

METAPOPULATION DYNAMICS AND EXTINCTION IN PRISTINE HABITATS - A DEMOGRAPHIC EXPLANATION

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Abstract

*Demographic and age-structured modelling of local populations in a pool frog (*Pelophylax lessonae*) metapopulation reveals that the natural emigration from a population is of a magnitude which, if all emigrants are lost from the system, enhances local extinction risk in comparison to if the emigrants become immigrants in other local populations. In the latter case, annual population growth rate averaged $\lambda = 1.2$, while in the former λ averaged 0.994. Simulations indicated that single local populations in pristine habitat with emigration and no immigration have an extinction probability of 0.532 in 100 years, with extinction occurring from 11 years after isolation and mean time to extinction of 61 years. Such isolated populations were also highly vulnerable to additive mortality. In comparison, two local populations interconnected by dispersal were resilient to increased and higher local mortality provided that connectivity and the source population of immigrants were unaffected. This provides a demographic explanation of extinction patterns observed in the pool frog and other taxa that likely has general relevance for the conservation and management of subdivided populations in various landscapes.*

Key words: demographic modelling, extinction, metapopulation, *Pelophylax lessonae*.

INTRODUCTION

The use of metapopulation dynamics theory (Levins, 1969; Hanski and Gilpin, 1997; Hanski and Gaggiotti, 2004) in ecology, genetics, and in biodiversity conservation and management, has increased greatly since the 1980s (e.g., Sjögren, 1988); its application to organism groups has also been discussed (e.g. Harrison, 1991; Marsh and Trenham, 2001). In southern Sweden, the pond-dwelling pool frog (*Pelophylax lessonae*; Figure 1) occurs with a metapopulation structure along part of the Baltic Coast where local populations inhabit ponds and adjoining terrestrial habitat that together serve as “patches”. In this system, local extinction may occur deterministically due to low quality or deterioration of local patch habitat (Sjögren, 1991a; Sjögren-Gulve, 1994), but also in seemingly pristine habitats. The latter type of extinction was characterized by greater isolation from other occupied ponds, larger pond size, lower mean water temperature, closer proximity to other local extinctions, and presence of large-scale forestry between ponds; the latter also reduced (re-) colonization rates of vacant ponds (Sjögren-

Gulve, 1994; Sjögren-Gulve and Ray, 1996). Sjögren-Gulve (1994) also showed that spatially correlated local extinctions were not due to a spatial correlation of habitat quality.



Figure 1. Adult female (left) and male pool frog (*Pelophylax lessonae*) from Östra Granskärdsdammen, Sweden (photo: © Per Sjögren-Gulve, used by permission)

Then, what can explain this greater extinction propensity of relatively isolated local populations also in pristine habitats? And why was there still a greater extinction risk at larger pool frog ponds even though the effect of the comparably colder water temperature in larger ponds had already been taken into account in

the extinction analysis (Sjögren-Gulve and Ray, 1996; Table 6.3). I set out to explore this using a combination of multiple-years field data on age-specific survival of the pool frogs, recorded dispersal between local pool frog populations (Sjögren, 1988; 1991b; Sjögren-Gulve, 1998), demographic analysis and simulation modelling.

MATERIALS AND METHODS

The population studies providing the field data and demographic data for these analyses were carried out during 1984-1992 in the landscape surrounding the village Klungsten at the northern Baltic coast of the Uppland county in southern Sweden.

Field work

The work and methods pertaining to hand-net captures, use of drift fences and individual marking of the pool frogs are described by Sjögren (1988, 1991b) and by Sjögren-Gulve (1998). Much of the results on the demography of the local population at Östra Granskärsdammen, in focus here, are presented by Sjögren (1988; 1991b); a few have been updated due to supplementary findings and data obtained after 1988. Review and updating of results regarding dispersal rates have also been done since Sjögren-Gulve (1998).

Local samples of pool frogs (n) captured at other ponds amounted to $50 < n < 150$. In the estimation of annual age-specific (0- and 1-year olds, 2-yr-olds and adults, respectively) numbers of pool frogs that had emigrated, it was assumed that emigrants experienced the same annual mortality at the immigration locality as did non-emigrants of the same age in the source patch.

Demographic analysis

The age-specific survival and fecundity of the female pool frogs are shown in Table 1, where “-home” denotes that only individuals which returned to their natal pond the following year were included as survivors in parameter estimation. “-all” denotes that also emigrants to other ponds in the landscape were included. Sjögren (1988; 1991b) found that the average life-span did not differ significantly between males and females, but there was a tendency

($p = 0.07$) of higher mortality among adult females than among adult males.

