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Population Dynamics and Conservation of the Sand Lizard (*Lacerta agilis*) on the Edge of its Range

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ACTA
UNIVERSITATIS
UPSALIENSIS
UPPSALA
2005

ISSN 1651-6214
ISBN 91-554-6218-9
urn:nbn:se:uu:diva-5750

Dissertation presented at Uppsala University to be publicly examined in Friessalen, EBC, Uppsala, Friday, May 13, 2005 at 13:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

Abstract

Berglind, S-Å. 2005. Population Dynamics and Conservation of the Sand Lizard (*Lacerta agilis*) on the Edge of its Range. Acta Universitatis Upsaliensis. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 41. 42 pp. Uppsala. ISBN 91-554-6218-9.

The sand lizard (*Lacerta agilis*) reaches the northern periphery of its distribution in south-central Sweden, where small, isolated relict populations occur in pine heath forests on sandy sediments. Modern forestry and fire suppression have reduced the amount of suitable open habitat for the species in this area and seem to be important for its decline. Main objectives of this thesis were to evaluate the efficiency of different management strategies, and if the sand lizard can function as an umbrella species for biodiversity conservation.

Over a 16-year period, the estimated annual numbers of adult females in each of two study populations fluctuated between 23 and 3. Simulations of stochastic future population growth showed that the risk of extinction was highly dependent on population growth rate, which in turn was strongly affected by juvenile survival as indicated by elasticity analysis.

Simulations of population growth for 50 years showed that the quasi-extinction risk (threshold ≤ 10 females) was $> 56\%$ for patches ≤ 1 ha; which is the observed average size of suitable habitat for inhabited patches during a 10-year period. In managed metapopulation networks with highly co-fluctuating local populations, among-population dispersal was not important to reduce extinction risks over a 50-year horizon.

In the field the preferred microhabitat of sand lizards was successfully restored using tree felling and patch-soil scarification. The lizards gradually colonized the restored patches, and 16 years after restoration, sand lizards where mainly found there.

Pine-heath area, and patch area within individual pine heaths, were of major importance for long-term population persistence at regional and landscape scales, respectively. Analyses of nested species subsets and an umbrella index suggest that the sand lizard can be a useful cross-taxonomic umbrella species on both scales for other red-listed species.

Keywords: demography, extinction, habitat, Lacerta agilis, management, metapopulation, peripheral populations, population dynamics, population viability analysis, reintroduction, reptiles, umbrella species

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ISSN 1651-6214
ISBN 91-554-6218-9
urn:nbn:se:uu:diva-5750 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-5750)

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List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Berglind, S-Å. 2000. Demography and management of relict sand lizard (*Lacerta agilis*) populations on the edge of extinction. – In: Sjögren-Gulve, P. & Ebenhard, T. (eds), *The use of population viability analyses in conservation planning*. Ecological Bulletins 48, pp. 123-142.

II Berglind, S.-Å. 2004. Sand lizard (*Lacerta agilis*) in central Sweden – modeling juvenile reintroduction and spatial management strategies for metapopulation establishment. – In: Akcakaya, H. R. et al. (eds), *Species conservation and management: case studies*. Oxford Univ. Press, New York, pp 326-339.

III Berglind, S.-Å. Habitat tacking and population dynamics of an early successional lizard in a changing pine forest landscape. Manuscript.

IV Berglind, S.-Å. 2004. Area-sensitivity of the sand lizard and spider wasps in sandy pine heath forests – umbrella species for early successional biodiversity conservation? – In: Angelstam, P. et al. (eds), *Targets and tools for the maintenance of forest biodiversity*. Ecological Bulletins 51, pp. 189-207.

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Contents

Introduction

> "Species are likely to be 'rare' near the margins of their distribution and outside the distribution they are 'extinct'. Because distribution and abundance are but two aspects of one phenomenon, the study of abundance in different parts of the distribution is itself a study of the causes of rareness and commonness in species." (Andrewartha & Birch 1954, p. 665)

Species are not evenly distributed throughout their geographic range. Abundance tends to decrease towards the periphery of a species range, but the pattern is normally more complex than a gradual decline (e.g. Brown 1984, Lawton 1995, Brown & Lomolino 1998, Gaston 2003). Relict populations close to the range boundary often exhibit relatively low rates of population increase and low densities, the magnitudes of which can be expected to depend on whether the populations have retreated to marginal habitats or into former ”hotspots” (Lawton 1993, 1995). In theory, the conservation of geographically peripheral populations poses particular difficulties since population densities and number of habitat types occupied are lower (Lawton 1993, Gaston 1994). Peripheral populations are also expected to be particularly liable to environmental and catastrophic variation, which generally have profound effects on extinction probabilities (e.g. Thomas 1990, Lande 1993, Caughley 1994), especially in species with low potential rates of population increase (Menges 1998). However, recently Channel & Lomolino (2000) showed that peripheral populations may be no more "doomed to extinction" than populations in the centre of a species´ range, and in fact often less so.

In Scandinavia many species are at the northern limit of their range. A large number of these are included in the national red-lists, and there is a need to know more about their population dynamics for long-term conservation (Berg and Tjernberg 1996, Gärdenfors 2000). The study of relict populations known to have survived since pre-historic times is of particular interest since confounding effects of recent long-distance dispersal on population survival can be ruled out. In south-central Sweden, a small number of peripheral populations of the sand lizard (*Lacerta agilis*) occur (Fig. 1) that are considered to be relicts from the postglacial warm period ca 7000-500 B.C. (Gislén and Kauri 1959, Gullberg et al. 1998). Most of these populations are restricted to large, sandy areas dominated by pine (*Pinus sylvestris*) forest

(Berglind et al. 2004). Berglind (1988) suggested that the survival of these populations in the past was largely dependent on recurrent forest fires and former human activities which may have created suitable early successional, open habitat patches with a mosaic of exposed sand and a rich field layer of heather (*Calluna vulgaris*). This thesis presents results from a 16-yr study of an isolated relict population of the sand lizard in south-central Sweden that consists of a few local populations. The need for conservation action to save this geographic population was realized some years ago (Berglind 1988), and here I evaluate some alternative conservation actions and management strategies.

After Graeme Caughley (1994) pointed out what he saw as two disparate directions in conservation biology, there has been progress in blending the so called ”small-population paradigm” (primarily studying threatened species using stochastic models for small populations) with the ”declining-population paradigm” (empirical investigations of declining populations that tend to be case-specific). Still, much remains to be done (Boyce 2002). Caughley (1994) encouraged a profitable synergism among the two approaches since the small-population paradigm needs more practice, and the declining-population paradigm more theory. This thesis sets out to consider both approaches.

I evaluate the consequences of smallness by using population viability analysis (PVA), which can be described as a way to predict the probability of population extinction by using actual life-history information in models and project it forward using stochastic computer simulation (Brook et al. 2000). Although PVAs have become a cornerstone of conservation science (Beissinger 2002), it is essential to bear in mind that predictions of future population sizes can be accurate only if the models are parameterized using data that adequately capture the distribution of population growth rates and/or vital rates (Coulson et al. 2001). There now seems to be a consensus that PVAs are particularly useful for comparing the consequences of alternative management or conservation strategies, and reveal uncertainties and needs of complementary data collection (e.g. Sjögren-Gulve & Ebenhard 2000, Burgman & Possingham 2000, Coulson et al. 2001, Akcakaya et al. 2004).

Furthermore, I address reasons for populations becoming small by studying the consequences of vegetation succession on habitat quality and population dynamics. Such deterministic habitat change is known to be crucial in the population dynamics of both plants, invertebrates and vertebrates (e.g. Thomas 1991, Sjögren-Gulve 1994, Webb & Thomas 1994, Sutcliffe et al. 1997, Tiebout & Anderson 1997, Coulson et al. 1999, Bergman 2001, Cousins & Eriksson 2001). Thus, understanding the history of a local area or habitat, plus the processes involved, is vital for correct management and for successful conservation.

Paper I and II in this thesis present PVAs where different management alternatives for the sand lizard are being evaluated. The results are of particular interest because PVAs on reptiles are few (Sjögren-Gulve 2004). Moreover, on the northern periphery of their range reptiles are highly dependent on the amount of sunshine for thermoregulation and successful reproduction, making them susceptible to environmental stochasticity, which need to be considered in management scenarios. Paper III presents results of an analysis of habitat requirements, population dynamics and effects of habitat restoration. Paper IV analyses area-sensitivity on different spatial scales of the sand lizard and a family of insects (spider wasps) with similar habitat requirements as the sand lizard. It explores the potential use of umbrella species for biodiversity conservation in the focal habitat, and whether the management of the sand lizard in central Sweden can be the foundation for conservation of several other early successional species that have declined in the Scandinavian sandy pine forests during the last decades.

