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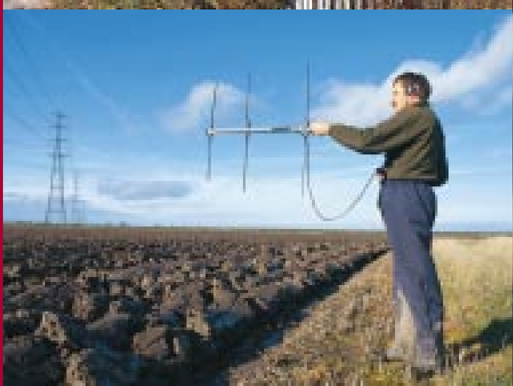
English Nature Research Reports



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A population viability analysis for the reintroduction of the pool frog (*Rana lessonae*) in Britain

Clair Williams and Richard A. Griffiths

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Contents

1 Introduction

Contrary to traditional views, recent findings by amphibian workers have suggested that the pool frog *Rana lessonae* is native to Britain. However, the last remaining native population has probably recently gone extinct (Snell 1994; Gleed-Owen & Joslin 1996; Beebee & Griffiths 2000). Consequently, the pool frog is the subject of a Species Action Plan species in the UK, and work is required to investigate potential strategies for reintroduction. Population Viability Analysis (or 'PVA') is a modelling process used to assess the risk of extinction of a population (eg Soulé 1987; Boyce 1992; Sjögren-Gulve & Ebenhard 2001), but has been little used on amphibians. When reintroduction is an option, PVA can therefore be used to inform and guide reintroduction protocols, particularly with regard to the numbers of individuals and numbers of populations required to found a viable metapopulation.

With a financial contribution from English Nature, this report describes a Population Viability Analysis (PVA) using data from Swedish pool frog populations. The aim of the work was to assess the viability of different reintroduction strategies and provide recommendations on a reintroduction protocol.

2 Methods

2.1 Construction of models using RAMAS Metapop

The computer program "RAMAS Metapop" (Akcakaya 1998) was used to perform a population viability analysis (PVA) for single and multiple populations of the pool frog, *Rana lessonae*. RAMAS was used to construct stochastic models of age-structured pool frog populations. Models were replicated 1000 times, and calculated the average risk of extinction over 50 years. RAMAS enabled the incorporation of the effects of environmental and demographic stochasticity, dispersal, catastrophes and population management. The program was run in Windows 95.

RAMAS has formerly been used to build an age-structured model of an existing pool frog metapopulation in Sweden (Akcakaya 1998), using data obtained by Sjögren (1991a,b). Our models were constructed using this model as a basis. The age-structured model uses postmetamorphic stages only. Consequently, estimates of 'fecundity' are based on the numbers of new individuals recruited to the first age class (ie metamorphs) rather than on numbers of eggs laid. In the recommendations section we provide a method for converting numbers of recruits to numbers of eggs or larvae, which may be more tractable for reintroduction purposes.

Specifically, rates of recruitment and survival; population age-structure; fluctuations in survival and recruitment with environmental and demographic stochasticity, and the effects of distance on dispersal and environmental correlation were all obtained from Sjögren's model (Akcakaya 1998). Density dependence was incorporated using a ceiling model. Models were based solely on females, as Sjögren (1988, 1991a,b) observed lower survival in females and found that population extinction was preceded by only males being present. As the purpose of this work was to investigate reintroduction strategies, the number of individuals in each population (N), the carrying capacity of each pond (K), the number of ponds and inter-pond distances were based on hypothetical values (Table 2.1). As true carrying capacities for pool frogs are largely unknown, K was used in a broader sense within the models in that it was used as a measure of pond quality and/or pond size. Introductions were modelled using the Population Management option in RAMAS. As we did not have sufficient data to incorporate pre-juvenile life stages, all introductions were made up of 1-year-old individuals. These results can be extrapolated to give the number of eggs or metamorphs (see Section 4: recommendations). The effects of recruitment failure (eg due to drought) were modelled using the Catastrophe option in RAMAS. When they occurred, catastrophes resulted in the complete failure of recruitment of 1-year-old individuals.

2.2 Summary of models

To assess the viability of different re-introduction strategies, a series of models were constructed to determine the effects of variation in the following parameters on metapopulation extinction risk: number of ponds, number of individuals present/introduced (N), the distance between ponds (= dispersal rate), the spread of introduced individuals among ponds, the number of yearly introductions made, pond carrying capacity and the frequency of recruitment failure (Table 2.1).

Table 2.1 Summary of the PVA models created using RAMAS Metapop to assess the viability of different strategies for re-introduction of the pool frog, *Rana lessonae*

Model summary
Models of Established Populations: ***For all models:*** • *To enable comparison, the same values for the number of individuals (N) and the pond carrying capacity (K) were used for each set of models. 4 pairs of values were used:* *N=12, K=24* *N=40, K=80* *N=100, K=200* *N=200, K=400.* • *K=2N for all models.* • *Model sets 2 and 3 were repeated with zero, low (inter-pond distance=500 m) and high (inter-pond distance = 50 m) dispersal among ponds. Only 1 and 2 year old individuals dispersed among ponds.* Sets of models were constructed to assess the viability of the following: 1. Extinction risk of single populations of N=12, N=40, N=100 and N=200. 2. Extinction risk of a 4 pond metapopulation with 1xN=12, 1xN=40, 1xN=100 and 1xN=200. 3. Extinction risk of an 8 pond metapopulation with 2xN=12, 2xN=40, 2xN=100 and 2xN=200.

