. The distance between the fence and the pond shoreline varied between 1 and 3 m. Trapped animals were registered and released on the other side of the fence daily. The number of immigrated adult individuals registered was used as a population size estimate.

Ponds no. 1–5, 7–11, 13–14, and 16–18 were monitored using funnel traps (Griffiths 1985, Malmgren et al. 2005). The traps were constructed of 1.5- and 2-liter plastic bottles with the neck cut off, turned inside out and fastened on the bottle. The traps had small holes for flowing of water and flaps for emptying. They were fixed horizontally on 1.5 m poles and placed in the watersides at a distance of about 5 m from each other. Due to desiccation, the number of traps used fluctuated in some of the ponds. The traps were placed at the bottom at a depth of between 0.1–0.4 m below the surface with the openings mainly directed towards the centre of the pond. Traps were placed at

Table 1. Characteristics of monitored ponds with great crested newt, population monitoring method, estimated adult population sizes (\pm SD), and absence (–) or presence (+) of reproduction in 2003 and 2004, respectively. Surroundings are described within a radius of 500 metres from the pond. Reproduction data of 2003 from Karlsson (2003). Ponds 13, 17 and 18 were not monitored for reproduction in 2003.

No	Type	Surroundings	Size (m ²)	Monitoring method	Population size estimate (adults)	Reproduction 2003/2004
1	Forest tarn	Coniferous forest	>1000	Funnel traps	357 (\pm 133)	+/+
2	Farm pond	Pasture/coniferous forest	100–500	Funnel traps	344 (\pm 74)	+/+
3	Farm pond	Pasture/coniferous forest	<50	Funnel traps	163 (\pm 141)	+/+
4	Farm pond	Pasture/coniferous forest	<50	Funnel traps	32 (\pm 54)	+/+
5	Farm pond	Pasture/coniferous forest	<50	Funnel traps	0	–/–
6	Garden pond	Garden/pasture/ coniferous forest	<50	Visual observation	1	–/–
7	Forest marsh/ pond	Garden/pasture/ coniferous forest	100–500	Drift fence	620	+/+
8	Farm pond	Pasture/coniferous forest	<50	Funnel traps	14 (\pm 19)	+/–
9	Farm pond	Pasture/coniferous forest	<50	Funnel traps	5 (\pm 13)	–/–
10	Farm pond	Pasture/coniferous forest	<50	Funnel traps	10 (\pm 24)	–/–
11	Farm/forest marsh	Pasture/coniferous forest	100–500	Funnel traps	314 (\pm 182)	–/+
12	Roadside ditch	Coniferous forest	<50	Visual observation	6	–/–
13	Forest marsh	Coniferous forest	<50	Funnel traps	92 (\pm 52)	/–
14	Forest marsh	Coniferous forest/garden/ pasture	100–500	Funnel traps	187 (\pm 86)	–/–
15	Ditch/marsh	Pasture/coniferous forest	<50	Visual observation	77	–/+
16	Marsh/farm pond	Pasture/coniferous forest	500–1000	Funnel traps	402 (\pm 217)	+/+
17	Farm pond	Pasture/coniferous forest	<50	Funnel traps	99 (\pm 61)	/–
18	Farm pond	Pasture/coniferous forest	<50	Funnel traps	67 (\pm 44)	/–

dusk and checked the following dawn. To prevent newts from drowning, the traps were checked at maximum 10 h intervals.

Funnel trapping took place between April 12 and May 17 2004, using five trap nights in each pond (except pond 13 with two trap nights, and pond 7 with eight). Monitoring pond no. 7 with both drift fence and funnel traps made it possible to estimate the catch efficiency of the funnel traps and estimate population sizes in the ponds only monitored with funnel traps. The regression function that best explained the variation in catch efficiency was a polynomial equation where catch efficiency is a function of time (Fig. 2). The bell-shaped relationship between catch efficiency and time was probably due to variation in breeding intensity. When breeding intensity is high, the activity of the newts is high, and as a consequence, more newts enter the traps. Since climatic conditions probably do not differ much between sites in the study area, we assumed correlation among the ponds in variation of breeding intensity and catch efficiency. Further, we assumed that equal proportions of the population sizes were caught by using the same trap density (1 trap per 5 m) in all ponds and all trap nights. Thus, we used the catch efficiency equation for pond no. 7 to calculate adult population sizes in the ponds monitored with funnel traps only.

Ponds no. 6, 12 and 15 were monitored after dusk by visual observation through torching, using a halogen head lamp. These ponds are small, shallow and relatively free from vegetation, and permit counting all newts being in

water at the moment. Visual observations in these ponds were carried out between April 21 and May 11 2004 with five observation nights in each pond. The highest observed number of individuals was used as a population size estimate.

All trapped and observed newts were classed by sex and stage. Since size is an unreliable predictor of age in great crested newts (Hagström 1980, Francillon-Vieillot et al. 1990), the newts were not stage-classed by age, only as adults or juveniles. Newts showing secondary sexual characteristics (cloacal swelling, dorsal crests in males) were defined as adults, whereas newts not showing secondary sexual characteristics were classed as juveniles.

To find out whether reproduction had occurred, the ponds were searched for larvae of the great crested newt using a hand net. The hand net (size 30 × 25 cm) was systematically swept from side to side 1 m along the water-side at a depth of 1–4 dm below the surface for 3 seconds every 5 m (Gustafson and Malmgren 2002, Malmgren et al. 2005). Netting was carried out once in every pond during the period August 13 to August 26 2004.

PVA model structure and simulation of the model

A demographically and spatially structured PVA model was performed using the software RAMAS GIS ver. 3.0 (Akçakaya 1998). We structured the populations demographically by the postmetamorphic stages adult and juve-

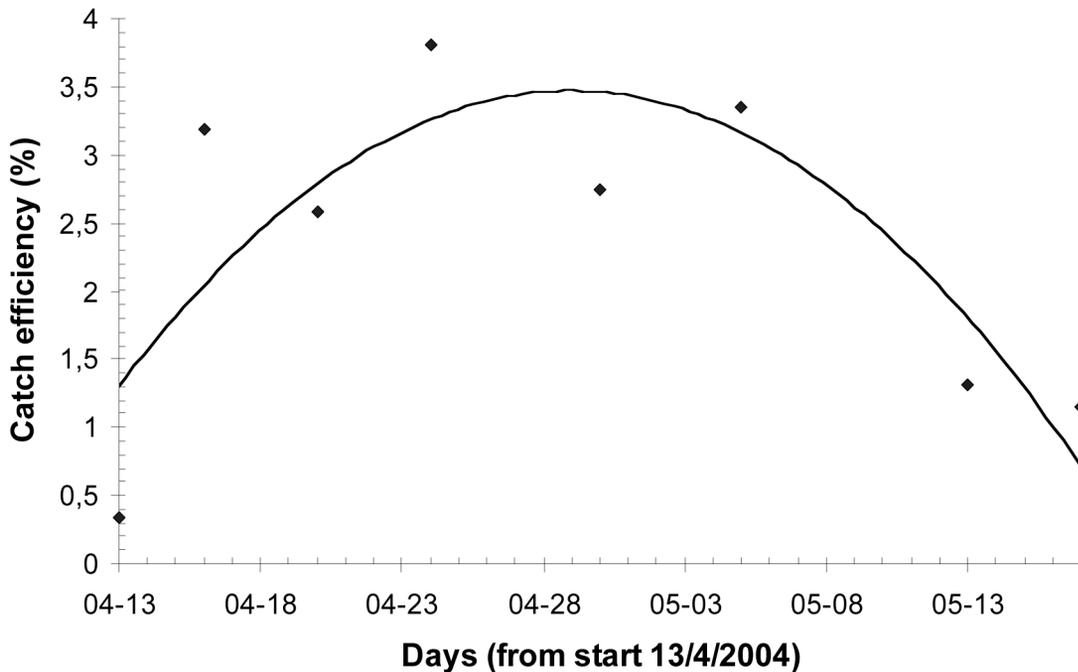


Fig. 2. Catch efficiency (percentage of the population size captured per trap night) of funnel traps in pond 7 during the study period. The number of immigrated adult individuals that was registered by means of drift fence and pitfall trapping was used as a population size estimate. $R^2 = 0.663$.

