Estimating Population Sizes, Viability and Sensitivity of the Crested Newt (*Triturus cristatus*) at a Landscape Scale

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Abstract

Population sizes, viability and sensitivity of the threatened amphibian crested newt (*Triturus cristatus*) were estimated in an area of 144 km^2 in southeastern Sweden. Eighteen ponds were monitored during spring and summer 2004 using drift fence with pitfall traps, funnel traps, visual observation and netting. Estimated adult population sizes ranged between 0 and 620 individuals, and the mean (±SD) in local populations was 297 ±233 individuals. Viability with and without management, and sensitivity of different parameters were simulated with a demographically and spatially structured stochastic model. Due to uncertain 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 1.2%. However, just by setting the most sensitive parameter, juvenile survival, to its lower bound, the quasi-extinction risk increased to nearly 100%. The sensitivity of juvenile survival points out the importance of focusing conservation efforts and research on this life stage. Management measures in form of restoration of ponds and increased pond density had only marginal effects on the quasi-extinction risk. Nevertheless, these measures decreased the risk for the species to end up below certain abundances after 50 years considerably, making the study populations more viable at a longer term. Concrete management measures for the study area are presented.

Svensk sammanfattning (Swedish summary)

Den större vattensalamandern (*Triturus cristatus*) är en art som anses ha minskat kraftigt under det senaste seklet. Den främsta orsaken till nedgången tros vara att artens livsmiljöer förstörts. I dagsläget är den större vattensalamandern rödlistad som missgynnad (NT) i Sverige. Den har en hög skyddsstatus och är upptagen i Bernkonventionens annex II, och i EU:s Habitatdirektiv där den skyddas i nätverket Natura 2000. Den större vattensalamandern har fått allt större uppmärksamhet inom naturvården det senaste decenniet. Fortfarande är dock kunskapen om artens utdöenderisk och vilka faktorer som bestämmer populationsdynamiken (ökningar och minskningar över tiden) bristfällig. Ett sätt att erhålla kunskap i dessa frågor är att göra en sårbarhetsanalys för arten. En sårbarhetsanalys innebär att man låter en dator utföra simuleringar av en modell som beskriver en arts populationsdynamik i en förmodad framtida situation. I denna studie uppskattar jag populationsstorlekar och gör en sårbarhetsanalys för den större vattensalamandern i ett 144 km^2 stort område i södra Östergötland med 18 kända förekomstdammar. Syftet med studien är att uppskatta sårbarheten för arten i området och hur denna påverkas av naturvårdsåtgärder, samt att identifiera vilka faktorer som tycks ha störst betydelse för populationsdynamiken.

I min sårbarhetsanalys gjorde jag i datorprogrammet RAMAS GIS 3.0 flera modeller för hur salamanderpopulationerna i studieområdet kommer att utvecklas under de närmaste 50 åren. Modellerna tog hänsyn till både dynamiken i de enskilda populationerna och dynamiken i studieområdet som helhet genom t ex spridning mellan de olika populationerna. För att kunna göra sådana modeller krävs en stor mängd data för olika faktorer som på ett realistiskt sätt beskriver populationsdynamiken, slumpmässiga händelser och förväntade förändringar i artens livsmiljö. Exempel på sådana faktorer är hur stora populationerna är, hur många salamandrar som överlever från ett år till ett annat, hur många ungar varje salamander ger upphov till, spridningen mellan olika lekdammar samt hur olika väderförhållanden och igenväxning av lekdammarna påverkar salamandrarna. En stor del av de värden jag har använt för dessa faktorer har jag baserat på litteraturuppgifter som t ex studier av den större vattensalamandern och väderstatistik. För att uppskatta hur stora populationerna var övervakade jag med hjälp av olika metoder de 18 förekomstdammarna under den större vattensalamanderns lekperiod. I en damm fångades alla salamandrar på väg för att leka i dammen genom att ett s k driftstaket sattes upp runt hela dammen längs med vilket fallfällor placerades (se foton i appendix 1). I 14 dammar (inklusive den med driftstaket) fångade jag salamandrar med s k flaskfällor (en slags mjärde tillverkad av en PET-flaska) (se foton i appendix 1). Eftersom jag visste hur många salamandrar som befann sig i dammen med driftstaket, kunde jag beräkna hur stor del av dammens salamandrar (populationsstorleken) som flaskfällorna fångade. Detta mått på flaskfällornas fångsteffektivitet användes för att uppskatta populationsstorlekarna i de dammar där endast flaskfällor använts. I tre dammar räknade jag samtliga synliga salamandrar efter skymningen med hjälp av pannlampa. För att konstatera om salamandrarna fortplantat sig håvade jag under sensommaren efter salamanderlarver. De uppskattade populationsstorlekarna varierade mellan 0 och 620 vuxna individer, med ett medelvärde på 297 individer i lekdammarna.

Mycket av den data jag använde i min sårbarhetsanalys var osäker. Det är t ex inte säkert att litteraturuppgifter för den större vattensalamandern från ett annat område gäller i mitt studieområde. Jag tog hänsyn till denna dataosäkerhet genom att göra flera simuleringar med olika data. Jag gjorde en simulering med de data som bör ge den högsta utdöenderisken ("sämsta värden"), en simulering med genomsnittsdata, och en simulering med de data som bör ge den lägsta utdöenderisken ("bästa värden"). På så sätt kunde jag få fram gränser inom vilket det är troligt att den verkliga utdöenderisken finns. En sårbarhetsanalys största värde ligger emellertid inte i att ta fram precisa värden på utdöenderisker. Det finns alltid ett stort

osäkerhetsmoment i sådana resultat eftersom man ju aldrig exakt kan veta hur framtiden kommer att te sig. En sårbarhetsanalys är tillförlitligare i undersökningar av relativ karaktär, som hur olika naturvårdsåtgärder påverkar arten och vilka faktorer som tycks ha störst betydelse för artens populationsdynamik. I min sårbarhetsanalys undersökte jag hur den större vattensalamandern i studieområdet skulle påverkas av restaurering av vissa dammar och en ökad dammtäthet genom skapande av nya dammar. Ökad dammtäthet simulerades genom att göra en modell där antalet dammar fördubblades, med de nya dammarna inom spridningsavstånd från de redan existerande. Vidare undersökte jag vilken faktor i modellen som hade störst betydelse. Detta gjordes genom att ändra varje faktor till dess sämsta respektive bästa värde, medan de andra faktorerna hölls konstanta, och se utfallet av detta.

På grund av dataosäkerheten varierade mina uppskattningar av utdöenderisken för den större vattensalamandern i studieområdet stort. Vid simuleringen med de sämsta värdena var utdöenderisken inom 50 år 100%, medan den med de bästa värdena var obefintlig. Det är dock osannolikt att alla de sämsta eller alla de bästa värdena skulle sammanfalla år efter år i 50 år. Simuleringen med genomsnittsvärdena får därför betraktas som den bästa uppskattningen av utdöenderisken. Utdöenderisken för studieområdet var vid denna simulering mycket låg, 1,2%, men antalet salamandrar och antalet populationer minskade successivt under de 50 åren. Detta kan innebära en högre utdöenderisk på längre sikt. Bara genom att sätta ungöverlevnaden till dess sämsta värde ökade också utdöenderisken till nästan 100%. Ungöverlevnaden verkar således vara den faktor som har störst betydelse för den större vattensalamanderns populationsdynamik i studieområdet. Eftersom man i dagsläget vet mycket lite om var ungarna till den större vattensalamandern lever och hur de beter sig, är detta ett viktigt forskningsområde. Förmodligen uppehåller sig dock ungarna mestadels på land under sina första levnadsår, vilket innebär att förändringar i landmiljön runt en lekdamm kan vara kritiska för en population av större vattensalamander.

Restaurering och/eller ökad dammtäthet påverkade inte utdöenderisken i särskilt hög grad. Detta beror förmodligen på att utdöenderisken med genomsnittsvärdena redan var mycket låg, utdöenderisken kunde inte sjunka så mycket ifrån denna. Däremot så minskade dessa naturvårdsåtgärder risken för att antalet salamandrar skulle sjunka under vissa värden. Effekten var som störst för att minska risken att antalet salamandrar skulle falla under 2268 individer i studieområdet. Denna risk minskade med nästan 26% om restaurering och dammtäthet kombinerades. Naturvårdsåtgärder kan således göra den större vattensalamandern i studieområdet mer livskraftig i ett längre tidsperspektiv genom att bibehålla en hög individtäthet. Detta beror på att ett större antal dammar naturligtvis medger ett större antal salamandrar. Dessutom verkade de redan existerande dammarna dra nytta av invandring från de nya dammarna. Försvinner salamandrarna från en damm, kan denna åter bli bebodd genom invandring från en annan damm. Man bör dock vara medveten om att om den större vattensalamandern dött ut i en damm beror det oftast på att dammen genom igenväxning, skuggning av träd eller andra faktorer inte längre är användbar för salamandrarna som fortplantningslokal. Dammen måste då restaureras för att salamandrar ska kunna kolonisera den igen.

Mina resultat kan användas för att göra konkreta naturvårdsåtgärder i studieområdet. Dammtätheten kan, förutom att gräva nya dammar, ökas genom att restaurera salamandertomma dammar inom spridningsavstånd från de befintliga salamanderdammarna. Ungefär 100 m nordväst om damm 1 (Lilla Flogen) (se figur 1, sid. 2, för dammarnas geografiska positioner) finns en skogstjärn (Starrpölen) som bör kunna hysa större vattensalamander. Anledningen till att den i dagsläget inte verkar fungera som fortplantningslokal är okänt, men kan bero på försurning. Ytterligare undersökningar och eventuellt kalkning är därför lämpliga åtgärder. Ungefär 200 m nordost om damm 5

(Appeldalen 4) finns en damm i en övergiven betesmark där större vattensalamander inte har påträffats. Dammen är förmodligen för kall för att större vattensalamander ska kunna reproducera sig i den eftersom den skuggas av träd, och kan restaureras genom att dessa träd tas bort. I damm 9 (Pikedal 2) påträffades endast en hane av större vattensalamander, och den verkar inte fungera som lekdamm. Genom att göra den större och djupare bör den dock kunna bli lämplig som lekdamm. Damm 9 skulle då göra stor nytta genom att vara en länk mellan den lilla och sårbara populationen i damm 8 (Pikedal 1) och damm 11 (Lilla Farsbo). I några av de nu befintliga dammarna är restaurering förmodligen nödvändig för att behålla livskraftiga populationer av större vattensalamander. I damm 14 (Snokpölen) är läget akut. Ingen reproduktion har konstaterats i dammen, vilket sannolikt beror på att den ofta torkar ut p g a igenväxning, samt att den skuggas av träd och därmed blir för kall. Denna damm bör grävas ut, samt avlägsnas från träd i söderläge. Damm 11 (Lilla Farsbo) omgärdas till stor del av planterad granskog, vilken förmodligen missgynnar den större vattensalamanderns reproduktion genom skuggning och försurning. En avlägsning av granskog vid dammen skulle minska utdöenderisken i denna damm, som i dagsläget verkar lida av bristande reproduktion. Damm 15 (Haneberg) utgörs av ett mindre dike som delvis är beläget i ett igenvuxet kärr. En utgrävning av detta kärr till en damm skulle göra denna population livskraftigare. Damm 2 och 3 (Appeldalen 1 och 2) ligger grannar med en damm där det finns abborre. Abborre och större vattensalamander kan inte existera tillsammans eftersom abborren äter upp salamandrarnas larver. Damm 2 och 3 hotas därför av att abborre invandrar till dessa dammar. Bäst vore naturligtvis om abborrbeståndet helt kunde tas bort, men då detta kan vara både komplicerat och kostsamt är hinder för vattenflöde mellan dammarna ett sätt att minska utdöenderisken.