Table 2.1 Continued.

Introduction Models (I)

For all models:

- *To enable comparison, the same values for the number of individuals (N) and the pond carrying capacity (K) were used for each set of models. 4 pairs of values were used:*

  N=12, K=24
  N=40, K=80
  N=100, K=200
  N=200, K=400.

- *K=2N for all models.*
- *N was kept constant for all years of introduction* *<u>except</u>* *in model sets 8 and 9.*
- *Introductions were made for 1, 2, 3 or 4 years in succession.*
- *Only 1 year old individuals were introduced.*
- *Model sets 4-9 were repeated with zero, low (inter-pond distance=500 m) and high (inter-pond distance = 50 m) dispersal among ponds. Only 1 and 2 year old individuals dispersed among ponds.*

Sets of models were constructed to assess the viability of the following introduction strategies:

4. Introduction of N=12, N=40, N=100 or N=200 to 1 pond in a 4 pond metapopulation.
5. Introduction of N=12, N=40, N=100 or N=200 to 1 pond in an 8 pond metapopulation.
6. Introduction of N=12, N=40, N=100 or N=200, with N divided equally among 4 ponds.
7. Introduction of N=12, N=40, N=100 or N=200, with N divided equally among 8 ponds.
8. Introduction into a 4 pond metapopulation with N increasing from N=12 to N=200 over 4 years.
9. Introduction into an 8 pond metapopulation with N increasing from N=12 to N=200 over 4 years.

Introduction Models (II)

Following the previous analyses, the model with the lowest extinction risk was used as a basis for the construction of more sets of models to investigate the following:

10. Determination of the values of N and K required to achieve an extinction risk of 5% in an 8 pond metapopulation, for inter-pond distances ranging from 100-500 m.
11. Determination of the values of N and K required to achieve an extinction risk of 5% in an 8-pond metapopulation when there is periodic failure of recruitment. This was modelled in 2 ways:

(a) Regional model - Zero recruitment occurred in all ponds during the same year, with a probability of either in 5 or 1 in 10 years.

(b) Local model - Zero recruitment occurred during different years in different ponds. Ponds experienced zero recruitment with a probability of either 1 in 5, 1 in 10 or 1 in 20 years.

(a) A comparison of the values of N and K required to obtain an extinction risk of 5% for metapopulations of 4, 8 and 16 ponds.

For the above models:

- *Values of N and K differed among models but were kept constant among years.*
- *Introductions were made for 4 years in succession.*
- *Only 1 year old individuals were introduced.*
- *N was divided equally among all ponds.*
- *Ponds were 500 m apart unless stated otherwise.*
- *Dispersal was incorporated into all models in sets 10-12. Only 1 and 2 year old individuals dispersed among ponds.*

3 Results

3.1 Models of established populations

In established populations with N ranging from 12 to 200 individuals, an 8 pond metapopulation was found to have a lower extinction risk than both single populations and a 4-pond metapopulation (Tables 3.1-3.3).

Table 3.1. Extinction risk of single populations ranging in size from N=12 to N=200

N	Dispersal Rate	Extinction Risk	95% Confidence Interval
12	None	0.996	0.968-1.000
40	None	0.811	0.783-0.839
100	None	0.438	0.410-0.466
200	None	0.203	0.175-0.231

Table 3.2. Extinction risk of a 4 pond metapopulation with and without dispersal. Ponds were separated by 50 m (High dispersal) and 500 m (Low dispersal). Population sizes were as follows: 1xN=12, 1xN=40, 1xN=100 and 1xN=200.

Inter-pond distance	Dispersal Rate	Extinction Risk	95%Confidence Interval
50m	None	0.142	0.114-0.170
500m	None	0.093	0.065-0.121
50m	High	0.26	0.232-0.288
500m	Low	0.112	0.084-0.140

Table 3.3 Extinction risk of an 8 pond metapopulation with and without dispersal. Ponds were separated by 50 m (High dispersal) and 500 m (Low dispersal). Population sizes (N) were as follows: 2xN=12, 2xN=40, 2xN=100 and 2xN=200.

Inter-pond distance	Dispersal Rate	Extinction Risk	95% Confidence Interval
50m	None	0.063	0.035-0.091
500m	None	0.024	0.000-0.052
50m	High	0.157	0.129-0.185
500m	Low	0.016	0.000-0.044

3.2 Introduction models (I)

3.2.1 Extinction risks following a single introduction

The extinction risk for all metapopulations decreased in line with increasing values of N (Figure 3.1). Following a single year of introduction of N=12 and N=40, extinction risks were similarly high for both 4 and 8 pond metapopulations (Figure 3.1, Table 3.4). However, when N was increased to N=100 and N=200, extinction risks were lower in the 8-pond metapopulation (Figure 3.1, Table 3.4).

