The Northern Leopard Frog (*Rana pipiens*)

Population Viability and Re-introduction Analysis

Contract No: 45181366

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1 Summary

This report summarizes efforts of a population viability analysis (PVA) for the Northern Leopard Frog (*Rana pipiens*). The underlying population model was developed in collaboration with Cyndi Smith and Kris Kendell. The model was built based on empirical data and expert knowledge and presents current understanding of the population biology and life cycle of the Northern Leopard Frog. The model could not be validated on empirical data, but it is believed that the model reflects important aspects of the particular population dynamics of the Northern Leopard Frog. Apart from standard PVA assessments, a comprehensive sensitivity analysis was performed using GRIP – an automated sensitivity analysis generator for Ramas@Metapop based population models. This is in fact the first study allowed to use GRIP outside from a lab environment and the author is grateful to the authors of GRIP for generously making this program available despite a pending publication.

The results of this PVA revealed insights with potential implications for re-introduction attempts as planned for historic habitat sites in Waterton National Park, Alberta. Interpretation of the results indicates that the Northern Leopard Frog may not be able to persist in single, isolated populations over an extended period of time. The intrinsic risk of local extirpations seems mainly attributed to density dependent regulations at the tadpole stage and to stochastic variations in demographic and environmental factors. The inherent growth potential of Northern Leopard Frog populations, however, seems to allow for quickly occupying and utilizing existing habitat. This demographic fingerprint indicates that the Northern Leopard Frog may be adapted to exist in spatially distributed but connected populations. Such a metapopulation arrangement may be the most efficient response to mitigate risks of local extirpations by means of dispersal and connectivity. More specific, but also sensible outputs from the PVA suggest minimum viable abundances of close to 30 2+ year adult females distributed across two spatially distinct populations. Viable abundance levels decrease with increasing number of connected populations. Re-introduction attempts may be more efficient and likely more successful if re-introduced individuals (tadpoles or YoY frogs) are distributed across multiple, connected populations. Connectivity may be as low as 1 percent average exchange of YoY frogs during one season. Simulation results furthermore indicate that a staged re-introduction effort over 2-3 years may reduce short time population decline and facilitate a more continuous population growth.

Finally, the revealed importance of connectivity to the viability of spatially distributed Northern Leopard Frog populations may support hypotheses related to the simultaneous extinction of this species across wide ranges of its natural habitat in western and central Canada. Connectivity may have supported and facilitated a sudden outbreak of a disease, which could otherwise not have spread across such a large spatial extent.

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Notice

The results provided in this report are subject to an unknown degree of uncertainty. There is substantial uncertainty in the knowledge of demographic data, such as fecundity, survival and dispersal distances. This uncertainty and its propagation over time is partly considered in the demographic and environmental stochasticity of the population model. Due to the stochastic nature of the population model, simulation runs were replicated 1000 times and results are averages out of those replicate simulation runs. Absolute numbers should be interpreted with caution. Instead trends and differences between different simulation runs (scenarios) are generally more trustworthy. All information used in this work have been discussed with members of the recovery team and verified as well as substantiated from the scientific, peer-reviewed literature. The work therefore represents our best possible educated “guess” based on our current knowledge of the biology, life history and habitat requirements for this species.

2 Demography of the Northern Leopard Frog

This chapter summarizes essential information about the life cycle and demographic characteristics of the Northern Leopard Frog, in particular as they contribute to and define the population model used for the population viability analysis presented in this report. The Northern Leopard Frog has a reported live span between 4 and 5 years. Frogs reach sexual maturity at the age of 2 years. Their reproductive potential depends on body mass and size. Observed sex ratios in Northern Leopard Frog populations are close to 1:1. Sexually mature females produce on average 1.5 egg masses per year (i.e. number of egg masses averaged over female adults). Each egg mass may contain between 1000 and 7000 eggs. Eggs turn into tadpoles, which grow into froglets. The tadpole stage is the most fragile during the life cycle of a Northern Leopard Frog with survival chances as low as 1 percent, but generally much higher (up to 34 or even 90 percent) in protected rearing ponds. Tadpoles grow in shallow breeding ponds and compete for resources. In case of insufficient resources, all tadpoles may grow slower with potential negative effects on their future reproductive potential. This type of competition is usually referred to as “scramble competition” with significant effects on the dynamics of affected populations. In addition, occasional micro-catastrophic events, such as breeding pond dry-outs or floods may wipe out an entire generation. The Young of the Year (YoY) frogs may disperse to new breeding ponds or over-wintering habitats, preferably along streams (reported up to 8 km), but also across land (reported up to 2 km). Winter mortality of YoY frogs is high and may reach up to 93 percent. After their first year, adult frogs may have an annual chance of survival of about 60 percent. Population densities are difficult to estimate, but observation records indicate relatively small numbers of adult frogs at or near one breeding site or pond. It is assumed that 30 adult female frogs (and their male counterparts) may occur at an average breeding site in one season.
Most of this information has been reported in the following documents (Adama and Kendell 2004, Alberta 2003, 2005, COSEWIC 2000, Kendell, 2004, Romanchuk and Quinlan 2006), but also discussed with and validated by Cyndi Smith and Kris Kendell.

3 Population Model

We used the demographic fingerprint of the Northern Leopard Frog populations as known today and described in section 2 for building an age-structured, female only population model based on Ramas©MetaPop (Akçakaya and Root 2002).

3.1 Model parameters and assumptions

3.1.1 Time Step

The model operates on a time step of one year. That decision implies that the development from eggs to one year adult frogs must be aggregated into one age class.

3.1.2 Age Classes

The population is partitioned into 5 age classes as follows:

- 1 Year adults (YoY over-winter survivors)
- 2 Year adults (sexually mature adult females)
- 3 Year adults (sexually mature adult females)
- 4 Year adults (sexually mature adult females)
- 5 Year adults (sexually mature adult females)

3.1.3 Vital Rates

3.1.3.1 Fecundity

Fecundity refers to the number of one year adult females per one sexually mature adult female (i.e. 2 to 5 Year adult females). This aggregation is necessary, because the model operates on a one year time step. It is therefore necessary to consider the entire process from egg laying, hatching, metamorphosis, and over-wintering survival of YoY frogs in the calculation of the fecundity value according to the following rationale:

1. egg masses per sexually mature adult female: 1.5
2. number of eggs per egg mass: 1000 – 7000
3. sex ratio: 1:1, we therefore consider only 50% (female) eggs of all laid eggs
4. survival rates of eggs to metamorphosed tadpoles: 1-6%
5. over-winter survival rate of YoY frogs: 8% - 12%

The minimum fecundity for a sexually mature female adult therefore calculates as follows:

1.5 * 1000 * 0.5 * 0.01 * 0.08 = 0.6

The maximum fecundity for a sexually mature female adult is calculated likewise:

1.5 * 7000 * 0.5 * 0.06 * 0.12 = 37.8

The average fecundity would then be 19.2 with a variation of +/- 18.6.

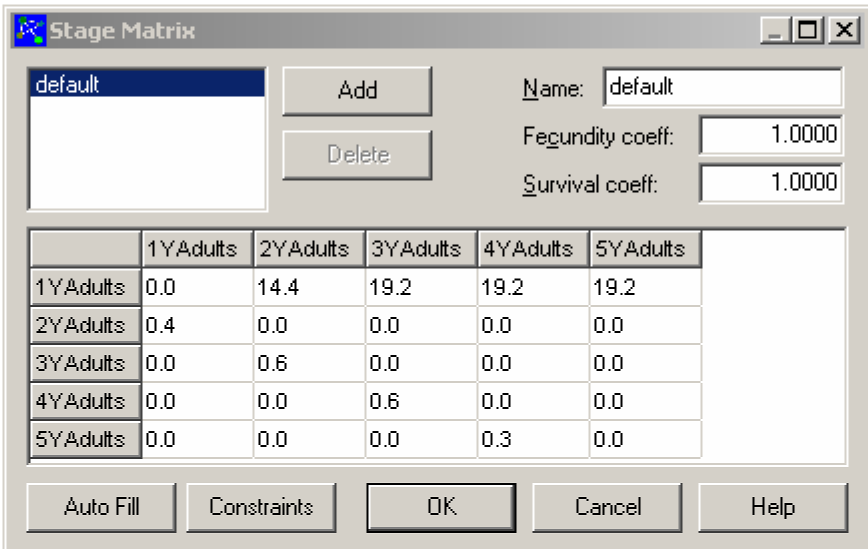
It was furthermore assumed that 2 year old female adults may have a somewhat lower reproductive potential compared to 3-5 year female adults, because of a potentially lower body mass and body size, but also perhaps due to lack of experience. It was therefore decided to reduce average fecundity for 2 year adult females to 75%.