En god strategi när man restaurerar och nyskapar dammar är att ett år innan man restaurerar en damm anlägga en ny damm i närheten. En sådan "reservdamm" buffrar mot den förändring i livsmiljön som en restaurering medför.

Med tanke på hur sårbara ungarna visat sig vara i min studie, så är det sannolikt viktigt att även ta hänsyn till livsmiljön på land vid naturvårdsåtgärder. Salamandrarnas liv på land är emellertid hemlighetsfullt och dåligt känt, men skogsmark verkar vara viktigt för födosök, skydd och spridning. Genom att bevara och nyskapa ytförstorande strukturer på marken såsom död ved, stenrösen och lövhögar i fuktig och skuggig skogsmark så nära lekdammen som möjligt gynnar man förmodligen salamandrarna.

Slutligen bör man ha i minnet att man genom ovan beskrivna åtgärder inte bara gynnar den större vattensalamandern, utan även många andra djur och växter som är beroende av dammar. Dammar har visat sig bidra avsevärt till ett områdes mångfald av arter.

Contents

Introduction

From the late 1950s until today a substantial global decline of amphibian populations has been recorded (Houlahan *et al.* 2000). Today is almost a third of the world's amphibians thought to be under threat of extinction (Stokstad 2004). The decline received attention in the late 1980s (Barinaga 1990, Wake 1991), and since then the interest of what has caused this remarkable decrease has been great (Alford & Richards 1999).

One of the amphibian species focused by conservationists during the last decade is the crested newt *Triturus cristatus* (Laurenti), Caudata: Salamandridae (see e.g. Gent & Bray 1994, Langton *et al.* 2001). The crested newt is a widespread species which is distributed over most of northern and central Europe (Gasc *et al.* 1997). However, it is thought to have declined rapidly during the last century (Beebee 1994, 1997, Malmgren 2002b). The species lives a secretive life on land for most part of the year, except for spring and early summer when it resides in ponds for breeding (Griffiths 1996). It can be found in a broad variety of habitats, but it is considered to have more demanding requirements than other widespread amphibians in Europe (Dolmen 1988, Arntzen & Teunis 1993, Beebee 1996). Due to the larvae's long development time, 3-4 months (Griffiths 1996), and susceptibility to predation of fish (Dolmen 1982, Beebee 1997, Baker & Halliday 1999, Oldham *et al.* 2000, Malmgren 2001, Niesel & Berglind 2003), the species is dependent on permanent and fish-free ponds for successful reproduction. Moreover, it has been shown that a number of water quality parameters such as pH (Niesel & Berglind 2003), temperature (Andersen 2001) and content of phosphorus (Karlström & Sjögren-Gulve 1997) affects the suitability of a breeding pond. The crested newt probably also have specific requirements of the terrestrial habitat – for instance ground cover like stones and dead wood may be important for foraging and cover (Latham *et al.* 1996). The habitat requirements, combined with a rather poor ability to disperse (at most 1-1.3 km; Arntzen & Wallis 1991, Kupfer 1998), have made the crested newt vulnerable to urban development and intensification of agriculture and forestry. Habitat destruction of breeding ponds due to introduction of fish, draining, filling, acidification, eutrophication and natural succession along with loss of terristrial habitat and fragmentation are considered as the main threats (Malmgren 2002b).

The crested newt is currently listed in the category lower risk/conservation dependent (LR/CD) in the global redlist (European Reptile & Amphibian Specialist Group 1996). 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 in the network Natura 2000 (Cederberg & Löfroth 2000). The Natura 2000-protection obliges the EU countries to maintain "favourable conservation status" for the species (Cederberg & Löfroth 2000). In Sweden the crested newt is currently redlisted as near threatened (NT) (Gärdenfors 2000). About 500-600 breeding ponds are known (Malmgren 2002b), but size and viability of the populations are poorly known.

How then to monitor "favourable conservation status"? Despite the attention the crested newt has received, much is still unknown about extinction risks and parameters regulating the population dynamics. One way to increase the knowledge in these issues is performing a population viability analysis (PVA), i.e. simulating a model of a species population dynamics in the future (see Akcakaya & Sjögren-Gulve 2000 and Beissinger 2002 for overviews). PVAs have received much criticism for being nothing but "games played with guesses" (Caughley 1994), with unreliable estimates of extinction risks (Ludwig 1998, Fieberg & Ellner 2000). Since data for a PVA commonly are uncertain (Caughley 1994), the results of a PVA should be interpreted with caution, especially absolute extinction risks at longer terms (Akcakaya & Sjögren-Gulve, 2000, Fieberg & Ellner 2000). PVAs are probably most useful

when comparing extinction risks under different scenarios (Hanski & Simberloff 1997). Nevertheless, PVA predictions have been shown to be surprisingly accurate (Brook *et al.* 2000). Furthermore, data uncertainties can be incorporated by using ranges of parameters (Akcakaya & Sjögren-Gulve 2000) to build, for instance, best-case and worst-case scenario models (e.g. Akcakaya & Raphael 1998). Data uncertainties can also be analysed through a sensitivity analysis to identify important assumptions and parameters to guide further fieldwork (Akcakaya & Sjögren-Gulve 2000, Mills & Lindberg 2002), something that is missing in amphibian decline research (Biek *et al.* 2002). PVAs have been used on several amphibian species (e.g. Sjögren-Gulve & Ray 1996, Sutherland *et al.* 2000, Vos *et al.* 2000, Hels & Nachman 2002, Conroy & Brook 2003, Funk & Mills 2003), including the crested newt (Halley *et al.* 1996, Griffiths & Williams 2000, Etienne *et al.* 2003, Griffiths 2004, Sohlman Wiessing 2004).

In this study I estimate population sizes and perform a PVA on the crested newt in a restricted area in southeastern Sweden. Since persistence of amphibians is thought to take place at a regional spatial scale (Hecnar & M´Closkey 1996, Alford & Richards 1999), the study area constitutes of 144 km^2 with nine known local populations of the crested newt. The objective with the study is to estimate the extinction risks under different scenarios, identify parameters that seem to be important in the population dynamics and to discuss measures to maintain "favourable conservation status" for the crested newt in this area.

Methods

Study area

The study area is 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).
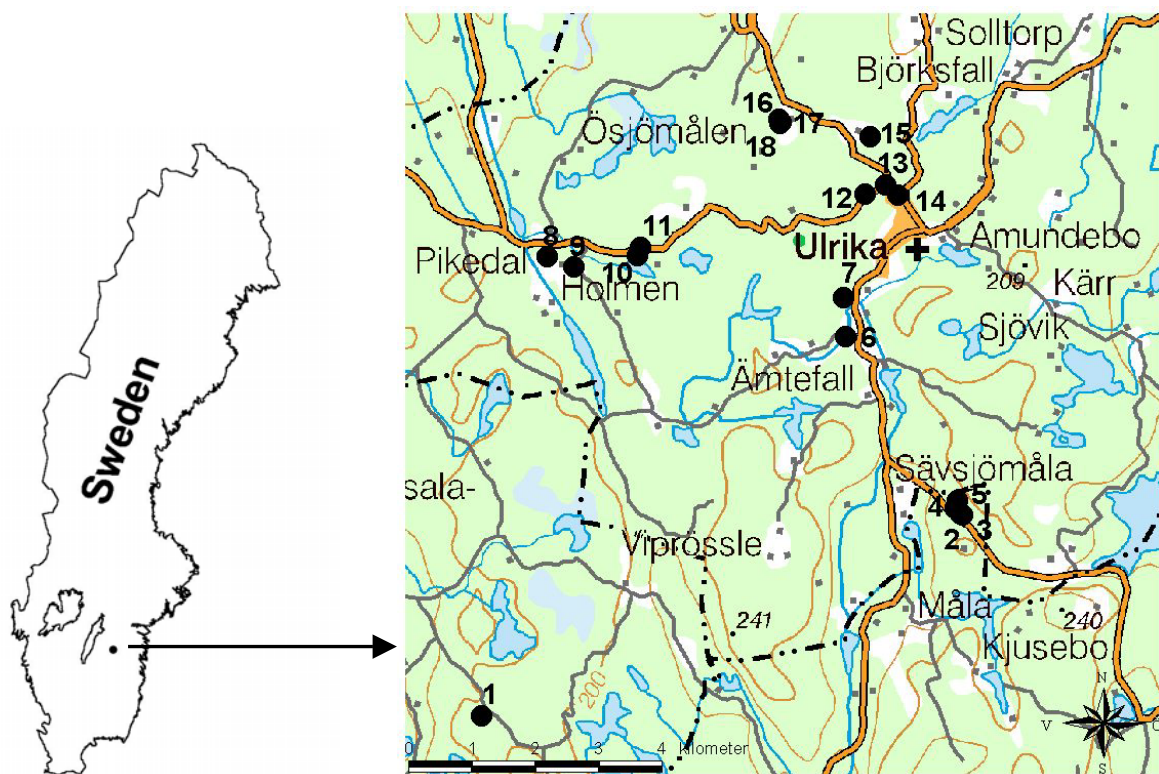
Figure 1. Location of the study area with positions of the monitored ponds.

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The area is situated on the edge of the southern Swedish highlands and consists of hilly coniferous woodland with great numbers of smaller lakes and wetlands. Cultivated land is concentrated to built-up areas and is rich in pastures and meadows (Lindahl 1997).

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

Table 1. Characteristics of monitored ponds with crested newt. Surroundings are described within a radius of 500 metres from the pond.