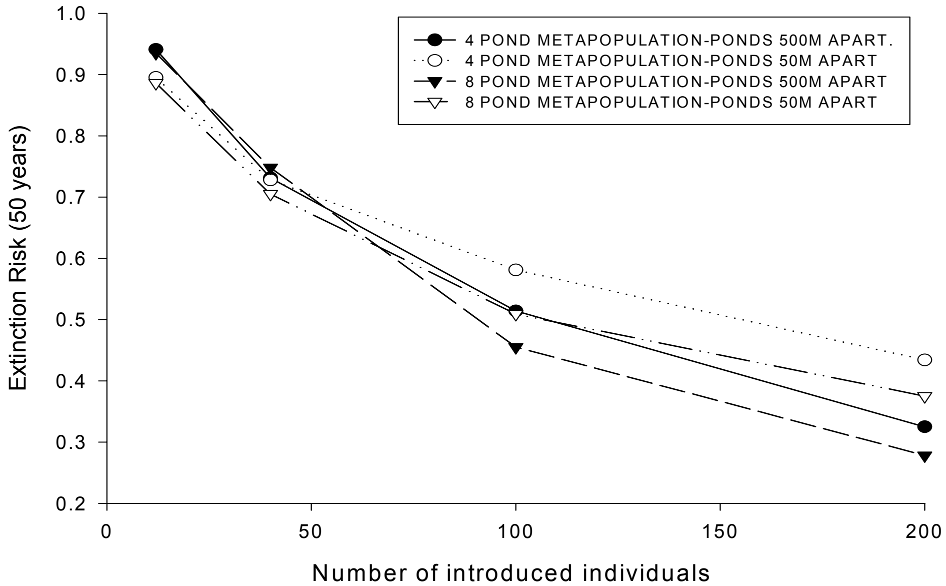


Figure 3.1 Extinction risk of 4 and 8 pond metapopulations following single introductions of 12-200 individuals to 1 pond

3.2.2 The relationship between inter-pond distance and extinction risk

For both 4 and 8 pond metapopulations, extinction rates were lower when ponds were separated by 500 m rather than 50 m, ie when dispersal was low (Figure 3.1, Table 3.4). Dispersal was modelled using the distance function calculated by Sjögren (Akcakaya 1998). This led to very high rates of dispersal when ponds were separated by only 50 m, with 12-17% of one and two-year-old individuals dispersing between ponds each year (ie a metapopulation behaves as one single population as a result of high levels of dispersal). When the distance between ponds was increased to 500 m, the proportion of individuals dispersing was reduced to 1-4%. Similarly, in Sjögren's model, the rate of dispersal ranged from 0.1-12.7% (Akcakaya 1998).

3.2.3 The spread of introduced individuals among ponds

Extinction risks for both 4 and 8 pond metapopulations were generally lower when the introduced individuals were divided equally among all the ponds, rather than being introduced to just one of the ponds in a metapopulation (Figure 3.2, Table 3.4). This relationship was more pronounced when the number of introduced individuals was low.

