

## Sand Lizard (*Lacerta agilis*) in Central Sweden

### *Modeling Juvenile Reintroduction and Spatial Management Strategies for Metapopulation Establishment*

---

SVEN-ÅKE BERGLIND

A common consequence of habitat loss and fragmentation is the creation of nonequilibrium metapopulations in which the local populations have become so isolated that among-population dispersal no longer occurs (Harrison 1994, Gilpin 1996). Metapopulations that have reached this state are destined to extinction unless the loss and fragmentation of habitat is reversed (Hanski 1997). In this situation, restoration and reintroduction at the scale of metapopulations should be considered (Huxel and Hastings 1999). Since introduced populations in general are small—and thus highly susceptible to environmental fluctuations, catastrophes, demographic stochasticity, and inbreeding depression—it is crucial to maximize the efficiency of initial introductions in order to shorten the period during which the populations would be exposed to these risks (Komers and Curman 2000).

In central Sweden a small number of nonequilibrium metapopulations of the sand lizard (*Lacerta agilis* L.) occur on “biotope islands” of large, glaciofluvial sand deposits covered by pine (*Pinus sylvestris*) heath forests. These populations are some of the northernmost in the world (Gasc et al. 1997) and represent genetically differentiated relicts from an ancient continuous distribution during the postglacial warm period ca. 7000–500 B.C. (Gislén and Kauri 1959, Gullberg et al. 1998). The sand lizard is a Eurasian species that has declined in most of northwestern Europe during the last decades, mainly due to loss of open, sandy, early successional habitats (Glandt and Bishoff 1988), and it is red-listed as “Vulnerable” in Sweden (Gärdenfors 2000). It is a ground-dwelling, medium-sized lizard that feeds mainly on insects and spiders.

The past forest structure on the sandy areas in central Sweden was strongly shaped by frequent fires that may have created a spatiotemporal mosaic of open patches with exposed sand used for egg-laying by the sand lizard and a rich field layer of heather (*Calluna*

*vulgaris*) used for foraging and shelter (Berglind 1988, 1999). However since the beginning of the twentieth century, effective forest fire suppression and afforestation have resulted in a dramatic increase in tree canopy formation, with subsequent loss of such open patches. It is probable that the number and size of sand lizard populations have decreased in parallel and that the present-day areas of occupancy are minute in comparison to the past. In 2001, only four local populations remained on the 11,000-ha nature reserve Brattforsheden, which is one of the largest of these sandy areas in central Sweden (Figure 29.1). All populations were completely isolated from each other by commercially managed pine forest at a distance of 2.5 to 10 km, and the number of adult females per population was estimated at < 5, 5, 8, and 13, respectively (Berglind 2000 and unpublished data). Each of the two largest populations was analyzed independently (Berglind 2000) by constructing age-structured, stochastic, single-population models using RAMAS Meta-pop 3.0 (Akçakaya 1998). These analyses predict that combined habitat and demographic management could dramatically improve the otherwise slim chances for population persistence (Berglind 2000; Sjögren-Gulve, Chapter 24, this volume).

However, beyond rescuing the present small sand lizard populations on Brattforsheden from imminent extinction, there is a need to transform this highly vulnerable metapopulation into a metapopulation of viable and more-or-less connected local popula-

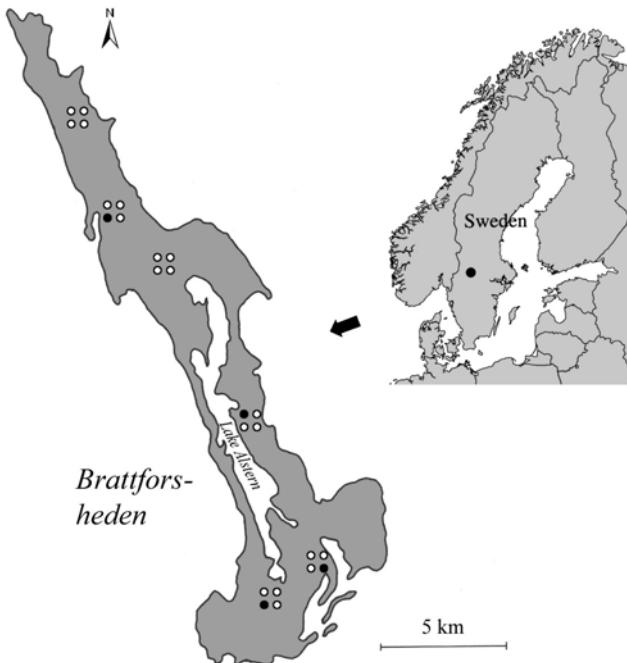


Figure 29.1 The nature reserve Brattforsheden in southcentral Sweden: the spatial distribution of inhabited patches by the sand lizard *Lacerta agilis* (filled circles) and the hypothetical future patches to be restored for reintroduction of sand lizards (empty circles). In this example there are six metapopulation networks, with four patches per network. The actual location of future restored patches will depend on a combination of suitable aspect, soil texture, potential for among-patch dispersal, and negotiation success with the landowners.

tions that require little demographic management for persistence. Because most of the area is subject to conventional forestry and because the past natural disturbance regimes are no longer operating (and will not do so in the foreseeable future), it is necessary to create networks of managed habitat for long-term conservation (Figure 29.1). After habitat restoration, one option is simply to let the few present populations colonize adjacent sites through natural dispersal. Another option, which potentially could create metapopulations much faster and not necessarily close to the existing populations, is to introduce lizards to restored sites. Sand lizards are comparatively easy to breed, and by introducing captive-born juveniles to new sites there are good chances for population establishment (Corbett 1988, Moulton and Corbett 1999, Berglind 2000).