No	Name	Type	Surroundings	Size
1	Lilla Flogen	Forest tarn	Coniferous forest	>1000 m²
2	Appeldalen 1	Farm pond	Pasture/coniferous forest	100-500 m²
3	Appeldalen 2	Farm pond	Pasture/coniferous forest	<50 m²
4	Appeldalen 3	Farm pond	Pasture/coniferous forest	<50 m²
5	Appeldalen 4	Farm pond	Pasture/coniferous forest	<50 m²
6	Ljungstorp	Garden pond	Garden/pasture/coniferous forest	<50 m²
7	Högliden	Forest marsh/pond	Garden/pasture/coniferous forest	100-500 m²
8	Pikedal 1	Farm pond	Pasture/coniferous forest	<50 m²
9	Pikedal 2	Farm pond	Pasture/coniferous forest	<50 m²
10	Lilla Farsbo 1	Farm pond	Pasture/coniferous forest	<50 m²
11	Lilla Farsbo 2	Farm/forest marsh	Pasture/coniferous forest	100-500 m²
12	Boxholmsvägen	Roadside ditch	Coniferous forest	<50 m²
13	Boxholmskorset	Forest marsh	Coniferous forest	<50 m²
14	Snokpölen	Forest marsh	Coniferous forest/garden/pasture	100-500 m²
15	Haneberg	Ditch/marsh	Pasture/coniferous forest	<50 m²
16	Sörstugan 1	Marsh/farm pond	Pasture/coniferous forest	500-1000 m²
17	Sörstugan 2	Farm pond	Pasture/coniferous forest	<50 m²
18	Sörstugan 3	Farm pond	Pasture/coniferous forest	<50 m²

Population monitoring

Population sizes were estimated by three methods; drift fence with pitfall traps, funnel traps and visual observation. Pond 7 was completely encircled by a drift fence with pitfall traps from April 4 to May 17 in 2004 (see photos in appendix 1). The idea of a drift fence is that newts are hindered by the fence when migrating to the pond, then follow the fence and fall into a pitfall trap. For a detailed description see Arntzen *et al.* (1995) or Halliday (1996). The fence was constructed of milk 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 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 desiccation and predators. Stones were placed in the traps as counterweights against upwelling water, as covers 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.

Pond 1-5, 7-11, 13-14, and 16-18 were monitored by means of funnel traps. Funnel traps for newts were originally described by Griffiths (1985). The traps used in this study are a variant developed by Berglind (see Niesel & Berglind 2003) and were constructed of 1.5- and 2-litres plastic bottles with the neck cut off, turned inside out and fastened on the bottle (see photos in appendix 1). The traps have small holes for flowing of water and flaps for emptying. The traps 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 1-4 dm below the surface with the openings mainly directed towards the centre of the pond. Since the crested newt is mainly nocturnal (Dolmen 1983a), traps were placed at dusk and checked the following dawn. To prevent the newts from drowning, the traps were checked within no longer than 10 hours.

The funnel trapping took place between April 12 and May 17 2004, using five trap nights in each pond (except pond 13 two trap nights and pond 7 eight).

Pond 6, 12 and 15 were monitored by visual observation after dusk with a halogen head lamp (Silva M2, 2.4 W). 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 5 observation nights in each pond.

All trapped and observed newts were classed by sex and stage. Since size is a weak predictor of age of 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 (swollen cloaca and crest at the male) were defined as adults and newts not showing secondary sexual characteristics as juveniles.

To find out whether reproduction had occurred, the ponds were searched for larvae of the crested newt using a hand net. The hand net (size 30 x 25 cm) was carried to and fro 1 m along the waterside at a depth of 1-4 dm below the surface for 3 seconds every 5 m (see Gustafson & Malmgren 2002). The 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

I built a demographically and spatially structured model (see Akcakaya 2000) using the software RAMAS GIS version 3.0 (Akcakaya 1998). In RAMAS GIS the populations are demographically structured by age or stage in a Leslie matrix or a Lefkovitch matrix (see Caswell 2001) respectively, in which the population growths are simulated. Since data on age structure in the study populations were missing, I structured the populations by the postmetamorphic stages adult and juvenile. Because males of the crested newt may mate with several females (Hedlund 1990), the number of males may not affect the fecundity too much (Akcakaya 2000). Therefore, only females were modelled. I considered the study populations as "prebreeding censused birth-pulse populations" (see Caswell 2001), and used a projection interval of one year. This resulted in the following stage matrix:

	Time *t*	
	Juvenile	Adult
Time *t* + 1		
Juvenile	S_j	F
Adult	$S_{j\text{-}a}$	S_a

where S_j is annual juvenile survival, $S_{j\text{-}a}$ 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 birth day. Parameterisation of the matrix is described in the "Parameterisation of the model – Demography" section.

Spatial structure in RAMAS GIS is defined through the geographic configuration, and dispersal and correlation among a set of local populations. In this study, breeding ponds were assumed to be equivalent to local populations. However, not all of the monitored ponds were assumed to act as breeding ponds. Ponds no. 5, 6, 9, 10, 12 and 13 had small estimated population sizes and/or no reproduction were ascertained (see Tab. 2). These ponds are probably to small and/or not sufficiently permanent to act as breeding ponds for the crested newt 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 (pond 1, 2/3, 4, 7, 8, 11, 14, 15, 16/17/18) were modelled.

Because data for several parameters were uncertain, I did simulations with minimum, medium and maximum estimates of these parameters to estimate lower and upper bounds of viability. I selected parameter values suggested to give the lowest, average and highest risks (following guidelines in Akcakaya 1998), and grouped them together.

To simulate the impact of management measurements in accordance with the Swedish conservation guidance for the crested newt (Schreiber 2003), I also built a model with a different spatial structure and simulated it with a different parameterisation. Schreiber states (after Oldham *et al*. 2000) that pond density should be at least 0.7 breeding ponds per km^2, and preferably 4 breeding ponds per km^2 in areas favourable for the crested newt. To simulate an increased pond density by creation of new ponds in the study area, I added one pond at a distance of 400 metres (average dispersal distance of the 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, I simulated restoration by excavation and removal of shading trees in some ponds. Parameterisation of this restoration is described in the "Paramerisation 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, I examined the probability for each population to go quasi-extinct, i.e. fall below a threshold value of 10 female individuals (adults + juveniles). This because demographic and genetic stochasticity may have strong effects on very small populations (Lande 1993, Simberloff 1998b), making it difficult to predict the behaviour of such populations (Akcakaya 1998). Furthermore, such small populations may be doomed due to inbreeding depression and difficulties for the individuals to find mates (Simberloff 1998b).

Each simulation was run with 10000 replicates with a time frame of 50 years.

Parameterisation of the model

Initial abundances

As initial abundances (the number of individuals in each stage and population at the start of a simulation) for adults, I used the proportion of females of the estimated adult population sizes that are presented in table 2. Regarding populations monitored with funnel traps, I did not use the actual sex ratio, because funnel trapping may be male biased (Griffiths 1985, Nilsson 1998). Instead, I assumed a 1:1 sex ratio, since the sex ratio is commonly even in populations of the crested newt (Hagström 1979, Verrell & Halliday 1985, Miaud *et al.* 1993, Oldham 1994). The mean population sizes were used as medium values and the means minus and plus the standard deviations as minimum and maximum, respectively. When negative values of initial abundances arose due to high standard deviations, the minimum values were set to five females.

For populations monitored with drift fence or visual observation (pond 7 and 15), I used the actual sex ratio when calculating initial abundances. These population size estimates are considered as minimum estimates. Consequently, I used these estimates as minimum values. I also used these estimates as medium values, since they are considered as "best estimates". As maximum values the population size estimates were increased with 20%, due to possible underestimating.

Most juveniles probably live a terrestrial life (Hedlund 1990), and will not be detected when monitoring breeding ponds. I 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 I assumed a 1:1 sex ratio.

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

Demography

I parameterised the vital rates survival and fecundity by using data from the literature. Published estimates on mean annual adult survival of the crested newt range from 0.49 to 0.78 (Hagström 1979, Hedlund 1990, Arntzen & Teunis 1993, Baker 1999, Cooke and Arnold 2003), averaging on 0.66. Mean annual juvenile survival has been estimated to 0.22 (Arntzen & Teunis 1993), 0.59 (Baker 1999) and 0.75 (Cummins & Swan 2000), averaging on 0.52. Following this data, annual survival rate for adults was set to minimum 0.49, medium 0.66 and maximum 0.78. However, Cummins & Swans (2000) estimate of juvenile survival seem unrealistically high, since juvenile survival of amphibians is thought to be low (Beebee 1996). Therefore, I chose 0.22 as minimum, 0.59 as maximum and the mean of these 0.40 as medium for annual juvenile survival, which is a conservative assumption. The age when crested newts become sexual mature, i.e. the transition of juvenile to adult, varies between 2 to 5 years old, with an average of 3 years old (Dolmen 1983b, Hagström 1984, Francillon-Vieillot *et al.* 1990, Arntzen & Teunis 1993, Miaud *et al.* 1993, Baker 1999). The annual proportion of juveniles that survives to the adult stage was therefore calculated as the juvenile survival during two years (first year is included in fecundity, see below). This resulted in the following values: minimum 0.048, medium 0.16 and maximum 0.35.

Estimated clutch sizes per female crested newt range from 189 to 220 (Hedlund 1990, Arntzen & Teunis 1993), averaging on 204. About 50% of the eggs die due to a cromosomal deficiency (Malmgren 2001). In addition to this, egg/larval mortality is thought to be 95% (Griffiths & Williams 2000). Fecundity was calculated with 189 as minimum, 204 as medium and 220 as maximum clutch size, and taking account of 50% egg abortion, 95% egg/larval mortality and juvenile survival of the metamorphs during their first seven months with 0.38 as

minimum, 0.75 as medium and 1.00 as maximum (derived from annual juvenile survival). Since only females were modelled, these products were divided with two, assuming a 1:1 sex ratio. This resulted in the following fecundity values: minimum 0.90, medium 1.91 and maximum 2.75.

Density dependence

Population growth in amphibians is commonly considered as density dependent because some individuals receive more resources than others at high densities by contest competition (Van Buskirk & Smith 1991, Beebee 1996). Population studies of the crested newt also suggest density dependent regulation of a contest competition type (Arntzen & Teunis 1993, Cooke & Arnold 2003). However, the knowledge about density dependence in populations of crested newt is poor. I 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 the 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 crested newt exists. I therefore assumed carrying capacities to 1.20 of the maximum initial abundances, except for pond 8 where I set the carrying capacity to 1.30 of the maximum initial abundance. This pond has been excavated during the autumn 2004 (Sven-Olof Karlsson, personal communication), which is supposed to increase the resources for the crested newt.