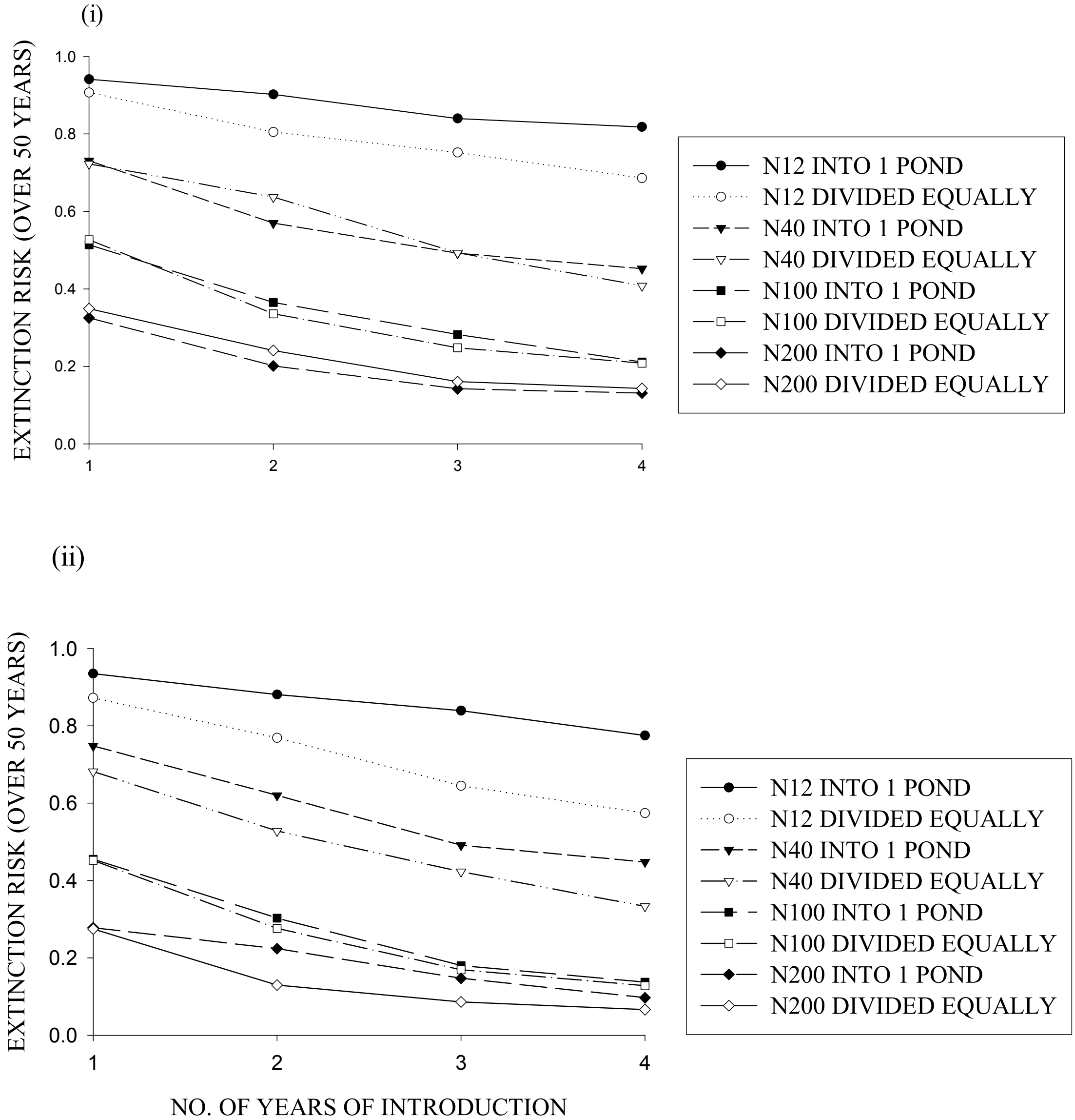


Figure 3.2 Extinction risks of (i) a 4 pond metapopulation and (ii) an 8 pond metapopulation following 1-4 years of introduction, with either all individuals having been introduced to 1 pond or individuals having been divided equally among all ponds. N ranged from 12-200 and the inter-pond distance was 500 m.

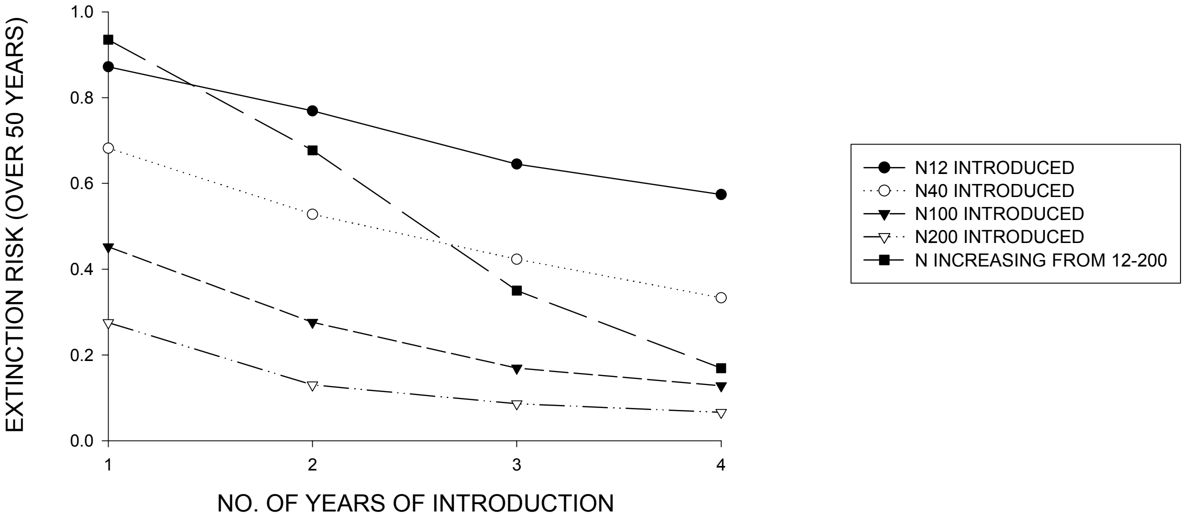
3.2.4 Multiple introductions models

For all values of N (No. introduced), the extinction risk of both 4 and 8 pond metapopulations decreased in line with increased number of annual introductions (Figure 3.3, Table 3.4). The lowest extinction risk was achieved by the introduction of 200 individuals per year for 4 years into an 8-pond metapopulation (Figure 3.3).

3.2.5 Multiple introductions where N increases from year to year

If introductions are to be facilitated by a captive breeding program, it is likely that the number of individuals available for introduction will increase over time as the program becomes more established. When the number of introduced individuals was modelled as increasing over 4 years from N=12 to N=200, the extinction risk was similar to that resulting from the introduction of 100 individuals every year for 4 years (Figure 3.3, Table 3.5).

(i)



(ii)

