

# Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*)

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Local extinction along the intrinsic isolation gradient within metapopulations is reviewed with particular reference to a study of the pool frog (*Rana lessonae*) on the northern periphery of its geographical range. As in the pool frog, many other different taxa show significantly increased extinction probabilities with increased interpopulation distance. Present data imply that the relative impact of demographic and genetic factors in such stochastic extinctions depends on the genetic history of the metapopulation; data also imply that populations fluctuate more greatly in size than predicted from demographic models which have been commonly referred to. By mitigating such fluctuations and inbreeding, and compensating for emigration, immigration undoubtedly 'rescues' local populations from extinction. In this way, and not just in terms of recolonization, connectivity is concluded to be a key to metapopulation persistence. Implications for conservation are also presented.

**KEY WORDS:**—Metapopulation – extinction – isolation – population fluctuations – demography – fertility – heterozygosity – *Rana lessonae*.

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## INTRODUCTION

Metapopulation theory (e.g. Levins, 1969, 1970; Hanski, 1987, 1989, 1991) regards extinctions of populations as a natural component of a species' regional dynamics. In this context, metapopulations and their dynamics provide a fundamental focus of study for conservation biologists (population vulnerability analysis: Gilpin, 1987).

Apart from deterministic extinctions and catastrophes (Lovejoy *et al.*, 1986; Ewens *et al.*, 1987; Simberloff, 1988; Pimm & Gilpin, 1989), studies of population persistence stress that local extinctions also can be due entirely to fluctuations in population size and composition caused by demographic and environmental stochasticities (Richter-Dyn & Goel, 1972; Leigh, 1981; Shaffer,

1981, 1987; Gilpin & Soulé, 1986; Gilpin, 1987, 1990; Goodman, 1987a; Simberloff, 1988; Pimm & Gilpin, 1989; Ebenhard, 1991) and to inbreeding effects (e.g. Frankel & Soulé, 1981; Berry, 1983; Schonewald-Cox *et al.*, 1983; Ralls, Harvey & Lyles, 1986; Ralls Ballou & Templeton., 1988). However, the relative importance of demographic and genetic factors in such extinctions of natural populations remains unclear (Lande, 1988).

For a variety of taxa, there is direct or indirect empirical evidence that the risk of local extinction increases with degree of isolation from conspecific populations (grouse: Fritz, 1979; pika: Smith, 1980; arthropods: Brown & Kodric-Brown, 1977; Toft & Schoener, 1983; mice: Fahrig & Merriam, 1985; shrews: Hanski, 1986; frogs: Sjögren, 1988, unpublished); the 'indirect evidence' usually being decreased average patch occupancy. Furthermore, higher extinction rates have been reported for fluctuating populations as compared to relatively stable ones (Leigh, 1981; Karr, 1982; Pimm, Jones & Diamond, 1988), and for populations in smaller habitats (Smith, 1980; Toft & Schoener, 1983; Bengtsson, 1989, 1991; Forney & Gilpin, 1989) and of smaller size (Toft & Schoener, 1983; Schoener & Spiller, 1987; Pimm *et al.*, 1988; Bengtsson, 1989, 1991; Forney & Gilpin, 1989). However, since inbreeding depression (Ralls & Ballou, 1983) is more likely to occur in smaller populations as well as in isolated ones, the fact that none of the above studies looked for inbreeding effects still leaves us unable to discriminate between demographic and genetic explanations; despite the urgent need, there are virtually no firm data on the role of inbreeding depression in extinctions of natural populations (Ralls *et al.*, 1986). As metapopulations naturally have an intrinsic range of interpopulation distances and (sub)population sizes, they provide opportunities to examine this issue.

This paper reviews recent results from an empirical study of a northern metapopulation of the pool frog (*Rana lessonae* Camerano; Sjögren, 1988, unpublished) and, briefly, results from other studies to examine and discuss the above 'distance effect' on population persistence and degree of patch occupancy. As far as possible, I will evaluate the relative importance of demographic and genetic factors in the local extinctions and discuss implications for population conservation and management.