Due to natural succession, pond 11 and 14 will probably undergo habitat deterioration (shading by trees and/or overgrowing with weeds) during the simulated time period. To simulate this I used a temporal negative trend in the carrying capacities of these ponds by -1.5% as minimum, -1% as medium and -0.5% as maximum of the initial carrying capacities each time step.

When simulating the management scenario, I set the carrying capacities in the 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 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" (Akcakaya 1998). I used data on dispersal capacities of the crested newt from the literature to use a simplified variant of the dispersal-distance function in RAMAS GIS:

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

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

where m_{ij} is the migration 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 crested newt has been reported to take place within 400 m (Baker & Halliday 1999), 860 m (Kupfer & Kneitz 2000), 1000 m (Laan & Verboom 1990) and 1290 m (Kupfer 1998). Arntzen & Wallis (1990) estimated the dispersal rate per year to 1000 m. However, Joly *et al.* (2001) assumed the average dispersal distance of the crested newt to be 400 m. I therefore set b to 400 m. D_{max} was set to 1200 m based on Kupfer (1998). Possible effects of landscape structure on dispersal was not taken in consideration.

Among-population dispersal of the crested newt is thought to take place mainly by juveniles (Dolmen 1982, Hedlund 1990, Kupfer & Kneitz 2000, Cooke & Arnold 2003), but is however reported for adults too (Arntzen & Teunis 1993, Miaud *et al.* 1993). I 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.

Correlation

It is not known to what extent variation in vital rates (survival and fecundity) among the local populations are correlated. Therefore, I arbitrarily set correlation in vital rates among the populations to minimum 0.75, medium 0.50 and maximum 0.25.

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" (Akcakaya 1998).

Environmental stochasticity was modelled by using standard deviations of survival rates, fecundities and carrying capacities within these parameters varies randomly during the simulations by drawing values from a lognormal distribution. Environmental stochasticity of survival rates, fecundities and carrying capacities were assumed to be correlated.

Standard deviations of published annual adult survival range from 0.11 to 0.25 (Hedlund 1990, Arntzen & Teunis 1993, Baker 1999, Cooke & Arnold 2003), averaging on 0.19. The only available standard deviation of annual juvenile survival is 0.20 (Arntzen & Teunis 1993). I used 0.25 as minimum, 0.19 as medium and 0.11 as maximum for standard deviations of adult survival rate. Standard deviations of juvenile survival and annual proportion of juveniles that survives to adults were set to 0.20 as medium, and the arbitrarily assumed values 0.30 and 0.10 as minimum and maximum respectively.

Standard deviations of fecundity were set to medium 0.20 following Griffiths & Williams (2000). Minimum and maximum values were arbitrarily assumed to 0.30 and 0.10 respectively.

Standard deviations of carrying capacities were arbitrarily assumed to minimum 0.30, medium 0.20 and maximum 0.10.

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

I modelled summers with severe drought, causing high mortality of eggs and larvae, as catastrophes. I used a probability of 0.09 for total mortality (= fecundity * 0) to occur, based on the frequency of summers with severe drought (annual precipitation < 150 mm) in Sweden 1900-2000 (SMHI 2003). These droughts were assumed to be regional, i.e. all populations were modelled to being hit at the same time step. In addition, I modelled a higher egg/larvae mortality in ponds 11, 14 and 15 based on reproduction data (Tab. 2), and my observations on the ponds tendencies to desiccate. I set the impact of these catastrophes to 50 % mortality (= fecundity * 0.5) 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 risk of being hit were independent of each other. When simulating the management scenario, these catastrophes in ponds 11, 14 and 15 were not used.

Sensitivity analysis

To identify what parameters that had most impact on the outcome of the simulations, I performed a sensitivity analysis of the "manual perturbation" approach (see Mills & Lindberg 2002). The procedure was to change each parameter up and down while keeping the other parameters at the medium estimates. I principally used the minimum and maximum estimates described in the "Parameterisation of the model" section. However, annual juvenile survival and annual proportion of juveniles that survives to the adult stage were considered as one parameter in the sensitivity analysis because the latter depends on the former. Furthermore, parameters that not have specified maximum and minimum values in the "Parameterisation of the model" section, were changed as follows. The carrying capacity values were changed -40% and +40%, respectively. The probability of catastrophes (total egg/larvae mortality) was changed to 0.15 and 0.05, respectively. The proportion of dispersing individuals per time step were changed by changing b, the constant representing the average dispersal distance, to 200 m and 600 m, respectively. However, the main part of the populations is 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 that reason I 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 impacts of changes in dispersal rates are more likely to be detected.

Results

Population size estimates

A total of 684 crested newts immigrated to and 17 emigrated from the drift fence pond (no.7, Högliden) (Fig. 2). Following other drift fence studies (e.g. Gill 1978, Kupfer & Kneitz 2000), the population size is presented as the number of immigrating individuals. Of these, 620 were classed as adults and 64 were classed as juveniles. The adults were classed as 413 females and 207 males, which gives a sex ratio of 2:1.

Monitoring pond 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 percentage of the number of individuals in pond 7 captured with funnel traps per trap night (catch efficiency) varied between 0.34% and 3.81%. The regression function that best explained the variation in catch efficiency was a polynomial equation where catch efficiency is a function of time ($y = -0.0085x^2 + 646.04x -1E+07$, $R^2 = 0.6626$) (Fig. 3). 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 don't differ in the study area, I assume correlation among the ponds in variation of breeding intensity and catch efficiency. Further, I assume 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, I used the catch efficiency equation for pond 7 to calculate adult population sizes in the ponds monitored with funnel traps. These estimates, which are presented as means of the trap nights, ranged from 0 to 402 adult individuals (Tab. 2). Estimates of adult population sizes by visual observation are presented as the highest observed number of individuals, since I assume total census, and ranged from 1 to 77 newts (Tab. 2). The average population size estimate ±SD was 155 ±179 individuals, and if only taking local populations (see the "PVA model structure and simulation of the model" section) in account 297 ±233. Reproduction was ascertained in eight ponds, which, together with reproduction data from 2003 (Karlsson 2003b), is shown in table 2.
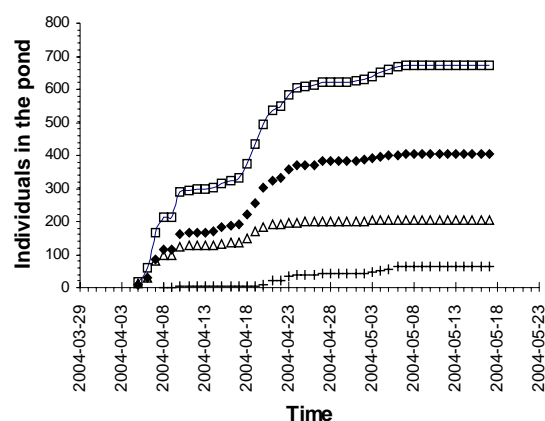
Figure 2. Number of crested newts (□ = total; ♦ = females; Δ = males; + = juveniles) in pond 7 during the study period.
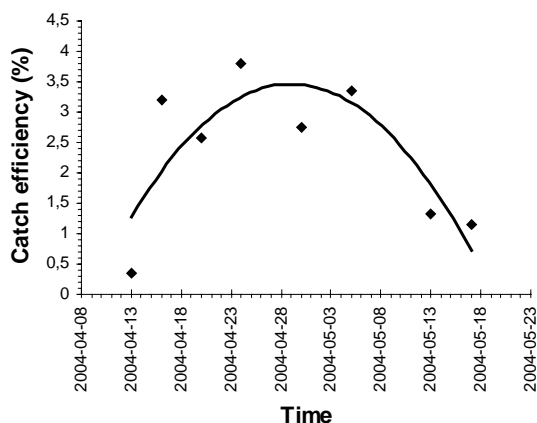
Figure 3. Catch efficiency (percentage of the number of individuals in the pond captured per trap night) of the funneltraps in pond 7 during the study period. Regression equation is $y = -0.0085x^2 + 646.04x - 1E+07$ ($R^2 = 0.6626$).

Table 2. Estimated adult population sizes (± SD), population monitoring method and absence (-) or presence (+) of reproduction 2003 and 2004 respectively. 2003 reproduction data from Karlsson (2003b). Pond 13, 17 and 18 were not monitored for reproduction in 2003.

| No	Name	Population size estimate (adults)	Method	Reproduction 2003/2004
1	Lilla Flogen	357 (± 133)	Funnel traps	+/+
2	Appeldalen 1	344 (± 74)	Funnel traps	+/+
3	Appeldalen 2	163 (± 141)	Funnel traps	+/+
4	Appeldalen 3	32 (± 54)	Funnel traps	+/+
5	Appeldalen 4	0	Funnel traps	-/-
6	Ljungstorp	1	Visual observation	-/-
7	Högliden	620	Drift fence	+/+
8	Pikedal 1	14 (± 19)	Funnel traps	+/-
9	Pikedal 2	5 (± 13)	Funnel traps	-/-
10	Lilla Farsbo 1	10 (± 24)	Funnel traps	-/-
11	Lilla Farsbo 2	314 (± 182)	Funnel traps	-/+
12	Boxholmsvägen	6	Visual observation	-/-
13	Boxholmskorset	92 (± 52)	Funnel traps	/-
14	Snokpölen	187 (± 86)	Funnel traps	-/-
15	Haneberg	77	Visual observation	-/+
16	Sörstugan 1	402 (± 217)	Funnel traps	+/+
17	Sörstugan 2	99 (± 61)	Funnel traps	/-
18	Sörstugan 3	67 (± 44)	Funnel traps	/-

Viability

The extinction risk for the crested newt in the study area varied considerably between different scenarios. Simulation with minimum estimates resulted in a 100% quasi-extinction probability of the crested newt in the study area within 50 years, with a median time to quasi-extinction of 6.8 years (Tab. 3). With medium estimates, the probability that the crested newt in the study area will end up quasi-extinct after 50 years was only 1.2%. However, 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 5.4 after 50 years (Tab. 3). Populations with high extinction probabilities were ponds 8, 11, 14 and 15 (Tab. 4). With the maximum estimates, there was no risk of quasi-extinction in the study area (Tab. 3).