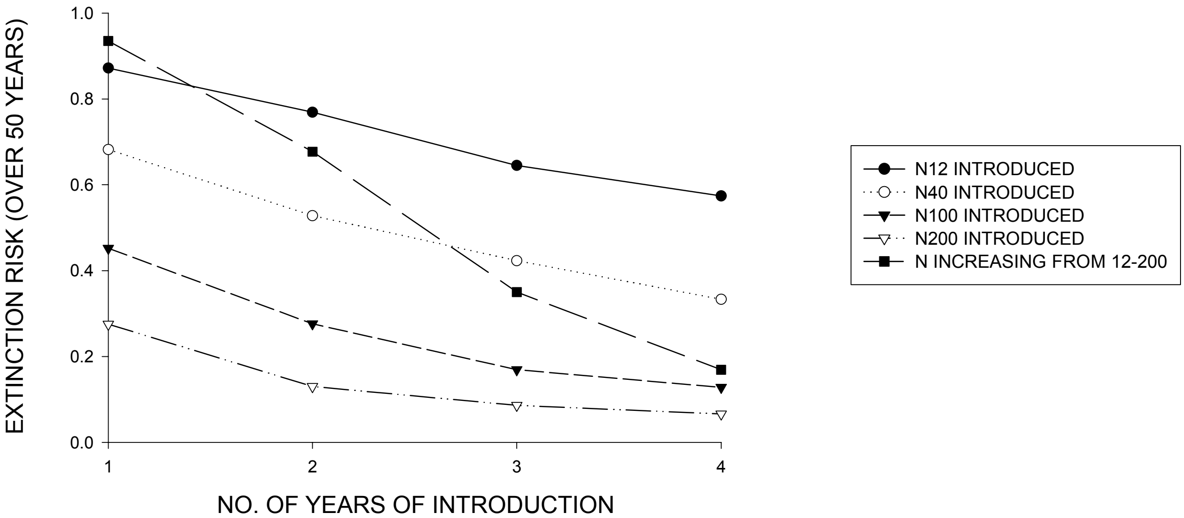


Figure 3.3 Extinction risk following repeated introductions of individuals over 1-4 years into (i) a 4 pond and (ii) an 8 pond metapopulation. The number of introduced individuals was either kept constant with individuals being divided equally among all ponds, or N increased from year to year with individuals introduced to a different pond each year. N introduced ranged from 12-200 and the inter-pond distance was 500 m.

Table 3.4 Summary of the results from the single and multiple introductions models. '1 Pond' models involved all individuals being introduced to just one of the ponds in either a 4 or 8 pond metapopulation. 'All ponds' models involved the introduced individuals being divided equally among the 4 or 8 ponds. * No. of annual introductions. ** Extinction Risk when there was No Dispersal with ponds 50 m/500 m apart, Low dispersal (ponds 500 m apart) and High Dispersal (ponds 50 m apart).[1]N=16 for 8 pond models. [2]N=104 for 8 pond models. [3]Model with lowest extinction risk.

			4 Ponds			8 Ponds		
			Extinction Risk			Extinction Risk		
Model Type	Total N introduced	*No. of Intro	**Dispersal Rate None	Low	High	**Dispersal Rate None	Low	High
1 Pond	12	1	0.996 / 0.999	0.941	0.895	0.996/ 0.999	0.935	0.886
		2	0.999 / 0.999	0.902	0.816	0.999/ 0.999	0.881	0.79
		3	0.992 / 0.992	0.840	0.752	0.992/ 0.992	0.839	0.726
		4	0.984 / 0.984	0.818	0.702	0.984 / 0.984	0.775	0.668
1 Pond	40	1	0.869 / 0.843	0.731	0.728	0.869 /0.843	0.748	0.705
		2	0.782 / 0.782	0.570	0.620	0.782 /0.782	0.620	0.558
		3	0.750 / 0.750	0.492	0.534	0.750 /0.750	0.491	0.486
		4	0.704 / 0.704	0.452	0.453	0.704 /0.704	0.448	0.392
1 Pond	100	1	0.549 / 0.552	0.514	0.581	0.549 /0.552	0.455	0.509
		2	0.447 / 0.447	0.365	0.44	0.447 /0.447	0.303	0.366
		3	0.425 / 0.425	0.282	0.359	0.425 /0.425	0.180	0.293
		4	0.382 / 0.382	0.211	0.331	0.382 /0.382	0.137	0.239
1 Pond	200	1	0.363 / 0.389	0.325	0.434	0.363 / 0.389	0.278	0.375
		2	0.265 / 0.265	0.201	0.357	0.265 /0.265	0.224	0.266
		3	0.203 / 0.203	0.142	0.289	0.203 /0.203	0.147	0.182
		4	0.196 / 0.196	0.131	0.275	0.196 /0.196	0.097	0.141
All Ponds	[1]12	1	0.917 / 0.925	0.907	0.909	0.923 /0.911	0.872	0.856
		2	0.843 / 0.856	0.805	0.821	0.834/0.840	0.769	0.742
		3	0.812 / 0.787	0.752	0.773	0.768/0.743	0.645	0.647
		4	0.764 / 0.746	0.686	0.710	0.702/0.71	0.574	0.546
All Ponds	40	1	0.804 / 0.775	0.723	0.745	0.814 /0.782	0.682	0.693
		2	0.67 / 0.662	0.637	0.578	0.658/0.644	0.528	0.531
		3	0.58 / 0.536	0.493	0.530	0.565/0.529	0.423	0.431
		4	0.514 / 0.460	0.408	0.465	0.475/0.476	0.333	0.331
All Ponds	[2]100	1	0.627 / 0.616	0.527	0.589	0.609/ 0.562	0.452	0.483
		2	0.444 / 0.431	0.336	0.467	0.460/0.372	0.276	0.298
		3	0.355 / 0.312	0.248	0.390	0.307/0.287	0.169	0.242
		4	0.285 / 0.243	0.208	0.360	0.274/0.205	0.128	0.182
All Ponds	200	1	0.434 / 0.414	0.349	0.451	0.427 /0.371	0.275	0.326
		2	0.271 / 0.264	0.241	0.316	0.266/0.224	0.130	0.201
		3	0.234 / 0.208	0.161	0.276	0.182/0.147	0.086	0.166
		4	0.194 / 0.146	0.143	0.278	0.122/0.128	[3]**0.066**	0.125

Table 3.5 Extinction risk of 4 and 8 pond metapopulations following a series of introductions whereby the number of individuals introduced per year increased from N=12 to N=200. Introductions were made into different ponds each year. * No. of annual introductions. **N = No. of individuals introduced per time step, eg 12 + 40 = 12 in year 1 and 40 in year 2. *** Extinction Risk when there was 'no dispersal' with ponds 50 m/500 m apart, 'low dispersal' (ponds 500 m apart) and 'high dispersal' (ponds 50 m apart).