#### STUDY SYSTEM AND RESULTS

Frogs in the temperate region occur as natural metapopulations; reproduction is confined to distinct water bodies and often involves conspicuous calling which permits easy detection and delimitation of local populations. Combined use of drift fences and hand-net captures permits close population monitoring where frogs can be individually marked to estimate population size, survivorship and dispersal rates between different breeding localities (e.g. Sjögren, 1988, unpublished; Berven, 1990). Furthermore, annual growth rings in toe phalanges can provide data on age structure (e.g. Leclair & Castanet, 1987), and egg masses and larvae in the water verify that reproduction has occurred. Since inbreeding depression primarily is manifested in reduced fertilization capability in males and increased offspring mortality at early life stages (Ralls & Ballou, 1983), the average proportion of fertilized eggs within egg masses provides a fertility index for examination of inbreeding effects in local populations.

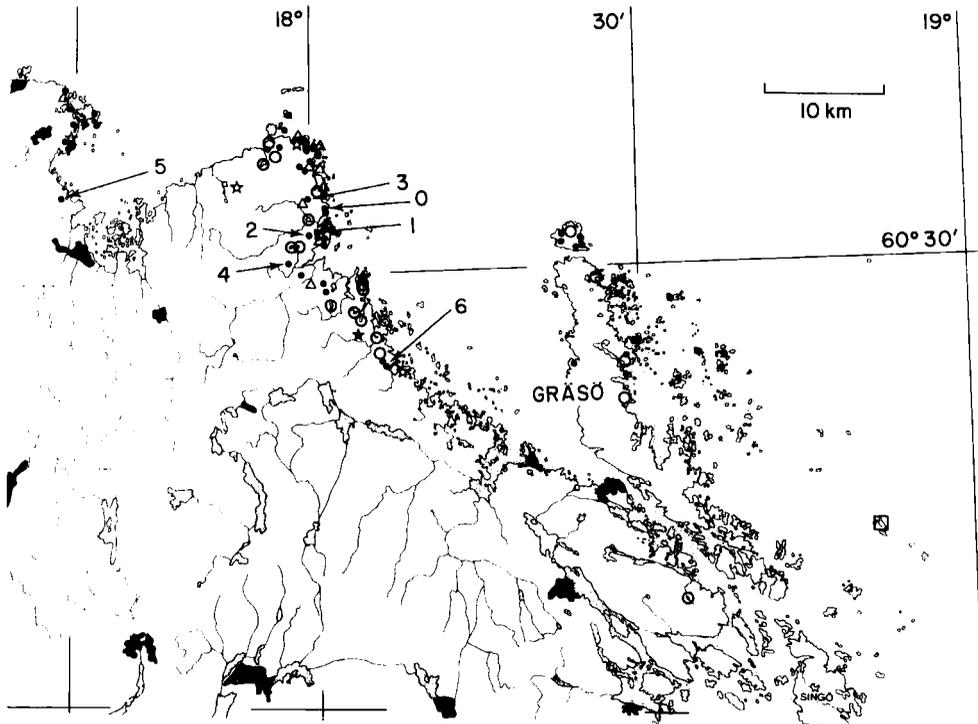


Figure 1. The regional distribution of the pool frog (*Rana lessonae*) along the Baltic coast of east-central Sweden in 1987/89. ●, Reproducing population (status 2, see text); △, locality with calling male(s) but without reproduction (status 1); ○, extinction(s) between 1962 and 1983 (status E); ☆, extinction(s) between 1983 and 1987 (status E); ◇, extinction between 1987 and 1989; ★, declining population with status 2 in 1987 and status 1 in 1989; □, locality reported by Forselius (1962) not visited in 1983 or 1987/89; four observations are hidden (status E and 1). 0 to 6 show localities at which proportions of fertilized eggs within egg masses were examined (Fig. 3). Changes in status from 1 to 2 occurred at localities 2 and 4 between 1983 and 1987, and at locality 5 between 1987 and 1989 (cf. Sjögren, 1988, unpublished). Black areas other than dots show villages.

The pool frog belongs to the shore-dwelling *Rana 'esculenta'*-complex (water frogs: Berger, 1983) and occurs at some 60 localities along the Baltic coast of east-central Sweden (Fig. 1). These local populations form an isolated metapopulation on the northern fringe of the species' distribution (60°N; Sjögren, Elmberg & Berglind, 1988). Because high water temperatures are required to initiate breeding, the pool frog reproduces 3–5 weeks later in spring than do the other anurans in the region. The short season thus imposes a time constraint on the pool frog's reproduction, which fails in cold years because of delayed spawning and retarded larval development (Sjögren, 1988, unpublished). Consequently, the species inhabits and reproduces successfully only in warm and permanent waters (Sjögren, 1988, unpublished).