nile in a Lefkovich matrix (Caswell 2001). Because males of the great crested newt may mate with several females (Hedlund 1990), the number of males may not affect the fecundity to a high extent (Akcakaya 2000). Therefore, only females were modelled. We considered the study populations as “prebreeding censused birth-pulse populations” (Caswell 2001), and used a projection interval of one year. This resulted in the following stage matrix:

$$\begin{array}{c}
 \text{Time } t+1 \\
 \begin{array}{cc}
 \text{Juvenile} & \text{Adult} \\
 \text{Juvenile} & \left[\begin{array}{cc} S_j & F \\ S_{j-a} & S_a \end{array} \right] \\
 \text{Adult} &
 \end{array}
 \end{array}$$

where S_j is annual juvenile survival, S_{j-a} is annual proportion of juveniles that survives to the adult stage, S_a is annual adult survival, and F is fecundity. Fecundity was defined as a product of clutch size per female and survival of egg, larvae and metamorphs up to their first birthday.

Spatial structure in RAMAS GIS is defined through the geographic configuration, as well as dispersal and correlation among a set of local populations. In this study, we assumed that breeding ponds were equivalent to local populations, and the model was based on breeding ponds discovered during 2003–2004. In the region, unoccupied ponds that still appeared suitable for breeding were not situated within dispersal distance from the occupied ponds. We therefore excluded these from the model. Suitable ponds for breeding were defined, based on the biology of the species (Arntzen 2003), as permanent and fish-free ponds which are not severely shaded by trees. Ponds no. 5, 6, 9, 10, 12 and 13 had small estimated population sizes and/or no reproductions were ascertained (Table 1). These ponds are probably too small and/or not sufficiently permanent to act as breeding ponds for the great crested newt (the other ponds in the study are permanent ponds) and were not included in the model. Furthermore, ponds no. 2 and 3, and 16, 17 and 18 respectively, were considered as single local populations because of the short distance (<5 m) between the ponds. Therefore, altogether nine local populations (ponds no. 1, 2/3, 4, 7, 8, 11, 14, 15, 16/17/18) were modelled.

Because data for several parameters were uncertain, we simulated minimum, medium and maximum estimates of these parameters to estimate lower and upper bounds of viability. We selected parameter values suggested to give the lowest, average and highest risks (sensu Akcakaya 1998), and grouped them together.

To simulate the impact of management measures, in accordance with Swedish conservation guidelines for the great crested newt (Schreiber 2003, Malmgren 2007), we also built a model with a different spatial structure and simulated it with a different parameterisation. This suggests that the species requires a high pond density at the landscape scale (0.7 breeding ponds per km², and prefera-

bly 4 breeding ponds per km² sensu Oldham et al. 2000) to allow for among-pond dispersal and metapopulation dynamics. To simulate an increased pond density from constructing of new ponds in the study area, we added one pond at a distance of 400 metres (average dispersal distance of the great crested newt; Joly et al. 2001) to every present breeding pond. These new ponds were positioned to increase connectivity between existing ponds when possible. Furthermore, we simulated restoration by excavation and removal of shading trees in some ponds. Parameterisation of this restoration is described in the “Parameterisation of the model – density dependence, and – stochasticity” section. If nothing else is stated, the other parameters were simulated with the medium estimates.

Instead of examining the risk of total extinction, we examined the probability for each population to go quasi-extinct, i.e. decline below a threshold value of 10 female individuals (adults + juveniles). This was because demographic and genetic stochasticity may have strong effects on very small populations (Lande 1993, Simberloff 1998), making it difficult to predict the behaviour of such populations (Akcakaya 1998). Furthermore, small populations may be doomed due to inbreeding depression and difficulties for individuals to find mates (Simberloff 1998).

Each simulation was run with 10 000 replicates with a time frame of 50 years.

Parameterisation of the model

Initial abundances

As initial abundances for adults, we used the proportion of females of the estimated adult population sizes (Table 1). Regarding populations monitored with funnel traps, we did not use the actual sex ratio, because funnel trapping may be male biased (Griffiths 1985, Nilsson 1998). Instead, we assumed a 1:1 sex ratio, since the sex ratio is generally fairly equal in populations of the great crested newt (Hagström 1979, Verrell and Halliday 1985, Miaud et al. 1993, Oldham 1994). Mean population sizes estimated with funnel traps were used as medium values and the means (\pm SD) as minimum and maximum, respectively. When negative values of initial abundances arose due to high standard deviations (Table 1), the minimum values were arbitrary set to five females.

For populations monitored with drift fences or visual observation (ponds no. 7 and 15), we used the observed sex ratio when calculating initial abundances. The observed numbers of individuals were considered minimum estimates of population size. We also used these estimates as medium values, since they were considered as “best estimates”. As maximum values the population size estimates were arbitrary increased with 20%, due to possible underestimating.

Estimating juvenile abundance is difficult since most juvenile great crested newts are likely to lead a predomi-

nantly terrestrial life until maturity (Hedlund 1990, Malmgren 2002). Thus they are only detected in very small numbers when monitoring breeding ponds. We therefore derived initial abundances for juveniles from the initial adult abundances, using Oldhams (1994) estimate of stage distribution: 20% adults and 80% juveniles. For juveniles we assumed a 1:1 sex ratio.

Initial abundances of newly created ponds simulated in the management scenario were set to 0.

Demography

We parameterised the vital rates for survival and fecundity by using data from the literature. Published estimates on mean annual adult survival of great crested newts range from 0.49 to 0.78 (Hagström 1979, Hedlund 1990, Arntzen and Teunis 1993, Baker 1999, Cooke and Arnold 2003), averaging 0.66. Mean annual juvenile survival has been estimated to 0.22 (Arntzen and Teunis 1993), 0.59 (Baker 1999) and 0.85 (Cummins and Swan 2000), averaging 0.55. Following this data, annual survival rate for adults was set to 0.49 (min.), 0.66 (medium) and 0.78 (max.), and annual survival rate for juveniles to 0.22 (min.), 0.55 (medium) and 0.85 (max.). The age when great crested newts become sexual mature (i.e. the transition from juvenile to adult), varies between 2 to 5 years old, with an average of 3 years (Dolmen 1983, Hagström 1984, Francillon-Vieillot et al. 1990, Arntzen and Teunis 1993, Miaud et al. 1993, Baker 1999). Due to lack of data of the annual proportion of juveniles that survives to the adult stage, a medium value for this parameter was used that in a matrix analysis gave a finite rate of increase close to 1.0 and a stable stage distribution of 24% adults and 76% juveniles, which is close to Oldhams (1994) estimate of stage distribution. This means that in the absence of stochasticity, density dependence and dispersal, the population will be stable over time. As minimum and maximum values the medium value ± 0.05 were used. This resulted in the following values: 0.06 (min.), 0.11 (medium) and 0.16 (max.).