Simulated management measures decreased the risk that the crested newt in the study area will end up quasi-extinct after 50 years only marginally, but had greater impact on the probability for the species to end up below certain abundances in the study area after 50 years. Restoration of three ponds decreased the quasi-extinction probability in the study area from 1.2% to 0.5% (Tab. 3), and decreased the probability of falling below 1244 individuals (threshold abundance where management had most effect) in the study area with 8.1% (Fig. 5). However, despite restoration, the number of occupied ponds decreased from 9 to an average of 6.4 after 50 years (Tab. 3). If the pond density was increased in addition to restoration, the quasi-extinction probability in the study area decreased to 0.2% (Tab. 3), and the probability of falling below 2268 individuals (threshold abundance where management had most effect) in the study area decreased with 25.8% (Fig. 5). Furthermore, an increased pond density decreased the risk of quasi-extinction in the existent populations, especially the ponds with the highest extinction risks (Tab. 4).

Table 3. Extinction risks for the crested newt in the study area under the 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 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	6.8	0
Medium	0.056	0.012	>50	5.4
Maximum	0	0	>50	9
Management 1	0.037	0.005	>50	6.4
Management 2	0.036	0.002	>50	15.4
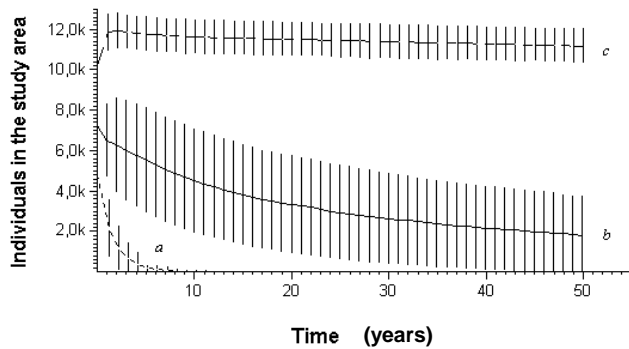
Figure 4. Trends in abundance of the crested newt in the study area during 50 years under the scenarios: *a*) minimum estimates of uncertain parameters; *b*) medium estimates; *c*) maximum estimates. Solid curves show the average abundance and vertical bars show ±1 SD.
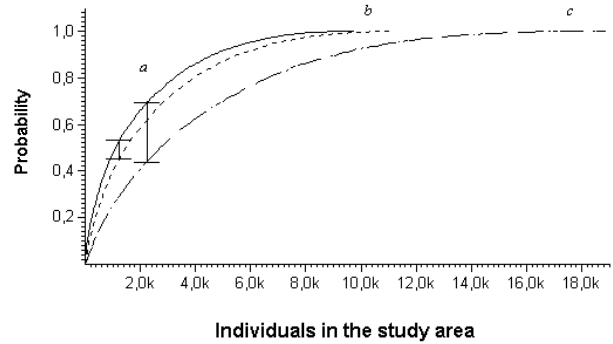
Figure 5. Extinction risks for the crested newt in the study area under the management scenarios: *a*) no management; *b*) restoration of three ponds; *c*) restoration of three ponds and increased pond density. The scenarios are simulated with medium estimates of uncertain paramaters. Extinction risk is expressed as the probability that the species will end up below a range of abundances after 50 years. The vertical bars show the maximum difference between the curves.

Table 4. Extinction risks for the local populations in the study area with no management, and with restoration of three ponds and increased pond density, respectively. 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
Pond 1	0.394 – 0.291	0.224 – 0.097	>50 – >50
Pond 2/3	0.394 – 0.268	0.127 – 0.046	>50 – >50
Pond 4	0.396 – 0.261	0.127 – 0.044	>50 – >50
Pond 7	0.276 – 0.208	0.143 – 0.059	>50 – >50
Pond 8	0.924 – 0.483	0.692 – 0.075	10.5 – >50
Pond 11	0.557 – 0.365	0.346 – 0.078	45.1 – >50
Pond 14	0.760 – 0.249	0.388 – 0.031	31.1 – >50
Pond 15	0.711 – 0.203	0.373 – 0.024	34.1 – >50
Pond 16/17/18	0.325 – 0.213	0.176 – 0.026	>50 – >50

Sensitivity

The most sensitive parameters for the model outcome were the demographic ones; juvenile survival, fecundity and adult survival. Of these the juvenile survival was the most important. Decreasing this parameter to its minimum estimate resulted in a 99.3% quasi-extinction probability in the study area within 50 years, while increasing it to its maximum estimate implied no risk of quasi-extinction (Tab. 5). Decreasing fecundity and adult survival to their minimum estimates resulted in 55% and 38.8% probabilities of the study area being quasi-

extinct after 50 years, respectively, while increasing these parameters to their maximum estimates implied no quasi-extinction risks (Tab. 5). Changes in the other parameters had only small effects on the quasi-extinction probabilities (Tab. 5).

Table 5. Sensitivity of parameters used in the simulations. Sensitivity is expressed as the extinction risk with a minimum and the 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 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
Juvenile survival	1 – 0	0.993 – 0	18.5 – >50	0 – 9
Fecundity	0.862 – 0.002	0.550 – 0	33.3 – >50	0.3 – 7.8
Adult survival	0.674 – 0.001	0.388 – 0	41.3 – >50	0.9 – 8.2
SD juvenile survival	0.221 – 0	0.069 – 0	>50 – >50	3.4 – 7.8
Correlation	0.126 – 0.019	0.035 – 0.002	>50 – >50	5.1 – 5.7
SD adult survival	0.090 – 0.013	0.022 – 0.001	>50 – >50	4.8 – 6.6
Catastrophe	0.111 – 0.035	0.023 – 0.006	>50 – >50	4.6 – 5.9
Carrying capacity	0.075 – 0.049	0.016 – 0.008	>50 – >50	4.8 – 5.6
Initial abundance	0.070 – 0.053	0.015 – 0.009	>50 – >50	5.1 – 5.6
SD fecundity	0.069 – 0.046	0.013 – 0.008	>50 – >50	5.1 – 5.6
Dispersal	0.036 – 0.044	0.003 – 0.004	>50 – >50	14.1 – 15
SD carrying capacity	0.001 – 0	0 – 0	>50 – >50	8.2 – 8.3

Discussion

Population size estimates

The catch efficiency of the funnel traps in pond 7 was rather low (Fig. 3). This is in line with catch efficiencies of crested newts in funnel traps reviewed by Griffiths & Raper (1994), there catch efficiencies ranged between 2% and 28% (standardised to 1 trap per 2 m). The poor catch efficiency of the funnel trap demonstrates the difficulties of using it to estimate population sizes. As showed by Nilsson (1998), using funnel traps in capture-recapture methods is almost impossible. Furthermore, the variation between ponds in catch efficiency showed by Griffiths & Raper (1994) implies that my population estimates with funnel traps, which are based on catch efficiency from only one pond, are uncertain. Population size estimates of the crested newt are also complicated by the fact that the number of breeding individuals may fluctuate between years (Hagström 1979, Hedlund 1990, Arntzen & Teunis 1993, Kupfer & Kneitz 2000). However, the low sensitivity of initial abundances implies that the uncertainty in my population size estimates not inflicted upon the outcome in the PVA, provided the real population sizes are within the estimated ranges. Nevertheless, a reliable and simple method of estimating population sizes of the crested newt is missing. On the other hand, using relative population estimates or just ascertain occurrence and reproduction might

be the only effective ways of monitoring the crested newt at a landscape scale (cf. Gustafson *et al*. 2004).

The estimated adult population sizes varied considerably (Tab. 2). The average population size estimate in the breeding ponds, 297, is very high if one consider the statements of Bell (1979) who suggests that the average adult population size is 10-20 individuals, and Feldmann (1981, cited in Arntzen & Teunis 1993) who only observed population sizes over 100 individuals in 3 out of 230 breeding ponds. My estimates are more in line with Malmgren (2002b), who suggests that the average population comprises of about 300 adult individuals.

The largest population was found in the pond monitored with drift fence, pond 7. The estimated adult population size, 620 in a pond of the size 100-500 m^2, is relatively high compared to estimated adult population sizes in other studies. Published population size estimates of equal-sized ponds range from 91 to 500 (Hagström 1979, Hedlund 1990, Arntzen & Teunis 1993, Baker 1999, Kupfer & Kneitz 2000, Malmgren 2002a, Hellberg *et al.* 2004), while Latham *et al.* (1996) reports population sizes up to about 1500 individuals in ponds of the size 600 and 1200 m^2. However, fence efficiency (the percentage of the population approaching the fence which was caught in the pitfalls) is not known for pond 7. Arntzen *et al.* (1995) report fence efficiency values between 23% and 76% for the crested newt, while Kufper & Kneitz (2000) had a fence efficiency of 67-100 %. As stated, a population size of about 600 individuals in a pond of the size of 100-500 m^2 is however a large population and correcting for fence efficiency may had overestimated the population size.

The sex ratio is commonly even in populations of the crested newt (Hagström 1979, Verrell & Halliday 1985, Miaud *et al.* 1993, Oldham 1994), but the males sometimes arrive to the breeding pond before females (Verrell & Halliday 1985, Cedhagen & Nilson 1991). The female biased sex ratio (2:1) in pond 7 may therefore indicate that a number of males entered the pond before the fence was erected. However, the equal migration patterns of females and males (Fig. 2) doesn't support this eventuality. Hedlund (1990) also found an uneven sex ratio, but in favour of males. The ratio altered from 1:1 to 2.8:1 within six years, with environmental stress as a possible explanation.

Viability and sensitivity

Due to uncertain estimates for several parameters, the estimated extinction risks for the crested newt in the study area range from 100% to no risk at all (Tab. 3). However, I consider the medium estimates as the best estimates. Thus, the simulations with these estimates should be the most realistic ones. It is rather unlikely that all minimum or maximum estimates would coincide year after year during a 50-year period. With the medium estimates, the extinction risk for the crested newt in the study area is almost non-existent (Tab. 3). However, the abundance and the number of local populations decreased during the simulated time period (Fig 4., Tab. 3), suggesting a higher extinction risk in a longer time horizon. I chose to not simulate longer time periods due to the increased uncertainty in such simulations (see Akcakaya & Sjögren-Gulve 2000). Due to the uncertainty, the strength of my PVA lies not in predicting absolute extinction risks, but in identifying the most important parameters and examining the impacts of management.