The demography and survivorship of the Swedish pool frogs resemble that of the North American wood frog (*Rana sylvatica* Le Conte: Berven, 1990) but differ in some important aspects. Sexual maturation occurs at 2 years of age, but the females spend their first season as adults growing eggs that will be deposited first in the following year. The average life span of the frogs is 2.5 years but some individuals survive to 8 years of age (Sjögren, 1988, personal observations).

Because of the body size-dependent fecundity in the females, the Swedish pool frogs have a generation time of *c.* 3.9 years (calculated from an  $l_x m_x$  matrix). Depending on the weather (i.e. larval mortality) and the proportion of adults that reproduce in a given year,  $R_0$  potentially ranges from *c.* 0.5 to 7 (Sjögren, unpublished, cf. Berven, 1990) but usually is  $0.7 < R_0 < 2$ . In pond no. 0 (Fig. 1), which is representative for the Swedish local populations, the yearly proportion of reproducing adults ranged from 0.112 to 0.291 during 1984–1988, and its effective size ( $N_e$ ) was estimated to be 35 in 1985–1988 when two reproductive failures occurred (in 1985 and 1987; Sjögren, unpublished). Since all surviving females with mature eggs reproduced in a given year (Sjögren, 1988, personal observations), these low proportions of reproducing adults derived from the combination of higher mortality in the females than in the males and the fact that virtually no 2-year-old females reproduced, resulting in male-biased sex ratios ( $1.19 \leq \text{male/female} \leq 2.09$  during 1984–1988; Sjögren, 1988, unpublished; cf. Berven, 1990) and few spawning females.

The striking warmth preference and basking behaviour in both adults and the 5–7 cm long larvae (Sinsch, 1984; Sjögren *et al.*, 1988; cf. Bradford, 1984), and the conspicuous calling of the males, who respond to playback or imitation calls, make the pool frog particularly suitable for studies of presence/absence and population turnover. Apart from the permanent waters not known to have supported the species (status 0 in Fig. 2) or at which the pool frogs have gone extinct (status E), two other types of occurrences exist: status 1 with calling male(s) during the breeding season, but with no reproduction; and status 2 with a reproducing pool frog population.

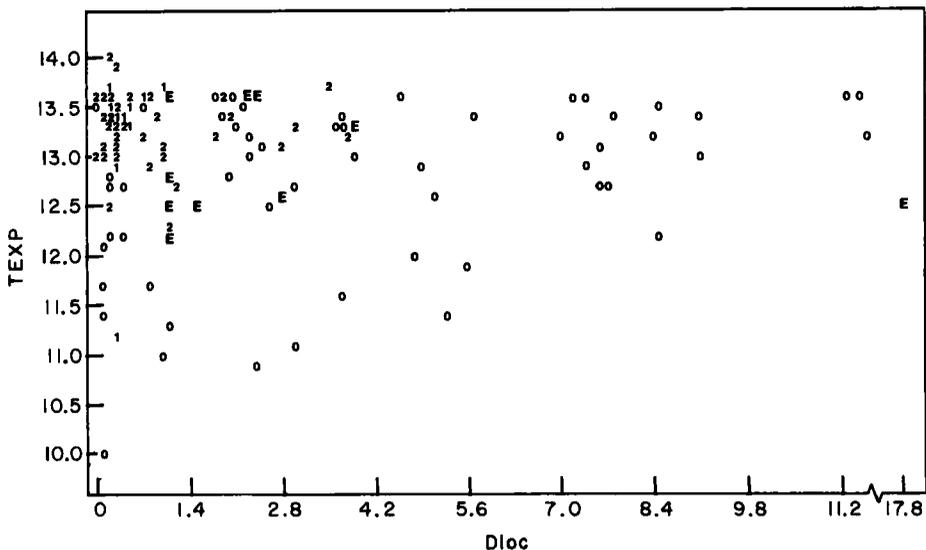


Figure 2. Plot of distance to the closest pool frog population [ $Dloc$  (km)] and local spring climate (= habitat quality) represented as estimated mean water temperature during May 25–31 1987 [ $TEXP$  ( $^{\circ}C$ )] of each of the 115 permanent waters analysed. 0, Water with pool frog absence (status 0); 1, calling locality without reproduction (status 1); 2, water with reproducing pool frog population; E, water at which the pool frogs have become extinct; all status data from 1987. Habitat quality, i.e.  $TEXP$ , was not spatially autocorrelated (i.e. to  $Dloc$ ,  $P > 0.10$ ; cf. Brown, 1984). Six observations are hidden (from Sjögren, unpublished).