Estimated clutch sizes for female great crested newts range from 189 to 220 (Hedlund 1990, Arntzen and Teunis 1993), averaging 204. About 50% of the eggs die before hatching due to a chromosomal deficiency (reviewed by Malmgren 2001). In addition to this, egg/larval mortality is thought to be 95% (Griffiths and Williams 2000). Fecundity was calculated with 189 as minimum, 204 as medium and 220 as maximum clutch size, and taking account of 50% egg lethality, 95% egg/larval mortality and juvenile survival of the metamorphs to the subsequent spring. Because we do not know how survival varies from metamorphosis to the subsequent spring, we used the values of annual juvenile survival, which can be considered as a conservative assumption. Because only females were modelled, these products were divided with two, assuming a 1:1 sex ratio. This resulted in the following fecundity values: 0.52 (min.), 1.4 (medium) and 2.34 (max.).

Density dependence

In amphibians, population growth is commonly considered as density dependent because some individuals receive more resources than others at high densities by contest competition (Van Buskirk and Smith 1991, Beebee 1996). Population studies of the great crested newt also suggest density dependent regulation of a contest competition type (Arntzen and Teunis 1993, Cooke and Arnold 2003). However, the knowledge about density dependence in populations of great crested newt is poor. We therefore modelled a density dependence similar to, but much simpler than, contest competition: the ceiling model. In the ceiling model, the population grows exponentially until it reaches carrying capacity, and then remains at that level.

The carrying capacities of the study populations were not known, and up to now no data on carrying capacities of the great crested newt exist. The inter-year fluctuation in population size for populations studied in Sweden (Hagström 1979, Hedlund 1990, Malmgren 2002) average 24.5%. We therefore arbitrarily assumed carrying capacities to 1.20 of the maximum initial abundances, except for pond no. 8 where we set the carrying capacity to 1.30 of the maximum initial abundance. This pond has been excavated during the autumn 2004, which can act to increase the resources for the great crested newt.

Due to natural succession, ponds no.11 and 14 will probably undergo habitat deterioration (shading by trees and/or overgrowing with weeds) during the simulated time period. To simulate this we used a temporal negative trend in the carrying capacities of these ponds by -1.5% (min.), -1% (medium) and -0.5% (max.) of the initial carrying capacities for each time step.

When simulating the management scenario, we set the carrying capacities for new ponds to 300 adults and 1200 juveniles. No temporal negative trend in carrying capacities of pond 11 and 14 were used in the management scenario. Instead, the carrying capacities of these ponds together with pond no. 15, were increased to 1.30 of the maximum initial abundances.

Dispersal

Dispersal in RAMAS GIS is defined "as the proportion of dispersing individuals per time step from one population to another" (the proportion of individuals in one population that actually arrive at another population; Akcakaya 1998). We used data on dispersal capacities of the great crested newt from the literature to apply a simplified variant of the dispersal-distance function in RAMAS GIS:

$$m_{ij} = \exp(-D_{ij}/b), \text{ if } D_{ij} \leq D_{\max}$$

$$m_{ij} = 0, \text{ if } D_{ij} > D_{\max}$$

where m_{ij} is the proportion of dispersing individuals per time step between population i and j , D_{ij} is the distance

between the populations, b is a constant representing the average dispersal distance of the species, and D_{\max} is the maximum distance the species can disperse. Among-population dispersal of the great crested newt has been reported up to 1290 m (Kupfer 1998), and Arntzen and Wallis (1991) estimated the dispersal rate per year to 1000 m. However, Joly et al. (2001) assumed the average dispersal distance of the great crested newt to be 400 m. We therefore set b to 400 m. D_{\max} was set to 1200 m based on Kupfer (1998). Possible effects of landscape structure on dispersal were not taken into consideration.

Among-population dispersal of the great crested newt is thought to take place mainly by juveniles (Hedlund 1990, Kupfer and Kneitz 2000, Cooke and Arnold 2003, Griffiths 2004), but has also been reported for adults (Arntzen and Teunis 1993, Miaud et al. 1993). We therefore used stage-specific dispersal, where juveniles disperse in accordance with the dispersal–distance function, but adults only disperse at one tenth of this dispersal rate, i.e. the migration probability for the adults are one tenth of the juveniles.

Stochasticity

Three different types of stochasticity were incorporated in the model: environmental stochasticity, demographic stochasticity and catastrophes. Catastrophes were defined as “extreme environmental events that adversely affect large proportions of a population” (Akçakaya 1998).

Environmental stochasticity was modelled by varying the parameters survival rate, fecundity and carrying capacity randomly during the simulations. The random values were drawn from a lognormal distribution constructed by the means and the standard deviations of these parameters. Environmental stochasticity of survival rates, fecundities and carrying capacities were assumed to be correlated under three levels of positive correlation. It is not known to what extent variation in vital rates (survival and fecundity) among the local populations are correlated. Therefore, we

arbitrarily set correlation in vital rates among the populations to 0.75 (min.), 0.50 (medium) and 0.25 (max.), assuming that correlation among local populations and metapopulation extinction risk are positively correlated (Akçakaya 1998).

Standard deviations of annual adult survival range from 0.11 to 0.25 (Hedlund 1990, Arntzen and Teunis 1993, Baker 1999, Cooke and Arnold 2003), averaging 0.19. The only available standard deviation of annual juvenile survival is 0.20 (Arntzen and Teunis 1993). We used 0.25 (min.), 0.19 (medium) and 0.11 (max.) for standard deviations of adult survival rate. Standard deviations for juvenile survival, annual proportion of juveniles surviving to adults, fecundity and carrying capacity were all set to 0.20 (medium), with 0.10 and 0.30 as max. and min. values, respectively. These estimates were arbitrarily chosen due to lack of more detailed data (for fecundity, see Griffiths and Williams 2000).

Demographic stochasticity was modelled during the simulations by randomly drawing survival values and fecundity values from a binomial distribution and a poisson distribution, respectively.

We modelled summers with severe drought, causing high mortality of eggs and larvae, as catastrophes. We incorporated a probability of 0.09 for total reproductive failure to occur, based on the frequency of summers with severe drought (annual precipitation < 150 mm) in Sweden between 1900–2000 (SMHI 2003). These droughts were assumed to be regional, i.e. all populations were modelled to be hit at the same time step. In addition, we modelled a higher egg/larval mortality in ponds 11, 14 and 15 based on reproduction data (Table 2), and our observations on the ponds tendencies to desiccate. We set the impact of these catastrophes to 50% mortality and the probability to 0.2 in pond 11 and 15, and 0.5 in pond 14. These droughts were assumed to be local, i.e. the ponds risks of being hit were independent of each other. When simulating the management scenario, catastrophes in

Table 2. Extinction risks for the great crested newt in the study area under different scenarios: minimum estimates of uncertain parameters; medium estimates; maximum estimates; medium estimates with restoration of three ponds (Management 1); medium estimates with restoration of three ponds and increased pond density (Management 2). Extinction risk is expressed as the probability of a quasi-extinction in the study area (the population size in each of the populations in the study area falling below 10 females [adults + juveniles]) at least once during 50 years (interval extinction risk); the probability that the great crested newt in the study area will end up quasi-extinct after 50 years (terminal extinction risk); the median time to quasi-extinction in the study area in years (time to quasi-extinction); the average number of occupied ponds in the study area after 50 years (no. of occupied ponds).