Objectives

The main objectives of this thesis were to: 1) analyse the demography and population dynamics of local populations (paper I and III), 2) evaluate alternative demographic and spatial management strategies to increase population size and chance of population persistence (paper I and II), 3) identify important structural components of the preferred habitat for the sand lizard and methods to restore these components (paper III), and 4) evaluate the usefulness of the sand lizard as an umbrella species for biodiversity conservation and monitoring in this habitat (paper IV).

Methods

The sand lizard

The sand lizard is considered primarily a "forest steppe" species and occurs in a variety of semi-open habitats from central Europe to central Asia (Bishoff 1984). It reaches the northern limit of its range in south-central Sweden with a few isolated populations confined to glaciofluvial sand deposits (Fig. 1). The area of occupancy in the northwestern part of its range has decreased considerably during the last decades due to loss of suitable habitat, principally afforestation of heathlands, overgrowth of dry meadows, and exploitation of coastal dune areas (Glandt & Bishoff 1988, Gasc et al. 1997).

During the postglacial warm period (ca 7000-500 B.C.), the favourable climate made it possible for this thermophilous lizard to immigrate to Sweden via a temporary land-bridge that connected the present-day southern Scandinavian peninsula to the European continent, and to disperse northwards throughout southern and central parts of Sweden. When the climate subsequently became cooler, the species retreated to southern Sweden but also survived on a few large, sandy pine forest areas in the central part (Gislén & Kauri 1959, Andrén & Nilson 1979, Gullberg et al. 1998). Today the sand lizard is believed to have a more or less continuous distribution in some parts of southern and southeastern Sweden where it occurs in various sand, gravel and/or rocky habitats. In the inland parts of south-central Sweden there are some small, isolated relict populations (Gislén & Kauri 1959, Andrén & Nilson 1979, Berglind 1988, Ahlén et al. 1995, Lydänge & Berglind 2003, Wallgren & Berglind 2004, Berglind et al. 2004) (Fig. 1). All occurrences in Sweden include areas with long historical continuity of exposed situations. Furthermore, these areas are characterized by suitable microclimatic conditions for embryo-development in the eggs, which are buried at oviposition and then left without parental care. The common factor for all habitats is availability of suitable environments for thermoregulation, shelter and foraging, and for egg incubation.

Adult sand lizards are normally philopatric between successive years and home ranges have been estimated to between 85-2000 m^2 (Nature Conservancy Council 1983, Nicholson & Spellerberg 1989, Olsson et al. 1997, Berglind 1999).

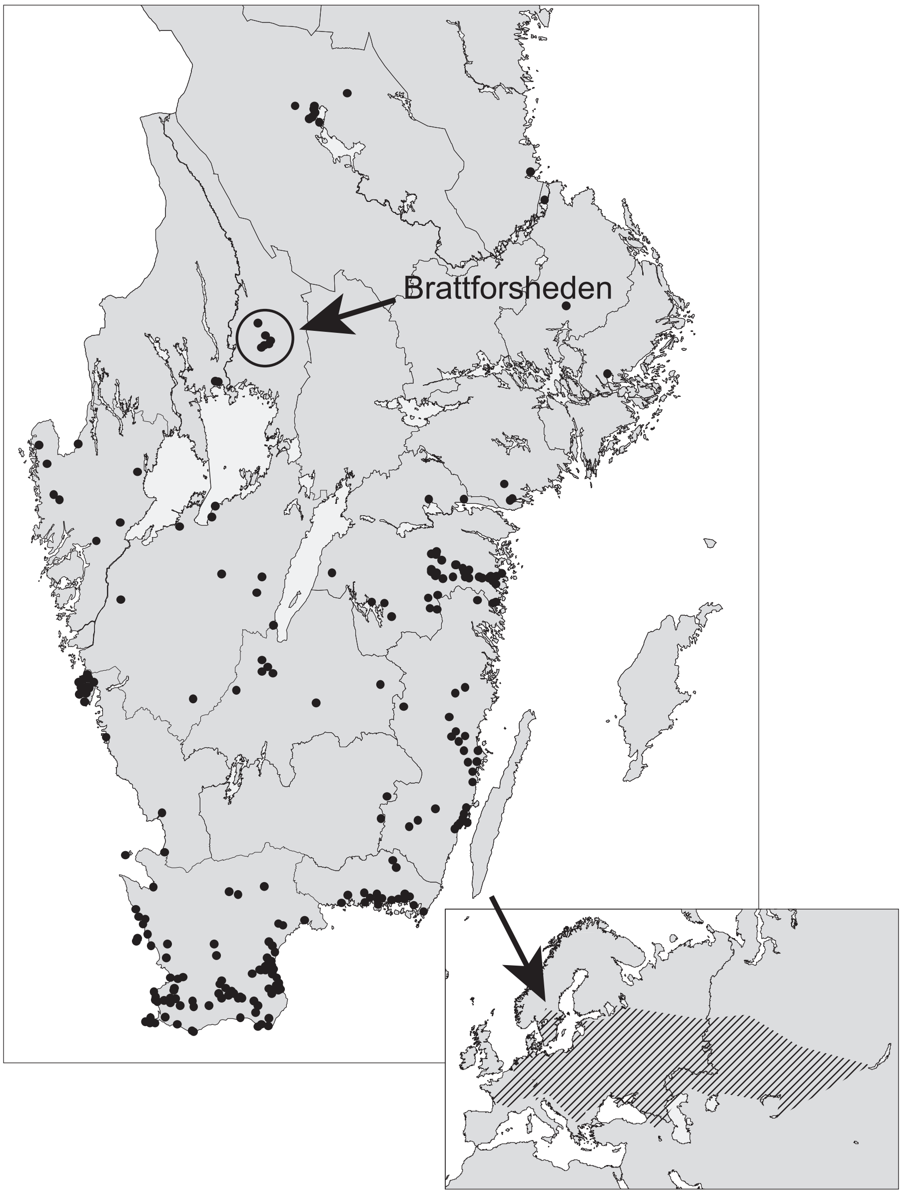

Figure 1. The distribution of the sand lizard (*Lacerta agilis*) in Eurasia and Sweden, with the local populations of the study area Brattforsheden marked. The Swedish records are data from Gislén & Kauri (1959) and the Swedish Species Information Center, Uppsala, with some modifications.

In June the female deposits 2-15 eggs, usually in sandy soil with high solar exposure. Normally the eggs hatch between mid August - beginning of September. The lizards hibernate in the ground from the end of August - mid October until the end of March - end of April; the time varies depending on age, latitude and yearly variations in climate. Sexual maturity is reached after 3 to 4 years (hibernations); the mean age of the reproducing part of Swedish populations is ca 4 to 7 years (Olsson 1992, Berglind, this study). One gravid female in my study area reached an age of 19 years (after having been marked as a 4 year old), which may be the oldest known sand lizard in the world (Berglind unpubl.).

Genetic analyses by Gullberg et al. (1998) and Madsen et al. (2000) have demonstrated low variability in the Swedish sand lizard populations, measured as number of alleles and degree of heterozygosity, compared to a central European reference population (where the sand lizard occurs with much larger populations). A bottleneck at the time of immigration may explain the low variability within the total Swedish population. The existing genetic variability was shown to be subdivided between regions but also between local populations within the same region, indicating that the relict populations have diverged on both levels (Gullberg et al. 1998).

Population study area

The field work was mainly performed on the 11 000 ha, glacifluvial sand area Brattforsheden (59°40´N) in south-central Sweden (Fig. 1). The topography is characterized by flat plateaus and areas of undulating topography, the latter mainly represented by fossil sand dunes (Hörner 1927, Furuholm et al. 1994). The vegetation is dominated by pine forest (*Pinus sylvestris*) with a ground- and field layer dominated by reindeer lichens (*Cladina* spp.), mosses (mostly *Pleurozium schreberi* and *Dicranum* spp.), lingon berry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*). Presently, afforestation and effective forest-fire suppression keep the area almost completely wooded with managed pine forest of various ages. Brattforsheden is isolated by 50 and 160 km, respectively, from the nearest two other sandy areas where the sand lizard occurs, also as small and isolated populations (Fig. 1). The landscape in between is unsuitable for the species at this latitude, and dominated by spruce (*Picea abies*)/mixed forests interspersed with agricultural land and lakes.

Population monitoring (I-III)

All occupied sand lizard patches at Brattforsheden were censused several times per season, and most potential patches at least once per season, from 1984 to 2004. Two populations separated by dense pine forest for a distance of ca 3 km at the sites FL and SB, were subject to demographic studies from 1988 to 2004. These sites were monitored for lizards on average 1-4 hours every second day during suitable weather from mid May to mid September 1988-1991 (corresponding to a few weeks after adult emergence from hibernation until the beginning of next hibernation), and for about 15 to 20 days during May-September 1992-2004. The lizards were captured by hand, measured (snout-vent length), photographed from their right (including dorsal) side, permanently marked by toe-clipping, and released on the same spot within 5-10 min. The phalanges were preserved in 4% formaldehyde, and later sectioned and stained in eosin-haematoxylin in accordance with Hemelaar (1985) for a skeletochronological analysis.