This chapter explores the potential for metapopulation establishment of the sand lizard by reintroduction, by modeling the effect of differences in (1) patch size, (2) number of patches, (3) number of introduced juveniles, and (4) among-patch dispersal. The study is part of the planning for a conservation action program for the sand lizard on Brattforsheden and is directed at determining optimum reintroduction strategies. My basic model is a spatially explicit, age-structured metapopulation model developed using RAMAS Metapop 4.0 (Akçakaya 2002). The computer files are available on the CD that accompanies this volume.

## Methods

### Models

Models were constructed for females only, and the matrices were based on postbreeding census (see Akçakaya 2000, Caswell 2001). The basic model included 15 age classes (ranging from 0- to 14-year-olds); demographic and environmental stochasticity; one type of catastrophe (regional cold summers); contest-type density dependence; and a hypothetical metapopulation system with one, two, four, and eight local populations, respectively, all of the same initial size and structure, and connected by dispersal. Comparisons were also made without dispersal. In addition, a sensitivity analysis was made to compare extinction risks of individual patches of different size.

All models used a simulation that ran for 50 years with 1,000 replicates. The basic model used survival and fecundity data from “Scenario II, site FL” in Appendix 1 in Berglind (2000), corresponding to a relatively conservative deterministic effect on the population growth rate ( $\lambda = 1.03$ ) after “optimal” habitat management (cutting of dense tree stands, excavation of new sand patches, and enhancement of heather growth). Details of parameterizations, except those of dispersal and density dependence, are given in Berglind (2000).

### Demography

Annual survival rates were estimated from a 10-year mark-recapture study during 1988–1998 undertaken for the two largest sand lizard populations (site FL and SB) on Brattforsheden, central Sweden (Berglind 2000). Additional survival rate data for juveniles were taken from a 7-year mark-recapture study by Strijbosch and Creemers (1988) of a stable sand lizard population in a similar habitat in The Netherlands. In

all, this gave the following annual survival rates: juveniles (0-year-olds) = 38.4 %, subadults (pre-reproductive ages; 1- to 2-year-olds) = 61.4%, and adults (that have hibernated 3 times or more) = 69.4%. Following Strijbosch and 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 and Creemers (1988). Maternity (the average number of female offspring hatched per year per reproductive female) was measured as 3.113 over a 9-year period for site FL. Age-specific fecundities ( $\bar{f}_x$ ) were calculated as the product of adult survival rate, probability of reproduction, and maternity.

### Environmental Stochasticity and Catastrophes

Environmental stochasticity was modeled as randomly drawn values from lognormal distributions. The environmental stochasticity for yearly survival was calculated as the standard deviation (SD) of the series of annual recapture rates and yielded the following SDs: 0-year-olds = 0.176, 1- to 2-year-olds = 0.155, 3+-year-olds = 0.109 (Berglind 2000). These estimates are crude and also include effects of demographic stochasticity and sample error (but see Brook 2000).

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 1988–1997 ( $CV = 0.18$ ) as in Berglind (2000). Catastrophic events were ignored in these variance estimates. Catastrophes were incorporated as 0% survival for 0-year-olds every tenth year (Berglind 2000).

There was no within-population correlation between yearly adult survival and fecundity during year 1989–1996 for site FL (Pearson's  $R = -0.36$ ;  $p = 0.38$ ). Thus, no correlation between adult survival and fecundity was used in my models.

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 (Pearson's  $R = 0.73$ ;  $p = 0.0029$ ). In the hypothetical metapopulation systems modeled here, the distance between the most adjacent local populations was 750 m (from center to center), which gives a 91% correlation using this function.

### Density Dependence

Density-dependent phenomena are suspected to be prominent in lizards, since population sizes are thought to fluctuate moderately compared to other vertebrates (Clobert et al. 1994). In this study I first compared the effects of exponential (no density dependence), ceiling, and contest types of density dependence, because the type of density dependence can strongly influence extinction risks. For the contest model, the equilibrium population size ( $K$ ) was set at 60 females (including hatchlings)/ha, which is the average population size for site FL during 1992–2001, when the amount of habitat was restricted to ca. 1 ha. The maximal rate of population increase ( $R_{\max}$ ) was set to 1.10 (as compared to  $\lambda = 1.03$  of the basic model's yearly population growth rate), which assumes an increase in juvenile survival to the mean between the above given estimates

for juvenile and subadult survival (cf. scenario III in Berglind 2000). For the ceiling model, carrying capacity ( $K$ ) was set at 120 females/ha, which is simply twice the observed equilibrium population density.

In the basic model I used contest type density dependence, for which there is evidence in populations of the common lizard (*Lacerta vivipara*) (Massot et al. 1992, Lena et al. 1998), a close and often sympatric relative to the sand lizard. Since my two study populations have fluctuated moderately under constant habitat size conditions during the 10-year period 1992–2001, and individuals have been homogeneously distributed within habitat patches (Berglind, unpublished data), it is reasonable to assume that contest type density dependence is operating also in these sand lizard populations. Note, however, that neither the sand lizard nor the common lizard is territorial; instead, intraspecific competition probably occurs by preemptive use of (micro-)sites that differ in suitability (Olsson et al. 1997, Ronce et al. 1998), which is one type of contest competition (Rodenhouse et al. 1997, 2000). In the common lizard, 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). In the sand lizard, young individuals occur rather frequently in places uninhabited by adults (Yablokov et al. 1980, Nature Conservancy Council 1983), and intraspecific competition also occurs to varying degrees by adult predation on juveniles (Corbett and Tamarind 1979).