Scenario	Interval extinction risk	Terminal extinction risk	Time to quasi extinction	No. of occupied ponds
Minimum	1	1	6.2	0
Medium	0.465	0.192	>50	1.7
Maximum	0	0	>50	9
Management 1	0.411	0.163	>50	2.1
Management 2	0.447	0.098	>50	5.6

ponds 11, 14 and 15 were not used, because restoration of these ponds was assumed to decrease the risk of desiccation.

impacts of changes in dispersal rates are more likely to be detected.

Sensitivity analysis

To identify which parameters that affected the simulations the most, we performed a sensitivity analysis using the “manual perturbation” approach (Mills and Lindberg 2002). The procedure was to change each parameter up and down while keeping the other parameters at the medium estimates. We principally used the minimum and maximum estimates described above. Parameters that had no specified minimum and maximum values, were changed as follows. The carrying capacity values were changed with -40% and $+40\%$, respectively. The probability of catastrophes was changed to 0.15 and 0.05, respectively. The effect of dispersal was investigated by changing b , the constant representing the average dispersal distance, to 200 m and 600 m, respectively. However, most populations are isolated from each other due to distance. Decreasing or increasing the proportion of dispersing individuals may therefore have small effects on viability in the study area. For this reason we analysed sensitivity in dispersal by using the management model with a higher pond density (described in the “PVA model structure and simulation of the model” section). In this model possible

Results

Population size estimates

A total of 684 great crested newts immigrated to the drift fence pond (no. 7) (Fig. 3). Following other drift fence studies (Kupfer and Kneitz 2000), the population size is presented as the number of immigrating individuals. Of these, 620 were classed as adults, with a 2:1 sex ratio (413 females and 207 males), and 64 were classed as juveniles. The drift fence was removed just before the onset of post-breeding emigration from the pond. By then, 17 newts had already been caught leaving the pond and released outside the fence, where they were assumed to set off to their terrestrial habitat.

The catch efficiency (i.e. the percentage of individuals captured with funnel traps per trap night) varied in pond no. 7 from 0.34% to 3.81% (Fig. 2). We used the catch efficiency equation for pond no. 7 to calculate adult population sizes in the ponds monitored with funnel traps only. These estimates, which are presented as means for the trap nights, ranged from 0 to 402 adult individuals (Table 1).

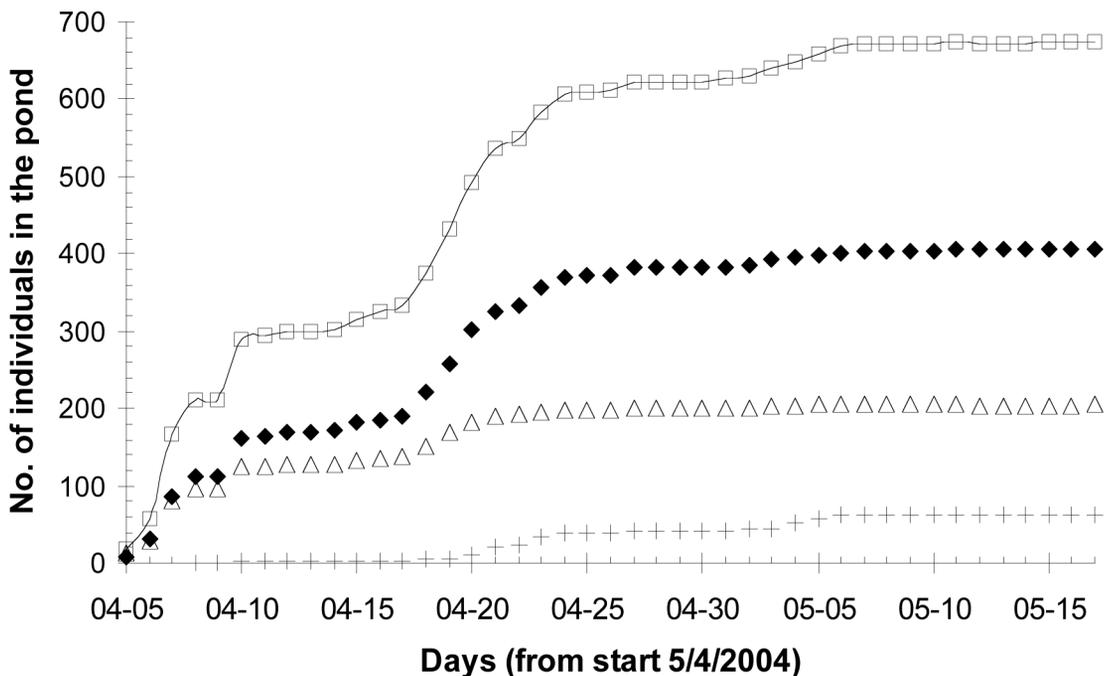


Fig. 3. Number of great crested newts (□ = total; ◆ = females; △ = males; + = juveniles) in pond 7 during the study period. The pond was monitored by means of a drift fence with pitfall traps during April 4 to May 17 in 2004. Trapped animals were registered and released on the other side of the fence daily.

Estimates of adult population sizes by visual observation are presented as the highest observed number of individuals, since we assumed total census success, and ranged from 1 to 77 newts (Table 1). The average population size estimate \pm SD was 155 ± 179 individuals, and if only taking local populations in account, 297 ± 233 newts. Reproduction was ascertained in eight of the ponds (Table 1).

Viability

The extinction risk for great crested newts in the study area varied considerably between different scenarios. Simulation with minimum estimates resulted in a 100% quasi-extinction probability of the great crested newt in the study area within 50 years, with a median time to quasi-extinction of 6.2 years (Table 2). With medium estimates the quasi-extinction probability was reduced to 19.2%. There was a negative trend in abundance with these estimates (Fig. 4), and the number of occupied ponds decreased from 9 to an average of 1.7 after 50 years (Table 2). Populations with high extinction probabilities were ponds no. 8, 11, 14 and 15 (Table 3). With the maximum estimates, there was no risk of quasi-extinction in the study area (Table 2).

Restoration of three ponds decreased the quasi-extinction probability in the study area from 19.2% to 16.3% (Table 2). Despite restoration, the number of occupied ponds decreased from 9 to an average of 2.1 after 50 years (Table 2). If the pond density was increased in addition to restoration, the quasi-extinction probability in the study area decreased to 9.8% (Table 2). Furthermore, an increased pond density decreased the risk of quasi-extinction

in existing populations, especially for the ponds with the highest extinction risks (Table 3).

Sensitivity

Demographic parameters such as fecundity, juvenile survival, adult survival and transition from juvenile to adult affected the model outcome to a high extent. Decreasing these parameters to their minimum estimates resulted in 80–100% quasi-extinction probabilities in the study area within 50 years, while increasing them to their maximum estimates inferred no or very small risks of quasi-extinction (Table 4). Changes in the other parameters had only small effects on the quasi-extinction probabilities (Table 4).

Discussion

Population size estimates

Estimated adult population sizes varied between 0 and 620 individuals. This is roughly in the same magnitude as published population estimates of the great crested newt, although these vary considerably (Arntzen and Teunis 1993).