During the egg laying period, which normally occurred during the first two-three weeks in June, all filled burrows dug by female sand lizards on the limited number of open sand patches at the study sites were discretely marked out with small twigs in all years from 1988 to 2004. In late autumn after the hatching period, which normally occurred from mid August to late September, the clutches were excavated. Each clutch was tightly clustered ca 5-7 cm below the ground surface. Hence, the number of deposited eggs, their hatching success, and the minimum number of females participating in reproduction each year were monitored in detail.

Demographic modelling (I and II)

Using the capture-recapture data gathered during 1988-1998, capture-history matrices with a time-step of one year were constructed for animals marked at different ages. These matrices were used as input files for the computer software MARK 1.6 (White 2000), sub-programme ”Recaptures only”, designed to obtain maximum-likelyhood estimates of survival and capture probability rates from the resightings of marked individuals. MARK provides parameter estimates under the Cormack-Jolly-Seber model (e.g. Lebreton et al. 1993). A model accounting for age (3 age classes) and locality (except for the adult age class) was applied to the data for the animals marked as juveniles or subadults, and estimates for juveniles and subadults were taken from this model. To the data for the animals marked as adults, a

Table 1. Survival rates (ϕ) and capture probabilities (p) for the sand lizard (*Lacerta agilis*) at sites FL and SB, estimated under two models for different subsets of the data. The estimates for non-adults were derived from a model allowing survival rates and capture probabilities to vary between age classes (juveniles 0 years old, subadults 1 or 2 years old, adults 3 years or older) and also between sites (except for the adult age class). The estimates for adults were derived from a model where the survival rates and capture probabilities differ only between the sexes.

		ϕ				p			
				95% confidence interval				95% confidence interval	
Age class	Site	Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper
0	FL	0.245	0.179	0.046	0.684	0.050	0.061	0.004	0.389
1-2	FL	0.614	0.182	0.261	0.878	0.026	0.026	0.003	0.173
0	SB	0.479	0.195	0.165	0.810	0.174	0.127	0.036	0.544
1-2	SB	0.631	0.098	0.428	0.796	0.437	0.102	0.256	0.637
3+ females	FL + SB	0.694	0.046	0.597	0.776	0.359	0.062	0.249	0.487
3+ males	FL + SB	0.538	0.074	0.394	0.677	0.495	0.120	0.277	0.715

model accounting only for sex differences was applied, and estimates for adult males and females were taken from this model. The survival estimates from these models were then used as the survival rates in life table analysis and in Leslie matrices of the stochastic models (below).

Deterministic population growth was quantified by life table analysis of the female populations at FL and SB. Fecundity was estimated using the overall mean clutch size, minus unhatched eggs, for all adult age classes and from each study population under field conditions. Following Strijbosch & Creemers (1988), the age-specific probability of reproduction was set to 52.3% for 3-year olds, 82.4% for 4-year olds, and 100% for 5+ year olds. The sex ratio among the offspring was set to 50% females, also in accordance with Strijbosch & Creemers (1988). Maternity (the average number of female offspring hatched per year per reproductive female) was measured as 3.113 over a nine-year period for site FL. Age-specific fecundities used in the PVAs (below) were calculated as the product of adult survival rate, probability of reproduction, and maternity.

A Leslie matrix parameterized with post-reproduction survival and fecundity data was subjected to elasticity analysis using RAMAS GIS (Akçakaya 1998) to assess which age-specific survival or fecundity rates are the most important in contributing to the finite rate of increase under asymptotic population growth (for overview, see de Kroon et al. 2000).

Simulation studies (I and II)

Future population growth of the study populations with stochasticity added, and with or without management, were simulated with RAMAS Metapop 3.0 and 4.0, respectively (Akçakaya 1998, 2002), which can be parameterized to meet the assumptions of stochastic, age-structured population models (Akçakaya 2000). The models used a simulation that ran for 20 years (paper I) and 50 years (paper II) respectively, with 1000 replicates. Contest type density dependence was included in simulations that ran for 50 years (paper II), and no density dependence in simulations that ran for 20 years (paper I).

Environmental stochasticity was modelled as randomly drawn values from lognormal distributions. The environmental stochasticity for yearly survival was calculated as the standard deviation of the series of annual recapture rates, measured as number of individuals captured in year x and number of these known to be alive in year x + 1 (i.e., recaptured in year x + 1 or later). This gave the following SDs, respectively: 0-year olds = 0.176, 1-2-year olds = 0.155, 3+ year olds = 0.109 (paper I). These estimates of environmental stochasticity are crude, and also include effects of demographic stochasticity and sample error..

The measure of environmental stochasticity for fecundity was calculated using the coefficient of variation of numbers of hatched eggs per clutch per year at site FL during 1988-97 (CV = 0.18), multiplied by the age-specific fecundity (f_x) to give corresponding standard deviation values for RAMAS (paper I). Catastrophic events were ignored when these fecundity variances were calculated.

Catastrophes were incorporated as 0% survival for 0-year olds every 10th year. This estimate is based on observed regional hatching failure in 1987 and near failure in 1998, because of unusually cold and rainy summers, and corroborated by captures of individuals of cohorts from 1979-1986 and 1988-1997 (paper I).

Correlation in environmental variation between local populations was established using the RAMAS correlation-distance function, with $a = c = 1$ and $b = 8000$, such that there was 100% correlation for a 0 m distance and 73% correlation for a 2500 m distance between populations. The latter value is equivalent to the correlation for adult female population sizes between site FL and SB (situated 2500 m apart) during the 14-year period 1988-2001. In the hypothetical metapopulation systems modelled here, the distance between the most adjacent local populations was 750 m (from centre to centre), which gives a 91% correlation using this function.

I modelled hypothetical (meta-)populations composed of 1-, 2-, 4-, and 8 local populations, each corresponding to a 5 ha patch (equilibrium population size $K = 300$) and connected to the most adjacent patches by a distance of 750 m (centre to centre). Maximum dispersal, D_{max}, was set to 1200 m per year. This function gives an annual dispersal rate of 1.3% per population in the 2-patch system, and 3% and 6% for the least and most connected patches, respectively, in the 8-patch system. I used relative dispersal weightings of 1.0 for immatures (0-, 1-, and 2-year olds), and 0 (i.e. no dispersal) for adults. Dispersal was assumed to be density dependent and the above rates represent maximum dispersal at $K = 300$.

For the models used to test effects of different patch size and types of density dependence, initial population size was based on the observed population density of 60 females/ha, with a stable age distribution. The smallest patch size, 0.1 ha, is the smallest observed on Brattforsheden (a now extinct population).

For the basic model used for juvenile introduction scenarios, I set $K = 300$ for each local population. The starting population (year 0) was composed of 10, 20 or 40 introduced juveniles per patch. For some scenarios, propagules of 10, 20 or 40 additional juveniles per patch were introduced for up to 2 subsequent years. The chosen propagule sizes and introduction time periods were a compromise between expected population establishment success, costs, and administrative continuity. In all, 36 introduction combinations (scenarios) were analysed.

For different alternatives to breed/raise juveniles for release, and a discussion of their potential survival rates, see paper I. It was assumed here that juveniles were introduced to restored habitat patches empty of sand lizards.

Demographic management scenarios (I)

I modelled future population growth for each population from 1998 and 20 years onwards under the following five management scenarios (presented in the order from assumed low to higher economic costs):

I) *No management*, without taking deterministic successional factors (mainly caused by increased pine canopy formation) into effect.

II) *Habitat management* (cutting of dense tree stands, excavation of new sand patches, and enhancement of heather growth), creating ”optimal” habitat conditions for the next 20 years within a 8 ha large area around 1-2 ha large sites. This would eliminate observed negative effects of shade from surrounding tree canopy on embryo development.

III) "*Headstarting" using artificial incubation* of eggs for 5 or 10 years, respectively, with eggs being dug up from the field shortly after deposition to be incubated artificially under ”optimal” temperatures. Alternatively, gravid females are caught just prior to egg deposition in the field to be temporally transferred to captivity to lay their eggs. This scenario allows for earlier hatching, and larger juveniles before hibernation after release in the field (Corbett 1988).

IV) *"Headstarting" using captive raising* (Caughley & Gunn 1996) for 5 or 10 years, with eggs being dug up from the field just prior to hatching in late summer or early autumn. Juveniles are reared and hibernated in captivity to be released the following spring. This results in substantially increased 0-yr old survival during the first hibernation. It was conservatively set to 0.80 and the standard deviation (yearly variability) to 0.08, in accordance with previous years´ pilot studies of rearing juveniles in captivity.

V) *Captive breeding* (Caughley & Gunn 1996) for 5 or 10 years, where 5 females are caught (the majority of the small populations in 1998) to reproduce in captivity during winter with two clutches per female, so that twice the number of juveniles can be released in spring each year. Normally, the sand lizard produces only one clutch per year in Sweden, but under optimal conditions in the laboratory two or even three clutches can be produced.