The parameters that were by far most important for the outcome of the simulations were juvenile survival, fecundity and adult survival (Tab. 5). This implies: 1) better estimates of these parameters would decrease the uncertainty in the model; 2) these parameters seem to be most important in the population dynamics, thus making them crucial in conservation efforts. Most sensitive was juvenile survival, where changes had dramatic effects on the extinction risk in the study area. The importance of juvenile survival for the crested newt is consistent

with Sohlman Wiessing (2004), who found that survival during the two first years were the most sensitive parameter. Sensitivity of juvenile and adult survival may be due to a life history with long life span and few offspring (Heppell *et al*. 2000), which is fairly in agree with the crested newt (Hedlund 1990, Miaud *et al*. 1993). The sensitivity of fecundity may partly be explained by the fact that survival of the juveniles during their first seven months is included in this parameter (see the "Parameterisation of the model – Demography " section). However, sensitivity of juvenile survival has recently also been reported for several other amphibian species with different life histories (Biek *et al*. 2002, Hels & Nachman 2002, Vonesh & De la Cruz 2002, Conroy & Brook 2003). This is in contrast to the general view of amphibian population dynamics mainly being regulated at the embryonic and larval stages (Hellriegel 2000, Vonesh & De la Cruz 2002, Conroy & Brook 2003, but see Wilbur 1980). However, the juvenile stage is the least studied stage of amphibians, mainly due to difficulties in monitoring the animals (Beebee 1996). Thus, studies on behaviour and ecology of juveniles should be given high priority in amphibian decline research.

Management measures had small effects on the extinction risk in the study area (Tab. 3). This is probably due to the already very small extinction risk with the medium estimates; the extinction risk cannot decrease much further. Management, especially increased pond density, had greater impact on the probability for the crested newt to end up below certain abundances in the study area after 50 years (Fig. 5). Thus, management may increase the viability in the study area on a longer term by maintaining a high abundance. The cause is quite obvious; an increased number of ponds enable higher newt abundance. Furthermore, extinction risks in the existing isolated ponds decreased by adding new ponds (Tab. 4), suggesting that the existing ponds benefit of dispersal from the new ponds due to a rescue effect (Brown & Kodric-Brown 1977). This was most evident for pond 8, which was the smallest population and had the highest extinction risk, while the larger populations were more viable when isolated. However, in contrast to this positive effect of 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 matter, not to what extent. Even a few individuals of the crested newt may be able to rapidly establish a population (Niesel & Berglind 2003). Otherwise are positive effects of dispersal consistent with Griffiths and Williams (2000), who in a PVA found that the crested newt persisted better in several connected small ponds than in a single and isolated large pond. However, in a PVA of Halley *et al*. (1996), isolated crested newt populations had small extinction risks if they were sufficiently large (> 40 adult females). Thus, small populations of the crested newt may be more dependent of connection with other populations for persistence than large populations.

The crested newt has generally been considered as performing metapopulation dynamics (Miaud *et al*. 1993, Griffiths & Williams 2000, Malmgren 2002b), and as a consequence requiring a certain pond density at the landscape scale (Oldham *et al*. 2000, Schreiber 2003). However, this view has been questioned by Niesel & Berglind (2003), who argued that extinctions of crested newt populations probably are mainly deterministic, not stochastic as they are assumed to be in classical metapopulation models (Hanski 1999). This is supported by a study of Beebee (1997), where most crested newt extinctions were caused by pond destruction, and by Sztatecsny *et al*. (2004), who found that parameters driven by pond succession best explained larval abundance. As pointed out by Niesel & Berglind (2003), even isolated populations may be viable if sufficiently large, and are of concern for conservation. This may be especially true in relative stable habitats, as forest tarns. However, a metapopulation approach may be useful even when extinctions mainly are deterministic (Hanski & Simberloff 1997, Hanski 1999). My simulations show positive effects of dispersal between crested newt populations, and to keep it simple, even without interactions between

local populations, multiple populations decrease the regional extinction risk (Hanski & Simberloff 1997, Akcakaya 1998). Nevertheless, it is important to be aware of the deterministic nature of crested newt extinctions. Just protecting networks of populations will not be enough for regional persistence; management of the local populations may be necessary to prevent deterministic extinctions (Marsh & Trenham 2001). Regarding the prescribed pond density in the Swedish conservation guidance for the crested newt (Schreiber 2003; see the "PVA model structure and simulation of the model" section), it lacks important definitions to be applicable. What are favourable areas for the crested newt, and at what spatial scale should the prescribed pond density be implemented?

My simulations demonstrate the need of management of local populations stated above. The highest extinction risks were predicted for ponds 8, 11, 14 and 15 (Tab. 4). For ponds 11 and 14, this is not surprising since these ponds are under habitat deterioration. Furthermore, I assumed a high mortality of eggs and larvae due to frequent droughts in ponds 11, 14 and 15. Simulating restoration in these ponds decreased the extinction risk considerably. An increased viability by restoration is in line with Sohlman Wiessing (2004), who in a PVA of an isolated crested newt population, decreased the extinction risk considerable when simulating restoration by increasing carrying capacity and maximum reproduction growth rate, respectively. Negative effects of a higher drought frequency are consistent with Griffiths & 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/larvae mortality) had only small effects on extinction risk in the study area. The reason to this contradiction is probably that the frequency of droughts has to be higher than in my sensitivity analysis to have severe effects on viability. Unless droughts are frequently occurring and/or occurring year after year, they may not be critical for crested newt populations due to their high life span (at least 16 years, Miaud *et al.* 1993; 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). Droughts have even been suggested to be positive for crested newt populations to a certain degree (once per decade) by reducing the number of invertebrates who predate on newt egg and larvae (Oldham 2000). However, in a study of Cooke (2001), no relationship between abundance of invertebrates and abundance of crested newt larvae could be found. The above discussion strengthens the view of crested newt extinctions as deterministic rather than stochastic. Further, it also points out the risk of not detecting such deterministic extinctions due to the long life span of crested newts. With perpetual reproduction failure, adult newts may just act as ghosts of the past.

PVAs are commonly considered to yield optimistic biased predictions due to the difficulties to incorporate all potential threats to a species (Brook 2000). In this PVA model, apart from taking account for severe inbreeding depression by using an extinction threshold value, genetic effects are not included due to the lack of data in this issue. The importance of genetics when predicting population viability has been debated (see e.g. Lande 1988, Frankham & Ralls 1998), but may be noteworthy in small and isolated populations (Allendorf & Ryman 2002). The estimated population sizes in the study area's breeding ponds were mostly rather large, but the populations are highly isolated from each other. The isolation implies a low gene flow between the populations, suggesting negative effects due to loss of genetic variation as a potential threat. Stensjö (1998) found a genetic subdivision between fairly isolated populations of the crested newt. On the other hand, populations of the crested newt may be genetically viable despite isolation (cf. Niesel 2003).

Further, adjacent (<5 m) to pond 2 and 3 is a pond inhabited by perch (*Perca fluviatilis*) (T. Karlsson 2004, unpublished data). Perch is probably a severe predator on the larvae of the crested newt, which makes coexistence between these species impossible (Oldham *et al.*

2000, Gustafson & Malmgren 2002, Niesel & Berglind 2003). Consequently, if perch colonise pond 2 and 3, these ponds would not act as breeding ponds any longer. However, it is difficult both to quantify and to incorporate the probability of a perch colonisation in my PVA model. The risk of this event was therefore not included in the model, but has to be considered when predicting the viability of these ponds. Possible effects of climate changes and air pollutions (e.g. acidification) are also difficult to predict and quantify, and were not incorporated in the model.

Finally, a disadvantage with the breeding pond focused approach used in this study is the disregard of the terrestrial habitat (Marsh & Trenham 2001). Adult crested newts spend a considerable amount of time on land (Griffiths 1996), and most juveniles probably live a terrestrial life (Hedlund 1990). The sensitivity of these life stages implies that processes occurring at the terrestrial habitat may be important in the population dynamics. Thus, destruction of the terrestrial habitat may constitute a threat. An indication of this has been reported by Latham *et al*. (1996), who observed a reduced newt density, especially juveniles, after clear-cutting. Furthermore, characteristics of the landscape between breeding ponds determine the ability for the newts to disperse between the ponds. However, the knowledge of terrestrial behaviour and ecology of the crested newt is still insufficient. In a study of Malmgren (2002a), both adults and juveniles dispersed towards an adjacent forest patch when leaving the pond, suggesting woodland as an important habitat and dispersing route. This is in line with Laan & Verboom (1990), who considered woodland as the most important landscape element for connectivity. Old deciduous forest has been suggested as optimal habitat (Latham *et al*. 1996, Malmgren 2001), but the species seems to accept a broad variety of habitats (Jehle 2000, Niesel & Berglind 2003). Leaf litter, mammal burrows, stones and dead wood seem to act as refuges (Latham *et al*. 1996, Jehle & Arntzen 2000), suggesting that ground cover structure may be important. The area directly adjacent to the breeding pond seems to be the most utilised by newts (Jehle 2000, Jehle & Arntzen 2000), and clear-cut forest and cultivated field in this area is probably unfavourable (Nilsson 1998, Joly *et al*. 2001). This suggests that delineation of terrestrial buffer zones around the breeding ponds may be an important conservation measure (see Semlitsch 1998 and Schabetsberger *et al*. 2004). Nevertheless, further characterisation of terrestrial habitat and dispersal routes is a crucial task in crested newt research.

Implications for conservation in the study area

According to my simulations, the crested newt is more likely to maintain "favourable conservation status" in the study area by management measures. Considering increased pond density, this may, besides from creating new ponds (see Langton *et al*. 2001 for practical guidance), be done by restoring already existing ponds within dispersal distance from the breeding ponds. About 100 m northwest from pond 1 is a forest tarn named Starrpölen located where crested newts not have been found (Karlsson 2003b, T. Karlsson 2004, unpublished data). Test-fishings (T. Karlsson 2004, unpublished data) and presence of the diving beetle *Dytiscus lapponicus* (Karlsson 2003a), which is mainly confined to fish-free waters (Nilsson & Holmen 1995), indicates that Starrpölen is devoid of fish. However, Starrpölen is more acid than pond 1 (pH 5.4 and 5.7, respectively; T. Karlsson 2004, unpublished data), which is a possible explanation for the absence of crested newts (but see Niesel & Berglind 2003). Therefore, further investigations and liming if necessary is conservation measures that would increase the viability of pond 1. Further, in a late-succession pasture about 200 m northeast from pond 5 is a pond located where crested newts not have been found (Karlsson 2003b, T. Karlsson 2004, unpublished data). This may be explained by low temperature (see Andersen 2001) due to shading of trees. This pond and pond 5 (which not seems to act as breeding

pond) constitutes suitable candidates for restoration (removal of trees and enlargement). Another suitable pond for restoration is pond 9, located about 500 m from pond 8. During the population monitoring one male crested newt was caught here, but it seems not to act as a breeding pond, probably due to its small depth and size. An enlargement of this pond would increase its suitability as a breeding pond and in this way increase the connectivity between pond 8 and 11.