### Dispersal and Population Geometry

Adult sand lizards are usually highly sedentary (Nature Conservancy Council 1983, Olsson et al. 1997, Berglind 1999). Most dispersal probably occurs among immatures (Yablokov et al. 1980, Nature Conservancy Council 1983), with considerable variation in dispersal tendencies (Olsson et al. 1996). No data exist on among-population dispersal rates, and there are few data on dispersal capacities. The longest dispersal distances reported seem to be of one individual found 2 km away from an isolated population (Strijbosch and van Gelder 1997) and of one subadult moving 500 m along a forest road within one season (Berglind 2000). Within forested areas, dispersal seems to be very limited outside open patches, probably occurring mostly along sun-exposed forest roads (Dent and Spellerberg 1988). In my models, it was assumed that suitably open dispersal corridors had been created between restored patches for introduction.

I modeled hypothetical (meta-)populations composed of one, two, four, and eight 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 (center to center). Dispersal among populations was modeled using the RAMAS dispersal-distance function, with  $a = 0.40$ ,  $b = 220$ , and  $c = 1$ . 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 two-patch system, and 3% and 6% for the least and most connected patches, respectively, in the eight-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  $K = 300$ . (Density-dependent dispersal as a function of source population size (slope), under the Populations dialog box, was set at stable age distribution, such that the curve crossed the origin and the total rate of dispersal, given as the sum under each population in the Dispersal matrix, was adjusted to the equilibrium population size  $K = 300$ .)

## Initial Population Structures

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). Although populations, not patches per se, are modeled in RAMAS Metapop, I here prefer to present the effects of differences in patch size (with the same initial population density) since “patch size” is the relevant term used by forest managers.

For the basic model 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 (cf. Snyder et al. 1996). In all, 36 introduction combinations (scenarios) were analyzed.

For different alternatives to breed and raise juveniles for release, and a discussion of their potential survival rates, see Berglind (2000). Here I assumed that juveniles were introduced to restored habitat patches empty of sand lizards. It is probable that this will result in increased juvenile survival and higher individual growth rates during population buildup, compared to what occurs in stable populations, since survivorship of juvenile lizards is negatively related to density of conspecific lizards (cf. Massot et al. 1992, Tinkle et al 1993). Such an effect is allowed for in my basic model by the incorporation of contest density dependence with a maximal yearly population growth rate of 10%.

## Results

### Effects of Patch Size and Type of Density Dependence

The quasi-extinction risk for populations inhabiting patches of six different sizes, each of which has three types of density dependence, is shown in Figure 29.2. The risk of decline was  $> 56\%$  for patches  $\leq 1$  ha, with relatively small differences between the three density dependence types. For patches 5 to 10 ha, the relative difference between contest-type density dependence, on one hand, and exponential and ceiling, on the other, is larger, with the first (probably most realistic) type showing a risk of decline from 6% to 1%. Thus, suitable habitat patches between 5 and 10 ha seem to offer “acceptable” chances of population persistence over a 50-year period. Larger patches contribute only a little more to persistence.

### Effects of Number of Patches and Introduced Juveniles

Since several of my introduction populations started very small, and with small introductions in following years, interval risk of decline is not so informative. Instead, I used expected minimum abundance, extinction risk, terminal risk of decline (threshold of 10 females per population), and interval probability of increase (threshold of 300 females per population) as risk-based outputs (Table 29.1).

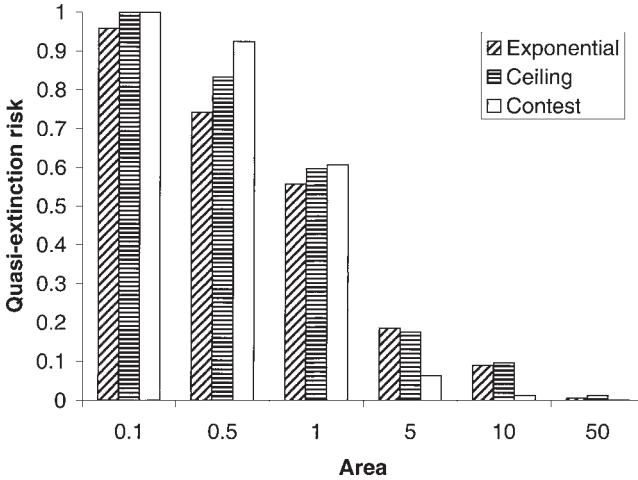


Figure 29.2 Quasi-extinction risks in relation to patch area and density dependence for female sand lizards on Brattforsheden. The quasi-extinction threshold is set to  $\leq 10$  individuals (including hatchlings). For all models, initial abundance = 60 individuals/ha  $\times$  patch area (ha), except patch size 0.1 ha, where initial abundance was set to 12 individuals. For the ceiling model,  $K = 120$  individuals/ha  $\times$  patch size; for the contest model,  $K = 60$  individuals/ha  $\times$  patch size.  $R_{\max} = 1.10$ .