Simulations and model parameterization

Simulations and their programming were carried out with the Population Viability Analysis program VORTEX ver. 10 (Lacy and Pollak, 2018) using an age-structured model. The SD of the age- and sex-specific annual survival and mortality from field data took into account observed variation during a more detailed 6-years study period, and regarding juvenile survival also considered the reproductive “failures” during cold years observed since the 1950s (Sjögren, 1991b; S. Forselius, *pers. comm.*). The SDs of the annual mortality rates used in the simulations were subtracted with the variation expected from demographic stochasticity [variance expected from a binomial distribution = $p_x(1-p_x)/(n_x-1)$] already programmed in the software, so that the entered SDs parameterizing year to year environmental variation (stochasticity) did not include demographic stochasticity too. Years with extremely cold weather caused “reproductive failure”; at worst with no pool frog larvae metamorphosing in such a year nor surviving to the next (Sjögren, 1991b). The SD of the estimated 0-yr-old mortality (p_0) in Table 1 was hence reduced so that the 99% of the variation ($2.58 \cdot \text{SD}$) would be within the limit of a mortality rate 1.0 at maximum. Adult pool frog survival had an opposite trend to reproductive success, probably because the frogs experience less mortality during years with cloudy and rainy weather due to less exposure to predation while basking. Thus, a negative correlation (-0.2433) between annual adult survival and reproductive success based on field data was included in all simulations.

Each simulation started with the local population(s) at stable age distribution before reproduction and no larvae nor metamorphs at start. The sequence of annual part-processes (e.g., reproduction, mortality, dispersal) in simulations was equal to the default used in the VORTEX software.

Since all emigrants found at other pool frog localities were captured closely after the annual breeding period, dispersal between the local populations in simulations was not modelled with mortality during dispersal. Females and males

were assumed to be equally prone to emigrate and the slightly male-biased recaptures of emigrants were assumed to be due mainly to their generally lower mortality than that of females of the same age (Sjögren-Gulve, 1998). Emigration and dispersal were much more frequent among juveniles and subadults than among adults (Sjögren, 1988; Sjögren-Gulve, 1998). Therefore, all scenario models with two local populations included age-differentiated dispersal among frogs up to 3 years of age; older frogs did not emigrate. These models also had an 89% correlation of the local populations' environmental variation in vital rates as quantified for correlated population fluctuations by Sjögren-Gulve (1994). Simulations were run with a local-specific "ceiling" adjusted to consider all living frogs, also the 0-yr-old metamorphs (juveniles). This ceiling did not vary between years nor have any temporal trend. All simulation scenarios were run with 10,000 replicates each. Local extinction was defined as no frog remaining.

RESULTS AND DISCUSSIONS

With p_x -home parameter values (Table 1), which only included the survival of pool frogs that return to their natal pond the following year(s), the expected asymptotic annual growth rate (λ) of the local pool frog population became 0.994. When also including all emigrant frogs, which were found at the neighbouring pool frog locality Klubbenviken, 270 meters away sometime during the 5 years recapture study (i.e. using the p_x -all instead), the average λ became 1.20 (Table 1).

The estimated annual percentage of frogs that emigrated was 38.3% among 0-yr-olds, 5.9% among 1-yr-olds (subadults), and 1% among adults (2-yr-olds and older).

Simulations were carried out using alternative p_x values from the "home" and "all" demographic scenarios. Each alternative scenario was simulated forward for 100 years, which is often used in the general time-frame of Minimum Viable Population analyses.

Table 1. Life table for females of the local pool frog population (*Pelophylax lessonae*) at Östra Granskärsdammen

Age (x)	p_x -home	SD-home	p_x -all	SD-all	l_x -home	l_x -all	$P_{repr}(x)$	m_x	$l_x m_x$ -home	$l_x m_x$ -all
0	0.109	0.066	0.153	0.107	1.0	1.0	0	0	-	-
1	0.2847	0.082	0.3345	0.096	0.1090	0.1534	0	0	-	-
2	0.1968	0.042	0.2328	0.050	0.0310	0.0513	0.0283	1.46	0.0452	0.0748
3	0.2643	0.056	0.3003	0.064	0.0061	0.0119	0.6765	85.24	0.5206	1.0183
4	0.2808	0.060	0.2808	0.060	0.0016	0.0036	0.9333	157.3	0.2538	0.5642
5	0.5	0.236	0.5	0.236	0.0005	0.0010	1.0	182.5	0.0827	0.1838
6	0.5	0.236	0.5	0.236	0.0002	0.0005	1.0	206.5	0.0468	0.1040
7	0.2	-	0.2	-	0.0001	0.0003	1.0	220	0.0249	0.0554
8	0	-	0	-	0.00002	0.00005	1.0	220	0.0050	0.0111
								$R_0 = \Sigma$	0.979	2.01
								$\lambda =$	0.994	1.20