However, our population estimates are tentative. Drift fence catch efficiency (i.e. the percentage of the population approaching the fence and caught in the pitfalls) is not known for pond no. 7. Arntzen et al. (1995) report fence efficiency values between 23% and 76% for the great crested newt, while Kufper and Kneitz (2000) had a fence effi-

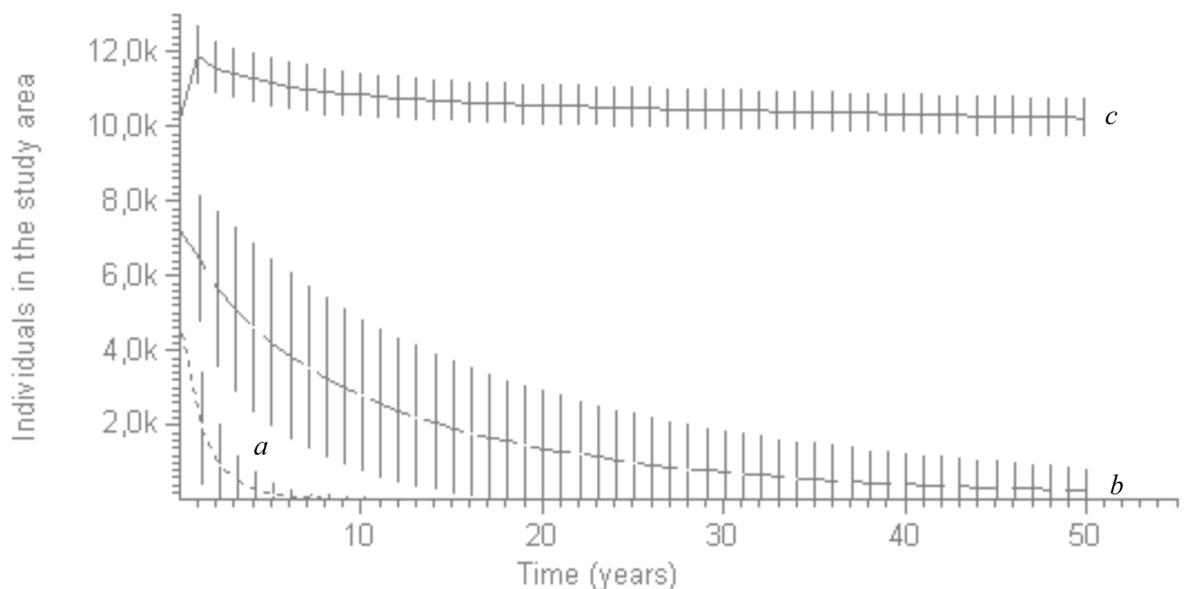


Fig. 4. Trends in abundance of the great crested newt in the study area during 50 years under different scenarios: a) minimum estimates of uncertain parameters; b) medium estimates; c) maximum estimates. Solid curves show the average abundance and vertical bars show ± 1 SD.

Table 3. Extinction risks for the local populations in the study area under two different scenarios I: no management, and II: with restoration of three ponds and increased pond density. Extinction risk is expressed as the probability of a quasi-extinction in the population (population size falling below 10 females [adults + juveniles]) at least once during 50 years (interval extinction risk); the probability that the population will end up quasi-extinct after 50 years (terminal extinction risk); the median time to quasi-extinction in the population in years (time to quasi-extinction).

Population	Interval extinction risk	Terminal extinction risk	Time to quasi extinction
Scenario	I / II	I / II	I / II
Pond 1	0.815 / 0.794	0.626 / 0.496	30.1 / 30.9
Pond 2/3	0.852 / 0.800	0.538 / 0.398	28.7 / 30.8
Pond 4	0.852 / 0.806	0.557 / 0.399	28.7 / 30.2
Pond 7	0.735 / 0.704	0.521 / 0.396	36.3 / 37.4
Pond 8	0.994 / 0.896	0.932 / 0.503	7.0 / 21.0
Pond 11	0.889 / 0.867	0.722 / 0.488	26.2 / 25.8
Pond 14	0.963 / 0.784	0.784 / 0.357	19.9 / 30.6
Pond 15	0.958 / 0.765	0.779 / 0.316	20.2 / 32.8
Pond 16/17/18	0.766 / 0.765	0.558 / 0.353	34.2 / 32.9

ciency of 67–100 %. Taking this into account, the data presented here may be underestimates of the true population size in pond no. 7. On the other hand the female-biased sex ratio (2:1) we observed in pond no. 7 may indicate that a number of males may have entered the pond before the fence was erected since males often arrive to the breeding pond before the females (Verrell and Halliday 1985, Arntzen 2002). However, the pond was partly covered by ice when the drift fence was erected and migration patterns of females and males were otherwise very similar. We therefore consider this risk as marginal at this particular site.

Further, the catch efficiency of the funnel traps in pond no. 7 was rather low (0.34% – 3.81%) and in line with catch efficiencies of great crested newts in funnel traps reviewed by Griffiths and Raper (1994) (2 – 28%). The variation between ponds in catch efficiency showed by Griffiths and Raper (1994) implies that our population estimates with funnel traps, which are based on catch efficiency from one pond only, are uncertain. As stated by Schmidt (2003), count data not adjusted for detection probabilities are not reliable and capture-recapture methods are preferable for the estimation of population sizes. Concerning funnel traps, Nilsson (1998) has however

Table 4. The sensitivity of different parameters for the model outcome. Sensitivity is expressed as the extinction risk at a minimum and maximum estimate, respectively, of a parameter when all other parameters are set at the medium estimates. Extinction risk is expressed as the probability of a quasi-extinction in the study area (the population size in each of the populations in the study area falling below 10 females [adults + juveniles]) at least once during 50 years (interval extinction risk); the probability that the great crested newt in the study area will end up quasi-extinct after 50 years (terminal extinction risk); the median time to quasi-extinction in the study area in years (time to quasi-extinction); the average number of occupied ponds in the study area after 50 years (no. of occupied ponds). The parameters are arranged in falling order by sensitivity in terminal extinction risk.

Parameter	Interval extinction risk	Terminal extinction risk	Time to quasi extinction	No. of occupied ponds
Estimate	min. / max.	min. / max.	min. / max.	min. / max.
Fecundity	0.996 / 0.044	0.935 / 0.008	22.5 / >50	0 / 5.7
Juvenile survival	0.981 / 0	0.869 / 0	24.8 / >50	0 / 8.6
Adult survival	0.961 / 0.031	0.832 / 0.003	26.9 / >50	0.1 / 6.0
Transition juvenile-adult	0.962 / 0.048	0.818 / 0.008	27.6 / >50	0.1 / 5.5
Correlation	0.568 / 0.348	0.278 / 0.106	45.9 / >50	1.6 / 1.9
SD juvenile survival	0.570 / 0.329	0.270 / 0.104	46.4 / >50	1.3 / 2.4
SD adult survival	0.507 / 0.337	0.229 / 0.097	49.6 / >50	1.6 / 2.3
Catastrophe	0.557 / 0.400	0.248 / 0.152	47.1 / >50	1.3 / 2.1
Initial abundance	0.510 / 0.420	0.226 / 0.164	49.4 / >50	1.5 / 1.9
SD fecundity	0.498 / 0.429	0.218 / 0.166	>50 / >50	1.6 / 1.8
Carrying capacity	0.504 / 0.440	0.214 / 0.176	49.8 / >50	1.5 / 1.8
SD carrying capacity	0.466 / 0.451	0.190 / 0.177	>50 / >50	1.7 / 1.8
Dispersal	0.434 / 0.438	0.112 / 0.115	>50 / >50	4.5 / 4.5

showed that capture-recapture studies are all but impossible. Furthermore, outcomes from the PVA's demonstrated low sensitivity to differences in modelled values for initial abundances. Hence, the results should not inflict upon the confidence of their accuracy due to this uncertainty alone, provided true population sizes are within the estimated ranges.