As expected, extinction risks decreased with larger propagule sizes of introduced juveniles and with increasing number of introductions. Table 29.1 shows that with 40 juveniles introduced per patch for 3 years (years 0–2) the extinction risk is  $\leq 5\%$  (given in bold) for all patch systems, including only one patch (scenario 9). Also low risk are the two-, four-, and eight-patch systems with 40 juveniles introduced per patch for 2 years. A propagule size as low as 10 juveniles per patch also gives  $< 5\%$  extinction risk for a four-patch system given three introductions (scenario 21) or an eight-patch system given at least two introductions (scenarios 29–30), but with such small propagule sizes the interval probability of increase is low (Table 29.1).

It seems that the same total number of introduced juveniles gives roughly the same extinction risk irrespective of whether these individuals are placed in one patch or divided into several, as in scenarios 9, 15, and 21. This result is also corroborated by the similar values for expected minimum abundance (Table 29.1). However, the probability of increase is lower for multipatch systems. Thus, given that the supply of juveniles is limited, it seems that in the highly correlated metapopulation networks simulated here (see also next section), 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.

### Effects of Among-Population Dispersal

Table 29.2 shows that introduced metapopulation networks with and without low and high rates of dispersal, respectively, had similar abundances and extinction risks, irrespective of the number of local populations in each network (scenarios a–c). Hence,

dispersal does not seem to be important over a 50-year horizon to reduce extinction risks for these types of highly correlated, managed metapopulation networks of the sand lizard. This was also confirmed by testing the effects of absence of among-population correlation in environmental variation, which increased expected minimum abundance and reduced extinction risks relatively more (Table 29.2, scenarios d–e).

The potential for substantial dispersal is of course still necessary for metapopulation establishment if we assume that juveniles are not introduced into all patches in each network. An example of metapopulation development after introducing 40 juveniles for three successive years into one patch in a connected four-patch network is given in Figure 29.3. The expected minimum abundance for this metapopulation was 24 and the extinction risk was 7.5%, which are figures similar to those for the corresponding one-patch introduction scenario 9 in Table 29.1.

Furthermore, simulations over 500 years showed that dispersal is important on longer (evolutionary) time scales. The four-patch metapopulation scenarios 24 f–g in Table 29.2 reveal substantially higher expected minimum abundance and metapopulation occupancy, and lower extinction risk, for the dispersal scenario.

## Discussion

Habitat restoration and reintroduction techniques have been employed for the sand lizard in England (Corbett 1988). To establish viable populations in England, three annual releases each of around 50 juveniles (both sexes) are recommended (Moulton and Corbett 1999). These numbers and introduction periods are similar to the “acceptable” one-patch scenario 9 in my simulations (Table 29.1). However, evaluation data from the English reintroductions are scarce. No doubt there is a need to maximize efficiency of sand lizard introductions to overcome demographic and stochastic problems during the buildup phase, especially since the supply of captive-born juveniles will normally be limited.

This study indicates that 5- to 10-ha suitable habitat patches have acceptably low extinction risks over a 50-year horizon. Dispersal among local populations had negligible effects on metapopulation persistence over the same time frame. Dispersal is generally expected to have little effect on local population persistence when growth rates of local populations in the system are highly correlated (Burgman et al. 1993, Stacey et al. 1997), like the ones in my basic metapopulation systems (91% correlation between adjacent local populations). However, in the past landscape of Brattforsheden and other Scandinavian sandy pine forests, dispersal was probably a much more important component for metapopulation survival than is implied here. In this landscape, with a natural forest fire regime and extensive human activities like forest grazing by cattle, sand lizard colonizations and extinctions might have occurred in a shifting spatial mosaic of habitat, with lizards tracking early successional habitats. Thus, continuity of suitable habitat within dispersal distance must have been critical to persistence (cf. Thomas 1994, 1996). In such a landscape it is likely that there was spatiotemporal variation in growth rates within sand lizard metapopulation networks, due to differences in successional stage, patch size, local topography (affecting microclimate and egg-hatching success), catastrophic short-term effects of forest fires, and so on.

Today and in the foreseeable future, however, we probably have to rely on habitat management to “freeze” patches in suitably early successional stages. Such manage-

Table 29.1 Juvenile sand lizard introduction scenarios and their effect on female metapopulation abundance and persistence over the next 50 years