"home" denotes age-specific survival (p_x) and its standard deviation (SD) based only on the fraction of frogs which returned to their natal pond the next year. Corresponding values labelled "-all" denote estimates including both surviving emigrants and frogs that returned to their natal pond the next year. l_x is the fraction of juveniles (0-yr-olds) that survive to the age x . $P_{repr}(x)$ is the age-specific probability of reproduction for females, m_x is the resulting estimated average number of female offspring per female of age x ; it was calculated from the number of eggs expected from an average-size female of age x multiplied by the sex ratio 0.5, $P_{repr}(x)$ (Sjögren 1991b) and estimated survival from egg to metamorph. R_0 is the net reproductive rate per generation; λ is the asymptotic population growth rate per year. Since the pool frog is a birth-pulse breeder (reproduction only c. 1 month of the entire year), r is not used. Female generation time (T_c) became 3.65 years

Scenarios in isolation - full emigration and no immigration

Scenarios with the age-specific survival p_x -home, m_x , emigration, no immigration, and no additional mortality, resulted in an average decline of an isolated local population and an extinction probability (P_{ext}) of 0.532 in 100 years. The variation in population trajectories is exemplified in Figure 2.

Under the premise of no added extra mortality, 47% of such local populations survived for 100 years (Figure 3).

In this scenario, the first extinctions occurred after 11 years, the mean time to extinction for the local population was 61.3 ± 21.7 years (mean \pm SD) and the median 95 years, indicating that most extinctions took long time.

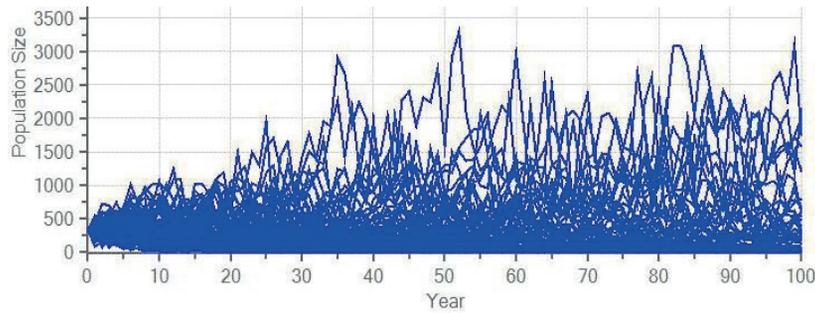


Figure 2. Population trajectories (1-yr-old and older frogs) of a subset of 100 simulation replicates of an isolated local pool frog (*Pelophylax lessonae*) population, initially with 340 frogs, when all emigrants experience mortality in the surrounding landscape (“matrix”). Asymptotic growth rate $\lambda = 0.994$ and $R_0 = 0.969$. Mean final size: 158 ± 400 (SD)

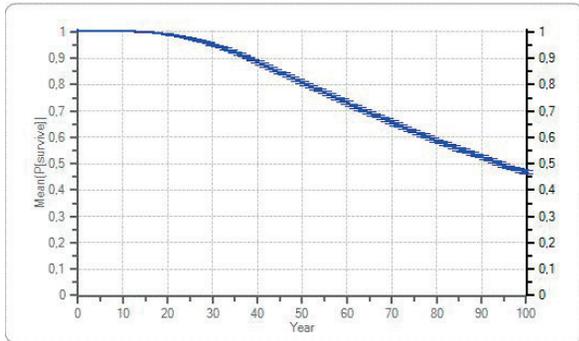


Figure 3. Yearly survival probability \pm SD of an isolated local pool frog (*Pelophylax lessonae*) population with natural emigration and no immigration during 10,000 simulation replicates. $\lambda = 0.994$. The extinction risk in 100 years $P_{ext} = 0.532$

In this scenario, the first extinctions occurred after 11 years, the mean time to extinction for the local population was 61.3 ± 21.7 years (mean \pm SD) and the median 95 years, indicating that most extinctions took long time. However, such an isolated population was also highly vulnerable to increased (additive) mortality. In a scenario with only slight additive mortality, e.g. 5% per year for all age classes, a “tipping point” appeared where the simulated local population went extinct, which began after five years, and 100% of the replicates were extinct by year 28 (Figure 4).

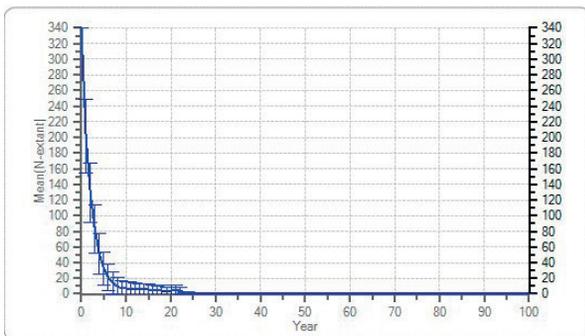


Figure 4. Mean yearly size \pm SD of an isolated local pool frog (*Pelophylax lessonae*) population with natural emigration, 5% extra mortality and no immigration

This implies that anthropogenic addition of mortality to isolated local populations may have drastic negative effects on local viability and persistence, but with a time-lag.

Scenarios with two subpopulations, full emigration and connectivity

The next set of simulations examined similar scenarios as above, but for two interconnected local populations, using the p_x -all demographic data where the populations’ emigration is not lost from the system.