3.1.3.2 Survival

Survival rates for 1 year adults are set to 0.4 +/- 20% standard deviation. Survival rates for 1-3 year adults are set to 0.6 +/- 10% standard deviation. Survival rates of 4 year adults is set to a lower value of 0.3 +/- 30% standard deviation. There is no direct empirical evidence for this decision, but it seems that there are fewer 5 year adults than 4 year adults, which may be caused by a lower survival rate from 4 year to 5 year adults.

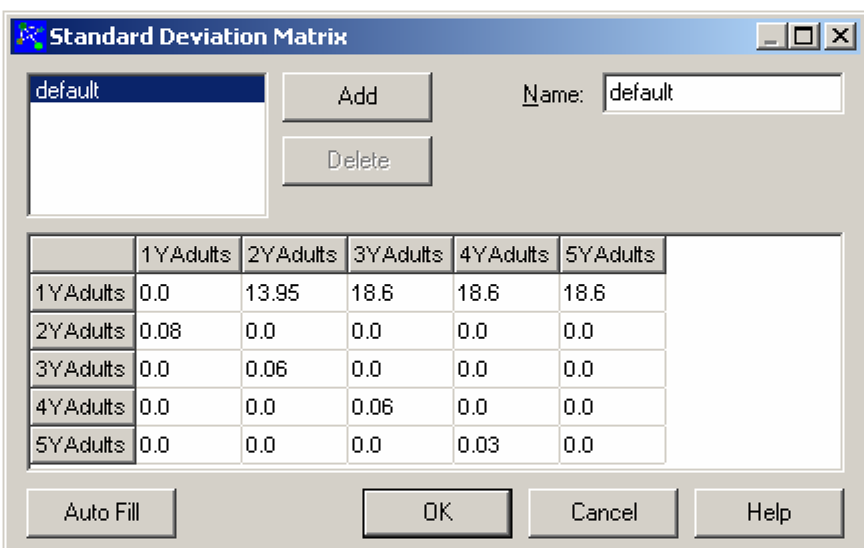
3.1.3.3 Leslie/Stage Matrices

Figure 1 shows the stage matrix with fecundity values in the upper row and survival values in the diagonal row. Figure 2 shows the corresponding standard deviation matrix for fecundity and survival values shown in Figure 1.



	1YAdults	2YAdults	3YAdults	4YAdults	5YAdults
1YAdults	0.0	14.4	19.2	19.2	19.2
2YAdults	0.4	0.0	0.0	0.0	0.0
3YAdults	0.0	0.6	0.0	0.0	0.0
4YAdults	0.0	0.0	0.6	0.0	0.0
5YAdults	0.0	0.0	0.0	0.3	0.0

Figure 1: Leslie matrix



	1YAdults	2YAdults	3YAdults	4YAdults	5YAdults
1YAdults	0.0	13.95	18.6	18.6	18.6
2YAdults	0.08	0.0	0.0	0.0	0.0
3YAdults	0.0	0.06	0.0	0.0	0.0
4YAdults	0.0	0.0	0.06	0.0	0.0
5YAdults	0.0	0.0	0.0	0.03	0.0

Figure 2: Standard deviations for vital rates

3.1.4 Sex Structure

The model includes females only.

3.1.5 Density Dependence

The reproductive strategy of the Northern Leopard Frog results in highly fluctuating populations. Population sizes are very likely constrained by resource limitations. There are two reported indicators suggesting density dependent effects on population dynamics:

1. higher tadpole densities result in smaller YoY frogs and higher YoY frog mortality
2. the maximum number of observed adult Northern Leopard Frogs per pond was 30

It seems logical to model the competition of tadpoles for resources as “scramble competition” type in Ramas©MetaPop. The resources in a breeding pond are shared equally among tadpoles and because of that there won’t be sufficient resources for all individuals at high densities. This will reduce the population size of tadpoles with negative effects on the growth rate of the entire population. See also a citation from the Ramas©MetaPop help regarding scramble competition in Appendix 8.

3.1.6 Stochasticity

The model is stochastic with 3 sources for stochasticity:

1. demographic stochasticity: “This will cause the number of survivors and dispersers (emigrants) to be sampled from binomial distributions, and the number of young from a Poisson distribution” – important for small population sizes.

2. environmental stochasticity: - fluctuations in vital rates, not correlated, means that a year with high mortality but also high fecundity may occur

3. catastrophes: The model will consider occasional breeding pond dry-outs with a complete loss of all YoY frogs for that particular year.(i.e. all tadpoles die and no 1Year adults will emerge) for that year.

3.1.7 Catastrophes

Based on the observed probability of early breeding pond dry-outs or floods, the model will consider such rare events. The model will simulate breeding pond dry-outs with a probability of 5% (or 1 out of 20 years on average). Such a “catastrophic event” will result in a complete loss of YoY frogs.

4 Model expectations

4.1 Age Class Distribution

A ratio of 120:1 YOY to sexually mature adults was observed in a breeding population in Cypress Hills, AB (see also Leclair and Castanet 1987). Considering an average over-wintering survival rate of YoY frogs between 8% and 12% (see 3.1.3.1), a ratio of roughly 10:1 to 15:1 1 year adults to sexually mature adults should be expected. The population model as described in section 3 produces a ratio of about 16:1 1 year female adults to sexually mature adults.

4.2 Population Trend

The Northern Leopard Frog was described as widespread across many regions in Canada. The observed decline between 1970 and 1980 was likely not caused by sudden changes in habitat loss or increased habitat fragmentation, although populations responses to such causes may have been delayed and can therefore not directly be linked to changes in habitat configuration. The sudden and widespread decline was more likely the result of other primary causes. Without those, the populations are expected to be viable in their natural habitats. Our population model should therefore produce a balanced population, which size is primarily dictated by the inherent growth rate of the model and density dependent constraints on the growth of the population.

5 Results

The results section is structured around two model configurations – a non-spatial, single population model and a spatially explicit metapopulation model with 5 populations. The purpose of the non-spatial population model is to analyze and understand population dynamics without considering dispersal and correlations between separated populations. The spatially explicit model reveals insight into the importance of dispersal and correlations in a spatially distributed setting. The time span of the simulations was 100 years or 100 generations. Each simulation run was repeated 1000 times and averages or probabilities were derived from those 1000 repetitions.

5.1 Non-spatial, single population model

The non-spatial population model was initialized with 200 individuals, 28 of which were 2+ year adult females and 172 where 1 year adult females. This initial distribution corresponds to the estimated stable age-class distribution. The carrying capacity for scramble competition was set to 1100 1 year adult females. This value was chosen arbitrarily to produce a final abundance of about 30 2+ year adult females after 100 years. This final abundance corresponds to the observed maximum number of female adults observed at one average-sized breeding pond.

5.1.1 Population trajectory

The population model produced an average abundance trajectory of 2+ year old female adults as shown in Figure 3. The grey bars show the standard deviations around the mean value (blue line). The population was initialized with 28 2+ year old adult females and the final abundance was 27 2+ year old adult females. The initial spike was caused by an overabundance of 1 year old females, which was determined by an estimated stable age-class distribution (~ 6:1). The realized age class distribution (~16:1), however, differed greatly from the estimated distribution, because the estimated distribution did not consider stochasticity and scramble competition.