Scenario	No. of Populations	Propagule size	Introduction Year	Final Abundance $\pm 1$ SD	Expected Minimum Abundance	Extinction Risk	Terminal Quasi-extinction Risk	Interval Probability of Increase	Terminal Probability of Increase	Median Time to Quasi-extinction	Metapopulation Occupancy $\pm 1$ SD
1	1	10	0	43 $\pm$ 88	1.3	0.583	0.61	0.05	0.026	0.5	0.4 $\pm$ 0.5
2	1	10	0-1	62 $\pm$ 98	3	0.41	0.456	0.08	0.026	1.5	0.6 $\pm$ 0.5
3	1	10	0-2	79 $\pm$ 100	5.4	0.297	0.347	0.146	0.044	2.8	0.7 $\pm$ 0.5
4	1	20	0	63 $\pm$ 93	3	0.406	0.448	0.088	0.031	0.6	0.6 $\pm$ 0.5
5	1	20	0-1	92 $\pm$ 114	7.2	0.238	0.302	0.163	0.063	3.3	0.8 $\pm$ 0.4
6	1	20	0-2	112 $\pm$ 113	12.5	0.121	0.164	0.209	0.069	>50	0.9 $\pm$ 0.3
7	1	40	0	86 $\pm$ 105	6.7	0.274	0.323	0.168	0.046	1.7	0.7 $\pm$ 0.5
8	1	40	0-1	109 $\pm$ 108	14.8	0.151	0.193	0.255	0.071	>50	0.8 $\pm$ 0.4
<b>9</b>	<b>1</b>	<b>40</b>	<b>0-2</b>	<b>137 <math>\pm</math> 119</b>	<b>24.1</b>	<b>0.053</b>	<b>0.088</b>	<b>0.338</b>	<b>0.092</b>	<b>&gt;50</b>	<b>0.9 <math>\pm</math> 0.3</b>
10	2	10	0	82 $\pm$ 136	3	0.39	0.582	0.036	0.015	0.5	1.0 $\pm$ 0.9
11	2	10	0-1	125 $\pm$ 157	7.5	0.235	0.397	0.059	0.015	1.5	1.3 $\pm$ 0.9
12	2	10	0-2	153 $\pm$ 179	13.4	0.133	0.212	0.094	0.035	2.9	1.6 $\pm$ 0.7
13	2	20	0	126 $\pm$ 170	6.9	0.274	0.355	0.063	0.03	0.7	1.3 $\pm$ 0.8
14	2	20	0-1	188 $\pm$ 202	16.4	0.114	0.192	0.142	0.054	4.6	1.6 $\pm$ 0.7
15	2	20	0-2	215 $\pm$ 210	26.9	0.066	0.129	0.17	0.063	>50	1.8 $\pm$ 0.5
16	2	40	0	172 $\pm$ 195	14.5	0.191	0.255	0.14	0.043	1.7	1.5 $\pm$ 0.8
<b>17</b>	<b>2</b>	<b>40</b>	<b>0-1</b>	<b>234 <math>\pm</math> 213</b>	<b>32.7</b>	<b>0.054</b>	<b>0.095</b>	<b>0.227</b>	<b>0.068</b>	<b>&gt;50</b>	<b>1.8 <math>\pm</math> 0.5</b>
<b>18</b>	<b>2</b>	<b>40</b>	<b>0-2</b>	<b>273 <math>\pm</math> 229</b>	<b>52</b>	<b>0.026</b>	<b>0.057</b>	<b>0.311</b>	<b>0.088</b>	<b>&gt;50</b>	<b>1.9 <math>\pm</math> 0.4</b>

19	4	10	0	169 ± 223	7.2	0.264	0.41	0.019	0.01	0.5	2.2 ± 1.7
20	4	10	0-1	278 ± 338	17.4	0.097	0.225	0.072	0.03	1.5	3.0 ± 1.4
<b>21</b>	<b>4</b>	<b>10</b>	<b>0-2</b>	<b>352 ± 372</b>	<b>29.2</b>	<b>0.04</b>	<b>0.142</b>	<b>0.093</b>	<b>0.04</b>	<b>3</b>	<b>3.4 ± 1.1</b>
22	4	20	0	284 ± 395	16.6	0.169	0.268	0.071	0.028	0.7	2.9 ± 1.5
<b>23</b>	<b>4</b>	<b>20</b>	<b>0-1</b>	<b>372 ± 371</b>	<b>37.1</b>	<b>0.054</b>	<b>0.122</b>	<b>0.122</b>	<b>0.041</b>	<b>8.7</b>	<b>3.4 ± 1.2</b>
<b>24</b>	<b>4</b>	<b>20</b>	<b>0-2</b>	<b>453 ± 401</b>	<b>58.9</b>	<b>0.019</b>	<b>0.074</b>	<b>0.181</b>	<b>0.069</b>	<b>&gt;50</b>	<b>3.7 ± 0.8</b>
25	4	40	0	357 ± 385	31.3	0.139	0.206	0.129	0.038	1.7	3.1 ± 1.5
<b>26</b>	<b>4</b>	<b>40</b>	<b>0-1</b>	<b>483 ± 455</b>	<b>72.8</b>	<b>0.024</b>	<b>0.072</b>	<b>0.218</b>	<b>0.07</b>	<b>&gt;50</b>	<b>3.7 ± 0.8</b>
<b>27</b>	<b>4</b>	<b>40</b>	<b>0-2</b>	<b>535 ± 425</b>	<b>110</b>	<b>0.006</b>	<b>0.025</b>	<b>0.294</b>	<b>0.076</b>	<b>&gt;50</b>	<b>3.9 ± 0.5</b>
28	8	10	0	380 ± 574	16	0.178	0.335	0.018	0.011	0.5	4.8 ± 3.0
<b>29</b>	<b>8</b>	<b>10</b>	<b>0-1</b>	<b>583 ± 660</b>	<b>38.3</b>	<b>0.04</b>	<b>0.158</b>	<b>0.061</b>	<b>0.022</b>	<b>1.5</b>	<b>6.6 ± 2.0</b>
<b>30</b>	<b>8</b>	<b>10</b>	<b>0-2</b>	<b>711 ± 678</b>	<b>62.9</b>	<b>0.015</b>	<b>0.094</b>	<b>0.089</b>	<b>0.031</b>	<b>3</b>	<b>6.9 ± 1.9</b>
31	8	20	0	527 ± 597	33.1	0.124	0.237	0.056	0.017	0.6	5.8 ± 2.9
<b>32</b>	<b>8</b>	<b>20</b>	<b>0-1</b>	<b>820 ± 788</b>	<b>78</b>	<b>0.027</b>	<b>0.087</b>	<b>0.131</b>	<b>0.059</b>	<b>19</b>	<b>7.1 ± 1.8</b>
<b>33</b>	<b>8</b>	<b>20</b>	<b>0-2</b>	<b>944 ± 833</b>	<b>126.8</b>	<b>0.003</b>	<b>0.054</b>	<b>0.169</b>	<b>0.063</b>	<b>&gt;50</b>	<b>7.5 ± 1.3</b>
34	8	40	0	699 ± 695	65.3	0.108	0.172	0.106	0.024	1.8	6.4 ± 2.7
<b>35</b>	<b>8</b>	<b>40</b>	<b>0-1</b>	<b>991 ± 817</b>	<b>148.4</b>	<b>0.011</b>	<b>0.04</b>	<b>0.214</b>	<b>0.06</b>	<b>&gt;50</b>	<b>7.5 ± 1.4</b>
<b>36</b>	<b>8</b>	<b>40</b>	<b>0-2</b>	<b>1101 ± 870</b>	<b>232</b>	<b>0.001</b>	<b>0.018</b>	<b>0.299</b>	<b>0.09</b>	<b>&gt;50</b>	<b>7.8 ± 0.8</b>