TABLE 1. Differences in eight environmental variables between permanent waters with extant (status 1 and 2) and extinct (status E) pool frog populations in 1987 using stepwise logistic regression (BMDPLR: Dixon *et al.*, 1988). *ALK*, Alkalinity (equivalents  $m^{-3}$ ); *AREA*, water surface area (ha); *CAL*,  $[Ca^{2+}]$  (ppm); *Dext*, distance to the closest habitat with local extinction of the pool frog recorded (km); *Dloc*, distance to closest pool frog locality (km); *Dsea*, distance to the Baltic sea (km); *PIKE*, presence/absence of pike (*Esox lucius* L.); *TEXP*, estimated mean water temperature in late May 1987 ( $^{\circ}C$ ); means and SD shown by group in columns. Step selections were based on maximum likelihood ratio; regression coefficient ( $\beta$ ) and its SE shown for each entered variable ( $P < 0.05$ ) (from Sjögren, unpublished).

Variable entered	Status 1+2 $\bar{x} \pm SD$	Status E $\bar{x} \pm SD$	$\beta$	SE	$\chi^2$	P
1 LN ( <i>AREA</i> )	$-1.03 \pm 0.95$	$0.55 \pm 1.25$	-2.262	0.838	16.30	0.0001
2 <i>Dloc</i>	$0.74 \pm 0.90$	$3.50 \pm 5.11$	-2.193	0.783	24.96	< 0.0001
3 <i>Dext</i>	$2.87 \pm 2.08$	$2.53 \pm 4.39$	2.654	0.978	29.38	< 0.0001
Not entered:						
a <i>Dsea</i>	$0.39 \pm 0.46$	$0.84 \pm 0.64$	—	—	3.08	0.0790
0 Constant			—	—	1.97	0.1608
b <i>TEXP</i>	$13.3 \pm 0.5$	$12.9 \pm 0.5$	—	—	1.82	0.1776
c <i>CAL</i> †	$38.79 \pm 18.35$	$47.02 \pm 20.31$	—	—	1.20	0.2730
d <i>ALK</i> †	$2.14 \pm 0.95$	$2.34 \pm 1.24$	—	—	1.12	0.2904
e <i>PIKE</i> *	—	—	—	—	0.22	0.6385
N =	49	10				

Goodness of fit:  $\chi^2 = 16.90$ ,  $df = 56$ ,  $P = 1.000$ .

\*  $N_{1+2} = 36$ ,  $N_E = 8$ ,  $\chi^2$  given with effects of variables 1, 2 and 3 removed.

†  $N_{1+2} = 22$ ,  $N_E = 9$ ,  $\chi^2$  given with effects of variables 1, 2 and 3 removed.

Forselius (1962) surveyed the regional distribution of the pool frog in central Sweden in the 1950s but did not discriminate between localities of status 2 and status 1. In more recent surveys (1983 and 1987: Sjögren, 1988, unpublished), two types of local extinctions were recorded in this metapopulation: (1) deterministic extinctions due to vegetational overgrowing or ditching of pool frog waters, and (2) extinctions of populations with a distance to the closest neighbouring pool frog population (= *Dloc*) greater than 1.0 km that were observed also in high-quality habitats (Fig. 2, Table 1). None of the extinction localities was recolonized in subsequent years (1984–1988).

In the type (2) extinctions, the extinct populations typically inhabited larger permanent waters than the extant ones, and had a shorter distance to the closest extinct neighbour (Table 1); the latter indicated a moderate spatial correlation of the local extinctions (Sjögren, unpublished). Focusing on area and interpopulation distance, adult population size was not significantly correlated to pond area ( $r = -0.43$ ,  $P = 0.40$ ; Fig. 3), but data and personal observations imply that pool frog populations in waters with pike (*Esox lucius* L.) were smaller than at pike-free localities (Fig. 3). As large water area was the sole significant predictor of pike presence (logistic regression:  $\chi^2 = 73.26$ ,  $df = 1$ ,  $P < 0.0001$ ; Sjögren, unpublished; Fig. 3), the inverse 'area effect' probably derived from predation by pike, which did not affect population persistence significantly until a critical degree of isolation was reached (Fig. 2; cf. Toft & Schoener, 1983). Demographically, a *Dloc* of 1.0 km would correspond to an immigration rate of between 2 and 15 frogs per generation (*c.* 4 years) (Sjögren, 1988, unpublished).