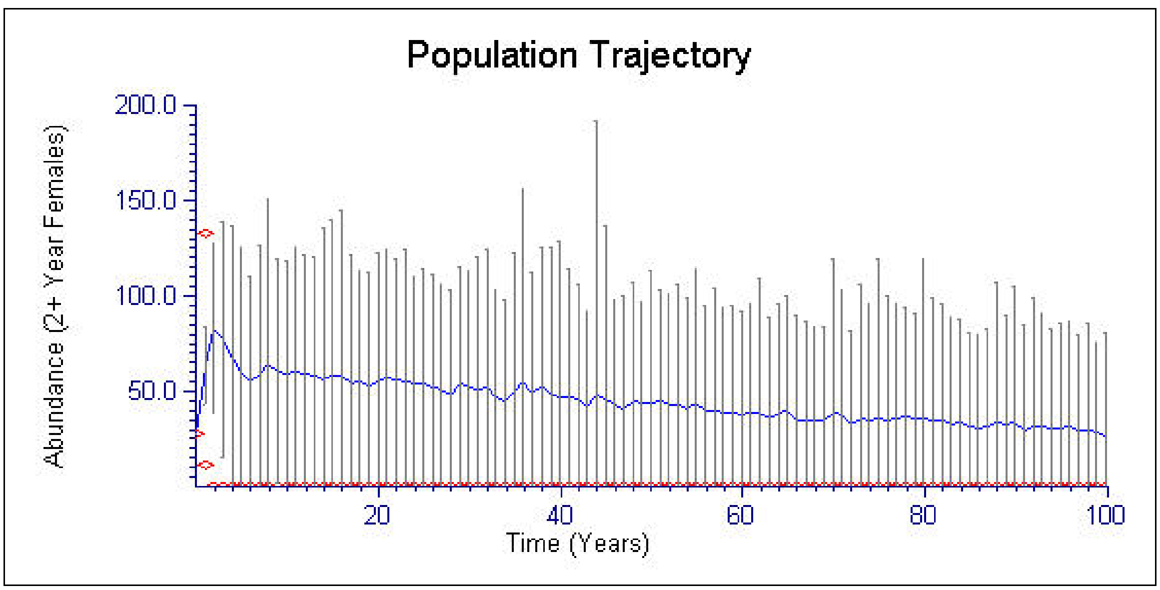


Figure 3: Abundance of 2+ year adult females over 100 years

The population trajectory indicates a highly fluctuating population abundance (large standard deviations) and an overall steady decline in 2+ year adult females despite an estimated growth rate (lambda or eigenvalue of the leslie matrix) of 2.8. Abundance is therefore primarily controlled by effects of scramble competition at or near the carrying capacity for the 1 year adult females (see 5.1), as well as by demographic (large standard deviations around fecundity and survival rates) and environmental stochasticity.

5.1.2 Extinction risk

The probability that one single population could go extinct within 100 years amounts to about 56 percent. This probability corresponds to the proportion of repetitions (out of 1000), for which the population abundance went to zero, i.e. 556 out of 1000 repetitions resulted in a simulated population extinction within 100 years.

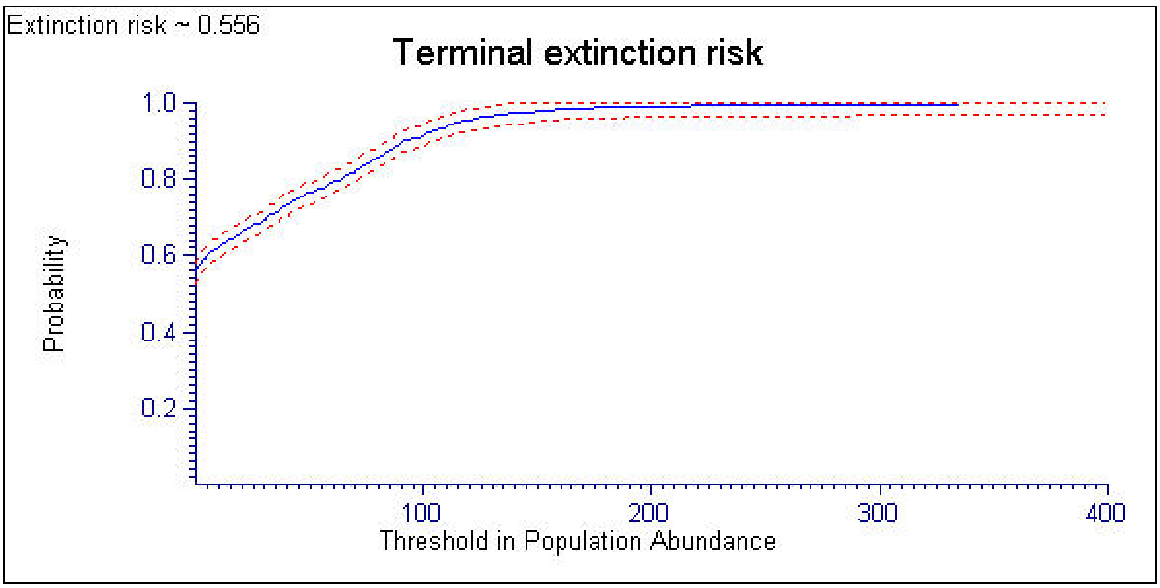


Figure 4: Probability of Extinction over 100 years

5.1.3 Minimum viable population size

The minimum viable population size or “target level” refers to the number of individuals necessary to ensure a viable population with a defined low risk of extinction over a defined period of time. The non-spatial, single population model did not reveal an initial population size resulting in a low risk (<= 5 percent) of extinction. Even very large initial population sizes did not significantly change extinction risk, but increased final population abundance. This result indicates a low relative importance or sensitivity of initial population size to extinction risk and a potential counter-productive effect of large population sizes on the growth rate due to scramble competition. This result also suggests that it is unlikely that one single isolated population of Northern Leopard Frogs may survive over a time period of 100 years, independent of the initial population size. This finding has also implications for re-introduction scenarios and will be discussed in section 5.3.

5.1.4 Sensitivity analysis using GRIP

In a conventional sensitivity analysis relationships between single model parameters and a simulated response variable (e.g. final abundance or extinction risk) are evaluated separately by varying one model parameter at a time. Such functional relationships are insightful, but do not consider interaction effects with other model parameters and they do not reveal the relative importance of this or all model parameters to the simulated response variable.

Another approach would be to vary all model parameters over a comparable range and simulate a factorial or randomized set of model parameter combinations. The simulated data set could then be scrutinized by statistical methods, which could reveal more comprehensive sensitivities and relative importance of all model parameters.

So far this has not been feasible using established population simulators such as Ramas©MetaPop. However, thanks to recent efforts by Janelle M. R. Curtis and Ilona Naujokaitis-Lewis at the Centre for Applied Conservation Research, University of British Columbia, a program GRIP was developed (supported in part by Parks Canada), which allows automated execution of a set of randomized model parameter combinations. GRIP (Curtis and Naujokaitis-Lewis 2007) varies model parameters randomly and executes RAMAS for each randomized parameter combination, hence providing for an automated sensitivity analysis based on randomized parameter variations of the initial Ramas@Metapop population model.

GRIP was made available for the purpose of this project in order to conduct a comprehensive sensitivity analysis of the population model. A slightly modified version of GRIP was used to vary the following model parameters randomly by drawing random numbers from normal distributions with a standard deviation of 20 percent. (fecundity, survival, initial abundance, carrying capacity, probability of pond dry-outs).

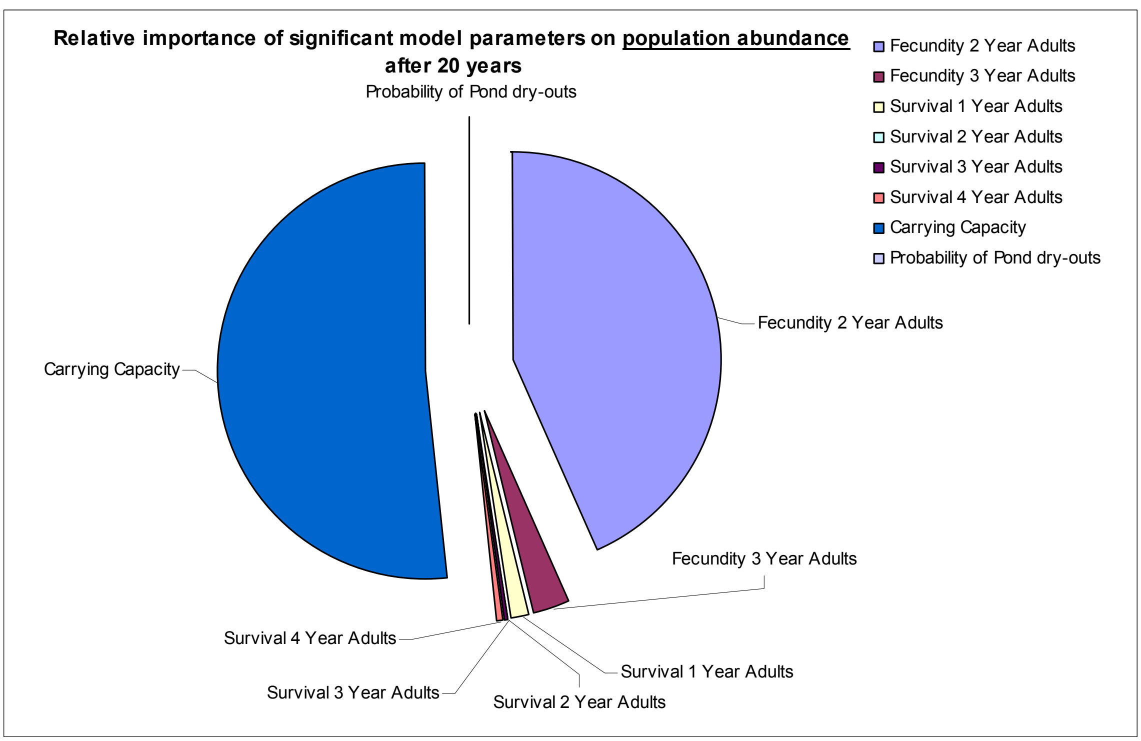


Figure 5: Relative importance of significant (p<0.05) model parameters on population abundance after 20 years.