Note: *Propagule size* = number of introduced juvenile females per patch. *Expected minimum abundance* = the average of the smallest metapopulation size that is expected to occur (cf. McCarthy and Thompson 2001). *Extinction risk* = the probability that metapopulation abundance will fall to zero. *Terminal quasi-extinction risk* = the probability that metapopulation abundance will be less than 10 individuals × number of populations at the end of the 50-year period. *Interval probability of increase* = the probability that metapopulation abundance will exceed 300 individuals × number of populations, at least once within the 50-year period. *Terminal probability of increase* = the probability that metapopulation abundance will end up above 300 individuals × number of populations, at the end of the 50-year period. *Median time to quasi-extinction* = the median time it takes the metapopulation size to fall below 10 individuals × number of populations. *Metapopulation occupancy* = average ± 1 standard deviation of the number of extant populations (i.e., occupied patches) during the 50-year period. Boldface = scenarios with ≤ 5% extinction risk.

Table 29.2 Juvenile sand lizard introduction scenarios with and without among-population dispersal and correlation, respectively, and the effects on metapopulation abundance and persistence over the next 50 years

Scenario	Dispersal	Correlation	No. of Populations	Propagule Size	Introduction Year	Final Abundance $\pm$ 1 SD	Expected Minimum Abundance	Extinction Risk	Terminal Quasi-extinction Risk	Interval Probability of Increase	Median Time to Quasi-extinction	Metapopulation Occupancy $\pm$ 1SD
15a	Yes	Yes	2	20	0–2	215 $\pm$ 210	26.9	0.066	0.129	0.17	>50	1.8 $\pm$ 0.5
15b	Yes 10x	Yes	2	20	0–2	234 $\pm$ 217	27.6	0.063	0.120	0.210	>50	1.8 $\pm$ 0.5
15c	No	Yes	2	20	0–2	217 $\pm$ 201	27.7	0.042	0.098	0.169	>50	1.7 $\pm$ 0.6
15d	Yes	No	2	20	0–2	231 $\pm$ 178	31.4	0.020	0.049	0.114	>50	1.9 $\pm$ 0.4
15e	No	No	2	20	0–2	216 $\pm$ 166	32.0	0.026	0.061	0.124	>50	1.7 $\pm$ 0.5
24a	Yes	Yes	4	20	0–2	453 $\pm$ 401	58.9	0.019	0.074	0.181	>50	3.7 $\pm$ 0.8
24b	Yes 10x	Yes	4	20	0–2	486 $\pm$ 437	59.9	0.019	0.066	0.206	>50	3.8 $\pm$ 0.7
24c	No	Yes	4	20	0–2	430 $\pm$ 395	59.8	0.018	0.074	0.156	>50	3.4 $\pm$ 1.0
24d	Yes	No	4	20	0–2	495 $\pm$ 270	74.2	0.003	0.009	0.053	>50	3.9 $\pm$ 0.4
24e	No	No	4	20	0–2	444 $\pm$ 257	74.1	0.003	0.010	0.038	>50	3.4 $\pm$ 0.8
24f	Yes 500 yrs	Yes	4	20	0–2	545 $\pm$ 436	36.0	0.08	0.090	0.952	298	3.6 $\pm$ 1.1
24g	No 500 yrs	Yes	4	20	0–2	326 $\pm$ 389	30.2	0.14	0.205	0.740	210	2.1 $\pm$ 1.4
33a	Yes	Yes	8	20	0–2	944 $\pm$ 833	126.8	0.003	0.054	0.169	>50	7.5 $\pm$ 1.3
33b	Yes 10x	Yes	8	20	0–2	1002 $\pm$ 912	124.0	0.005	0.050	0.192	>50	7.7 $\pm$ 1.1
33c	No	Yes	8	20	0–2	841 $\pm$ 740	120.2	0.003	0.048	0.129	>50	6.8 $\pm$ 1.6
33d	Yes	No	8	20	0–2	1030 $\pm$ 442	157.5	0.000	0.001	0.013	>50	7.9 $\pm$ 0.4
33e	No	No	8	20	0–2	876 $\pm$ 377	157.8	0.000	0.000	0.002	>50	6.8 $\pm$ 1.1

Note: The dispersal scenarios b (= “10x”) refer to about a 10 times higher annual dispersal rate than that used in the basic model (see Methods), and scenarios 24f–g (= “500 yrs”) refer to simulations over 500 years. For further details see Table 29.1.