With no added mortality, the expected mean λ of both populations was 1.2.

Even though significant and 89% correlated populations fluctuations occurred in the simulations due to spatially correlated poor reproduction during very cold years (Figure 5), none of the local populations went extinct in 100 years ($P_{ext} = 0$) provided that environmental conditions did not deviate from normal (Figure 6).

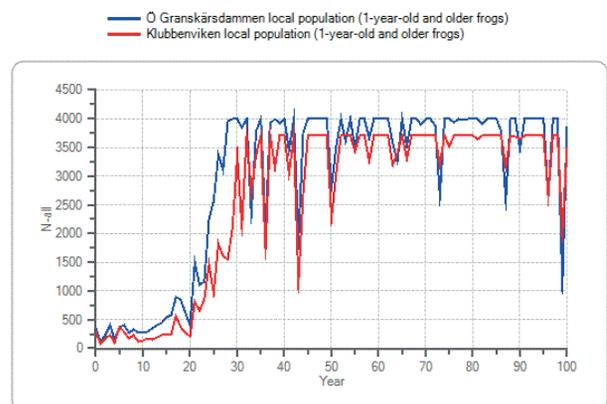


Figure 5. Population size trajectories of one simulation replicate of the two local pool frog populations Ö Granskärdsdammen (blue) and Klubbenviken (red) interconnected by dispersal and with no extra mortality

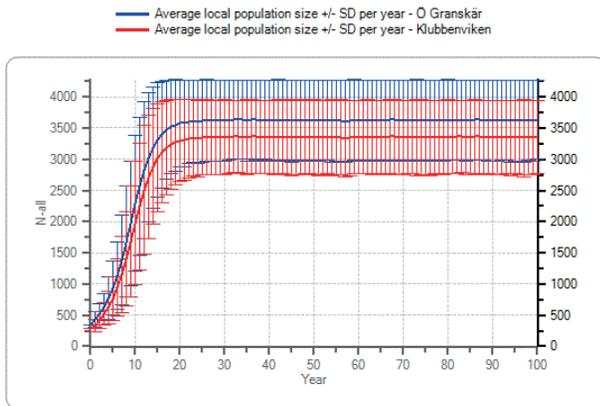


Figure 6. Yearly mean population size \pm SD during 10,000 simulation replicates of the two local pool frog populations (*Pelophylax lessonae*) at Östra Granskärssdammen and Klubbenviken, interconnected by dispersal and with no extra mortality added

Next, a number of scenarios explored the effect of various degrees of extra, additive mortality (5%, 10%, 15%, 20%, 25%, 30%) at the locality Klubbenviken while the other local population (Ö Granskärssdammen) remained unaffected. Even though the local population size at Klubbenviken became smaller in the simulations corresponding to the increased mortality, local extinction at this site did not occur at all with 5% extra yearly mortality. At 10% added mortality, local population size at Klubbenviken averaged 341 ± 1.2 (mean \pm SE including 1-yr old and older frogs) during simulations and 1 local extinction occurred with recolonization from Ö Granskärssdammen the following year. With additive mortality at 15%, the Klubbenviken subpopulation averaged 222 ± 0.8 pool frogs and 4 local extinctions occurred among the 10,000 replicates with recolonization after 1 or 2 years. At 20% additive mortality, it averaged 212 ± 0.8 frogs with 5 local extinctions; at 25%, it averaged 197 ± 0.8 with 21 local extinctions. At 30% additive mortality, the subpopulation averaged 179 ± 0.8 frogs (1-yr-olds and older) and experienced 76 local extinctions among the simulation replicates (Figure 7); recolonization occurred in all cases. In this case, most if not all frogs at Klubbenviken likely are immigrants.

Summarized, these results demonstrate significantly greater resilience of demographically (and genetically) interconnected sub- or local populations to withstand increased natural or anthropogenic environmental

pressures in comparison to that of isolated local populations. This resilience depends on that the dispersal connectivity and the “source” population(s) are unaffected, and demonstrates “source-sink” dynamics (Pulliam 1988).

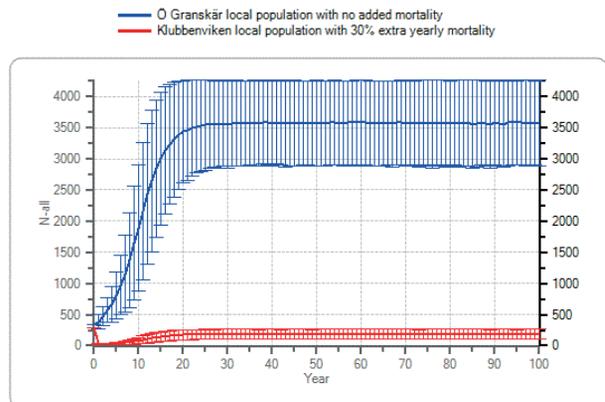


Figure 7. Yearly mean population size \pm SD during 10,000 simulation replicates of the two local pool frog populations (*Pelophylax lessonae*) at Östra Granskärssdammen and Klubbenviken, interconnected by dispersal and with 30% extra mortality at Klubbenviken

Already more than 30 years ago, scientists pointed to the need to distinguish between “source” and “sink” habitats in field studies of populations. This is important in both management and conservation. In his seminal paper, Pulliam’s (1988) argued and showed that active dispersal from source habitats can maintain even large “sink populations” and, furthermore, that such dispersal may be evolutionarily stable in the long term.