*No. of Intros	** Total N introduced	4 PONDS			8 PONDS		
		***Dispersal			**Dispersal		
		None	Low	High	None	Low	High
1	12	0.996/ 0.999	0.941	0.895	0.996 / 0.999	0.935	0.886
2	12+40	0.868/ 0.850	0.674	0.695	0.851 / 0.845	0.677	0.650
3	12+40+100	0.507 / 0.492	0.410	0.492	0.486 / 0.501	0.350	0.406
4	12+40+100+200	0.214 / 0.187	0.214	0.345	0.248 / 0.225	0.169	0.238

3.3 Summary of the best introduction strategy

In the previous models, the lowest extinction risk (6.6%) was achieved by introducing 200 individuals to 8 ponds for 4 consecutive years. Ponds were separated by 500 m and individuals were divided equally among the ponds, equivalent to introducing N=25 per pond per year.

3.4 Introduction models (II)

3.4.1 Determination of the values of N and K required to achieve an extinction risk of 5% in an 8-pond metapopulation when inter-pond distances range from 100-500m

Using the model described in Section 3.3 as a basis, we investigated how to reduce the extinction risk to an acceptable level (ie 5%) for a range of inter-pond distances. The results in Table 3.6 show the extinction risk following introduction of 200 individuals to an 8-pond metapopulation, for inter-pond distances ranging from 100-500 m. Increasing the number of individuals (N) introduced resulted in reduced extinction risks (Table 3.7). The number of individuals required per pond (per year) ranged from 30-150, with N decreasing with increased inter-pond distance. When ponds were modelled as being separated by 100 m, it was not possible to reduce the extinction risk below 0.0860 due to the carrying capacity of the ponds limiting population growth; at this point, further increases in N yielded no further reduction in extinction risk.

When the carrying capacity of each pond was increased, so that half of the ponds had K=200 and the other half K=400, the introduction of just 25 individuals per year reduced the extinction risk to 5% or less for all inter-pond distances (Table 3.8).

Table 3.6 Extinction risks for 8 pond metapopulations with inter-pond distances of 100-500m. In all models, 200 introduced individuals were divided equally among 8 ponds, and introductions were repeated for 4 consecutive years. *The carrying capacity (K) of the 8 ponds was as follows: 2 ponds K=24, 2 ponds K=80, 2 ponds K=200 and 2 ponds K=400.

Inter-Pond Distance (m)	Total N introduced / year	N per pond	*K	Extinction Risk	95% Confidence Interval
100	200	25	24-200	0.132	0.104-0.160
200	200	25	24-200	0.115	0.087-0.143
300	200	25	24-200	0.089	0.061-0.117
400	200	25	24-200	0.063	0.035-0.091
500	200	25	24-200	0.066	0.038-0.094

Table 3.7 Number of individuals required to reduce the extinction risk to 5% for 8 pond metapopulations with inter-pond distances of 100-500 m. In all models, the introduced individuals were divided equally among 8 ponds, and introductions were repeated for 4 consecutive years. *The carrying capacity (K) of the 8 ponds was as follows: 2 ponds K=24, 2 ponds K=80, 2 ponds K=200 and 2 ponds K=400.

Inter-Pond Distance (m)	Total N introduced / year	N per pond	*K	Extinction Risk	95% Confidence Interval
100	1200	150	24-200	0.086	0.077-0.133
200	800	100	24-200	0.057	0.029-0.085
300	360	45	24-200	0.054	0.026-0.082
400	320	40	24-200	0.052	0.024-0.080
500	240	30	24-200	0.052	0.024-0.080

Table 3.8 Extinction risk of 8 pond metapopulations with inter-pond distances of 100-500 m, following the increase of the carrying capacity (K) of all ponds. *The carrying capacity (K) of the 8 ponds was as follows: 4 ponds K=200 and 4 ponds K=400. In all models, 200 individuals were divided equally among 8 ponds, and introductions were repeated for 4 consecutive years.

Inter-Pond Distance (m)	Total N introduced / year	N per pond	*K	Extinction Risk	95% Confidence Interval
100	200	25	200-400	0.049	0.021-0.077
200	200	25	200-400	0.040	0.012-0.068
300	200	25	200-400	0.052	0.024-0.080
400	200	25	200-400	0.016	0.000-0.044
500	200	25	200-400	0.013	0.000-0.410

When attempting to reduce the extinction risk of an 8 pond metapopulation to 5%, modelling ponds as separated by 500 m was still the most efficient in terms of achieving the lowest extinction risk while minimising the number of individuals required per introduction (Tables 3.7 and 3.8).

3.4.2 Determination of the values of N and K required to achieve an extinction risk of 5% in an 8-pond metapopulation when there is periodic failure of recruitment

As the 500 m model still achieved the lowest extinction risk (see Section 3.5), the effects of recruitment failure were modelled using the original best strategy model described in Section 3.3, ie 200 individuals were divided equally among 8 ponds for 4 consecutive years, with ponds 500 m apart. Complete failure of recruitment at the same time in all ponds (ie the Regional model) led to the extinction risk being increased to between 24-48% (Table 3.9). When the timing of recruitment failure differed among ponds then the impact on extinction risk was reduced but, even with the introduction of 200 individuals per year for 4 years, the risk of extinction was still 11-41% (Table 3.9).