Viability and sensitivity

Due to uncertain estimates for several parameters, the estimated extinction risks for the great crested newt in the study area range from 100% to no risk at all. However, we consider the medium estimates to be those most informative and realistic, because it is unlikely that all minimum or maximum estimates would co-occur year after year during a 50-year period. The abundance and the number of local populations decreased during the simulated time period, suggesting a higher extinction risk in a longer time horizon. We chose not to simulate longer time periods due to the increased uncertainty of such simulations (Akçakaya and Sjögren-Gulve 2000).

Management measures, especially increased pond density, had greatest impact on the probability for the great crested newt to end up quasi-extinct in the study area after 50 years. Thus, management may increase the viability in the study area on a longer term since an increased number of ponds enable higher newt abundances. Furthermore, extinction risks in the existing isolated ponds decreased by adding new ponds, which suggests that existing ponds benefit from dispersal from new ponds due to a rescue effect (Brown and Kodric-Brown 1977). However, in contrast to this positive effect from dispersal, changing the proportion of dispersing individuals had negligible effects in the sensitivity analysis. An interpretation of this may be that it is the possibility to disperse that matters, not to what extent, since even very few individuals may be able to establish a population quite rapidly (Arntzen and Teunis 1993, Niesel and Berglind 2003). Positive effects of dispersal are otherwise consistent with Griffiths and Williams (2000) and Griffiths (2004), who found that the great crested newt persisted better in several connected small ponds than in a single and isolated large pond. However, Halley et al. (1996) demonstrated that isolated great crested newt populations had low extinction risks if they were sufficiently large (> 40 adult females).

The great crested newt may not perform classical metapopulation dynamics, since extinctions of great crested newt populations are probably mainly due to deterministic causes (Beebee 1997, Niesel and Berglind 2003, Sztatecny et al. 2004), not stochastic as they are assumed to be in classical metapopulation models (Hanski 1999). Nevertheless, a metapopulation approach seems to be useful for the conservation of the species. Our simulations show positive effects of dispersal between great crested newt popula-

tions, and even when there are no interactions between local populations, the very presence of several populations decrease the regional extinction risk (Hanski and Simberloff 1997, Akçakaya 1998). However, merely protecting networks of ponds will not be enough for regional persistence.

Our simulations demonstrate the need for well-designed management regimes for local populations. Ponds in a late succession stage and/or with a high drought frequency (ponds no. 8, 11, 14 and 15) had the highest extinction risks and benefited from restoration. Negative effects of a higher drought frequency are consistent with Griffiths and Williams (2000), who found an increased extinction risk when the frequency of drought increased. However, in the sensitivity analysis, the probability of regional catastrophes (droughts causing total egg/larval mortality) had only small effects on extinction risk in the study area. The reason for this contradiction is probably that the frequency of droughts has to be higher than in our sensitivity analysis to have severe effects on viability. Unless droughts are frequently occurring and/or occurring year after year, they are probably not critical for great crested newt populations due to their long life expectancy (Malmgren 2001), with maximum life spans reported to vary between 16–18 years in the wild (Dolmen 1982, Miaud et al. 1993) to about 27 years in captivity (Fog et al. 2001). This is supported by observations of persistence of isolated populations despite reproduction failure (Cooke 1995, Baker 1999). This highlights the risk of not detecting deterministic extinctions due to the long life span of great crested newts. In cases where surveys identify sites where newts occur, some sites may represent declining populations with a history of reproductive failure, and adult newts still present may simply represent ghosts of the past. Therefore, surveys and monitoring programmes should incorporate data on actual reproductive success to take this risk into account (Malmgren et al. 2005, Malmgren 2007).

The most important parameter for the outcome of the model was fecundity, followed by juvenile survival, adult survival and transition from juvenile to adult. This implies: 1) better estimates of these parameters would decrease the uncertainty in the model; 2) these parameters appear most important in the population dynamics, thus making them crucial in conservation. Fecundity includes survival of juveniles during their first seven months, and the fact that we estimated this with the values for annual juvenile survival may be a cause for the high sensitivity. This also highlights juvenile survival as an important parameter. Amphibian population dynamics are generally thought to be regulated at the embryonic and larval stages (Hellriegel 2000, Vonesh and De la Cruz 2002, Conroy and Brook 2003, but see Wilbur 1980). However, sensitivity of juvenile survival has recently been reported for several other amphibian species with different life histories (Biek et al. 2002, Hels and Nachman 2002, Vonesh and De la Cruz 2002, Conroy and Brook 2003, Hatfield et al. 2004). The im-

portance of juvenile survival for the great crested newt is consistent with Sohlman Wiessing (2004), who showed that survival during the first two years was the most sensitive parameter. Sensitivity to juvenile and adult survival rates are often due to life history constraints (Heppell et al. 2000), and the great crested newt is a species with a long life span that produce few offspring (Hedlund 1990, Maud et al. 1993). Proximate and ultimate causes to this, as well as implications for conservation, have been discussed in detail by Malmgren (2001). However, the juvenile stage is the least studied stage of amphibians, mainly due to difficulties in monitoring the animals (Beebee 1996). Cummins and Swan (2000) have demonstrated that passive integrated transponders (PIT tags) can be used to mark late-larval and newly metamorphosed great crested newts. This methodology and/or radiotracking (Jehle 2000, Jehle and Arntzen 2000) may provide means of investigating juvenile behaviour and ecology and estimating survival rate.

To reduce the uncertainty in adult and juvenile survival rates, the great crested newt is in need of additional demographic studies. Capture-recapture methods should be used to obtain reliable estimates of survival (Schmidt 2003). However, demographic studies of the great crested newt are complicated by the temporary emigration between the breeding pond and the terrestrial habitat. The number of breeding individuals has been shown to invariably fluctuate between years (Hagström 1979, Hedlund 1990, Arntzen and Teunis 1993, Kupfer and Kneitz 2000) and mortality may differ between the breeding pond and the terrestrial habitat. Multistate capture-recapture models may provide a mean to deal with this (Lebreton et al. 2003, Bailey et al. 2004, Schaub et al. 2004).

In conclusion, the strength of our PVA lies in identifying critical parameters and examining impacts from management, not in predicting absolute extinction risks. Furthermore, it demonstrates the potentially deceptive power of viability estimates if uncertainty of demographic data is not taken into account. Clearly, management and conservation of the great crested newt requires improved demographic data to produce refined viability prognoses. This is especially important for the juvenile stage. As there is rising evidence of a high sensitivity of this lifestage in amphibians, we recommend that studies on juvenile ecology should be given high priority in amphibian decline research. Another area of further research is the terrestrial ecology of the species. Great crested newts spend a considerable amount of time on land and processes occurring in the terrestrial habitat are probably important to population dynamics. However, terrestrial behaviour and ecology of the great crested newt is still poorly understood (Malmgren et al. 2007). Moreover, our results suggest that a metapopulation approach is useful for the conservation of great crested newt. Therefore, a successful management of this species requires a holistic landscape approach that ensures as well networks of breeding ponds as prevents extinctions of local populations.