Habitat restoration and lizard colonisation (III)

Since it was obvious that the two study sites had become, and were to become, smaller because of formation of surrounding pine stands (15 and 35 years old respectively), the sites were subject to habitat restoration in the winter and spring of 1988 and 1992. This included felling of dense tree sections and manually scraping off patches of the humus layer to create new sand patches. In 1992, two sections at each site were also subject to patch-soil scarification by a tractor, turning ca 0.4 x 1 m of the humus-layer upside down and creating an open sand patch of equivalent size, ca every 1 m. This was done evenly in each section. In all, these restoration measures doubled the area of suitable habitat to 2.0 ha at each locality. These new clearings did not decline in size over the study years, but because of increasing shade due to tree canopy formation at the original habitat sections, the overall habitat remained on average 1.0 ha until 1999 at SB and until 2001 at FL, respectively. In the autumn of these years, ca 10 ha at each site was subject to tree felling and patch scarification. In addition, an excavator created 11 ca 100-200 m^2 large sand patches at SB, and 7 such patches at FL.

Stepwise logistic regression was performed with the programme BMDP (Dixon 1992) ver. 2.0, to analyse which habitat variables correlate with the presence or absence of the sand lizard within 2x2 m quadrats. Logistic regression is a suitable method for determining the relationship between environmental variables and observed dichotomous responses such as species presence or absence.

Two parts of the site SB in 2004 were chosen to assess the effect of three different treatments on vegetation development and sand lizard microhabitat suitability (excluding the excavated new sand patches): 1) tree felling + patch scarification, 2) tree felling only, and 3) no treatment (control). The percentage cover of vegetation (mostly assessed to species), litter and bare ground was estimated by placing a 2x2 m quadrat on each of the three treatments in and around 8 pine groups in one 12-year old restoration area, and at 8 groups in one 5-year old area. Analysis of variance (ANOVA) were used to detect significant differences in vegetation development between the three treatments. Data were arcsin-transformed, and Shapiro-Wilks statistic was used to verify normality of means, and Levene´s test to verify homogeneity of variances, using the program package BMDP ver. 2.0.

To assess relative population changes in connection to habitat restoration, the number of observed clutches, adults and subadults were recorded within all larger sand patches (range 4-200 m^2) and a ca 30 m wide sector around each sand patch. These sand patches were all actual or potential egg-laying patches for sand lizards. The sector around the patches comprised a more or less rich field layer of predominantly *Calluna*, suitable for lizard activities beside egg-laying.

Adult female population size, mesured as the highest value of either number of females known to be alive or number of clutches (cf. paper I), were assessed from 1988 to 2004. From these data I calculated the finite rates of population increase (R), according to Akcakaya et al. (1997, p. 11).

Regional and landscape surveys and usefulness as an umbrella species (IV)

The sand lizard was surveyed in Värmland and Dalarna, the two northernmost counties in Sweden where the species has been reported during recent decades. Before the start of the surveys it was known that the sand lizard had been found on some of the largest sandy pine heaths with aeolian (wind blown) sand. Therefore all sand deposits > 4 km^2 and some smaller ones with aeolian sand, usually in the form of fossil sand dunes, were surveyed (n = 29). In addition, some other pine heaths > 1.0 km^2 with gravel-mixed sand, and close to dune areas, were surveyed (n = 11). Areas were localized and their size measured from quaternary sediment maps, scale 1:200 000 (G. Lundqvist 1948, J. Lundqvist 1958). Localized sand deposits were subsequently studied on aerial photographs, and all open patches with or without exposed sand (except for mires) were noted on topographic maps. Thereafter the patches were visited in the field.

In total, 11 sandy pine heaths were also surveyed for spider wasps, a family of insects often occurring in similar habitats as the sand lizard. Within each pine heath the majority of existing open patches with a mosaic of south-exposed sand and a rich field layer were localized with the same technique as described for the sand lizard. Patches were considered separate if > 300 m of unsuitable habitat (usually closed pine stands) was situated in between. The majority of patches were separated by > 1 km. On mostrveyed patches one yellow and one white water trap were used, but the number per patch varied somewhat. The water traps consisted of plastic, round pans with a diameter of 23 cm and a height of 11 cm. They were 3/4 filled with water, some drops of detergent, and a bottom-layer of coarse salt (to slow down the decay of the caught insects). The traps were inspected and emptied at least once every second week from the end of May to late August. All spider wasps were preserved in 70% alcohol and later identified to species using Oehlke & Wolf (1987) and van der Smissen (1996). In total, ca 5000 specimens were examined. Other caught insect taxa were preserved and identified.

Potential environmental correlates of extinction for local sand lizard populations were analysed using stepwise logistic regression and the statistical software package BMDP New System (Dixon 1992), ver. 2.0. Logistic regression quantifies how much independent (predictive or explanatory) variables can explain the variation in some dependent (outcome or response) variable. In this study the dependent variable was extinction or persistence of local sand lizard populations in patches known to have been occupied some time between 1977-1998, and the explanatory variables were patch area and isolation, as measured in 1998.

A nested subset analysis for spider wasps was carried out based on a presence-absence matrix for sandy pine heaths of different size. I used Atmar & Patterson´s (1993, 1995) Nestedness Temperature Calculator method and software to establish the extent at which my data were nested. Nestedness values can range from T = 0° for a perfectly ordered system (perfectly nested), to T = 100° for complete randomness.

To evaluate and rank potential umbrella species, the umbrella index developed by Fleishman et al. (2001a, b) was used. Originally, this index takes into account three components: mean co-occurrence of the species, its degree of ubiquity, and its sensitivity to human disturbance.

Results and Discussion

Population subdivision and demographic management (I)

Six local populations within the pine heath forest Brattforsheden were censused during 1984-1998. Two populations went extinct and the remaining four declined, each with less than ten adult females left in 1998. Efficient afforestation and fire suppression seem to be the most important factors behind the recent decline of the species, having reduced the amount of open, suitable habitat. In some years there were more or less complete egg hatching failures coinciding with cold, rainy summers with exceptionally few hours of sunshine. A significantly lower average number of hatched eggs at

Table 2. Life table for the female sand lizard population at site FL. x = age in years; p_x = probability to survive during age interval x; l_x = proportion alive at the start of year x; p_{repr} = probability to reproduce (age 3-9 according to Strijbosch and Creemers 1988); Fem_{young} = half of overall mean hatched clutch size; $m_x = p_{repr} \times Fem_{young}$; f_x = age-specific fecundity used in RAMAS = $p_x\ (m_{x+1})$.

x	p_x	l_x	p_{repr}	Fem_{young}	m_x	$l_x m_x$	$x l_x m_x$	f_x
0	0.245	1.000	0.000	0.000	0.000	0.000	0.000	0.000
1	0.614	0.245	0.000	0.000	0.000	0.000	0.000	0.000
2	0.614	0.150	0.000	0.000	0.000	0.000	0.000	0.954
3	0.694	0.092	0.523	2.969	1.553	0.143	0.430	1.697
4	0.694	0.064	0.824	2.969	2.446	0.157	0.627	2.060
5	0.694	0.044	1.000	2.969	2.969	0.132	0.660	2.060
6	0.694	0.031	1.000	2.969	2.969	0.092	0.549	2.060
7	0.694	0.021	1.000	2.969	2.969	0.063	0.445	2.060
8	0.694	0.015	1.000	2.969	2.969	0.044	0.352	2.060
9	0.694	0.010	1.000	2.969	2.969	0.031	0.275	2.060
10	0.694	0.007	1.000	2.969	2.969	0.021	0.212	2.060
11	0.694	0.005	1.000	2.969	2.969	0.015	0.162	2.060
12	0.694	0.003	1.000	2.969	2.969	0.010	0.122	2.060
13	0.694	0.002	1.000	2.969	2.969	0.007	0.092	2.060
14	0.000	0.002	1.000	2.969	2.969	0.005	0.069	0.000
						R_0=0.720	T_C=5.550	
						λ=0.943		

one locality seemed to be due to a more advanced formation of tree canopy and subsequent shading of the oviposition patches. Life table analysis of two populations implied an average 6% decline and 2% increase in population size per year, respectively ($\lambda = 0.94$ and 1.02) (see Table 2 for one example).