Regarding management of the local populations, restoration of pond 11 and 14 is probably necessary to maintain crested newt population in these ponds. Pond 11 suffers from a plantation of Norway spruce (*Picea abies*) adjacent to the pond. This plantation shades the pond and probably decreases the water temperature. Furthermore, it may acidify the pond. Reproduction seems to be poor in this pond (Tab. 2; Karlsson 2003b, T. Karlsson 2004, unpublished data), presumably due to the factors described above. Consequently, a spruce-free zone towards the pond would decrease the extinction risk. Pond 14 is in a late succession and seems to suffer from droughts of very high frequencies. Moreover, it is completely encircled by trees, which shades the pond. No reproduction has been ascertained in this pond (Tab. 2), although leks were observed during the population monitoring. This pond is in immediate need of excavation and removal of trees (see Langton *et al*. 2001 for practical guidance). Further, pond 15 constitutes of a small ditch, partly located in an overgrown marsh. Excavation of this marsh would make this population more viable. As discussed in the "Viability and sensitivity" section, pond 2 and 3 are at the risk of being colonised by perch. To decrease this risk, the best thing to do would of course be to remove the fish (see Langton *et al*. 2001 for practical guidance). Fish removals may, however, be complicated and costly. Preventing water flow between the pond 2 and 3 and the pond with perch is an alternative.

A good strategy when restoring and creating new ponds is to create a new pond in the vicinity a year before restoring an isolated pond (Jan C Malmgren, personal communication). Such a procedure buffer for the changes a restoration causes.

Hitherto, I have discussed conservation measures for the aquatic habitat. Due to the sensitivity of juveniles, taking the terrestrial habitat in consideration is probably crucial for maintaining "favourable conservation status" in the study area. This is a more difficult task, since the knowledge of juvenile ecology is insufficient. However, maintaining and creating ground cover structures such as stones, dead wood and leaf litter in moist and shaded woodland, as near the breeding pond as possible, would probably favour the newts (see Langton *et al*. 2001 for practical guidance). Such environments are presumably good dispersal routes too. Moreover, not all ponds were considered to act as breeding ponds, although newts were found in them. These "non-breeding" ponds may act as stepping-stones between breeding ponds and terrestrial habitat. Furthermore, in the present study and in Karlsson (2003b), pond 5 and 12 seemed to be mainly inhabited by juveniles, indicating that these small and shallow ponds may act as habitats for juveniles.

Finally, the effects of favouring the crested newt are not restricted only to this species. The crested newt has been suggested as an "umbrella species" (see Simberloff 1998a) for amphibians (Beebee 1996) and other pond organisms (Baker & Halliday 1999, Jehle 2000, Gustafson & Malmgren 2002). Moreover, ponds have been found to contribute considerable to regional biodiversity (Williams *et al.* 2003).

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References

Akcakaya, H.R. (1998). *RAMAS GIS: Linking landscape data with population viability analysis (version 3.0)*. Applied Biomathematics, Setauket, New York.

Akcakaya, H.R. (2000). Population viability analyses with demographically and spatially structured models. *Ecological Bulletins* 48:23-28.

Akcakaya, H.R. & Raphael, M.G. (1998). Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. *Biodiversity and Conservation* 7:875-894.

Akcakaya, H.R. & Sjögren-Gulve, P. (2000). Population viability analysis in conservation planning: an overview. *Ecological Bulletins* 48:9-21.

Alford, R.A. & Richards, S.J. (1999). Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30:133-165.

Allendorf, F.W. & Ryman, N. (2002). The role of genetics in population viability analysis. In: Beissinger, S.R. & McCullough, D.R. (eds). *Population viability analysis*. The University of Chicago Press, Chicago & London, pp 50-85.

Andersen, A. (2001). *Occurence of the crested newt, Triturus cristatus, in relation to water quality and submerged vegetation*. (In Swedish with English abstract). Degree Thesis. University of Karlstad, report 01:39.

Arntzen, J.W. & 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. *Herpetological Journal* 3:99-110.

Arntzen, J.W. & 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., Oldham, R.S. & Latham, D.M. (1995). Cost effective drift fences for toads and newts. *Amphibia-Reptilia* 16:137-145.

Baker, J.M.R. (1999). Abundance and survival rates of great crested newts (*Triturus cristatus*) at a pond in central England: monitoring individuals. *Herpetological Journal* 9:1-8

Baker, J.M.R. & Halliday, T.R. (1999). Amphibian colonization of new ponds in an agricultural landscape. *Herpetological Journal* 9:55-63.

Barinaga, M. (1990). Where have all the froggies gone? *Science* 247:1033-1034.

Beebee, T.J.C. (1994). Distribution and status of great crested newts in Britain. In: Gent, T. & Bray, R. (eds). Conservation and management of crested newts: Proceeding of a symposium held on 11 january 1994 at Kew Gardens, Richmond, Surrey. *English Nature Science Series* no. 20, pp 3-5.

Beebee, T.J.C. (1996). *Ecology and conservation of amphibians*. Chapman & Hall, London.

Beebee, T.J.C. (1997). Changes in dewpond numbers and amphibian diversity over 20 years on chalk downland in Sussex, England. *Biological Conservation* 81:215-219.

Bell, G. (1979). Populations of crested newts, *Triturus cristatus*, in Oxfordshire, England. *Copeia* 1979:350-353.

Biek, R., Funk, W.C., Maxell, B.A. & Mills, L.S. (2002). What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conservation Biology* 16:728-734.

Biessinger, S.R. (2002). Population viability analysis: past, present, future. In: Beissinger, S.R. & McCullough, D.R. (eds). *Population viability analysis*. The University of Chicago Press, Chicago & London, pp 5-17.

Brook, B.W. (2000). Pessimistic and optimistic bias in population viability analysis. *Conservation Biology* 14:564-566.

Brook, B.W., O´Grady, J.J., Chapman, A.H., Burgman, M.A., Akcakaya, H.R. & Frankham, R. (2000). Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385-387.

Brown, J.H. & 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 edn. Sinauer Associates, Sunderland, Massachusetts.

Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.

Cederberg, B. & 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.

Cedhagen, T. & Nilson, G. (1991). *Grod- och kräldjur i Norden* (In Swedish). Fältbiologerna, Sollentuna.

Conroy, S.D.S. & Brook, B.W. (2003). Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia. *Population Ecology* 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. *Herpetological Journal* 5:221-228.

Cooke, A.S. (2001). Invertebrate predation on larvae of the crested newt (*Triturus cristatus*). *Herpetological Bulletin* no. 77:15-19.

Cooke, A.S. & Arnold, H.R. (2003). Night counting, netting and population dynamics of crested newts (*Triturus cristatus*). *Herpetological Bulletin* no. 84:5-14.

Council of Europe. (1979). Convention on the conservation of European wildlife and natural habitats. http://conventions.coe.int/Treaty/FR/Treaties/Html/104-2.htm (Access 2004-11-04).

Cummins, C.P. & Swan, M.J.S. (2000). Long-term survival and growth of free-living great crested newts (*Triturus cristatus*) PIT-tagged at metamorphosis. *Herpetological Journal* 10:177-182.

Dolmen, D. (1982). Zoogeography of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia) in Norway, with notes on their vulnerability. *Fauna Norvegica Series A*. 3:12-25.

Dolmen, D. (1983a). Diel rhythms and microhabitat preference of the newts *Triturus vulgaris* and *T. cristatus* at the northern border of their distribution area. *Journal of Herpetology* 17:23-31.

Dolmen, D. (1983b). Growth and size of *Triturus vulgaris* and *T. cristatus* (Amphibia) in different parts of Norway. *Holarctic Ecology* 6:356-371.

Dolmen, D. (1988). Coexistence and nich segregation in the newts *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti). *Amphibia-reptilia* 9:365-374.

Etienne, R.S., Vos, C.C. & Jansen, M.J.W. (2003). Ecological impact assessment in data-poor systems: a case study on metapopulation persistence. *Environmental Management* 32:760-777.

European Reptile & Amphibian Specialist Group. (1996). Triturus cristatus. In: IUCN. *2003 IUCN red list of threatened species*. http://www.redlist.org/search/details.php?species=22212 (Access 2004-11-06).

Feldmann, R. (ed.) (1981). Die amphibien und reptilien Westfalens (In German). *Veröffentlichung der Arbeitsgemeinschaft für Biologisch-Ökologische Landeserforschung* 34:1-161.

Fieberg, J. & Ellner, S.P. (2000). When is it meaningful to estimate an extinction probability? *Ecology* 81: 2040-2047.

Fog, K., Schmedes, A. & Rosenørn de Lasson, D. (2001). *Nordens padder og krybdyr* (In Danish). Gads Forlag, Copenhagen.

Francillon-Vieillot, H., Arntzen, J.W. & Geraudie, J. (1990). Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. *Journal of Herpetology* 24:13-22.

Frankham, R. & Ralls, K. (1998). Inbreeding leads to extinction. *Nature* 392:441-442.

Funk, C.W. & Mills, L.S. (2003). Potential causes of population declines in forest fragments in an Amazonian frog. *Biological Conservation* 111:205-214.

Gasc, J.P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H. *et al.* (eds). (1997). *Atlas of amphibians and reptiles in Europe*. Societas Europaea Herpetologica and Muséum National D'Histoire Naturelle, Paris.

Gent, T. & 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 Nature Science Series* no. 20.

Gill, D.E. (1978). The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48:145-166.

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. *Herpetological Journal* 1:5-10.

Griffiths, R. (1996). *Newts and salamanders of Europe*. Poyser Natural History, London.

Griffiths, R. (2004). Great Crested Newts (*Triturus cristatus*) in Europe: Effects of metapopulation structure and juvenile dispersal on population persistence. In: Akcakaya, H.R., Burgman, M., Kindvall, O., Wood, C.C., Sjögren-Gulve, P., Hatfield, J.S. & McCarthy, M.A. (eds). *Species conservation and management case studies*. Oxford University Press, Oxford pp 281-291.

Griffiths, R.A. & Raper, S.J. (1994). *A review of current techniques for sampling amphibian communities*. Joint Nature Conservation Committee, Peterborough, report no. 210.

Griffiths, R.A. & Williams, C. (2000). Modelling population dynamics of great crested newts (*Triturus cristatus*): a population viability analysis. *Herpetological Journal* 10:157-163.

Gustafson, D. & Malmgren, J.C. (2002). *Inventering och övervakning av större vattensalamander (Triturus cristatus)* (In Swedish). Örebro University and County Administrative Board of Örebro, report no. 2002:02.

Gustafson, D., Hellberg, E., Andersen, A. & Malmgren, J.C. (2004). *Större vattensalamander i tio Natura 2000-områden i Örebro län: Test och utvärdering av övervakningsmetodik 2002* (In Swedish). County Administrative Board of Örebro, publication no. 2003:25.

Gärdenfors, U. (ed). (2000). *The 2000 red list of Swedish species.* Swedish Species Information Centre, SLU, Uppsala.