To investigate whether the significantly increased extinction probabilities at

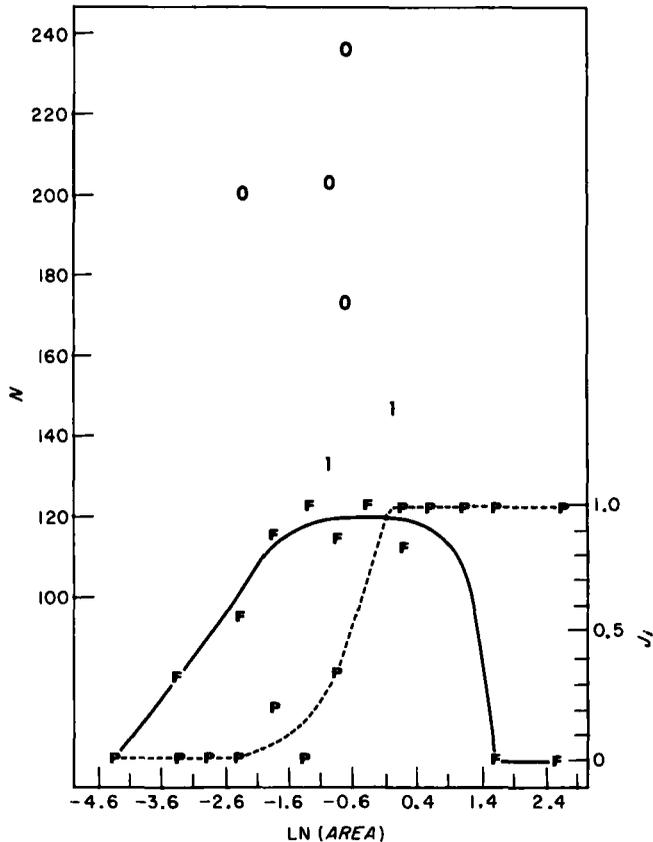


Figure 3. Size of six local pool frog populations ( $N$ ), and incidence ( $J_i$ ) of pike (*Esox lucius*; P) and the pool frog (*Rana lessonae*; F), in relation to pond size [ $\text{LN}(\text{AREA})$ ]. Population size data are from 1986 when the local populations were large and include frogs older than one year: 0, locality without pike; 1, locality with pike; presence/absence data for pike and the pool frog derive from the inventory made in 1987; population size was estimated from a Lincoln index (Southwood, 1978).

$D_{loc} > 1.0$  km had an apparent genetic explanation, i.e. inbreeding depression, the proportion of fertilized eggs within egg masses ( $FER$ ) was examined at seven breeding localities with different degrees of isolation (Fig. 1). These included two specific localities with  $D_{loc} = 1.1$  and  $1.2$  km (nos 2 and 4 in Figs 1 and 4), where the pool frogs did not reproduce in 1983 but did so in 1987 (Sjögren, unpublished). As is shown in Fig. 4, no significant reduction in fertility was found in populations with  $D_{loc} \leq 2$  km. Results from a stepwise regression analysis, including all continuous variables in Table 1, suggest an environmental rather than a genetic explanation for the pattern in Fig. 4: the mean proportion of fertilized eggs within egg masses (arcsine-transformed) showed a higher correlation to water alkalinity ( $ALK$ ), which explained 77% of the variance ( $r = -0.878$ ,  $F = 16.78$ ,  $df = 1,5$ ,  $P < 0.01$ ; the only variable entered), than to  $D_{loc}$  ( $F = 0.64$ ,  $df = 1,4$ ,  $P = 0.47$ ; effect of alkalinity removed). In the comparison of the habitats of extinct and extant pool frog populations, however, alkalinity did not differ significantly between the groups (Table 1).

## DISCUSSION

*Genetic versus demographic factors in extinctions*

My results do not indicate any signs of inbreeding depression in pool frog populations isolated by 2 km or less from the closest neighbouring population (*Dloc*). Since the observed reductions in the proportion of fertilized eggs within egg masses (Fig. 4) appear largely explained by water alkalinity, present data offer no support to the hypothesis that inbreeding depression had a major role in the type (2) extinctions within the pool frog metapopulation. They also imply that absence of egg-carrying females in some years, a severe demographic consequence of combined environmental and 'heterogeneous' demographic stochasticity in small and relatively isolated populations (Ebenhard, 1991), accounted for the change in pool frog status in study localities 2 and 4 between 1983 and 1987.