1000 model runs were performed, each with a different set of model parameter values. The resulting data set was analyzed by means of ANOVA (using SAS, SAS 1990) and the relative importance of each significant model parameter was then determined using Type III Sums of Squares. The results are shown in Figure 5 and 6.

Overall, close to 80 percent of the variation in abundance and extinction risk was explained by the varied model parameters. The remaining 20 percent are attributed to simulated demographic and environmental stochasticity. In other words, 20 percent of the abundance or extinction risk is solely caused and explained by stochastic influences. Figure 5 reveals the main drivers of the simulated abundance as being fecundity of 2 year old adults, carrying capacity (applied to 1 year old adults only in relation with scramble competition) and fecundity of 3 year old adults. Probability of pond dry-outs as well as survival rates did not contribute much to the observed population abundance.

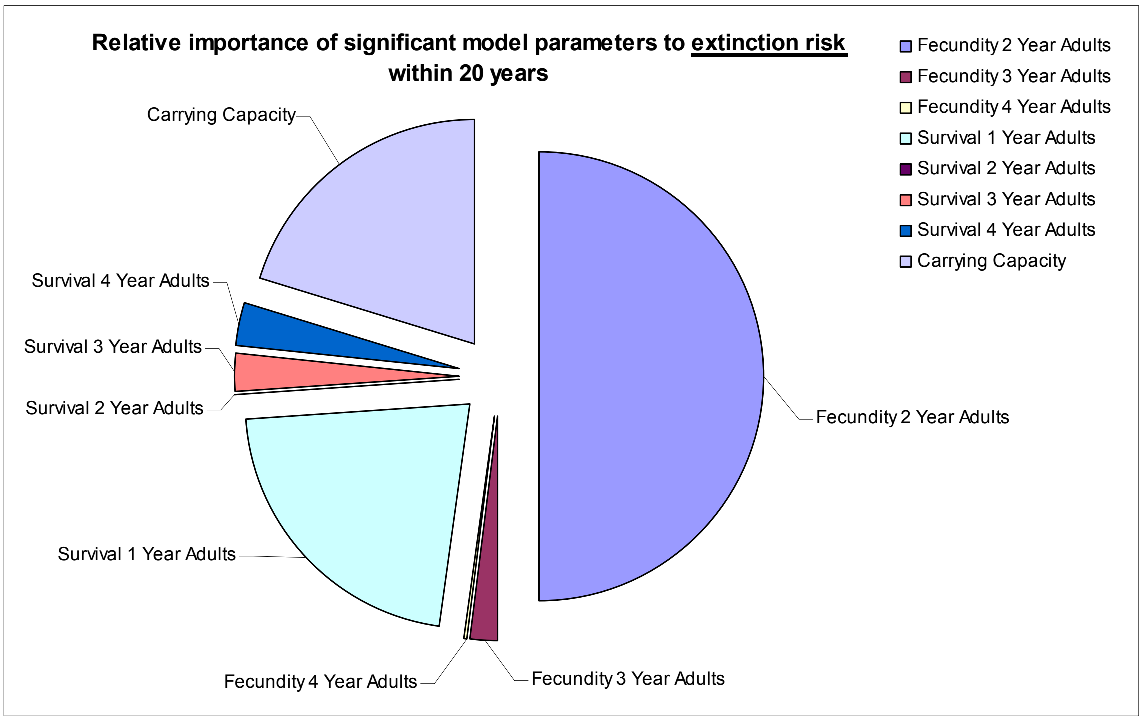


Figure 6: Relative importance of significant (p<0.05) model parameters on extinction risk within 20 years.

Figure 6 reveals a different partition of the sensitivity of model parameters to extinction risk. Again, carrying capacity has a major influence on extinction risk, indicating a strong effect of scramble competition on the viability of the population.

Overall, these results indicate that initial population size and occasional pond dry-outs do not substantially contribute to either population abundance or extinction risk. Abundance is likely mainly controlled and restricted by carrying capacity of 1 year adult females (effect of scramble competition on tadpole stage) and by the reproductive output of 2 year old females. Extinction risk, on the other hand, is mainly controlled by fecundity of 2 year adults, carrying capacity and by survival probability of all age classes.

5.1.5 Summary

The results of the non-spatial, single population model indicate that isolated Northern Leopard Frog populations may experience high fluctuations in population abundance with a substantial risk of local extirpation in the absence of connectivity to other populations. The population dynamics seem largely driven by density dependent regulations at the tadpole stage, but also by stochastic variations in demographic and environmental factors. It was not possible to determine a minimum viable population size for a single population, which would result in a viable population with an extinction risk of less than 5 percent over 100 years.
A model validation is not possible at this time, due to lack of data. However, the realized final age class distribution of 16:1 (1 year adults to 2+ year adults after 100 years) is one indicator that the internal model structure reflects part of the identified population biology of the Northern Leopard Frog.

5.2 Spatially explicit, metapopulation model

Results of section 5.1. suggest the importance of connectivity to other populations, simply to mitigate the risk of local extirpations. In order to evaluate potential effects of dispersal mitigated connectivity and correlation of environmental stochasticity between multiple populations a spatially explicit metapopulation model was created with 5 populations. The metapopulation model was initialized identically to the non-spatial population model. The overall initial abundance was 200 individuals, split equally across all 5 populations. Likewise, the carrying capacity of 1100 1 year adult females was partitioned equally across all 5 populations. The dispersal transition probability between all populations was set between 0.3 and 1.5 percent of 1 year old females. Correlation factors between populations varied between 1 and 3 percent. This hypothetical metapopulation represents a ‘loosely coupled’ set of 5 populations with very low dispersal rates and equally low correlation factors, i.e. environmental stochasticity would not affect all populations equally at a certain time.

5.2.1 Population trajectory

The metapopulation model produced an average abundance of about 65 2+ year adult females. The standard deviation around the mean abundance is smaller compared to those obtained from the non-spatial, single population model (compare to Fig 1.) The population abundance does not decline over time. It should be noted that this abundance trajectory is based on the same overall initial population size and carrying capacity as applied in the non-spatial, single population model. This abundance, however, is the sum over all 5 single population abundances. This means that each of the 5 populations may persist with 1/5 of 65 2+ year adult females or 13 adult females per population respectively when connected to a metapopulation.

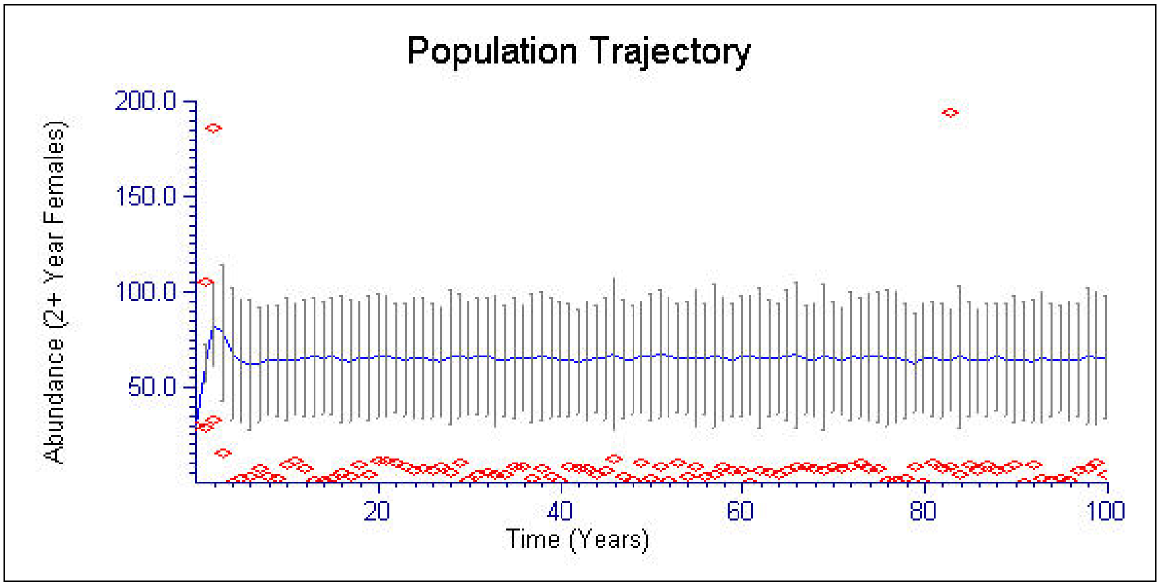


Figure 7: Overall Metapopulation abundance of 2+ year adult females over 100 years

5.2.2 Extinction risk

The extinction risk for the metapopulation over 100 years was zero percent (Figure 8).