Hagström, T. (1979). Population ecology of Triturus cristatus and T. vulgaris (Urodela) in SW Sweden. *Holarctic Ecology* 2:108-114.

Hagström, T. (1980). Growth of newts (*Triturus cristatus* and *Triturus vulgaris*) at various ages. *Salamandra* 16:248-251.

Hagström, T. (1984). Vattensalamandrarna i Västsverige, en ekologisk översikt (In Swedish with English summary). *Fauna & Flora* 79:117-128.

Halley, J.M., Oldham, R.S. & Arntzen, J.W. (1996). Predicting the persistence of amphibian populations with the help of a spatial model. *Journal of Applied Biology* 33:455-470.

Halliday, T.R. (1996). Amphibians. In: Sutherland, W.J. (ed). *Ecological census techniques: A handbook.* Cambridge University Press, Cambridge, pp 205-217.

Hanski, I. (1999). *Metapopulation ecology.* Oxford University Press, Oxford.

Hanski, I. & Simberloff, D. (1997). The metapopulation approach, its history , conceptual domain, and application to conservation. In: Hanski, I. & Gilpin, M.E. (eds). *Metapopulation biology: Ecology, genetics, and evolution.* Academic Press, San Diego, pp 5-26.

Hecnar, S.J. & M´Closkey, R.T. (1996). Regional dynamics and the status of amphibians. *Ecology* 77:2091-2097.

Hedlund, L. (1990). *Reproductive ecology of crested newts, Triturus cristatus (Laur.).* PhD Thesis. Swedish Unversity of Agricultural Sciences, report no. 16.

Hellberg, E., Gustafson, D., Malmgren, J.C. & Rygne, H. (2004). *Större vattensalamander (Triturus cristatus) i Örebro län: Inventering 2003 och sammanställning av kända lokaler 1989-2003* (In Swedish). County Administrative Board of Örebro, publication no. 2003:26.

Hellriegel, B. (2000). Single- or multistage regulation in complex life cycles: does it make a difference? *Oikos* 88:239-249.

Hels, T. & 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., Caswell, H. & Crowder, L.B. (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81:654-665.

Houlahan, J.E., Findlay, C.S., Benedikt, R.S., Meyer, A.H. & Kuzmin, S.L. (2000). Quantitative evidence for global amphibian population declines. *Nature* 404:752-755.

Jehle, R. (2000). The terrestrial summer habitat of radio-tracked great crested newts (*Triturus cristatus*) and marbled newts (*T. marmoratus*). *Herpetological Journal* 10:137-142.

Jehle, R. & Arntzen, J.W. (2000). Post-breeding migrations of newts (*Triturus cristatus* and *T. marmoratus*) with contrasting ecological requirements. *Journal of Zoology* 251:297-306.

Joly, P., Miaud, C., Lehmann, A. & Grolet, O. (2001). Habitat matrix effects on pond occupancy in newts. *Conservation Biology* 15:239-248.

Karlsson, T. (2003a). *Inventering av dykare och trollsländor i åtta småvatten i Boxholms, Kinda, och Linköpings kommuner* (In Swedish). Course Thesis. University of Kalmar, unpubl.

Karlsson, T. (2003b). *Inventering av större vattensalamander (Triturus cristatus) i delar av Boxholms, Kinda, Mjölby och Linköpings kommuner* (In Swedish with English abstract). Project course Thesis. University of Kalmar, unpubl.

Karlström, A. & Sjögren-Gulve, P. (1997). *Groddjur – indikatorer på biologisk mångfald* (In Swedish). Municipality of Stockholm, report 1997:4.

Kupfer, A. (1998). Wanderstrecken einzelner kammolche (*Triturus cristatus*) in einem agrarlebensraum (In German with English abstract). *Zeitschrift für Feldherpetologie* 5:238-242.

Kupfer, A. & Kneitz, S. (2000). Population ecology of the great crested newt (*Triturus cristatus*) in an agricultural landscape: dynamics, pond fidelity and dispersal. *Herpetological Journal* 10:165-171.

Laan, R. & Verboom, B. (1990). Effects of pool size and isolation on amphibian communities. *Biological Conservation* 54:251-262.

Lande, R. (1988). Genetics and demography in biological conservation. *Science* 241:1455-1460.

Lande, R. (1993). Risk of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911-927.

Langton, T.E.S., Beckett, C.L. & Foster, J.P. (2001). *Great crested newt conservation handbook*. Froglife, Halesworth. Also in PDF: http://www.froglife.org/Handbook%20PDF/GCNCH.htm (Access 2004-12-01).

Latham, D.M., Oldham, R.S., Stevenson, M.J., Duff, R., Franklin, P. & Head, S.M. (1996). Woodland management and the conservation of the great crested newt (*Triturus cristatus*). *Aspects of Applied Biology* 44:451-459.

Lindahl, C. (ed.). (1997). *Ängs- och hagmarker i Sverige* (In Swedish). Swedish Environmental Protection Agency, report no. 4819.

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 University, Örebro studies in biology 1.

Malmgren, J.C. (2002a). 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*). *Herpetological Journal* 12:29-35.

Malmgren, J.C. (2002b). Swedish Species Information Centre's fact sheet for the crested newt (In Swedish). http://www-umea.slu.se/MiljoData/webrod/Faktablad/trit_cri.PDF (Access 2004-11-04).

Marsh, D.M. & Trenham, P.C. (2001). Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15:40-49.

Miaud, C., Joly, P. & Castanet, J. (1993). Variation in age structures in a subdivided population of *Triturus cristatus*. *Canadian Journal of Zoology* 71:1874-1879.

Mills, L.S. & Lindberg, M.S. (2002). Sensitivity analysis to evaluate the consequences of conservation actions. In: Beissinger, S.R. & McCullough, D.R. (eds). *Population viability analysis*. The University of Chicago Press, Chicago & London, pp 338-366.

Niesel, J. (2003). Förekomst av större vattensalamander, *Triturus cristatus*, i relation till vatten- och omgivningsmiljö i Värmland (In Swedish with English abstract). Project course Thesis. University of Kalmar, unpubl.

Niesel, J. & 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 Administrative Board of Värmland, report 2003:16.

Nilsson, A.N. & Holmen, M. (1995). *The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. II. Dytiscidae*. E.J. Brill, Leiden.

Nilsson, J. (1998). *Analysis of habitat requirements and abundance of Triturus cristatus on the Hållnäs peninsula of nothern Uppland, eastcentral Sweden* (In Swedish with English summary). Degree Thesis. Uppsala University, unpubl.

Oldham, R.S. (1994). Habitat assessment and population ecology. In: Gent, T. & Bray, R. (eds). Conservation and management of crested newts: Proceeding of a symposium held on 11 january 1994 at Kew Gardens, Richmond, Surrey. *English Nature Science Series* no. 20, pp 45-67.

Oldham, R.S., Keeble, J., Swan, M.J.S. & Jeffcote, M. (2000). Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). *Herpetological Journal* 10:143-155.

Schabetsberger, R., Jehle, R., Maletzky, A., Pesta, J. & Sztatecsny, M. (2004). Delineation of terrestrial reserves for amphibians: post-breeding migrations of Italian crested newts (*Triturus c. carnifex*) at high altitude. *Biological Conservation* 117:95-104.

Schreiber, H. (2003). *Art- och naturtypsvisa vägledningar för Natura 2000 – Större vattensalamander (Triturus cristatus)* (In Swedish). Swedish Environmental Protection Agency. http://www.naturvardsverket.se, version 2003-04-16 (Access 2004-11-04).

Semlitsch, R.D. (1998). Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12:1113-1119.

Simberloff, D. (1998a). Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83:247-257.

Simberloff, D. (1998b). Small and declining populations. In: Sutherland, W.J. (ed). *Conservation science and action*. Blackwell Science, Oxford, pp 116-134.

Sjögren-Gulve, P. & Ray, C. (1996). Using logistic regression to model metapopulation dynamics: large-scale forestry extirpates the pool frog. In: McCullough, D.R. (ed). *Metapopulations and wildlife conservation*. Island Press, Washington, pp. 111-137.

[SMHI] Swedish Meteorological and Hydrological Institute. (2003). *Torka – Faktablad nr 16* (In Swedish). Norrköping.

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 University, unpubl.

Stensjö, J.O. (1998). *Population genetics of the common newt (Triturus vulgaris) and the crested newt (T. cristatus), with implications for conservation*. PhLic Thesis. Uppsala University.

Stokstad, E. (2004). Global survey documents puzzling decline of amphibians. *Science* 306:391.

Sutherland, G.D., Richardson, J.R. & Bunnell, F.L. (2000). Uncertainties linking tailed frog habitat and population dynamics with riparian management. In: Darling, L.M. (ed) *Proceedings of a conference on the biology and management of species and habitat at risk, Kamloops, B.C., 15-19 Feb., 1999. Volume two*. B.C. Ministry of Environment, Lands and parks, Victoria, B.C. and University College of the Cariboo, Kamlops B.C.

Sztatecsny, M., Jehle, R., Schmidt, B.R. & Arntzen, J.W. (2004). The abundance of premetamorphic newts (*Triturus cristatus, T. marmoratus*) as a function of habitat determinants: an *a priori* model selection approach. *Herpetological Journal* 14:89-97.

Van Buskirk, J. & Smith, D.C. (1991). Density dependent population regulation in a salamander. *Ecology* 72:1747-1756.

Verrell, P. & Halliday, T. (1985). The population dynamics of the crested newt Triturus cristatus at a pond in southern England. *Holarctic Ecology* 8:151-156.

Vonesh, J.R. & De la Cruz, O. (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia* 133:325-333.

Vos, C.C., Ter Braak, C.J.F. & Nieuwenhuizen, N. (2000). Incidence function modelling and conservation of the tree frog *Hyla arborea* in the Netherlands. *Ecological Bulletins* 48:165-180.

Wake, D.B. (1991). Declining amphibian populations. *Science* 253:860.

Wilbur, H.M. (1980). Complex life cycles. *Annual Reviews of Ecology and Systematics* 11:67-93.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. & Sear, D. (2003). Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation* 115:329-341.

Appendix 1.

Photos of material used in the population monitoring. All photos by the author.

Pond 7 encircled by the drift fence.

Damm 7(Högliden) omgärdad av driftstaketet.

The drift fence at pond 7 with a pitfall trap in the middle of the picture.

Driftstaketet vid damm 7 med en fallfälla i bildens mitt.

Funnel trap of the type used in this study.

Flaskfälla av den typ som användes i studien.

Funnel trap fixed on a pole in front of pond 2.

Flaskfälla monterad på en käpp framför damm 2 (Appeldalen 1).