Table 3.9 Extinction risk of an 8-pond metapopulation following periodic failure of recruitment. Recruitment failure either affected all ponds simultaneously ('regional' models) or occurred in different ponds in different years ('local' models). The periodicity of recruitment failure ranged from 1 in 5 to 1 in 20 years.

Model	Total N	N per pond	Extinction Risk if no catastrophe	Extinction Risk with catastrophe
Regional – 1 in 5 years	200	25	0.066	0.480
Regional – 1 in 10 years	200	25	0.066	0.236
Local – 1 in 5 years	200	25	0.066	0.411
Local – 1 in 10 years	200	25	0.066	0.192
Local – 1 in 20 years	200	25	0.066	0.105

For the two catastrophe models that were considered most likely to occur, the number of individuals introduced (N) was increased in an attempt to reduce the extinction risk to 5% (Table 3.10). When recruitment failure occurred once every 20 years at different times in different ponds ('local' model), the extinction risk was reduced to <5% by increasing the number of introduced individuals from 25 to 100 per pond per year. However, for the 'regional' model where zero recruitment occurred simultaneously in all ponds once every 10 years, there was no further reduction in extinction risk when N was increased above 150 due to the carrying capacity of the ponds preventing populations from reaching a size that could withstand periodic failures of recruitment. When the models were repeated using increased values for pond carrying capacity (K increased so that 50% of ponds had K=200 and 50% had K=400), the extinction risk was reduced to 5% for both regional (when N=100+) and local models (when N=25+) (Table 3.10).

Table 3.10 The effects of increasing the values of N and K on the extinction risk of an 8-pond metapopulation following periodic failure of recruitment. Recruitment failure either affected all ponds simultaneously 1 in 10 years ('regional' models) or occurred 1 in 20 years in different ponds in different years ('local' model).

Catastrophe Model	Total N	N per pond	K*	Extinction Risk if no catastrophe	Extinction Risk with catastrophe
Increasing N:					
Regional – 1 in 10 years	200	25	24-400	0.066	0.236
	800	100	24-400	0.066	0.1010
	1200	150	24-400	0.066	0.0930
Local – 1 in 20 years	200	25	24-400	0.066	0.105
	800	100	24-400	0.066	0.0470
Increasing N + K:					
Regional – 1 in 10 years	200	25	200-400	0.066	0.0870
	800	100	200-400	0.066	0.0320
	1200	150	200-400	0.066	0.0170
Local – 1 in 20 years	200	25	200-400	0.066	0.038
	800	100	200-400	0.066	0.005

3.4.3 Comparison of the values of N and K required to obtain an extinction risk of 5% for metapopulations of 4, 8 and 16 ponds

After repeating the model described in Section 3.3 for metapopulations of 4, 8 and 16 ponds (where N=200 and K ranges from 24-200), the extinction risk was lowest for the 16 pond metapopulation (Table 3.11). For all metapopulations, the number of occupied ponds remained fairly constant after 10 years (Table 3.11). In the 4-pond metapopulation, the mean size of the metapopulation decreased gradually throughout the 50-year simulation. In the 8-pond metapopulation the number of individuals remained relatively constant, while the 16 pond metapopulation continued to increase in size throughout the 50-year simulation (Table 3.11).

Table 3.11 Extinction risk for 4, 8 and 16 pond metapopulations. Ponds were separated by 500 m; 200 individuals were divided equally among all ponds and introductions were repeated for 4 consecutive years. *N =Total no. of individuals introduced per year.

**Carrying capacity of the ponds in each metapopulation was as follows: in 25% of ponds K=24, 25% K=40, 25% K=100 and 25% K=200.

No. of Ponds	*N	*K	Ext. Risk	95% Confidence Interval	Mean No. Ponds			Mean No. Individuals		
					10yrs	25yrs	50yrs	10yrs	25yrs	50yrs
4	200	24-200	0.143	0.115-0.171	4	3	3	284	238	205
8	200	24-200	0.066	0.038-0.094	8	7	7	355	412	389
16	200	24-200	0.029	0.001-0.057	15	15	15	426	632	799

Table 3.12 shows the results following increase of the K values for each metapopulation, so that 50% of ponds had K=200 and 50% had K=400. Increasing the carrying capacity meant that the extinction risk of the 16 pond metapopulation remained the same despite N being reduced to just 6 per pond per year (Tables 3.11 and 3.12). To obtain an extinction risk of <5% in the 4 pond metapopulation, it was necessary to increase the number of individuals introduced from 25 to 40 per pond, as well as increasing pond carrying capacity (Table 3.12).

Table 3.12 Extinction risk for 4, 8 and 16 pond metapopulations following increased pond carrying capacity. *Carrying capacity of the ponds in each metapopulation was as follows: 50% had K=200 and 50% had K=400. Ponds were separated by 500 m; individuals were divided equally among all ponds and introductions were repeated for 4 consecutive years. **N =Total no. of individuals introduced per year.

No. of Ponds	**N	N per pond	*K	Extinction Risk	95% Confidence Interval
4	160	40	200-400	0.049	0.021-0.077
8	200	25	200-400	0.013	0.000-0.410
16	96	6	200-400	0.030	0.002-0.058

4 Conclusions and recommendations

4.1 Number of ponds

- A metapopulation of 4, 8 or 16 ponds would be more viable than single populations.
- If frogs are reintroduced into a pond system, the greater the number of ponds, the lower the metapopulation extinction risk.
- The number of ponds required to achieve a given extinction risk can be reduced by increasing the number of individuals that each pond can support. When each pond could support at least 200 individuals, a 4-pond metapopulation had an extinction risk of <5 % following 4 yearly introductions of 160 individuals.