This northern sand lizard metapopulation exhibits several features typical for populations on the edge of extinction: 1) sharp spatial division among local populations with no dispersal between them, 2) small habitat patches, 3) small local populations, 4) low juvenile recruitment, 5) low finite rate of population increase (λ), and 6) large variation in λ (highly dependent on the effects of weather on juvenile survival) (cf. Leigh 1981, Goodman 1987, Harrison 1994, Lawton 1995, Hanski 1999). The study suggests that the sand lizard population on Brattforsheden presently can be viewed as a non-equilibrium metapopulation, where the local populations have become com

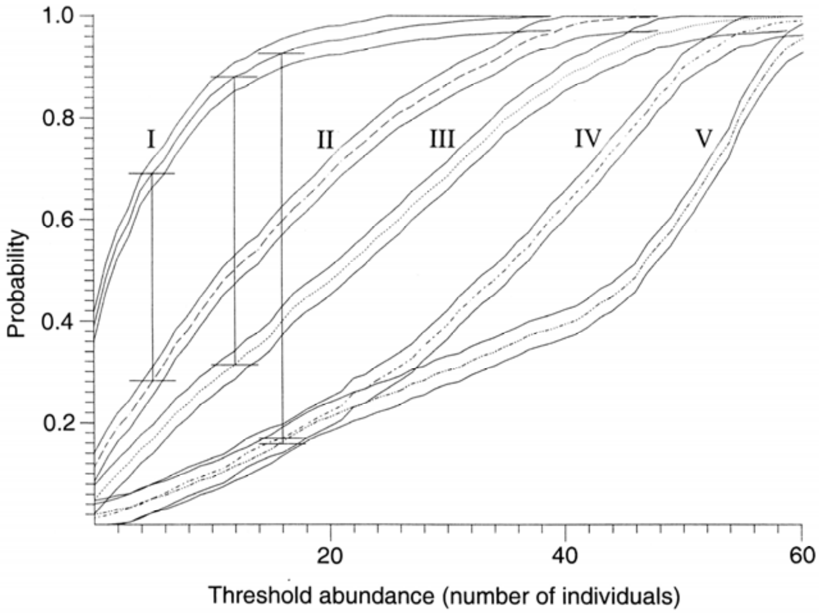

Figure 2. Quasi-extinction risks for the female sand lizard population at site FL under the management scenarios I) no management, II) habitat management, III) artificial incubation, IV) captive raising, and V) captive breeding. The curves show, for each threshold abundance, the probability of falling below that abundance sometime during the next 20 years from 1998. The vertical bars show the maximum difference between the indicated curves. The solid curves around the mean curves give 95% confidence intervals, based on Kolmogorov-Smirnov statistic, D. Scenarios III-V were practised during year 1-5, in parallel with II during year 1-20.

pletely isolated by deterministic environmental changes, i.e. overgrowth by pine and shading due to canopy formation in open habitat patches.

Simulations of stochastic future population growth for 20 years with no management predicted a 36% and 8% risk of extinction, respectively. Projected risks of population extinction and decline were highly dependent on the population growth rate, which in turn was greatly affected by the estimates of juvenile survival. Elasticity analysis demonstrated that this latter demographic parameter contributed most to population growth rate under asymptotic conditions. Simulations of five different conservation management options ranked a programme of captive raising (increased juvenile survival in captivity during the first hibernation) or captive breeding (using a breeding stock from the two populations, respectively), in parallel with habitat management, potentially to be the most effective options to drastically reduce the risk of extinction and decline (Fig. 2).

Modelling juvenile introduction and spatial management strategies for metapopulation establishment (II)

The potential for metapopulation establishment of the sand lizard in a sandy pine heath reserve in central Sweden was explored by modelling the effect of differences in: 1) patch size, 2) number of patches, 3) number of introduced juveniles, and 4) among-patch dispersal. My basic model was presented as a spatially explicit, age-structured, stochastic metapopulation model, and it was parameterized with long-term demographic data from two local populations inhabiting the area subject for this study. Simulations of population growth for 50 years showed that the quasi-extinction risk (threshold ≤ 10 females including hatchlings) was $> 56\%$ for patches ≤ 1 ha; which is the average size of suitable habitat for inhabited patches during a 10 year period. The quasi-extinction risk decreased to $< 6\%$ for patches ≥ 5 ha (Fig. 3). Extinction risks decreased with larger propagule size of introduced juveniles and with increasing number of annual introductions. The same total number of introduced juveniles gave roughly the same extinction risk irrespective of if these individuals were placed in 1 patch or divided into several patches in managed, highly correlated metapopulation networks.

Dispersal was not important to reduce extinction risks over a 50-year horizon for these types of metapopulation networks Fig. 4). Dispersal generally has little effect on local population persistence times when growth rates of local populations in the system are highly correlated (Burgman et al.

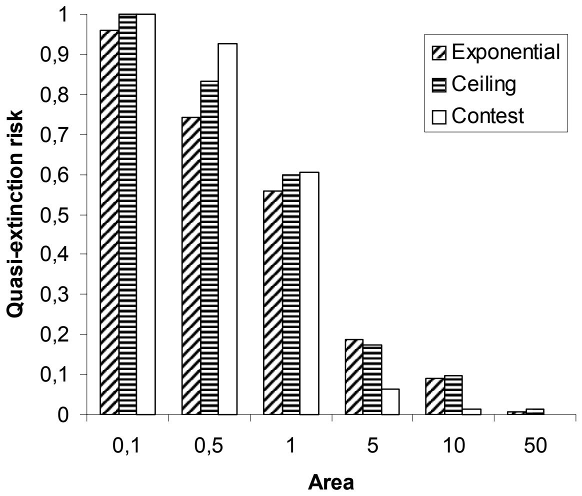

Figure 3. Quasi-extinction risks in relation to patch area and density dependence for female sand lizards on Brattforsheden. The quasi-extinction threshold is set to ≤ 10 individuals (including hatchlings). For all models, initial abundance = 60 individuals/ha x patch area (ha), except patch size 0.1 ha, where intial abundance was set to 12 individuals. For the ceiling model K = 120 individuals/ha x patch size, and for the contest model K = 60 individuals/ha x patch size, and R_{max} = 1.10.

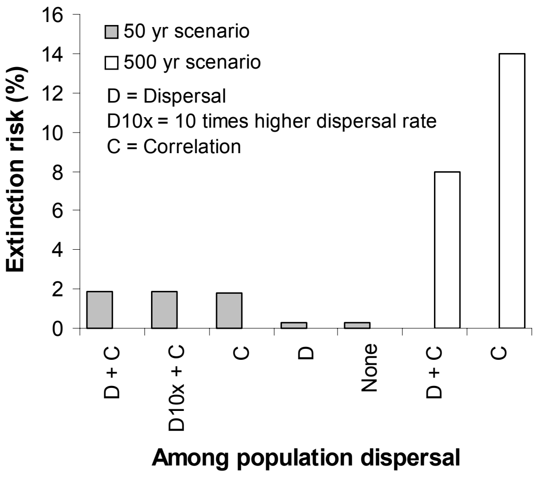

Figure 4. Relative importance of among-population dispersal and correlation for metapopulation extinction risk with simulations over 50 and 500 years, respectively, for a four-population network. Scenarios 24a-g in Table 29.2 in paper II.

1993, Stacey et al. 1997), like the ones in my basic metapopulation systems (91% correlation between adjacent local populations). Given that the supply of juveniles for release is limited, it seems that a wise strategy may be to introduce juveniles for three successive years into one patch in each of several metapopulation networks to minimize correlation among the initial populations. Dispersal was probably much more important in the past landscape, with a natural forest fire regime and extensive human activities like forest grazing by cattle, that created spatiotemporal variation in growth rates within sand lizard metapopulation networks (cf. Thomas 1994). Yet, the potential for substantial dispersal also within future restored networks is important for colonization of empty patches (assuming that juveniles are not introduced into all patches in each network), and for metapopulation persistence on longer, evolutionary time-scales.

My results support other modelling and empirical studies that an increase of the patch carrying capacity is more promising for population persistence than an increase in patch number or connectivity (Drechsler & Wissel 1998, Thomas et al. 2001). On the other hand, dispersal was experimentally shown to decrease metapopulation extinction probability in the common lizard (*Lacerta vivipara*) by dampening local stochasticity via homogenisation of population sizes (Lecomte et al. 2004).

Habitat restoration and habitat tracking (III)

Habitat restoration and management for species dependent on the early phase of vegetation succession after disturbance has become an increasingly important issue in biodiversity conservation (e.g. Webb & Thomas 1994, Sutherland 1998, Bergman 2001, Cousins & Eriksson 2001, Pullin 2002). Loss of open habitat patches in pine heath forests on sandy sediments have resulted in a decline of the sand lizard in south-central Sweden, where small, isolated relict populations occur on the northern periphery of the species´ range. Over a 16-year period, habitat tracking and population dynamics of the sand lizard, and habitat vegetation development, were studied experimentally in one pine heath forest in connection with habitat restoration at two sites. Using stepwise logistic regression, it was shown that a structurally complex microhabitat of open patches with bare sand and the pioneer moss *Polytrichum piliferum*, and a dense field layer of predominantly heather (*Calluna vulgaris*), had a positive association with presence of the sand lizard.