The second lesson (Lesson 2) from this case is that if emigration continues as normal, a local population in a pristine pond or patch that becomes isolated due to local extinction of neighbouring populations may still persist for quite a long time but faces a much higher extinction risk, similar to an “extinction debt” (Kuussaari et al. 2009). Since habitat quality *per se* was not spatially correlated in the Swedish metapopulation system, this increased extinction risk may also explain the spatially correlated extinction pattern in the pool frog metapopulation (Sjögren-Gulve, 1994). The extinction of a neighbouring “source” population may unfold a much higher local vulnerability of remaining populations.

Lesson 3 is that the results imply a risk of a “tipping point” phenomenon, in which isolated local populations may go extinct quite rapidly

since isolation commenced, due to only modestly increased or added mortality (Figure 4). Thus, introduction of predatory fish such as pike (*Esox lucius*) is detrimental (Sjögren-Gulve, 1994; Sjögren-Gulve and Ray, 1996), especially into ponds with source populations. Altogether, the results provide a demographic explanation of the isolation-associated extinction pattern observed in the Swedish pool frog metapopulation and also in other taxa.

Other amphibians

Regarding other European amphibians, Laan and Verboom (1990) examined the number of species and their presence/absence patterns in old vs. recently constructed pools in the Netherlands in relation to characteristics of the pools and the surrounding landscape. In both old and new pools, species number was positively correlated with vicinity of a wood, which was interpreted as a connectivity element in the landscape. Pool age was the prime predictor of species number in the new pools, and differences in pond colonization rate were related to the species' abundance, suggesting that dispersal was important in compensating for local extinctions in these local frog communities.

The above interpretation was corroborated by a field experiment by Mazerolle and Vos (2006) who presented edible frogs (*Pelophylax klepton esculenta*) with a choice between a short route through hostile environment and a longer but safer route to reach their focal pond. The frogs' ability to orient toward the pond decreased with pond distance and increased with distance to a hedgerow. Mazerolle and Vos concluded that both landscape and weather variables influence the movements of amphibians in agricultural settings, and that landscape quality thus can be important for population persistence.

In many European countries, the tree frog *Hyla arborea* has declined due to habitat fragmentation and loss of suitable breeding sites. Auffarth et al. (2017) predicted the viability of a *Hyla arborea* population of c. 70 adults inhabiting an isolated pond in the region of Hannover (Germany), by combining life history data with genotypic information from microsatellite markers. Their findings are in agreement with results in this pool frog analysis. Auffarth et al. found a high

probability of extinction within the next 50 years, with juvenile survival being a crucial demographic parameter for population persistence. Simulated natural immigration, or population supplementation, prevented genetic erosion and markedly increased the probability of population survival. They concluded that future management interventions should improve the pond habitat to enhance survival at young life stages, and create migration corridors to facilitate connectivity with adjacent local populations and/or consider translocation of individuals.

Similar conclusions were made for *Hyla arborea* populations in Switzerland by Angelone et al. (2011). They analysed how functional connectivity (frog movement and gene flow) among local populations depends on the landscape matrix between occupied habitat patches. They examined the effects of landscape elements and geographic distance on genetic differentiation among the local populations. Hedgerows and various structure-rich landscape elements affected gene flow positively. At distances < 2 km, only a larger river acted as a barrier to gene flow. At distances > 2 km, geographic distance had a negative effect on gene flow as had landscape elements such as forests and roads.

Findings by Ficetola and Bernardi (2004) are also in agreement with results presented here. They analysed patterns in amphibian presence/absence during the breeding season in 84 wetlands in Northern Italy in relation to their features and isolation. They found that amphibian presence depended strongly on habitat quality and isolation: the richest communities were found in fish-free, sunny wetlands near other occupied wetlands (cf. Lesson 1); the negative effects of isolation were not biased by spatial autocorrelation of habitat features. The system showed strong species nestedness, with species persistence dependent on the contemporary effects of species adaptability and mobility. The commonest species, the edible frog (*Pelophylax klepton esculenta*) and the Italian tree frog (*Hyla intermedia*) readily move through the landscape matrix using canals and hedgerows, and maintain metapopulations across the landscape, while the rarest species (newts and toads) are more sensitive to habitat change and

exhibited strong isolation effects (cf. Lessons 1-3). Ficetola and Bernardi concluded that if human exploitation of the studied landscape continues without consideration of such species groups, only the mobile and opportunistic few species will persist.