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References

- Akcakaya, H. R. 1998. RAMAS GIS: Linking landscape data with population viability analysis, ver. 3.0. – Appl. Biomath., Setauket, New York.
- Akcakaya, H. R. 2000. Population viability analyses with demographically and spatially structured models. – *Ecol. Bull.* 48: 23–28.
- Akcakaya, H. R. and Raphael, M. G. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. – *Biodiv. Conserv.* 7: 875–894.
- Akcakaya, H. R. and Sjögren-Gulve, P. 2000. Population viability analysis in conservation planning: an overview. – *Ecol. Bull.* 48: 9–21.
- Arntzen, J. W. 2002. Seasonal variation in sex ratio and asynchronous presence at ponds of male and female *Triturus* newts. – *J. Herpetol.* 36: 30–35.
- Arntzen, J. W. 2003. *Triturus cristatus* Superspezies – Kammolch-Artenkreis (in German). – In: Grossenbacher, K. and Thiesmeier, B. (eds). *Handbuch der Reptilien und Amphibien Europas: Schwanzlurche (Urodela) IIA, Salamandridae II: Triturus 1*. Aula-Verlag, Wiebelsheim, pp. 421–514.
- Arntzen, J. W. and Teunis, S. F. M. 1993. A six year study on the population dynamics of the crested newt (*Triturus cristatus*) following the colonization of a newly created pond. – *Herpetol. J.* 3: 99–110.
- Arntzen, J. W. and Wallis, G. P. 1991. Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. – *Evolution* 45: 805–826.
- Arntzen, J. W. et al. 1995. Cost effective drift fences for toads and newts. – *Amphibia-Reptilia* 16: 137–145.
- Arntzen, J. W. et al. 2004. *Triturus cristatus*. – In: IUCN 2006. 2006 IUCN Red list of threatened species. Url: www.iucnredlist.org (Access 14 september 2007).
- Bailey, L. L. et al. 2004. Estimating survival and breeding probability for pond-breeding amphibians: a modified robust design. – *Ecology* 85: 2456–2466.
- Baker, J. M. R. 1999. Abundance and survival rates of great crested newts (*Triturus cristatus*) at a pond in central England: monitoring individuals. – *Herpetol. J.* 9: 1–8.
- Beebee, T. J. C. 1994. Distribution and status of great crested newts in Britain. – In: Gent, T. and Bray, R. (eds). *Conservation and management of crested newts. Proceeding of a symposium held on 11 January 1994 at Kew Gardens, Richmond, Surrey*. T. English Nat. Sci. Ser., Rep. no. 20, Peterborough, pp. 3–5.
- Beebee, T. J. C. 1996. *Ecology and conservation of amphibians*. – Chapman and Hall.

- Beebee, T. J. C. 1997. Changes in dewpond numbers and amphibian diversity over 20 years on chalk downland in Sussex, England. – *Biol. Conserv.* 81: 215–219.
- Beissinger, S. R. 2002. Population viability analysis: past, present, future. – In: Beissinger, S. R. and McCullough, D. R. (eds). *Population viability analysis*. Univ. Chicago Press, pp. 5–17.
- Biek, R. et al. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. – *Conserv. Biol.* 16: 728–734.
- Brook, B. W. et al. 2000. Predictive accuracy of population viability analysis in conservation biology. – *Nature* 404: 385–387.
- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rate in insular biogeography: effect of immigration on extinction. – *Ecology* 58: 445–449.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation* (2nd ed.). – Sinauer.
- Caughley, G. 1994. Directions in conservation biology. – *J. Anim. Ecol.* 63: 215–244.
- Cederberg, B. and Löfroth, M. (eds). 2000. Swedish animals and plants in the European network Natura 2000 (in Swedish with English summary). – Swedish species information centre, SLU, Uppsala.
- Conroy, S. D. S. and Brook, B. W. 2003. Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia. – *Popul. Ecol.* 45: 105–114.
- Cooke, A. S. 1995. A comparison of survey methods for crested newts (*Triturus cristatus*) and night counts at a secure site, 1983–1993. – *Herpetol. J.* 5: 221–228.
- Cooke, A. S. and Arnold, H. R. 2003. Night counting, netting and population dynamics of crested newts (*Triturus cristatus*). – *Herpetol. Bull.* 84: 5–14.
- Council of Europe. 1979. Convention on the conservation of European wildlife and natural habitats. – Url: <http://conventions.coe.int/Treaty/FR/Treaties/Html/104-2.htm> (Access 14 september 2007).
- Cummins, C. P. and Swan, M. J. S. 2000. Long-term survival and growth of free-living great crested newts (*Triturus cristatus*) PIT-tagged at metamorphosis. – *Herpetol. J.* 10: 177–182.
- Dolmen, D. 1982. Skeletal growth marks and testis lobulation as criteria for age in *Triturus* spp. (Amphibia) in central Norway. – *Acta Zool.* 63: 73–80.
- Dolmen, D. 1983. Growth and size of *Triturus vulgaris* and *T. cristatus* (Amphibia) in different parts of Norway. – *Holarct. Ecol.* 6: 356–371.
- Edgar, P. and Bird, D. R. 2006. Action plan for the conservation of the crested newt *Triturus cristatus* species complex in Europe. – Council of Europe, Strasbourg. Url: http://www.coe.int/t/e/cultural_co-operation/environment/nature_and_biological_diversity/nature_protection/sc26_inf17_en.pdf (Access 6 september 2007).
- Etienne, R. S. et al. 2003. Ecological impact assessment in data-poor systems: a case study on metapopulation persistence. – *Environ. Manage.* 32: 760–777.
- Fieberg, J. and Ellner, S. P. 2000. When is it meaningful to estimate an extinction probability? – *Ecology* 81: 2040–2047.
- Fog, K. et al. 2001. Nordens padder og krybdyr (in Danish). – Gads Forlag, Copenhagen.
- Francillon-Vieillot, H. et al. 1990. Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. – *J. Herpetol.* 24: 13–22.
- Gasc, J. P. et al. (eds) 1997. Atlas of amphibians and reptiles in Europe. – Soc. Eur. Herpetol. Mus. Natl D’Hist. Naturelle, Paris.
- Gent, T. and Bray, R. (eds) 1994. Conservation and management of crested newts. Proceeding of a symposium held on 11 January 1994 at Kew Gardens, Richmond, Surrey. – English Nat. Sci. Ser., Rep. no. 20, Peterborough.
- Griffiths, R. 1985. A simple funnel trap for studying newt populations and an evaluation of trap behaviour in smooth and palmate newts, *Triturus vulgaris* and *T. helveticus*. – *Herpetol. J.* 1: 5–10.
- Griffiths, R. 2004. Great crested newts (*Triturus cristatus*) in Europe: effects of metapopulation structure and juvenile dispersal on population persistence. – In: Akcakaya, H. R. et al. (eds), *Species conservation and management case studies*. Oxford Univ. Press, pp. 281–291.
- Griffiths, R. A. and Raper, S. J. 1994. A review of current techniques for sampling amphibian communities. – Joint Nat. Conserv. Committee, Rep. no. 210, Peterborough.
- Griffiths, R. A. and Williams, C. 2000. Modeling population dynamics of great crested newts (*Triturus cristatus*): a population viability analysis. – *Herpetol. J.* 10: 157–163.
- Gustafson, D. and Malmgren, J. C. 2002. Inventering och övervakning av större vattensalamander (*Triturus cristatus*) (in Swedish). – Örebro Univ. and County Admin. Board of Örebro, Rep. no. 2002:02.
- Hagström, T. 1979. Population ecology of *Triturus cristatus* and *T. vulgaris* (Urodela) in SW Sweden. – *Holarct. Ecol.* 2: 108–114.
- Hagström, T. 1980. Growth of newts (*Triturus cristatus* and *Triturus vulgaris*) at various ages. – *Salamandra* 16: 248–251.
- Hagström, T. 1984. Vattensalamandrar i Västsverige, en ekologisk översikt (in Swedish with English summary). – *Fauna Flora* 79: 117–128.
- Halley, J. M. et al. 1996. Predicting the persistence of amphibian populations with the help of a spatial model. – *J. Appl. Biol.* 33: 455–470.
- Hanski, I. 1999. *Metapopulation ecology*. – Oxford Univ. Press.
- Hanski, I. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. – In: Hanski, I. and Gilpin, M. E. (eds), *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, pp. 5–26.
- Hatfield, J. F. et al. 2004. Houston toad (*Bufo houstonensis*) in Bastrop County, Texas: need for protecting multiple subpopulations. – In: Akcakaya, H. R. et al. (eds), *Species conservation and management case studies*. Oxford Univ. Press, pp. 292–298.
- Hedlund, L. 1990. Reproductive ecology of crested newts, *Triturus cristatus* (Laur.). – PhD thesis. Swedish Univ. of Agric. Sci., Rep. no. 16.
- Hellriegel, B. 2000. Single- or multistage regulation in complex life cycles: does it make a difference? – *Oikos* 88: 239–249.
- Hels, T. and Nachman, G. 2002. Simulating viability of a spadefoot toad *Pelobates fuscus* metapopulation in landscape fragmented by a road. – *Ecography* 25: 730–744.
- Heppell, S. S. et al. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. – *Ecology* 81: 654–665.
- Jehle, R. 2000. The terrestrial summer habitat of radio-tracked great crested newts (*Triturus cristatus*) and marbled newts (*T.*