In originally dense pine stands with a bottom-layer dominated by reindeer lichens, the cover of *Calluna* increased markedly after a combination of tree felling and patch-soil scarification. After 12 years there was no significant

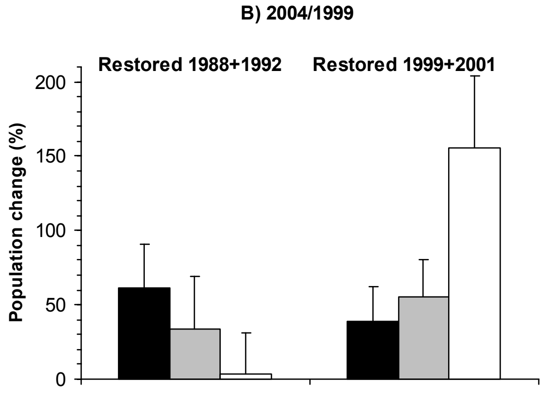

Figure 5. Changes (±SE) in relative population size in 2004 and 1999 for clutches (black), adults (grey) and subadults (white) in habitat sections that were restored during 1988 and 1992 (n = 9) and 1999 and 2001 (n = 18), respectively. The sections restored during 1999 and 2001 differed significantly from the sections restored earlier regarding changes in relative population size for subadults, but not for clutches or adults.

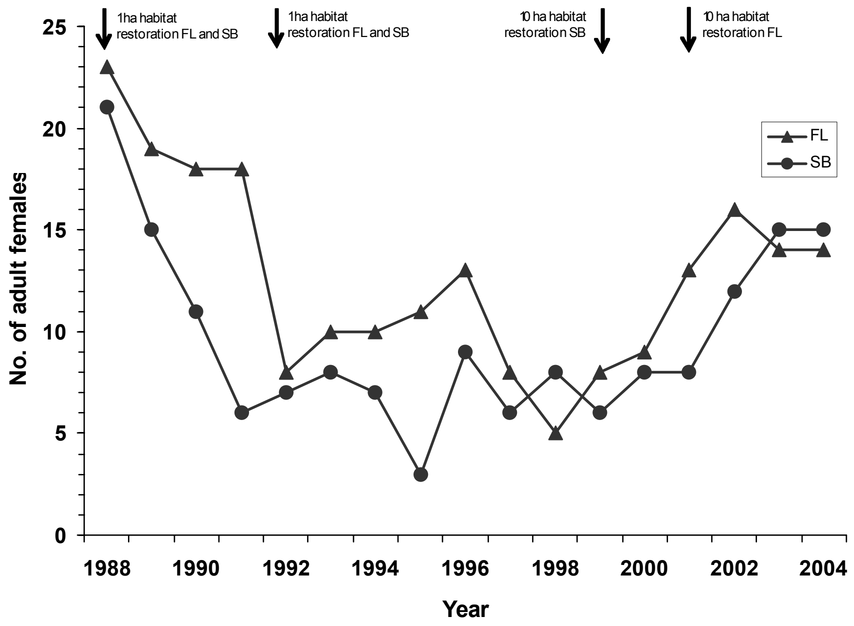

Figure 6. Estimated number of adult female sand lizards at sites FL and SB during 1988 and 2004. The arrows indicate year of habitat restoration at each site.

difference in *Calluna* cover in random quadrats at restored sections compared to that in quadrats around the observed lizards at other sections. In quadrats with tree felling only, and in control quadrats, the cover of *Calluna* was significantly smaller, as was the cover of *Polytrichum* and bare sand.

Sand lizards gradually colonized restored sections, especially as subadults (Fig. 5), while all originally occupied but unmanaged (control) sections had been abandoned after 16 years, probably due to canopy formation. Although the sand lizards colonized restored sections, the estimated yearly population growth rate for adult females at the two study sites during the first 10 years implied an average 9% and 11% decline, respectively (R ± SD = 0.91 ± 0.33 and 0.89 ± 0.71). However, during the last ca 6 years, the populations have increased by a yearly population growth rate of 19% and 11%, respectively (R ± SD = 1,19 ± 0.27 and 1,11 ± 0.27) (Fig. 6). This change may partly be due to a much larger habitat restoration than before. Because historical disturbance regimes are no longer operating, habitat restoration and long-term management seem necessary for conservation of the sand lizard.

The lack of increase in population growth rate during the first 10 years may be ascribed to the on average small amount of available habitat, and that the performed small-scale habitat restorations were insufficient to increase the carrying capacity of the sites. The increase in population growth rate during the last six years coincided partly with large-scale habitat restorations (Fig. 6). Furthermore, it seems that it was especially immature lizards that colonized the recently restored sections (Fig. 5). This may be due to density-dependent population regulation, promoting dispersal of immatures into "empty" habitat sections. Density-dependent processes occur in the common lizard (*Lacerta vivipara*), where juvenile mortality is positively related to population density (Massot et al. 1992), and adult female density is a major factor promoting juvenile dispersal (Lena et al. 1998). However, contrary to these findings, no effect of maternal nearness was shown on offspring dispersal in a sand lizard population in southern Sweden (Ryberg et al. 2004).

Area-sensitivity and usefulness as an umbrella species for biodiversity conservation (IV)

Since dry pine heath forests on sandy sediments occur as islands in an archipelago all over Fennoscandia, island biogeography theory may be relevant for conservation purposes. The degree of isolation from sources of colonisers would then determine the rate of immigration, while island area would determine the population size and thus the extinction rate (Lomolino 1999).

However, extinction is probably the dominant population process for low-vagility organisms in isolated transient landscapes, and the internal disturbance dynamics the critical key to long-term persistence (Pickett & Thompson 1978, Webb & Thomas 1994, Tiebout & Anderson 1997). If so, it is important to define the "minimum dynamic area" with a natural and anthropogenic disturbance regime which maintains internal recolonisation sources and hence minimises extinctions (Pickett & Thompson 1978).

Surveys of the sand lizard on a regional scale in south-central Sweden showed that populated pine heaths were significantly larger (median area 65 km^2) than those where the species was absent (median area 5 km^2) (Fig. 7). No effect of pine heath isolation was found. Moreover, on a landscape scale, occupied habitat patches within individual pine heaths were significantly larger than patches where the sand lizard had recently gone extinct (Fig. 8). Patch isolation had no significant effect. Furthermore, an analysis of presence/absence of ground-nesting spider wasps (Hymenoptera: Pompilidae) on sandy pine heaths of different size showed that species composition was significantly nested. The highest diversity, of all species and red listed ones, was found on the largest pine heaths, in sympatry with the sand lizard. However, some smaller pine heaths showed unexpectedly high species richness

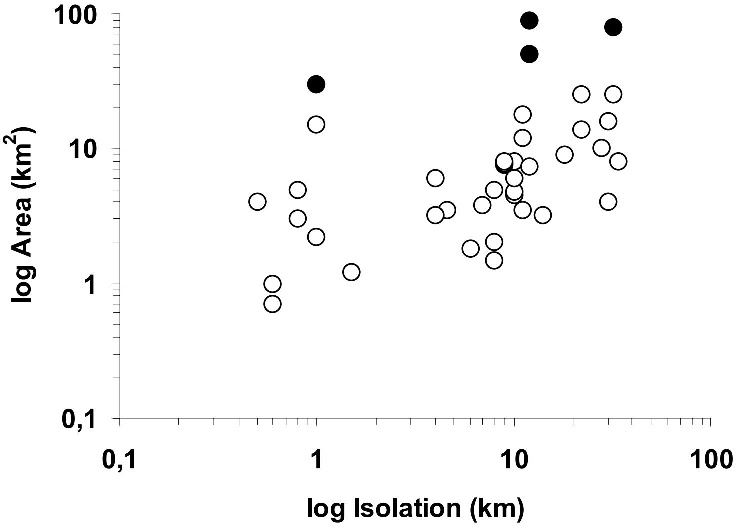

Figure 7. Area and isolation of sandy pine heaths with (filled circles) and without (open circles) populations of the sand lizard Lacerta agilis in Värmland and Dalarna. Aeolian sand, usually with fossil sand dunes, were present at 29 (72%) of the 40 surveyed areas, including the four occupied areas. Isolation = shortest distance of non-sandy soil from one sand deposit to the nearest other with aeolian sand

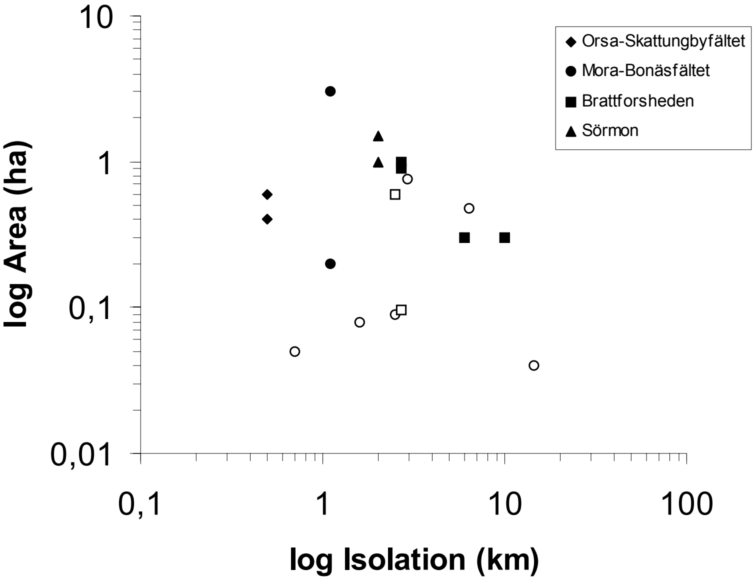

Figure 8. Area and isolation of patches with extant (filled symbols) and extinct (open symbols) local sand lizard populations on the four occupied sandy pine heaths in Värmland and Dalarna in 1998 (see panel). Isolation = distance to the nearest other occupied sand lizard patch.

with some rare species. It is argued that only the largest sandy pine heaths have provided historical continuity of suitable early successional habitat patches with exposed sand for the most dispersal-limited species. Because of forest fire suppression and afforestation since the beginning of the 20th century, many early successional species in sandy pine heath forests are now threatened due to loss of such patches. To provide habitat for these species, measures to re-create early successional patches must be taken.