In population simulations, Griffiths (2004) found that local populations of the great crested newt (*Triturus cristatus*) - also a species protected by the EU Habitats Directive (Council Directive 92/43/EEC) - had an annual λ of 1.12. The extinction risk declined with an increasing number of local populations in the metapopulation. In scenarios with no dispersal, at least 4 local populations with 200 newts each were required for system persistence times > 100 years. With interpopulation dispersal, similar persistence times could be achieved with a similar number of local populations, but then even if they were half as big (cf. Lesson 1).

Roads are one anthropogenic factor in the landscape that affects amphibians and other taxa (Elzanowski et al., 2009; Selva et al., 2011).

That emigrant survival is important, indirectly sheds light on results from a study by Lesbarrères et al. (2006) of the agile frog (*Rana dalmatina*) in France. They analysed the degree of genetic diversity and differentiation within and among seven local populations far from trafficked roads (“non-fragmented”) in France compared to that of four local populations situated pairwise on both sides of a major highway (“fragmented”). The landscapes surrounding the agile frog ponds were otherwise similar and no ecological pond habitat variables (e.g. pond size) differed significantly between the groups. The four fragmented local populations had much lower genetic variation and greater differentiation than those of the non-isolated populations, and their local population size was less than 1/3 of the average of the non-isolated populations. Viewed in light of the conclusions about significant mortality in amphibians caused by road traffic, for example by Elzanowski et al. (2009), Lesbarrères et al.’s (2006) results indicate that the fragmented agile frog populations likely have become much smaller and more depauperate in genetic variation because of high mortality among their

emigrants due to the trafficked road (cf. Figure 7 and Lessons 1-2).

A conservation example with amphibians in North America where this study’s Lessons 1 and 3 may apply is provided by Fellers and Drost (1993). They found that healthy, seemingly well-protected populations of the Cascades frog (*Rana cascadae*) - which from historic accounts and museum records was once abundant close to the Lassen Volcanic National Park in California (USA) - had disappeared for no obvious reason. Where biologists less than 15 years earlier found 40 or more frogs at some of the examined sites, Fellers and Drost located two frogs at a single locality. This decline seemed caused by a combination of the presence of non-native predatory fish (i.e. extra mortality), which restricted habitat and limited dispersal of the frogs, loss of breeding habitat due to a five-year drought, and a gradual loss of open meadows and associated aquatic habitats.

In another example, Harper et al. (2008) used model projections of wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*) populations and related the amount of high-quality terrestrial habitat surrounding isolated wetlands to the decline and risk of extinction of the local amphibian populations. The simulation results indicated that current U.S. state-level wetland regulations were inadequate to support viable populations of the pool-breeding amphibians. They found that species with different life-history strategies responded differently to the loss and degradation of terrestrial habitat. The wood frog, with a short life span and high fecundity, was most sensitive to habitat loss and isolation, whereas the longer-lived spotted salamander with lower fecundity was most sensitive to habitat degradation which reduced adult survival rates. Their results demonstrated that high local population persistence requires sufficient terrestrial habitat, maintenance of habitat quality, and connectivity among the local populations. They thus stressed the essential roles of adequate terrestrial habitat and connectivity for maintenance of wetland biodiversity and ecosystem function.

Other taxonomic groups

To what extent may findings from studies on amphibians apply also to other taxonomic groups? Mazerolle and Villard (1999) reviewed 61 studies which simultaneously examined the effects of landscape variables and patch variables on the presence/absence and abundance of some invertebrate taxa, amphibians, reptiles, birds and mammals in various landscapes. They found that patch habitat variables had significant effects on all examined groups in all landscape types. Landscape variables, such as area of suitable habitat within a certain distance, were significant predictors of presence/absence for the vertebrate species but not for the majority of the invertebrates. Mazerolle and Villard (1999) concluded that more consideration of landscape characteristics generally is likely to enhance strategies for species conservation in landscapes.

As likely were the case for the Klubbenviken pool frog population under higher additive mortality, the review by Millon et al. (2019) found that the number of immigrants exceeded locally born individuals in recruitment for most avian populations (median = 0.57 based on 37 studies); this was twice that estimated for mammalian populations (median = 0.26; 11 studies). They argued that overall, it is likely that most populations benefit from immigrants (cf. Lesson 1) without necessarily being “sink” populations and that quantitative estimates of immigration should be core to future demographic studies in various landscapes.

In a review of 432 papers - most of them focusing on birds, mammals, and forested systems - Heinrichs et al. (2019) found that source-sink theory has become increasingly relevant for species conservation and management. While 79% of the reviewed papers claimed to identify source-sink dynamics in these taxa - indicating potential relevance of the demographic explanation here - nearly 23% of the 432 studies used neither demographic nor movement metrics to make their conclusions. Heinrichs et al. stressed that future studies need to take a more rigorous approach to defining sources and sinks to better assess the prevalence of source-sink dynamics (cf. Lessons 1-3) in systems subject to management and/or conservation.