4.2 Number of introduced individuals required (N)

The value of N depends on:

- The number of ponds - N is lower when the number of ponds is greater, ie with 4 ponds, 160 individuals were required per year to achieve an extinction risk of 4.9%; with 16 ponds, an extinction risk of 3% was achieved by introducing just 96 individuals per year.
- The carrying capacity of the ponds - the greater the population size that can be supported by ponds, the lower the initial value of N required. For example, when 75% of ponds could only support <100 individuals, introducing 200 individuals into a 4-pond metapopulation for 4 years gave an extinction risk of 14.3%. When all ponds were modelled as supporting populations of at least 200 individuals, the extinction risk was reduced to 4.9%.

4.3 Inter-pond distance

- For a fixed number of introduced individuals, using the dispersal rates documented by Sjögren (in Akcakaya 1998), extinction risks decreased with increasing inter-pond distance up to 500 m. This is because when ponds are close together and dispersal levels are high, the metapopulation behaves as a single isolated population. If a series of ponds are created for pool frog reintroductions they must therefore be sufficiently distant from each other for their population dynamics to operate independently (eg they must not all desiccate at the same time), but close enough to permit some dispersal.
- When ponds could support populations of at least N=200, a <5% extinction risk was achieved by introducing 200 individuals per year for 4 years into ponds that were 100 m apart. When pond capacity restricted population size to <100 in 75% of ponds, then it was not possible to achieve an extinction risk of <5% for ponds 100 m apart.

4.4 Spread of individuals

- Lower extinction risks were achieved by spreading the introduced individuals equally among ponds rather than placing all individuals in one pond.

4.5 Number of introductions

- The viability of populations increased with the number of annual introductions. In most cases, the extinction risk of 4 and 8 pond metapopulations decreased by at least 5-10% with each additional year of introduction.

4.6 Pond management

- Following 4 annual introductions of 200 individuals to an 8 pond metapopulation, if 75% of ponds could only support populations of N<100, recruitment failure occurring simultaneously every 1 in 5 or 10 years led to the extinction risk being increased by 17% and 42% respectively. Recruitment failure occurring every 1 in 5, 10 or 20 years, at different times in different ponds, led to the extinction risk being increased by 35%, 13% and 5% respectively.
- If all 8 ponds were able to support populations of at least 200 individuals, the effects of periodic failure in recruitment were substantially reduced. If recruitment failure

occurred simultaneously every 1 in 10 years, the extinction risk was increased by just 4%. When recruitment failure occurred 1 in 20 years, at different times in different ponds, the extinction risk was increased by just 2.6%.

4.7 Summary of the best introduction strategies for difference sizes of metapopulation

- For a 4 pond metapopulation, when (1) the inter-pond distance was 500 m; (2) all ponds could support populations of at least N=200; (3) individuals were divided equally among ponds; and (4) introductions were repeated for 4 consecutive years, introducing 160 individuals per year gave an extinction risk of 4.9%.
- For an 8 pond metapopulation, when (1) the inter-pond distance was 500 m; (2) all ponds could support populations of at least N=200; (3) individuals were divided equally among ponds; and (4) introductions were repeated for 4 consecutive years, introducing 200 individuals per year gave an extinction risk of 1.3%.
- For a 16 pond metapopulation, when (1) the inter-pond distance was 500 m; (2) all ponds could support populations of at least N=200; (3) individuals were divided equally among ponds; and (4) introductions were repeated for 4 consecutive years, introducing 96 individuals per year gave an extinction risk of 3%.

4.8 Calculation of the number of males required

According to Sjögren (1991), in populations of the pool frog in Sweden the number of females per male ranges from 1.19-2.09. Therefore the values of N in our models should be multiplied by a value within this range to obtain an estimate of the number of males required.

4.9 Calculation of the number of eggs or metamorphosing tadpoles required

In the models, introductions were made up of 1-year-old individuals. As an example, the calculations below indicate how to calculate the number of metamorphosing tadpoles or eggs needed to provide N=200 1-year old individuals. The estimates of fecundity and egg and adult survival were documented by Sjögren (1988, 1991a,b).

1) Calculation of the number of eggs required to provide N=200 1-year olds:

1 small female produces >500 eggs, 1-2% of which survive to two years of age. The following calculations use the conservative (1%) estimate of egg survival:

- Survival rate from age 1-year to age 2-years = 0.247.
- Therefore, 200 1-year olds produce 49 2-year olds (200 x 0.247=49).
- No. of 2 year olds = 49 = 1% of eggs laid.
- No. of eggs required to produce 49 two year olds (ie 200 one yr. olds) = 100 x 49 = <u>4900 eggs</u>

2) Calculation of the number of metamorphosing tadpoles required to provide N=200 1-year olds:

- From the above calculations, 4900 eggs = N=200 1-year olds
- Survival from egg to metamorphosing tadpole stage is approximately 20%
- No. of tadpoles required to produce N=200 1-year olds = 20% x 4,900 eggs = 980 metamorphosing tadpoles

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Peter Wakely/English Nature 21,792
Bottom left: Radio tracking a hare on Pawlett Hams, Somerset.
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