Pine heaths and patches with the sand lizard had a disproportionately large number of red listed spider wasps and other early successional species on a regional and landscape scale. Because of the sand lizards' restricted dispersal capacity and association with structurally complex sand habitats (see above), this species indicates historical continuity of such habitats. Since the sand lizard is also conspicuous and rather easy to survey, it can be considered a suitable indicator species for patches of high early successional biodiversity value. Furthermore, potential habitat patches for the sand lizard are fairly easy to identify, which make surveys for "hot spot" patches straightforward.

In addition, since the sand lizard requires relatively large patches on at least a 50-yr horizon (> 5-10 ha; see above), it makes it a suitable umbrella species for early successional biodiversity conservation on large sandy pine heaths. This was also supported by the relatively high score of the umbrella index calculated for red listed species on Brattforsheden. However, two drawbacks with the sand lizard as an umbrella species for biodiversity conservation in pine heath forests are its restriction to the largest sandy areas, and its rarity within these at present. An ideal umbrella species should be neither too ubiquitous nor too rare but instead strike a balance between these two extremes (Fleishman et al. 2001b). Sites that are identified with an umbrella species should also encompass viable populations of both the umbrella and its beneficiary species (Roberge & Angelstam 2004). Importantly, this could be achieved after habitat restoration and subsequent population growth. To preserve the existing threatened biodiversity within a given pine heath (including the many pine heaths where the sand lizard is absent), a strategy of multiple umbrella species and demarcation of patches with key habitat components is needed.

Conclusions and long-term conservation

The ultimate factor behind the decline of my study populations seems to be the deterministic effect of afforestation and forest fire suppression during the 20th century. This has resulted in a reduction in the amount of open, early successional habitat patches suitable for the sand lizard. The surviving populations are so small that there is substantial risk that more or less stochastic factors, like cold summers, predation, emigration losses, traffic mortality and chance effects in birth and death rates, can lead to extinction within 20 years.

The survival of these populations in the past seems explained principally by: 1) the regular occurrence of forest fires and extensive human activities which maintained a network of suitable habitat patches, 2) the long life expectancy of adult sand lizards that buffers against reproductive failures in cold summers, and 3) a disproportionately high recruitment from cohorts of warm summers with high juvenile survival.

In order to save these lizard populations in the long run, short-term demographic management as outlined here is not enough. It must be combined with long-term habitat management. Successful management of the sand lizard requires creating unbroken series of successional stages in a spatial mosaic fine enough to permit constant recolonization. This would also favour a number of other succession-dependent species, like the nightjar (*Caprimulgus europaeus*), wood lark (*Lullula arborea*), pasqueflower (*Pulsatilla vernalis*), and a large number of insects, especially among the wasps, ants, flies and beetles, of which at least 30 uncommon and red-listed species have been found on Brattforsheden.

By practising combined demographic and habitat management, there is potentially a good chance of sand lizard population recovery. Moreover, several hectares around the present lizard populations must be cleared from dense forest stands to create a mosaic of open sand patches and a rich and varied field layer. A practical long-term conservation strategy for the species could be: 1) to focus on recurrent habitat management at a number of particularly suitable ”core” sites (with south-exposed slopes) in a network fine enough to permit interpopulation dispersal, and 2) to temporally create suitable habitat between these core sites by making clear-cuts colonizable. Clearence of trees to create broad, permanently open verges along forest roads would also be beneficial for dispersal. Although the demographic management options seem promising for sand lizard conservation, they carry several assumptions, risks during implementation, and higher costs than habitat management. Without explicit and relevant management, it seems likely that we will loose these unique relict populations in the near future.

One might argue that the peripheral populations of red listed species that occur in these Fennoscandian sandy pine heath forests are on the brink of extinction anyway, the positive effects of increased global warming not withstanding, and that conservation resources should be directed toward, for example, threatened boreal species occurring closer to their centres of range. However, recently Channel & Lomolino (2000) showed that peripheral populations are no more ”doomed to extinction” than populations in the centre of a species´ range, and in fact often less so. Furthermore, peripheral populations often exhibit unique genetic characteristics that make them especially valuable for biodiversity conservation (Lesica and Allendorf 1995), which has in fact been demonstrated for the central Swedish sand lizard populations (Gullberg et al. 1998). Large sandy pine heath forests may also be viewed as ”archives” with regard to early successional species connected to historical ecological processes, including forest fires and associated open sand habitats, which have only relatively recently been suppressed by human activities. Thus, there are strong reasons to direct conservation management priorities towards these heath forests without further delay.

Svensk sammanfattning

Populationsförändringar och bevarande av sandödla (*Lacerta agilis*) på norra gränsen av utbredningsområdet

Under den postglaciala värmeperioden (ca 7000-500 f.Kr.) invandrade sandödlan via en tillfällig landbrygga från kontinenten till Sverige och spred sig norrut i landet. Under efterföljande kallare klimatperioder anses arten ha överlevt endast på särskilt gynnsamma platser. Idag har sandödlan inga stora, sammanhängande förekomster någonstans i landet. Förekomsten är i de flesta fall mycket fläckvis, med ofta helt isolerade populationer. Flest lokala populationer finns i delar av Skåne, Halland, Blekinge, östra Småland och södra Östergötland. Norrut glesas förekomsten ut med isolerade populationer i norra Småland och Västergötland, samt i Södermanland, Värmland och Dalarna, varav åtminstone de nordligaste anses vara historiskt isolerade reliktpopulationer.

I Svealand är populationerna få och bestående av små, isolerade lokala populationer om några tiotal vuxna djur. I Värmlands län är totalt åtta lokala populationer kända under de senaste 20 åren, varav två (25%) dött ut. Under 2004 skattades antalet vuxna djur i sammanlagt fyra återstående lokala populationer på Brattforsheden till ca 90, varav de två största lokala populationerna rymde ca 25-30 vuxna djur vardera. Antalet könsmogna honor fluktuerade mellan 3-23 per år i var och en av dessa två populationer mellan 1988-2004. Könsmognad nås efter 3-4 år (övervintringar). En gravid sandödlehona i Värmland har konstaterats vara 19 år gammal, vilket torde vara den äldsta kända sandödlan i världen. Två andra honor i Värmland har uppnått 14 års ålder.

Arten har snävare krav på habitat (livsmiljö) längre norrut i utbredningsområdet. I Värmland och Dalarna är arten idag bara känd från de största isälvsavlagringarna med fossil flygsand. Livsmiljön här omfattar lokaler med lång kontinuitet i tillgång på väl solexponerade, sydsluttande sandmarker i tidig vegetationsfas, med ett rikt fältskikt av ljung- och/eller gräs och örter, samt spridda buskar och öppna sandytor. Typiska biotoper är sydsluttningar i sand- och grustag, skogsvägkanter, kraftledningsgator, samt i viss mån strandmiljöer och öppningar i äldre brandfält.

Skogsbränder var förr en viktig ekologisk faktor som kontinuerligt skapade öppna miljöer, inte minst på de större sandområdena i inlandet. Fr.o.m.

1900-talet har denna dynamik till stor del satts ur spel genom effektiv släckning av skogsbränder. Vidare höll människan skogen mera öppen förr genom svedjebruk, skogsbete och avverkning för träkolframställning m.m. Tillgången på lämplig livsmiljö för sandödlan i sandtallskogar har minskat drastiskt genom både spontan igenväxning och genom att öppna ytor aktivt planteras igen, med följd att kontinuiteten har brutits för miljöer som befinner sig i en tidig vegetationsfas. Det åtföljande kallare mikroklimatet slår på sikt ut hela populationer.

Sårbarhetsanalyser avseende populationer i Värmland har utförts med simuleringsprogrammet RAMAS Metapop. Analyserna visade att för en av de större lokala populationerna på Brattforsheden år 1998 var risken drygt 80% att den någon gång skulle minska till endast tio honor (inkl. årsungar) eller färre under de kommande 20 åren, med ca 40% risk för utdöende. Även med "optimal" habitatförbättring och varma somrar, så att äggens naturliga kläckbarhet är lika hög som den potentiella kläckbarheten (d.v.s. den negativa effekten av skuggiga/kyliga förhållanden på embryonal-utvecklingen elimineras), var risken för ovan nämnda typ av minskning respektive för utdöende oacceptabelt stor (45 respektive 11% inom 20 år). Risken för minskning respektive utdöende kunde enligt sårbarhetsanalyserna drastiskt reduceras med hjälp av uppfödningsverksamhet som höjer de juvenila ödlornas överlevnad första halvåret.