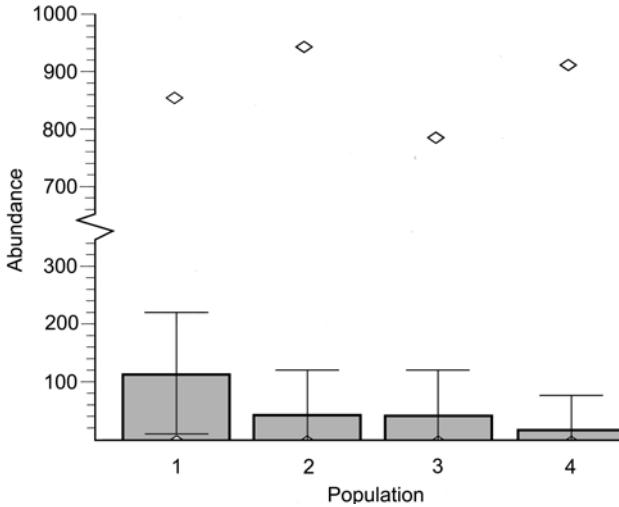


Figure 29.3 Simulated metapopulation structure of female sand lizards 50 years after the start of introduction of 40 juveniles for three successive years into one patch (patch 1) in a connected, empty four-patch network. The histogram shows the average  $\pm 1$  SD and the minimum and maximum number of individuals in each population. The annual dispersal rate was 3% per patch for 0-, 1-, and 2-year-olds, respectively. See “Methods” for details of dispersal parameterization.

ment is now undertaken on Brattforsheden, with felling of up to 10-ha large pine stands, and within these excavation of, on average, one sand patch  $\geq 100$  m<sup>2</sup> per ha for egg laying by the sand lizard. At the moment, ca. 20 new habitat patches (divided into six networks) are planned to be restored within the coming years. The lesson from this modeling exercise is that if a limited number of juveniles per year are available for introduction into these patches, it seems wise to introduce them into one patch in a restored network at a time. If fairly large numbers of juveniles are available, it may be a good strategy to divide them into several patches belonging to different, moderately correlated metapopulation networks in order to reduce the extinction risk for the entire regional metapopulation. When self-sustaining, viable local populations have been established, it may also be a plausible strategy to translocate eggs and juveniles from these populations to other restored, empty patches.

*Acknowledgments* Thanks to Reşit Akçakaya and Per Sjögren-Gulve for inviting me to contribute to this volume. Barry W. Brook and one anonymous reviewer gave much appreciated comments on the manuscript. Thanks also to Jan Bengtsson and Lars Furuholm for assistance in the practical and administrative sand lizard conservation work, and to the timber company Stora Enso for good cooperation with the habitat restoration measures undertaken so far. Financial support for the demographic studies was obtained from the Swedish World Wildlife Fund (WWF), Swedish Biodiversity Centre (CBM), County Administrative Board of Värmland, Swedish Environmental Protection Agency, Carl Tryggers foundation, and Oskar och Lili Lamms foundation.