In this situation, reduced survival and population size in the pool frogs due to predation by pike in larger waters (Fig. 3) will increase the extinction probability significantly. As only 1–2% of a female's offspring survive from embryo to adulthood in pike-free waters (Sjögren, unpublished), one adult immigrant could potentially have the same reproductive value as  $10^2$  additional offspring. With increased isolation, occasional absence of reproduction in small

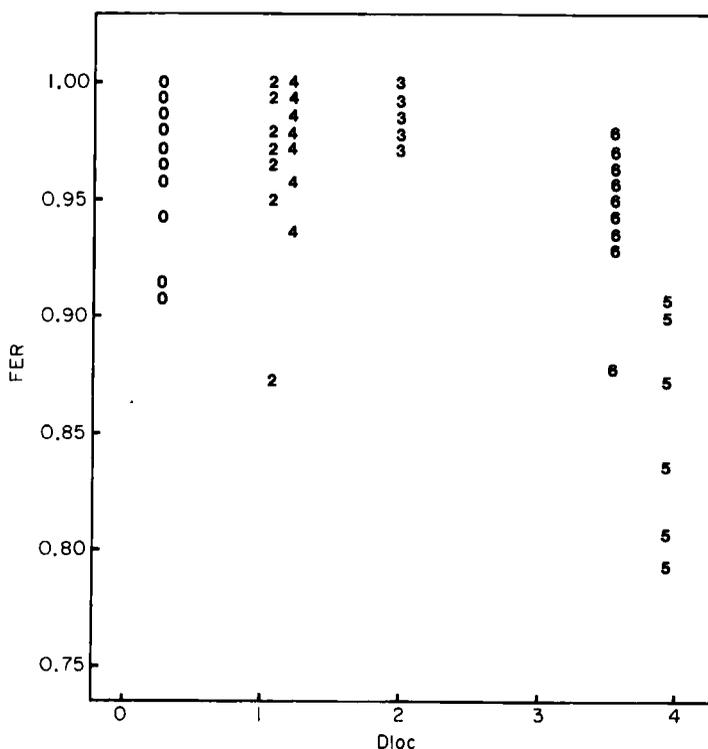


Figure 4. Plot of proportion of fertilized eggs per egg mass (*FER*) against distance to the closest neighbouring pool frog population [*Dloc* (km)] for breeding populations/localities 0 to 6 in Fig. 1. Fifty-nine observations are hidden, e.g. all from locality 1 (*Dloc* = 0.26 km); sample sizes were  $n_0 = 50$ ,  $n_1 = 6$ ,  $n_2 = 9$ ,  $n_3 = 7$ ,  $n_4 = 16$ ,  $n_5 = 6$ ,  $n_6 = 9$  (23 045 eggs).

populations as above becomes more likely, causing further and stronger fluctuations in population size and increasing the risk of extinction (Leigh, 1981; Karr, 1982; Pimm *et al.*, 1988; Forney & Gilpin, 1989). Hence, at a critical degree of isolation (Fig. 2), the pool frogs in larger waters with pike will be the first to become extinct; this is probably why *AREA* precedes *Dloc* in Table 1.

Since all isolated extinction localities at one time did support pool frog populations, and *Dloc* but not *AREA* has increased with time due to deterministic extinctions of intervening populations (type (1) above; Sjögren, unpublished), increased *Dloc* appears to be the ultimate extinction factor. Apart from mitigating population fluctuations (Reddingius & den Boer, 1970; Forney & Gilpin, 1989), immigration will stem inbreeding depression (Simberloff, 1988). However, the genetic effects of an immigration rate of 2–15 frogs per generation (at *Dloc* = 1.0 km) are likely to be greater than the demographic ones (cf. Crow & Kimura, 1970; Lacy, 1987). But in the most isolated populations, inbreeding effects cannot be ruled out. In the Swedish pool frogs, future reciprocal crosses of frogs from central and the most isolated populations will help clarify the genetic components of the pattern in Fig. 4.