Därtill har sårbarhetsanalyser utförts med avseende på optimering av utsättning av juvenila sandödlor till tomma, restaurerade lokaler. Dessa har visat att genom utsättning av mellan 40-80 juveniler (båda könen) per år under tre år i rad till en 5 hektar stor lokal, är risken för utdöende omkring 5% inom 50 år. Vidare tycks den bästa strategin vara att introducera alla juveniler till samma (restaurerade) lokal, i ett sammanhängande nätverk av lokaler, snarare än att sprida ut ungarna på flera lokaler.

Det ska poängteras att analyserna endast tagit hänsyn till effekter av miljömässig och demografisk variation på populationsöverlevnaden. Utdöenderisken är i själva verket mycket större om man också räknar med effekten av igenväxning av habitatytor.

Majoriteten lokaler i inlandet behöver aktiv skötsel för att inte krympa ytterligare. Denna inkluderar avverkning av skuggande träd, oftast i kombination med skapande av ett rikt fältskikt samt fler öppna sandytor vid lämpliga sydslänter. Hyggen inom sandtallskogar i Svealand erbjuder ofta ingen lämplig miljö för sandödla eftersom hyggena i regel ej utvecklar ett tillräckligt rikt fältskikt. Istället domineras de av renlavar som hämmar uppväxten av ett tätare fältskikt av ljung (eller gräs och örter) innan den nya skogsgenerationen slutit sig. En effektiv metod att skapa ett rikt fältskikt på renlavdominerade hyggen är med hjälp av lätt fläckmarkberedning. Metoden innebär att en markberedningstraktor skrapar upp fläckar av humustäcket samt skapar motsvarande sandblottor. Den har på prov praktiserats i Värmland, där ett tillräckligt väl utvecklat fältskikt av ljung (> 40% täckningsgrad) för sandödla har utvecklats efter mindre än 10 år (från den befintliga fröbanken), som ödlorna koloniserat.

Ett effektivt sätt att skapa nya sandytor är att med hjälp av grävmaskin skrapa bort växt- och humustäcket i lämpliga sydslutningar. På Brattforsheden och Sörmon i Värmland har nyligen ett 30-tal nya, i snitt 20x10 m stora, sandytor skapats på nämnda sätt inom tre restaurerade sandödlelokaler. På flera av dessa ytor har äggläggning ägt rum. Även inom i övrigt lämpliga kraftledningsgator vore framskrapning av sandytor i sydsluttningar en värdefull åtgärd för att förbättra sandödlornas äggläggningsmöjligheter.

Många av de lokaler där sandödlan lever är värdefulla även för andra rödlistade (mer eller mindre hotade) arter som har liknande krav på tillgång till öppna, tidiga vegetationsmiljöer. På de öppna sandmarker där sandödlan förekommer finns så gott som alltid också andra stora fauna- och floravärden. Genom att skydda sandödlans miljöer kan man skydda även många ytterligare rödlistade arter. Sandödlan är inom sandområden i inlandet en lämplig indikatorart för lokaler med hög artrikedom av andra rödlistade arter. Trots sandödlans sällsynthet här, är den därtill en förhållandevis god paraplyart, såtillvida att skydd av sandödlans lokaler skyddar en relativt stor andel av övriga rödlistade arters lokaler. De restaureringar för sandödla som utförts i Värmland har också visat sig vara positiva för nattskärra och trädlärka samt flera rödlistade insektsarter.

Tack/Acknowledgements

Varmt tack till Pekka Pamilo, Per Sjögren-Gulve och under senare tid Martin Lascoux och Ulf Lagercrantz, för hjälp och stöd under mina år vid avdelningen för naturvårdsbiologi och genetik (= avdelningen för evolutionär funktionell genomik, fr.o.m. i år). Er fördragsamhet över att jag ägnat mycken tid åt andra verksamheter än min avhandling (först redaktörskap för Entomologisk Tidskrift och senare att skriva diverse rapporter åt länsstyrelser), har varit oändligt uppskattad. Per har även lärt mig att tänka i naturvårdsbiologiska modeller och har alltid tagit sig tid att klokt kommentera manus. Din vänskap har också betytt mycket många gånger, alltsedan tiden i "gölgrode"stugan i Klungsten för många år sedan. Jan Bengtsson, Skogsvårdsstyrelsen i Karlstad, har varit av enormt stor betydelse för att restaureringsåtgärderna blivit gjorda inom mina studielokaler på Brattforsheden. Det är alltid en höjdare att sitta och skrocka med dig på "hea" och att planera nya åtgärder. Även Lars Furuholm, Länsstyrelsen i Värmlands län, har varit en viktig och entusiastisk kugge för att restaureringsåtgärderna blivit utförda. Under senare åt har jag också fått diverse god hjälp vid sandödlearbetet mm av Torbjörn Nilsson och Johan Bohlin, Länsstyrelsen i Värmlands län. Lasse Wikars har varit en klok diskussionspartner om branddynamik, hockey och livet, och som också tagit sig tid att läsa manus. Anna Lundhagen, min fd rumskompis på avdelningen: görmycket tack för all hjälp och stöd och uppfriskande sjuk humor genom åren! Jättetack även till AnnaCarin Andersson, Johan Fogelqvist, Thomas Källman och Per Sjödin, vid avdelningen, för all datorhjälp! Johan har också varit otroligt hjälpsam med att framställa snygga kartfigurer mm, och Per har alltid haft något tänkvärt att säga om rock'n'roll och akvariefisk. Solstrålarna Kerstin och Rose-Marie: tack för diverse hjälp och alla "goa" prat om allt mellan himmel och jord och för alla sjyssta fester vid inst! Alla vid nuvarande avdelningen (i rumsordning från V till O): Tanja, Harald, Per, Johan, Kerstin, jag själv, Susanne, Rose-Marie, Laura, Marita, Delal, Martin, Hanna, Rahel, Ulf, AnnaCarin, Nicklas och Thomas, som skapat en besynnerligt uppfriskande avslappnad och kreativ stämning på avdelningen, inkl för mig trots mina begränsade bidrag till genetikens utvecklande.. Thanks a lot also to my English brothers David B and Robert P, who separately joined the dept during the early 90s and made skating at Studenternas ice-rink a fine art, besides drinking beer and watching progressive rock bands at Barowiak. Tack också till Jonas W för alla sena telefonsamtal om Livet, Håkan L för många roliga snack om sandmarksdjur mm och till Janne M för åtskilliga kul snack om salamandrar och mycket annat genom åren. Och till Peter för viktiga snack om fiske på Alstern och allt möjligt närsomhelst och hursomhelst, och till Ingrid B, Ulla C, Lars, Jan, och Ellen, för uppmuntran genom åren. Jättetack till Jennie för hjälp med figurer och för att ha lyst upp den sista tiden av avhandlingsarbetet med alldeles särskild musik och många uppmuntrande ord. Tack också till Annika G, Mats O, Mats H, Björn C, Karin L, Märtha W och Annika L för diverse uppfriskande sandödleprat mm under tidigare och senare år. Och till Göran och Anna S för gästfrihet och kattprat. Fröet till den här avhandlingen hade förmodligen aldrig börjat gro om det inte vore för svunna, magiska stunder av utforskande av fåglar, fjärilar, fiskar och naturen kring Edsgatan med min gamle barndomsvän Börje E (†1999) och min unge barndomsvän Gunnar G. Gunnar har också på senare år hållit mig informerad om livet på Edsgatan över en och annan kopp té. Varmaste tack till mamma som alltid funnits tillhands under mina år i Uppsala, för uppmuntrande telefonprat, och för att jag kunnat bo hemma på Edsgatan under mina långa perioder med fältarbete i Värmland, och till mina syskon Gunilla, Ingvor och Lasse och era familjer som hjälpt mamma och uppmuntrat mig under åren i Uppsala. Finally, this thesis is almost dedicated to the extraordinary tunes of Slowdive, My Bloody Valentine, Cocteau Twins, Pale Saints, Kitchens of Distinction, Bleach, Lush, Curve, Cranes, Shelleyan Orphan and other late progressive British spray guitar bands for accompanying me on countless field trips on the sandy roads of the Brattfors heath. Allra sist men inte minst ett jättetack till de alldeles särskilda katterna Klara-Bella (†2000) och Maya som funnits till hands att krama därhemma när det blåst snålt inombords. Om jag råkat glömma någon kan han/hon ändå vara förvissad om min uppskattning.

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Editor: The Dean of the Faculty of Science and Technology

Distribution: publications.uu.se
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