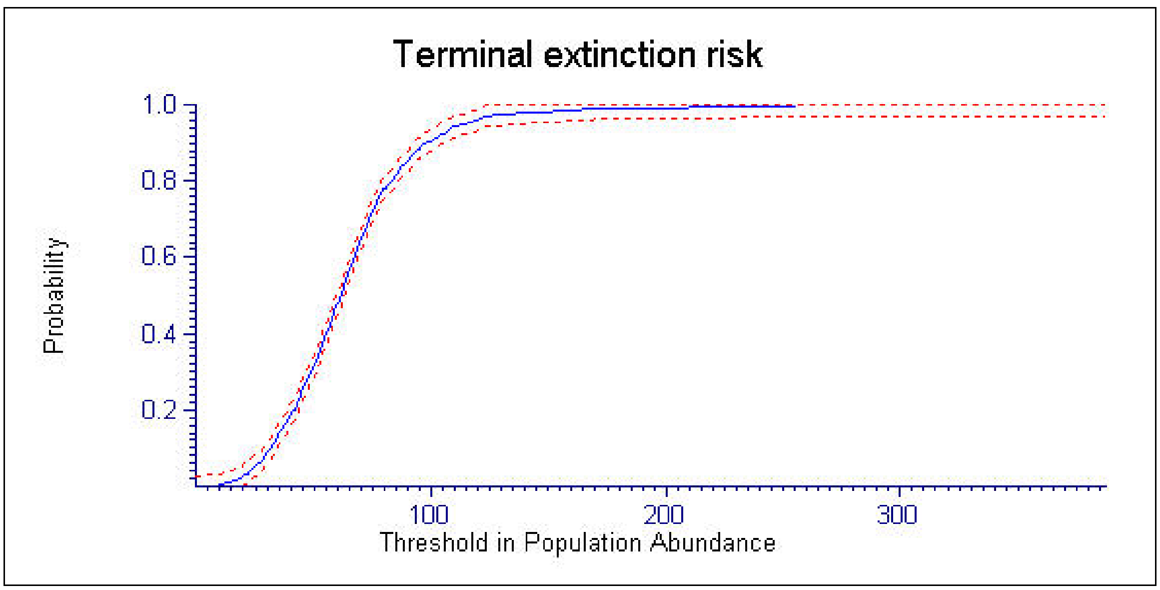


Figure 8: Probability of Extinction over 100 years

5.2.3 Minimum viable population size

The minimum viable population abundance was determined for the metapopulation with different numbers of populations (Figure 9). The initial metapopulation model with 5 populations revealed a minimum viable population abundance of about 10 2+ year adult female frogs, which corresponds to a total population size of about 160 female frogs (1 year adult females included).

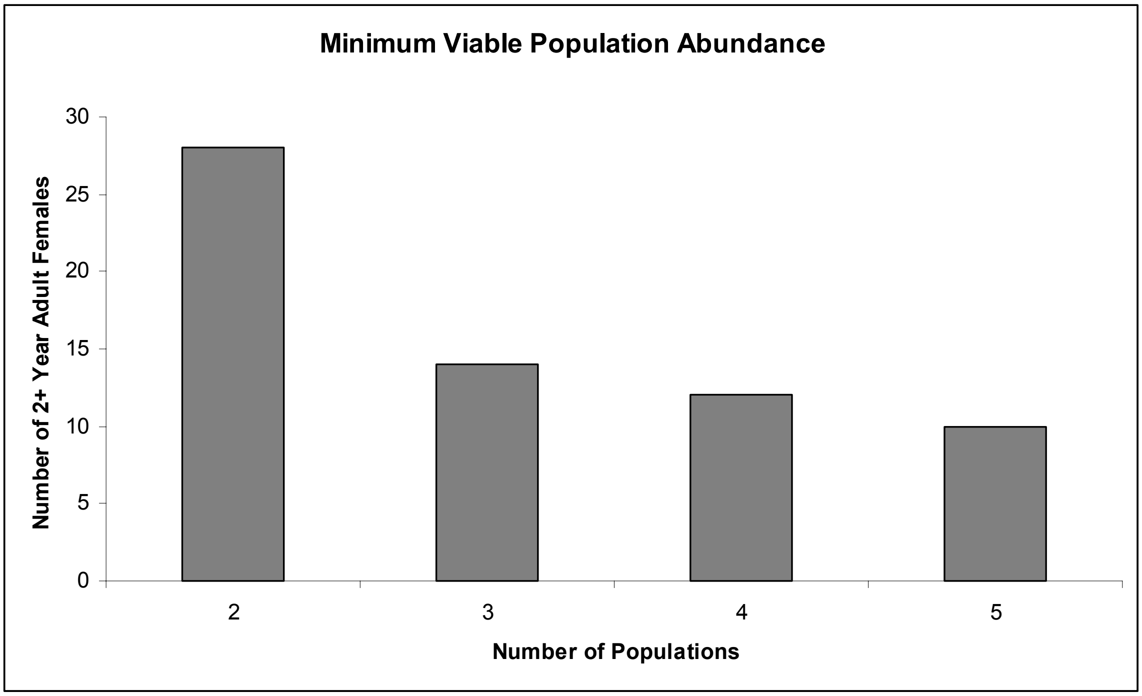


Figure 9: Minimum viable population abundances

Figure 9 shows that viable abundance levels strongly depend on the number of populations included in the metapopulation model. A viable metapopulation of 2 populations would require abundance levels twice of those necessary for a metapopulation comprised of 5 populations. This exercise, although rather hypothetical in nature, indicates that spatially separated, but connected populations are likely essential for the viability of the Northern Leopard Frog. A metapopulation arrangement seems more efficient in mitigating the risk of local extirpations than a higher population abundance, although both factors are likely to be important.

5.2.4 Sensitivity analysis using GRIP

A sensitivity analysis was conducted in a similar way as described in section 5.1.4. GRIP was used to change model parameters randomly. In addition to the model parameters varied in 5.1.4, the following additional parameters were varied for the metapopulation model (dispersal rate, disperser survival rate, correlation between populations). The results are shown in Figure 10 and 11.

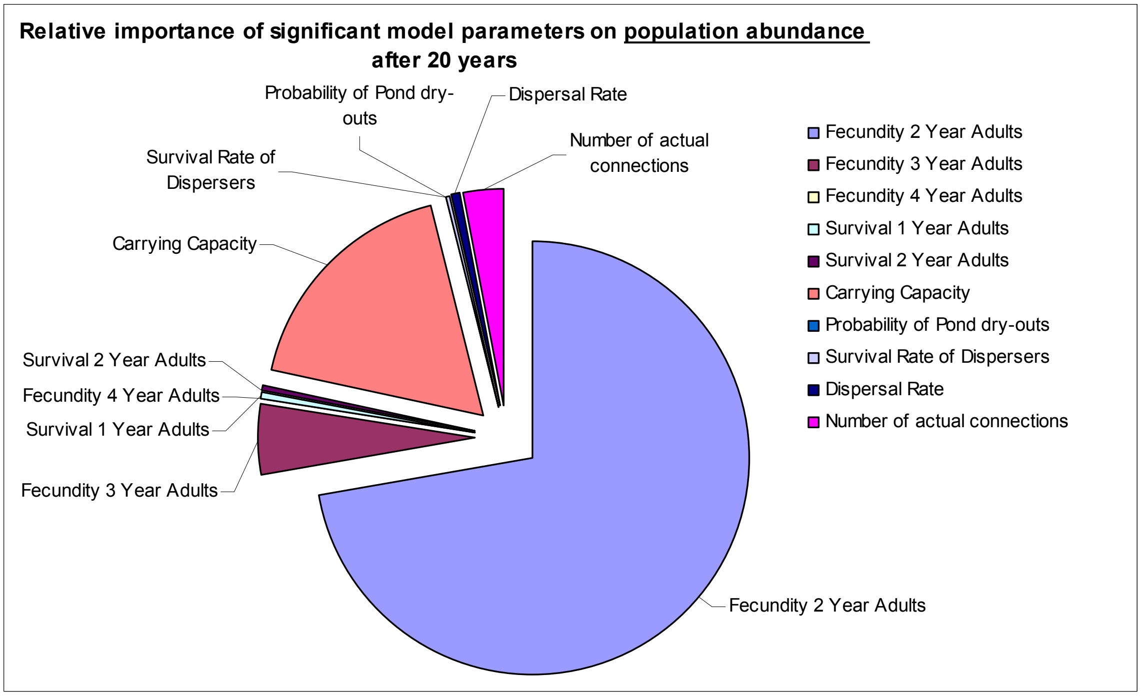


Figure 10: Relative importance of significant ($p<0.05$) model parameters on metapopulation abundance after 20 years.