Bommarco et al. (2014) examined species richness of habitat specialist and generalist butterflies, bees, hoverflies, and vascular plants in 45 seminatural grassland fragments of various size and degree of connectivity; those were situated in landscapes with contrasting land use conversion history. Habitat loss was estimated by comparing modern maps to ~45 years old aerial photographs. They found that bees responded rapidly to habitat loss, possibly because their primary nesting resource was destroyed. Species richness of specialist plants was best explained by historical habitat connectivity, richness of hoverflies by historical habitat area, and richness of butterflies by both historical habitat area and connectivity, indicating extinction debt for all these taxa (cf. Lessons 1-2). Habitat generalist butterflies and hoverflies, but not plants and bees, exhibited extinction debt mainly in relation to habitat area. No effect of landscape type *per se* was found.

They hypothesized that the slow extinctions (cf. Lesson 2) of persistent and long-lived plants might explain extinction debt for both plants and the herbivorous insects linked to these plants.

CONCLUSIONS

Amphibians are an important part of ecosystems and food webs (e.g. Gibbons et al., 2006).

This paper provides a demographic explanation of the isolation-associated extinction pattern observed in the Swedish pool frog metapopulation. Much indicates that the explanation has general relevance for the viability, conservation and management of subdivided populations of multiple organism groups - in forest, agricultural and mixed landscapes.

For several species of animals and plants, including amphibians, Bell et al. (2019) found that gene flow through immigration has helped prevent population extinction. Yet, they found that augmented gene flow is rarely used as a conservation strategy. In conservation actions for small isolated populations, they thus advocated that actions' focus should shift away from managing populations in isolation, and toward widespread restoration of gene flow.

In their recent review, Millon et al. (2019) found that a clear picture is still missing of how widely the immigration rate varies both among- and within-populations, in relation to extrinsic and intrinsic ecological conditions, even for the best studied avian and mammalian populations. They found that this empirical knowledge gap precludes the emergence of a sound conceptual framework that is important for conservation and population ecology.

In conclusion, my results and reviewed material confirm the significance of population connectivity, dispersal and gene flow in species conservation and in the landscape management to “protect, conserve and enhance the Union’s natural capital” (e.g. European Commission 2013). From an overarching “biodiversity, ecosystems, ecosystem services and nature-based solutions” standpoint, it is of key importance to identify and conserve source populations, and to restore “sink” populations and/or connectivity wherever it is relevant.

Most landscapes are under management in Europe, and management is under responsibility. Article 10 of the EU Habitats Directive (Council Directive 92/43/EEC) states that “*Member States shall endeavour, where they consider it necessary, in their land-use planning and development policies and, in particular, with a view to improving the ecological coherence of the Natura 2000 network, to encourage the management of features of the landscape which are of major importance for wild fauna and flora. Such features are those which, by virtue of their linear and continuous structure (such as rivers with their banks or the traditional systems for marking field boundaries) or their function as stepping stones (such as ponds or small woods), are essential for the migration, dispersal and genetic exchange of wild species.*”

ACKNOWLEDGEMENTS

I thank Dr. Adrian Asanica for inviting me as speaker and author at the 2020 year’s conference *Agriculture for Life*. Thanks go to the IUCN Conservation Planning Specialist Group for developing the VORTEX software. My research and writing time for this paper have been financed primarily by the Swedish

Environmental Protection Agency. The research was made possible also by grants from Olle Engqvist byggmästare, the World Wide Fund for Nature, Frans von Sydow’s Help Fund, the Uppland Foundation, and by formal permits from the Uppsala County Administration Board and the Uppsala University Ethical Committee for Scientific Use of Animals in Research. I am very grateful for all the field work done - with or without me - by Sven-Åke Berglind, Kjell Larsson, Ingrid Gulve, Lars Berg, Mats Höggren, Johan Elmberg and Kurt Elmqvist. Thank you!

REFERENCES

- Angelone, S., Kienast, F. & Holderegger, R. (2011). Where movement happens: scale-dependent landscape effects on genetic differentiation in the European tree frog. *Ecography*, 34, 714-722.
- Auffarth, J., Krug, A., Pröhl, H. & Jehle, R. (2017). A genetically-informed Population Viability Analysis reveals conservation priorities for an isolated population of *Hyla arborea*. *Salamandra* 53, 171-182.
- Bell, D.A., Zachary, A., Robinson, L., Funk, W.C., Fitzpatrick, S.W., Allendorf, F.W., Tallmon, D.A., & Whiteley, A.R. (2019). The exciting potential and remaining uncertainties of genetic rescue. *Trends in Ecology and Evolution* 34, 1070-1079.
- Bommarco, R., Lindborg, R., Marini, L. & Öckinger, E. (2014). Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Diversity and Distributions*, 20, 591-599
- Elzanowski, A., Ciesiolkiewicz, J., Kaczor, M., Radwańska, J. & Urban, R. (2008). Amphibian road-mortality in Europe: a meta-analysis with new data from Poland. *European Journal of Wildlife Research*, 55, 33-43.
- Ficetola, G.F. & De Bernardi, F. (2004). Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation*, 119, 219-230.
- Gibbons, J.W. et al. (2006). Remarkable amphibian biomass and abundance in an isolated wetland: Implications for wetland conservation. *Conservation Biology*, 20, 1457-1465.
- Griffiths, R.A. (2004). Great crested newts (*Triturus cristatus*) in Europe - Effects of metapopulation structure and juvenile dispersal on population persistence. In H.R. Akçakaya, Burgman, M.A., Kindvall, O., Wood, C.C., Sjögren-Gulve, P., Hatfield, J.S. & McCarthy, M.A. (Eds.) *Species conservation and management - case studies* (281-291), New York, USA: Oxford University Press.
- Hanski, I., Gaggiotti, O.E. (Eds.) (2004). *Ecology, genetics, and evolution of metapopulations*. London, England: Elsevier Academic Press.