To my knowledge, the relative importance of genetic and demographic factors in extinctions of natural populations has only been assessed in one other empirical study: the Bay checkerspot butterfly, *Euphydryas editha bayensis* Boisduval (Ehrlich, 1983; Ehrlich & Murphy, 1987). Both studies conclude that, apart from deterministic extinctions, combined environmental and demographic stochasticity was more important than genetic factors (heterozygosity, inbreeding depression) in the local extinctions (see also Lande, 1988; Simberloff, 1988). The fact that the same conclusion was reached for two such different taxa suggests that it has general validity, but such interpretations should be made with caution (see below); several more and comparable studies of metapopulations of different taxa are needed to examine this issue.

The *Euphydryas* and pool frog systems share some important features, such as a strong impact of environmental stochasticity causing extensive variation in population size between years (Ehrlich & Murphy, 1987; Harrison, Murphy & Ehrlich, 1988; Sjögren, 1988, unpublished). Two years after a reproductive failure, the local Swedish pool frog populations are reduced to half their size because of annual mortality and absence of two-year-old recruits. Two populations averaged 146 and 136 in size ( $\bar{N}$  excluding 1-year-olds) during five and three years respectively (Sjögren, 1988, unpublished), but their CV's ( $SD/\bar{N}$ ) were 38% and 52% which widely exceed that expected from 'pure' demographic stochasticity ( $= 1/\sqrt{\bar{N}}$ : Richter-Dyn & Goel, 1972; Leigh, 1981; see Ebenhard, 1991). Harrison *et al.* (1988) also showed that population fluctuations in the Bay checkerspot were environmentally induced. However, the great reproductive potential in both taxa allows rapid recovery from population 'bottlenecks'. In such systems with low to moderate vagility (cf. Ehrlich, 1983), reduction of genetic load is likely to have occurred and populations can experience relatively strong inbreeding without exhibiting inbreeding depression (see Lande, 1988). This has been suggested to explain the differing effect of inbreeding on reproductive success in natural bird populations (Gibbs & Grant, 1989).

Genetic data imply that the Swedish pool frogs historically have been subjected to inbreeding during recurrent strong fluctuations in population size

and founder events which have reduced their genetic load substantially (cf. Gilpin, 1991). In 28 enzyme loci examined with electrophoresis, the average heterozygosity ( $\bar{H}_s$ ) was 0.0047 in the most polymorphic local population (no. 0;  $\bar{n} = 71.1$  per locus) compared to the corresponding 0.0497 ( $n = 63$ ) in Polish conspecifics (Sjögren, unpublished). Recent studies of hypervariable minisatellite DNA sequences ('DNA fingerprinting': Tegelström & Sjögren, 1990) revealed monomorphic 'fingerprints' in population no. 0 while the Polish pool frogs exhibited normal variation. The fact that this low heterozygosity *per se* has not resulted in reduced fertility compared to that of other, more heterozygous, anuran populations (Sjögren, 1988, unpublished) suggests an 'inbreeding tolerance' in the Swedish pool frogs. But this may not apply to all metapopulations.

In a metapopulation of the tree frog *Hyla arborea* L. in southernmost Sweden, experimental reciprocal crosses of frogs from isolated/smaller and central/bigger local populations showed that the proportion of fertilized eggs within egg masses and the rate/success of larval development were significantly lower in clutches of frogs from isolated localities (A. Carlson & P. Edenhann, unpublished data). It is known that the sizes of central populations in this system may be up to five orders of magnitude larger than corresponding pool frog populations; this difference may explain the greater effects of isolation/inbreeding on fertility in the Swedish tree frogs. I conclude that if there is a general pattern in the relative importance of demographic and genetic factors in extinction processes, it will relate to the genetic history of the populations.

#### *Implications*

Leaving the genetic issue aside and just acknowledging that immigration has positive effects on population persistence for both demographic and genetic reasons, the fact that average patch occupancy decreases and local extinction probabilities increase with increased isolation in many different taxa (Brown & Kodric-Brown, 1977; Fritz, 1979; Smith, 1980; Toft & Schoener, 1983; Fahrig & Merriam, 1985; Hanski, 1986; Harrison *et al.*, 1988; Sjögren, 1988, unpublished) has important implications for metapopulation theory and conservation biology. Minimum viable population studies (e.g. Ewens *et al.*, 1987; Goodman, 1987b; Shaffer, 1987) stress that virtually no single population is immune to extinction. As long as local extinctions occur, even at very low rates, counterbalancing (re)colonization is the only way by which the number of local populations can be kept at a level where simultaneous extinction of them is unlikely (Hanski, 1991). This is also the logic of Levins's (1969, 1970) model.