Figure 10 shows that fecundity and carrying capacity are the main drivers of the population abundance. Sensitivity of model parameters is tendentiously similar to those observed for the non-spatial, single population model. Model parameters explained about 88 percent of the total variation in population abundance. This result indicates that stochasticity has an overall smaller effect on population abundance when compared to the non-spatial, single population model. This is also reflected in the lower standard deviations around the average population abundance as shown in Figure 7 (compare Figure 7 and Figure 3).

Figure 11 shows model parameter sensitivities for the metapopulation extinction risk over 100 years. The extended time frame (100 instead of 20 years) was necessary, because extinction risk was mostly zero after 20 years, i.e. extinction risk after 20 years did not vary sufficiently for a statistical analysis. Figure 11 impressively reveals the importance of connectivity as the main driver for population viability in a spatially structured metapopulation of Northern Leopard Frogs. The number of actual connections was calculated based on the varied dispersal rates. Due to random variations in the dispersal rate, some populations became 'disconnected' during the sensitivity analysis. The number of connections was determined and reported for each of the 1000 simulation runs. As it turns out, the number of connections, i.e. any dispersal transition probability between any two populations of greater than zero, accounts for more than 75 percent of the explained extinction risk.

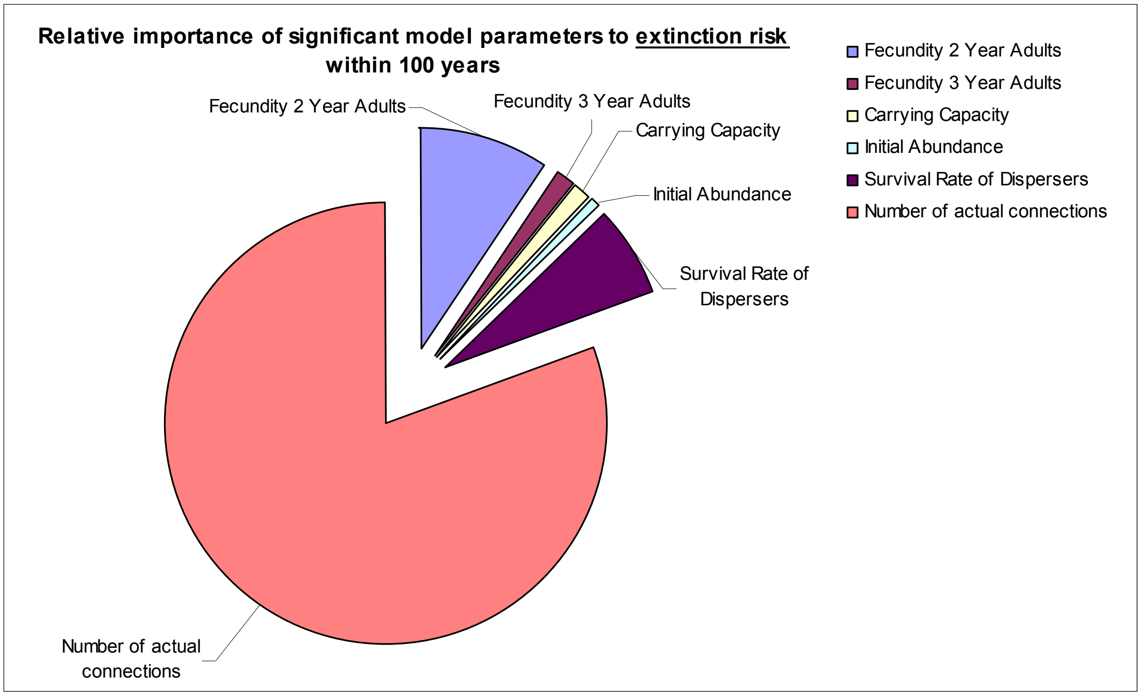


Figure 11: Relative importance of significant (p<0.05) model parameters on extinction risk within 100 years.

The survival rate of dispersers (modeled via a separate sink population in Ramas@Metapop) had a strong effect on extinction risk, which emphasizes the importance of connectivity even more. It is interesting that correlation between populations did not significantly contribute toward extinction risk and that no survival rate had a significant effect on extinction risk either. This does not mean, however, that those variables don't matter at all. Changes in the range of 20 % standard deviation did not significantly change the extinction risk. Different value ranges, in particular for the correlation factors, may have resulted in more significant contributions toward extinction risk and population abundance. Overall, only 57 percent of the extinction risk within 100 years was explained by the model parameters shown in Figure 11. This lower R^2 value compared to the other analyses indicates a higher significance of stochasticity and the propagation of uncertainty and/or stochasticity over time.

5.2.5 Summary

The results of the spatially explicit metapopulation model revealed a diminished extinction risk and abundance levels twice as high compared to those obtained from the non-spatial, single population model. These results are based on the very same overall initial abundances and carrying capacities as those used in the singe population model. The main difference is the actual spread of risk across multiple populations and the overall stabilizing effect of re-colonization or mutual exchange via dispersal, even at very low dispersal rates around 1 percent. Spreading of risk, low correlations of environmental factors and connectivity seem to be the major guaranties for population viability of the Northern Leopard Frog. The metapopulation model also allowed to estimate the minimum viable population abundance or target abundance level for potential re-introduction scenarios. This abundance level depends on the number of populations and could only be derived for at least 2 populations at about 28 2+ year old female adults.

5.3 Re-introduction scenarios

This section discusses options for optimal re-introduction scenarios based in part on the results obtained in sections 5.1 and 5.2.

5.3.1 Harvesting egg masses from existing populations

One concern may be to harvest egg masses from existing populations. Harvesting egg masses has a similar effect on population dynamics than local breeding pond dry-outs or floods, because it will partly or fully destroy one generation for the affected population. As the results revealed, probability of local catastrophic events did not register as a very important parameter in the sensitivity analyses. This indicates, that occasional breeding failures do not seem to seriously jeopardize population persistence. Such events may easily be compensated by the reproductive potential or intrinsic growth rate of the population, which is estimated to be around 2.8 (see 5.1.1).

Therefore, harvesting egg masses seems to be a minor intrusion in the overall population dynamics, but should still be executed with care. It would always be better to harvest egg masses from populations with known abundance records and in close vicinity to other occupied breeding ponds of the Northern Leopard Frog.

5.3.2 Re-introducing tadpoles into historic habitat sites

The results of the population viability analysis indicate that spreading of risk by means of multiple, connected populations seems to be a key factor for population persistence of the Northern Leopard Frog. Re-introduction attempts may therefore be more successful if multiple, connected populations are reared simultaneously. The two main variables for re-introduction attempts are:

1. number of re-introduced tadpoles
2. number of breeding sites for re-introduced tadpoles

Effects of both variables on population viability of re-introduced metapopulations were analysed and are described in the following sections. Since tadpoles are not an explicit stage or age class in the population model, re-introduction analysis was based on 1 year adult females.

5.3.2.1 Re-introduction numbers: tadpoles and target populations

The number of 1 year old females can be used as a surrogate for tadpoles or egg masses based on the known relationship between those life stages. One egg mass may produce on average around ten 1 year adult females according to the following rationale (see also 3.1.3.1).

1. average number of eggs per egg mass: 3500
2. sex ratio: 1:1, we therefore consider only 50% (female) eggs of all laid eggs
3. survival rates of eggs to metamorphosed tadpoles: 6%
   (may be even higher in protected rearing ponds)
4. over-winter survival rate of YoY frogs: 10%

The number of 1 year adult females would then calculate as follows:

$$3500 * 0.5 * 0.06 * 0.08 = 10.5$$

Using 10 expected 1 year adult females per one egg mass should be regarded as a conservative estimate considering much higher survival rates for tadpoles in protected rearing ponds.

Effects of starting 1 to 5 new connected populations with different numbers of 1 year old females were analysed and are shown in Figure 12 and 13.