## References

- Akçakaya, H. R. 1998. *RAMAS GIS: linking landscape data with population viability analysis (version 3.0)*. Applied Biomathematics, Setauket, N.Y.
- Akçakaya, H. R. 2000. Population viability analysis with demographically and spatially structured models. *Ecological Bulletins* 48: 23–38.
- Akçakaya, H. R. 2002. *RAMAS Metapop: viability analyses for stage-structured metapopulations (version 4.0)*. Applied Biomathematics, Setauket, N.Y.
- Berglund, S.-Å. 1988. The sand lizard, *Lacerta agilis* L., on Brattforsheden, south central Sweden: habitat, threats and conservation. *Fauna och flora* (Stockholm) 83: 241–255 (in Swedish with English summary).
- Berglund, S.-Å. 1999. Conservation of relict sand lizard (*Lacerta agilis* L.) populations on inland dune areas in central Sweden. Ph.Lic. thesis, Uppsala University.
- Berglund, S.-Å. 2000. Demography and management of relict sand lizard *Lacerta agilis* populations on the edge of extinction. *Ecological Bulletins* 48: 123–142.
- Brook, B. W. 2000. Pessimistic and optimistic bias in population viability analysis. *Conservation Biology* 14: 564–566.
- Burgman, M. A., Ferson, S., and Akçakaya, H. R. 1993. *Risk assessment in conservation biology*. Chapman and Hall, London.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. 2nd ed. Sinauer Associates, Sunderland, Mass.
- Clobert, J., Massot, M., Lecomte, J., Sorci, G., de Fraipont, M., and R. Barbault. 1994. Determinants of dispersal behavior: the common lizard as a case study. Pages 183–206 in L. J. Vitt and E. R. Pianka (eds.), *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, N.J.
- Corbett, K. F. 1988. Conservation strategy for the sand lizard (*Lacerta agilis agilis*) in Britain. *Mertensiella* 1: 101–109.
- Corbett, K. F., and Tamarind, D. L. 1979. Conservation of the sand lizard, *Lacerta agilis*, by habitat management. *British Journal of Herpetology* 5: 799–823.
- Dent, S., and Spellerberg, I. F. 1988. Use of forest ride verges in southern England for the conservation of the sand lizard *Lacerta agilis* L. *Biological Conservation* 45: 267–277.
- Gärdenfors, U. (Ed.). 2000. *The 2000 Red List of Swedish species*. Threatened Species Unit, Swedish University of Agricultural Sciences, Uppsala.
- Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J. P., Maruin, H., Oliveira, M. E., Sofianidou, T. S., Veith, M., and Zuiderwijk, A. (Eds.). 1997. *Atlas of amphibians and reptiles in Europe*. Societas Europaea Herpetologica and Muséum National d'Histoire Naturelle, Paris.
- Gilpin, M. 1996. Metapopulations and wildlife conservation: approaches to modeling spatial structure. Pages 11–27 in D. R. McCullough (ed.), *Metapopulations and wildlife conservation*. Island Press, Washington, D.C.
- Gislén, T., and Kauri, H. 1959. Zoogeography of the Swedish amphibians and reptiles. *Acta Vertebratica* 1(3): 193–397 (Special issue).
- Glandt, D., and Bishoff, W. (Eds.). 1988. Biologie und Schutz der Zauneidechse (*Lacerta agilis*). *Mertensiella* 1: 1–257.
- Gullberg, A., Olsson, M., and Tegelström, H. 1998. Colonization, genetic diversity, and evolution in the Swedish sand lizard, *Lacerta agilis* (Reptilia, Squamata). *Biological Journal of the Linnaean Society* 65: 257–277.
- Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. Pages 69–91 in I. A. Hanski and M. E. Gilpin (eds.), *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego.
- Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb (eds.), *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, Oxford.
- Huxel, G. R., and Hastings, A. 1999. Habitat loss, fragmentation, and restoration. *Restoration Ecology* 7: 309–315.
- Komers, P. E., and Curman, G. P. 2000. The effect of demographic characteristics on the success of ungulate re-introductions. *Biological Conservation* 93: 187–193.

- Lena, J., Clobert, J., de Fraipont, M., Lecomte, J., and Guyot, G. 1998. The relative influence of density and kinship on dispersal in the common lizard. *Behavioral Ecology* 9: 500–507.
- Massot, M., Clobert, J., Pilorge, T., Lecomte, J., and Barbault, R. 1992. Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* 73: 1742–1756.
- McCarthy, M. A., and Thompson, C. 2001. Expected minimum population size as a measure of threat. *Animal Conservation* 4: 351–355.
- Moulton, N., and Corbett, K. 1999. *The sand lizard conservation handbook*. English Nature, Peterborough, U.K.
- Nature Conservancy Council. 1983. *The ecology and conservation of amphibian and reptile species endangered in Britain*. Nature Conservancy Council, London.
- Olsson, M., Gullberg, A., and Tegelström, H. 1996. Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). *Journal of Evolutionary Biology* 9: 229–242.
- Olsson, M., Gullberg, A., and Tegelström, H. 1997. Determinants of breeding dispersal in the sand lizard, *Lacerta agilis* (Reptilia, Squamata). *Biological Journal of the Linnean Society* 60: 243–256.
- Rodenhouse, N. L., Sherry, T. W., and Holmes, R. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78: 2025–2042.
- Rodenhouse, N. L., Sherry, T. W., and Holmes, R. T. 2000. Site-dependent regulation of population size: a reply. *Ecology* 81: 1168–1171.
- Ronce, O., Clobert, J., and Massot, M. 1998. Natal dispersal and senescence. *Proceedings of the National Academy of Sciences USA* 95: 600–605.
- Snyder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone, W. D., and Miller, B. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10: 338–348.
- Stacey, P. B., Johnson, V. A., and Taper, M. L. 1997. Migration within metapopulations: the impact upon local population dynamics. Pages 267–291 in I. A. Hanski and M. E. Gilpin (eds.), *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego.
- Strijbosch, H., and Creemers, R. C. M. 1988. Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. *Oecologia* 76: 20–26.
- Strijbosch, H., and van Gelder, J. J. 1997. Population structure of lizards in fragmented landscapes and causes of their decline. Pages 347–351 in W. Böhme, W. Bishoff, and T. Ziegler (eds.), *Herpetologia bonnensis*. Societas Europaea Herpetologica, Bonn.
- Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology* 8: 373–378.
- Thomas, C. D. 1996. Essential ingredients of real metapopulations, exemplified by the butterfly *Plebejus argus*. Pages 292–307 in M. E. Hochberg, J. Clobert, and R. Barbault (eds.), *Aspects of the genesis and maintenance of biological diversity*. Oxford University Press, Oxford.
- Tinkle, D. W., Dunham, A. E., and Congdon, J. D. 1993. Life history and demographic variation in the lizard *Sceloporus graciosus*: a long-term study. *Ecology* 74: 2413–2429.
- Yablokov, A. V., Baranov, A. S., and Rozanov, A. S. 1980. Population structure, geographic variation, and microphylogenesis of the sand lizard (*Lacerta agilis*). Pages 91–127 in M. K. Hecht, W. C. Steere, and B. Wallace (eds.), *Evolutionary biology*, vol. 12. Plenum Press, New York.