- marmoratus*). – Herpetol. J. 10: 137–142.
- Jehle, R. and Arntzen, J. W. 2000. Post-breeding migrations of newts (*Triturus cristatus* and *T. marmoratus*) with contrasting ecological requirements. – J. Zool. 251: 297–306.
- Joly, P. et al. 2001. Habitat matrix effects on pond occupancy in newts. – Conserv. Biol. 15: 239–248.
- Karlsson, T. 2003. Inventering av större vattensalamander (*Triturus cristatus*) i delar av Boxholms, Kinda, Mjölby och Linköpings kommuner (in Swedish with English abstract). – Project course thesis, Univ. of Kalmar, Sweden.
- Kupfer, A. 1998. Wanderstrecken einzelner kammolche (*Triturus cristatus*) in einem agrarlebensraum (in German with English abstract). – Z. Feldherpetol. 5: 238–242.
- Kupfer, A. and Kneitz, S. 2000. Population ecology of the great crested newt (*Triturus cristatus*) in an agricultural landscape: dynamics, pond fidelity and dispersal. – Herpetol. J. 10: 165–171.
- Lande, R. 1993. Risk of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911–927.
- Langton, T. E. S. et al. 2001. Great crested newt conservation handbook. – Froglife, Halesworth.
- Lebreton, J. D. et al. 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. – Oikos 101: 253–264.
- Ludwig, D. 1998. Is it meaningful to estimate probability of extinction? – Ecology 80: 298–310.
- Malmgren, J. C. 2001. Evolutionary ecology of newts. – PhD thesis. Örebro Univ., Sweden.
- Malmgren, J. C. 2002. How does a newt find its way from a pond? Migration patterns after breeding and metamorphosis in great crested newts (*Triturus cristatus*) and smooth newts (*T. vulgaris*). – Herpetol. J. 12: 29–35.
- Malmgren, J. C. 2007. Åtgärdsprogram för bevarande av större vattensalamander och dess livsmiljöer (*Triturus cristatus*). Rep. no. 5636. Naturvårdsverket, Stockholm. (in Swedish with English summary). Url: <http://www.naturvardsverket.se/Documents/publikationer/620-5636-0.pdf> (Access 6 September 2007).
- Malmgren, J. C. et al. 2005. Inventering och övervakning av större vattensalamander (*Triturus cristatus*). Surveying and monitoring plan. – Swed. Environ. Protection Agency, Stockholm (in Swedish). Url: http://www.naturvardsverket.se/upload/02_tillstandet_i_miljon/Miljoovervakning/undersokn_typ/vatmark/salamand.pdf (Access 14 September 2007).
- Malmgren, J. C. et al. 2007. Modelling terrestrial interactions and shelter use in great crested newts (*Triturus cristatus*). – Amphibia-Reptilia 28: 205–215.
- Miaud, C. et al. 1993. Variation in age structures in a subdivided population of *Triturus cristatus*. – Can. J. Zool. 71: 1874–1879.
- Mills, L. S. and Lindberg, M. S. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. – In: Beissinger, S. R. and McCullough, D. R. (eds), Population viability analysis. Univ. of Chicago Press, pp. 338–366.
- Niesel, J. and Berglind, S. Å. 2003. Habitat och hotsituation för större vattensalamander (*Triturus cristatus*): Sammanställning och utvärdering av inventeringar i Värmlands län 1991–2003 (in Swedish). – County Admin. Board of Värmland, Rep. 2003:16.
- Nilsson, J. 1998. Analysis of habitat requirements and abundance of *Triturus cristatus* on the Hällnäs peninsula of northern Uppland, eastcentral Sweden. (in Swedish with English summary). – Degree thesis. Uppsala Univ., Sweden.
- Oldham, R. S. 1994. Habitat assessment and population ecology. – In: Gent, T. and Bray, R. (eds), Conservation and management of crested newts. Proceeding of a symposium held on 11 January 1994 at Kew Gardens, Richmond, Surrey. T. English Nat. Sci. Ser., Rep. no. 20, Peterborough, pp. 45–67.
- Oldham, R. S. et al. 2000. Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). – Herpetol. J. 10: 143–155.
- Schaub, M. et al. 2004. Estimating survival and temporary emigration in the multistate capture-recapture framework. – Ecology 85: 2107–2113.
- Schreiber, H. 2003. Art- och naturtypsvisa vägledningar för Natura 2000 – Större vattensalamander (*Triturus cristatus*) (in Swedish). – Swed. Environ. Protection Agency. Url: <http://www.naturvardsverket.se, ver. 2003-04-16> (Access 14 september 2007).
- Schmidt, B. R. 2003. Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. – C. R. Biol. 326: 119–124.
- Simberloff, D. 1998. Small and declining populations. – In: Sutherland, W. J. (ed.), Conservation science and action. Blackwell, pp. 116–134.
- [SMHI] Swed. Meteorol. Hydrol. Inst. 2003. Torka – Faktblad nr 16 (in Swedish). – Norrköping, Sweden.
- Sohlman Wiessing, A. 2004. Sårbarhetsanalys (population viability analysis, PVA) av en population av större vattensalamander (*Triturus cristatus*) vid Gränby backe (in Swedish). – Course thesis. Uppsala Univ., Sweden.
- Sztatecsny, M. et al. 2004. The abundance of premetamorphic newts (*Triturus cristatus*, *T. marmoratus*) as a function of habitat determinants: an a priori model selection approach. – Herpetol. J. 14: 89–97.
- Van Buskirk, J. and Smith, D. C. 1991. Density dependent population regulation in a salamander. – Ecology 72: 1747–1756.
- Verrell, P. and Halliday, T. 1985. The population dynamics of the crested newt *Triturus cristatus* at a pond in southern England. – Holarct. Ecol. 8: 151–156.
- Vonesh, J. R. and De la Cruz, O. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. – Oecologia 133: 325–333.
- Wilbur, H. M. 1980. Complex life cycles. – Annu. Rev. Ecol. Syst. 11: 67–93.