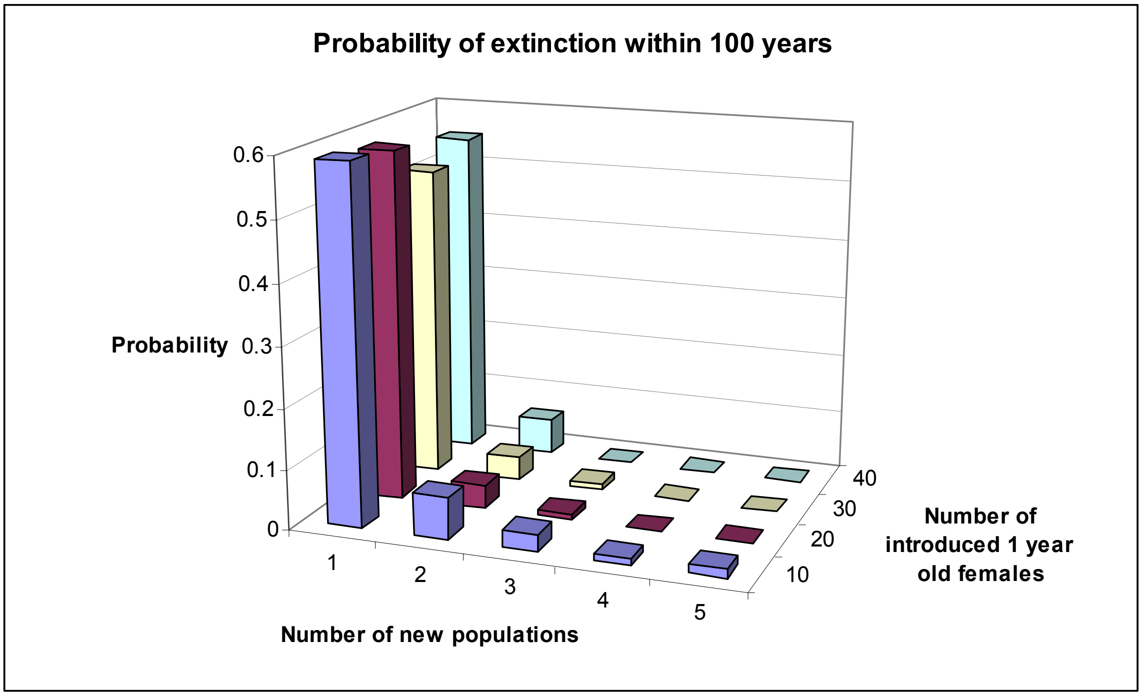


Figure 12: Extinction risk within 100 years as a function of number of new populations and number of introduced 1 year adult females

Figure 12 depicts effects of different re-introduction scenarios on the extinction risk of re-introduced populations. The results indicate that tadpoles or YoY frogs from at least two egg masses should be introduced to at least 3 breeding sites. The breeding sites or ponds should be spatially arranged to allow for dispersal of YoY frogs.

A similar conclusion can be drawn from abundance levels after 100 years as a function of numbers of populations and re-introduced 1 year adult females. It seems that 20 introduced 1 year adult females into 3 breeding sites may allow to fully max out the given carrying capacity of the corresponding metapopulation.

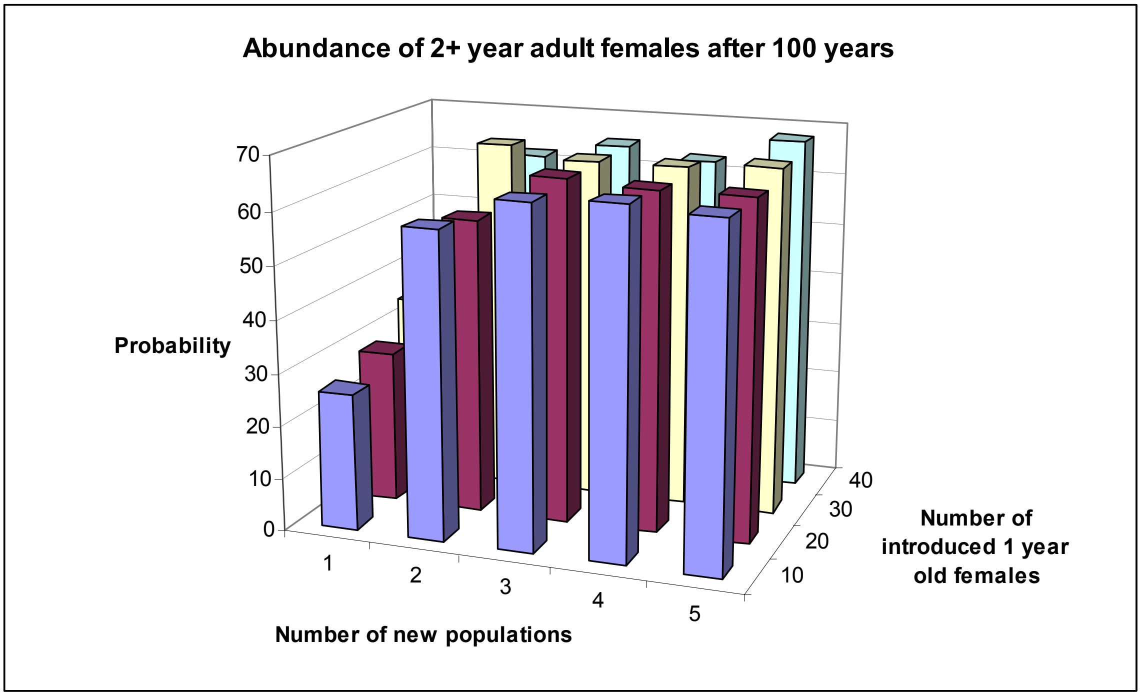


Figure 13: Abundance of 2+ year adult females after 100 years as a function of number of new populations and number of introduced 1 year adult females

5.3.2.2 Abundance trajectory for re-introduced populations

The success of re-introduction attempts can only be measured by closely monitoring population abundances for all re-introduced populations. Figure 14 shows a predicted abundance trajectory

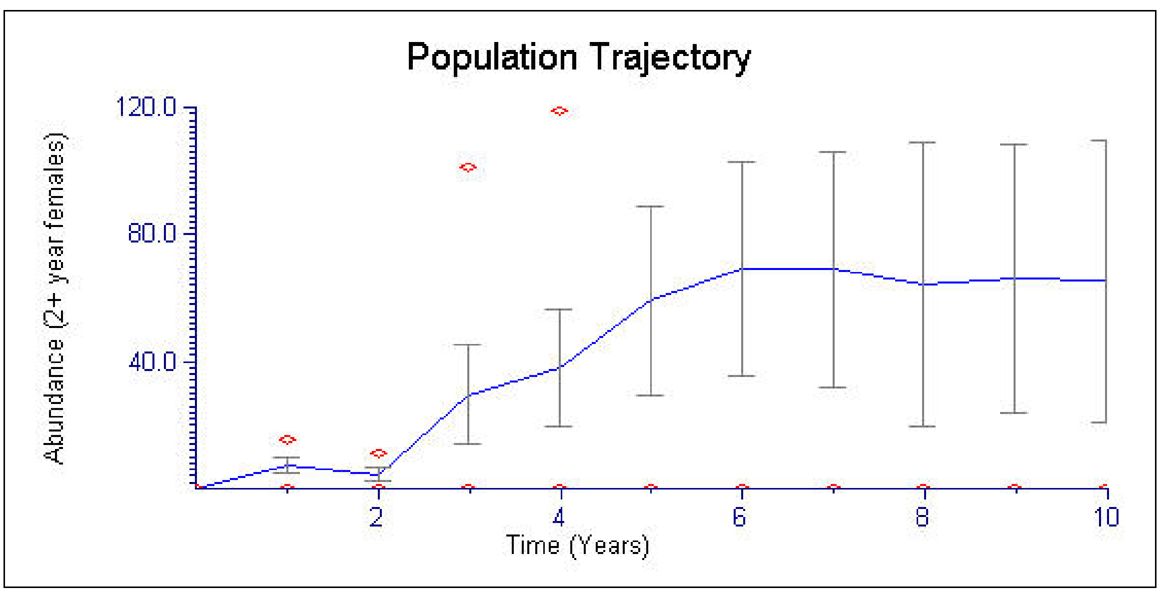


Figure 14: Abundance trajectory across 3 re-introduced populations with an initial population size of 20 1 year adult females.

after re-introducing 20 1 year old females (or the corresponding number of tadpoles or YoY frogs) into 3 separate, but connected breeding sites. According to the simulated prediction, it could be expected that a metapopulation may reach its carrying capacity within a time period of 10 years. It may also take 3 to 4 years until a significant population growth can be observed.