It is clear that immigration and colonization rates decrease with increased isolation of patches in most taxa (e.g. Gilpin & Diamond, 1981; Toft & Schoener, 1983; Sjögren, 1988; Harrison, 1989), but for many it is also evident that extinction probabilities increase along the same gradient, indicating that immigration affects local persistence through a 'rescue effect' (Brown & Kodric-Brown, 1977). Toft & Schoener (1983) reported increased absolute extinction rates with increased isolation in orb spiders on Bahamian islands without predatory *Anolis* lizards. Fahrig & Merriam (1985) demonstrated significantly lower growth rates in isolated populations of the white-footed mouse (*Peromyscus leucopus* Raf.) than in central ones due to the fact that density-independent emigration was not sufficiently compensated for by immigration. In

an experimental study with *Drosophila* flies, Forney & Gilpin (1989) showed that immigration mitigated size fluctuations in the recipient population and thus lowered the extinction rate (cf. Leigh, 1981; Karr, 1982; Pimm *et al.*, 1988). Preliminary results from stochastic simulations of population persistence in the pool frog concur with these findings (Sjögren, unpublished). The fact that extinctions of pool frogs due to isolation first occurred at interpopulation distances greater than 1.0 km (Fig. 2) but colonizations occurred 300 m from reproducing populations (Sjögren, unpublished) suggests that a smaller number of immigrants suffice to 'rescue' an existing population than to successfully found a new (cf. Ebenhard, 1991). All this emphasizes the importance of the 'rescue effect' for local and regional persistence, and for average patch occupancy, in various systems (cf. Ray, Gilpin & Smith, 1991).

One implication for conservation is that the combination of deterministic and isolation-dependent stochastic extinctions in the Swedish pool frogs in fact is analogous to the extinction pattern associated with severe habitat fragmentation (Sjögren, unpublished). The fragmentation process poses a twofold extinction threat at local and regional levels. In addition to the increased risk of extinction following from the reduction in population size (e.g. Gilpin & Soulé, 1986; Goodman, 1987a; Shaffer, 1987), increased isolation of the remaining populations beyond a critical degree (above; Hanski, 1985) is likely to increase the risks of local and regional extinction further, and especially in taxa susceptible to environmental stochasticity (Sjögren, unpublished). As many frog populations belong to this category (e.g. Corn & Fogleman, 1984; Sjögren, 1988; Berven, 1990), this may similarly explain the sudden disappearance of individual populations from seemingly pristine, but isolated, reserves, highlighted in a recent conservation conference on the global decline of amphibians (Barinaga, 1990).

The implications for reserve 'design' and management are that reserves should include sets of interconnected local populations and vacant suitable habitats, or be located in groups so that connectivity is achieved. Apart from that it allows 'rescue effects' and (re)colonization, an equally important aspect of this strategy is that it increases the survival of dispersers/emigrants and, thus, enhances population growth rate (Fahrig & Merriam, 1985), and allows a more dynamic system with fewer density effects (Hansson, 1991). With reference to the spatial correlation of the local extinctions in Table 1, it may be questioned whether population proximity would not increase the risk of simultaneous or correlated extinction of all populations. However, present results undoubtedly show that the negative demographic/genetic consequences of isolation on local persistence in a metapopulation (i.e. increased size fluctuations, inbreeding, no compensation for emigration or high mortality) override its assumed benefits in terms of 'environmental independence' yielding independent local extinction probabilities (cf. Quinn & Hastings, 1987). According to Harrison & Quinn (1989), with an average extinction rate of 0.021 per year or 0.085 per generation as in the pool frogs, even a 100% correlation of the local extinction probabilities will have very little effect on overall persistence.

Empirical data confirm the existence of a critical isolation threshold for local and regional persistence within metapopulations (Smith, 1980; cf. Hanski, 1985) and which is not due to spatial autocorrelation of habitat quality (Harrison *et al.*, 1988; Sjögren, unpublished; cf. Brown, 1984), thus suggesting a 'rescue'

effect. Future empirical studies of to what degree population fluctuations and local extinction probabilities are spatially autocorrelated in metapopulations (cf. Reddingius & den Boer, 1970; Roff, 1974; Goodman, 1987b; Gilpin, 1990) will make important contributions to metapopulation theory and conservation biology.

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