- Hanski, I., Gilpin, M.E. (Eds.) (1997). *Metapopulation biology - ecology, genetics and evolution*. San Diego, USA: Academic Press.
- Harper, E.B., Rittenhouse, T.A.G. & Semlitsch, R.D. (2008). Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. *Conservation Biology*, 22, 1205-1215.
- Harrison, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, 42, 73-88.
- Heinrichs, J.A., Walker, L.E., Lawler, J.J., Schumaker, N.H., Monroe, K.C. & Bleisch, A.D. (2019). Recent advances and current challenges in applying source-sink theory to species conservation. *Current Landscape Ecology Reports*, 4, 51-60.
- Kuussaari, M. et al. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24, 564-571.
- Laan, R. & Verboom, B. (1990). Effect of pool size and isolation on amphibian communities. *Biological Conservation*, 54, 251-262.
- Lacy, R.C. & Pollak, J.P. (2018). VORTEX: A Stochastic Simulation of the Extinction Process. Version 10.3.1. Brookfield, Illinois, USA: Chicago Zoological Society.
- Lesbarrères, D., Primmer, C.R., Lodé, T. & Merilä, J. (2006). The effects of 20 years of highway presence on the genetic structure of *Rana dalmatina* populations. *Écoscience*, 13, 531-538.
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15, 237-240.
- Marsh, D.M. & Trenham, P.C. (2001). Metapopulation dynamics and amphibian conservation. *Conservation Biology*, 15, 40-49.
- Mazzerolle, M.J. & Villard, M.-A. (1999). Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Écoscience*, 6, 117-124.
- Mazzerolle, M.J. & Vos, C.C. (2006). Choosing the safest route: Frog orientation in an agricultural landscape. *Journal of Herpetology*, 40, 435-441.
- Millon, A., Lambin, X., Devillard, S. & Schaub, M. (2019). Quantifying the contribution of immigration to population dynamics: a review of methods, evidences and perspectives in birds and mammals. *Biological Reviews*, 94, 2049-2067.
- Pulliam, H.R. (1988). Sources, sinks and population regulation. *The American Naturalist*, 132, 652-661.
- Selva, N., Kreft, S., Kati, V., Schluck, M., Jonsson, B.-G., Mihok, B., Okarma, H. & Ibsch, P.L. (2011). Roadless and Low-Traffic Areas as Conservation Targets in Europe. *Environmental Management*, 2011, 865.
- Sjögren, P. (1988). Metapopulation biology of *Rana lessonae* Camerano on the northern fringe of its distribution. Acta Universitatis Upsaliensis Comprehensive Summaries of Uppsala Dissertations, 157. 35 pp. (PhD dissertation).
- Sjögren, P. (1991a). Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society*, 42, 135-147.
- Sjögren, P. (1991b). Genetic variation in relation to demography of peripheral pool frog populations (*Rana lessonae*). *Evolutionary Ecology*, 5, 248-271.
- Sjögren-Gulve, P. (1994). Distribution and extinction patterns within a northern metapopulation of the pool frog (*Rana lessonae*). *Ecology*, 75, 1357-1367.
- Sjögren-Gulve, P. (1998). Spatial movement patterns in frogs: Target-oriented dispersal in the pool frog (*Rana lessonae*). *Écoscience*, 5, 31-38.
- Sjögren-Gulve, P. & Hanski, I. (2000). Metapopulation viability analysis using occupancy models. *Ecological Bulletins*, 48, 53-71.
- Sjögren-Gulve, P. & Ray, C. (1996). Using logistic regression to model metapopulation dynamics: large-scale forestry extirpates the pool frog (*Rana lessonae*). In D. R. McCullough, (Ed.) *Metapopulations and Wildlife Conservation*, 111-137, Covelo, USA: Academic Press.
- ***European Commission, (2013). *Environment Action Programme to 2020*. <https://ec.europa.eu/environment/action-programme/> accessed on 10 May 2020.
- ***European Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. https://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm accessed on 10 May 2020.