5.3.2.3 Staged vs. one time re-introduction

It is certainly feasible to re-introduce tadpoles over multiple years into historic breeding sites. The one time introduction as analysed in section 5.3.2.2 revealed a strong potential for population growth, but also a temporary and consistent decline of 2+ year adult females at about 2 years after the re-introducing 20 1 year adult females into 3 connected breeding sites. This decline may reduce population levels to a critical size with potential negative allele effects (undercrowding) to population growth, i.e. if there are too few female and male adults, reproduction may become impossible. Figure 15 shows the same one-time re-introduction attempt based on introducing 60 1 year old female adults (or the corresponding number of YoY frogs or tadpoles) into 3 connected populations.

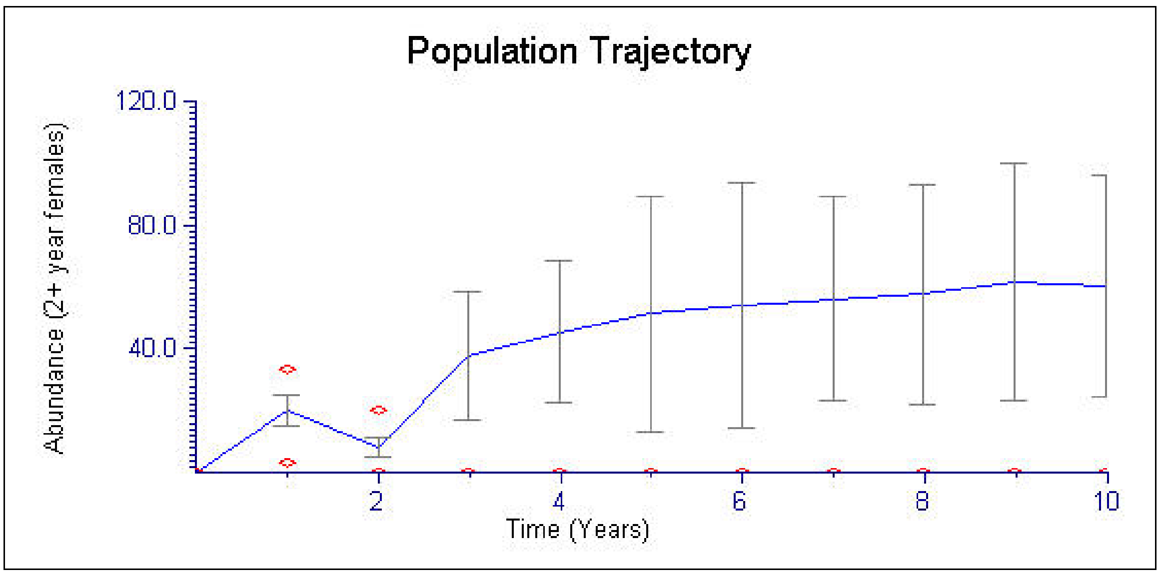


Figure 15: Abundance trajectory across 3 re-introduced populations with an initial population size of 60 1 year adult females.

The same pattern emerges although the number of 2+ year adult females at year #2 is larger compared to Figure 14. This result indicates that an increased number of re-introduced individuals may not necessarily change the principal pattern of population growth during the first 3-4 years with a risk of very low abundances 2 years after initial re-introduction.

A staged re-introduction approach may reduce this risk and lead to a more continuous population growth as shown in Figure 16. This result is based on introducing 20 1 year old adult females 3 times over 3 years, i.e. each year 20 individuals. The overall effort in terms of introduced individuals is equal to Figure 15, however the projected population growth is more continuous and does not show a short term decline after 2 years. A staged approach may therefore be more appropriate than a one-time effort.

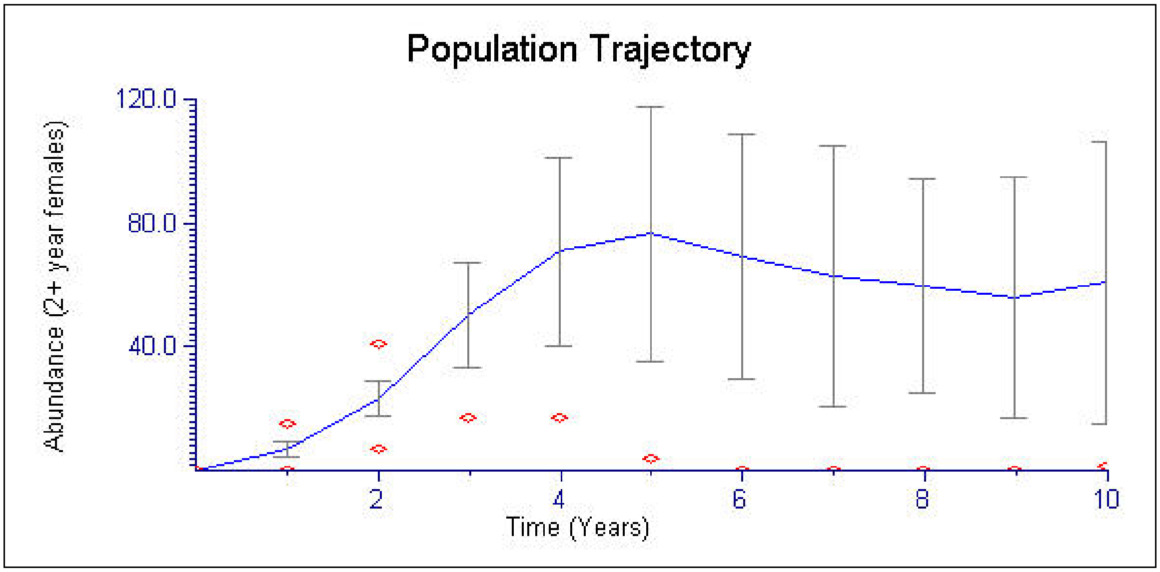


Figure 16: Abundance trajectory across 3 re-introduced populations for introducing 20 1 year adult females 3 times over 3 years – staged re-introduction

6 Conclusions

This population viability analysis indicates that Northern Leopard Frog populations may have a significant population growth potential and that population sizes are very likely limited by density dependent regulations at the tadpole stage but also by stochastic variations in demographic and environmental factors. It is therefore unlikely that single, isolated populations will survive over a long period of time due to the intrinsic risk of local extirpations. The results of the metapopulation analysis suggest that this risk can be mitigated effectively by the mere existence of multiple, loosely coupled populations, among which dispersal should be feasible. Connectivity seems to be the most important variable with respect to reducing extinction risk for a spatially distributed population of Northern Leopard Frogs.

These findings have implications for re-introduction scenarios and were confirmed by exploratory simulation experiments. Spreading of risk seems to be more important than initial abundance. It can therefore be concluded that efficacy and potential success of re-introduction attempts will increase with number of initiated populations but also with the number of released individuals. Visible population growth should be observable within 5 years after re-introduction and populations may max out the habitat specific carrying capacity within 10 years. A staged re-introduction approach may lead to a more continuous and stable population growth compared to a one-time effort. It may therefore be advisable to consider re-introducing the Leopard Frog over multiple years.f

The findings of this study may also be related to the sudden disappearance of the Northern Leopard Frog from most of its habitat between 1970 and 1980. As connectivity seems to be very important, any potential disturbance or disease could have been spread quickly among all connected populations. If Northern Leopard Frog populations existed mostly in isolation, an almost simultaneous wipe-out would have been more unlikely.

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8 Appendix

8.1 Types of Density Dependence

8.1.1 Scramble competition (logistic, Ricker)

As population size increases, the amount of resources per individual decreases. If the available resources are shared more-or-less equally among the individuals, there will not be enough resources for anybody at very high densities. This process of worsening returns leads to scramble competition, and can be modeled by logistic or Ricker equations. In both equations, the population size at the next time step, N(t+1), is a declining function of the population size at this time step, N(t), for large population sizes.

When you select "scramble" type of density dependence in RAMAS Metapop, at each time step of the simulation, the vital rates affected by density dependence are modified so that the average (deterministic) growth rate of the population (i.e., the eigenvalue of the stage matrix for that time step) is equal to the growth rate given by the Ricker equation for the current abundance. This growth rate (as a function of abundance) is represented in the Density Dependence in R curve. Thus, even if the Stage matrix suggests a declining population, it is assumed that the population would recover from low densities. For example, if the Stage matrix has an eigenvalue (finite rate of increase) of 0.9, and Rmax=1.05, then at low densities the population would have a deterministic growth rate of 5% per time step (which may fluctuate due to stochasticity), regardless of what the stage matrix is. In this case, the Stage matrix is assumed to represent the average decline of the population at an abundance over the carrying capacity.

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