Distribution and Extinction Patterns within a Northern Metapopulation of the Pool Frog, Rana Lessonae

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DISTRIBUTION AND EXTINCTION PATTERNS WITHIN A NORTHERN METAPOPULATION OF THE POOL FROG, *RANA LESSONAE*[1]

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Abstract. The distribution and extinction patterns within a northern metapopulation of the pool frog (*Rana lessonae*) were analyzed with reference to metapopulation theory. Occupied ponds were permanent and differed from unoccupied ones in terms of higher water temperature during May–June and a closer proximity to neighboring pool-frog localities, but local climate was not spatially autocorrelated. Two types of population extinctions occurred (average rate = 2% per population and year): (1) deterministic extinctions due to succession or draining of pool-frog ponds, and (2) extinctions of populations whose isolation had increased to a critical degree because of Type 1 extinctions of neighboring populations, increasing their susceptibility to predation and combined demographic/environmental stochasticity. The Type 2 extinctions were spatially correlated to a moderate degree, which may reflect the great impact of environmental stochasticity in the system. The results confirm and emphasize the importance of interpopulation proximity and connectivity for metapopulation persistence.

Key words: colonization; conservation; extinction; isolation; local climate; metapopulation dynamics; persistence; predation; Rana lessonae; *regional distribution.*

INTRODUCTION

The regional distribution of a species can be viewed as the net result of extinctions and colonizations among a set of local populations that constitute a metapopulation (Levins 1969, 1970, Hanski and Gilpin 1991). Where local extinction outweighs (re)colonization, the range of the species ends (Carter and Prince 1981).

Minimum Viable Population (MVP) theory suggests that no single population is immune to extinction (e.g., Soulé 1980, Shaffer 1987); consequently, the key to species persistence would be the existence of multiple populations, which reduces the risk of overall extinction (Goodman 1987*a*). However, few natural systems have been examined from this metapopulation perspective (Harrison 1991). One fundamental question is whether local extinctions occur randomly or can be predicted from a common pattern; another issue is to what degree local extinctions are spatially and temporally correlated, and how this affects the persistence of metapopulations (Goodman 1987*a*, Quinn and Hastings 1987, 1988, Gilpin 1988, 1990, Harrison and Quinn 1989).

The pool frog (*Rana lessonae* Camerano) is known from ≈60 Scandinavian localities, all of which are ponds situated along the Baltic coast of east–central Sweden (Forselius 1962, Ebendal 1979). These local populations form an isolated metapopulation on the northern fringe of the species distribution (60° N) and ≈380 km west–northwest of its main range (Sjögren 1991*a*). In 1948–1962, this system was surveyed by Forselius (1962) who found 50 pool-frog localities. Six were added by Haglund (1972) and Fernholm and Stolt (1976).

Forselius (1962) reported that many ponds in the area were not inhabited by pool frogs. An apparent explanation is that these ponds were unsuitable for the species, but the pattern is also predicted from Levins' (1969, 1970) theory of metapopulation dynamics. Accordingly, I investigated some proposed hypotheses for this patchy distribution: (A) the pool frog is restricted to a lime-rich region and, hence, specific requirements regarding lime content or pH/alkalinity of the ponds might explain its presence/absence pattern (Forselius 1948, 1962); (B) the absence of pool frogs at certain permanent ponds may be due to predation by pike (*Esox lucius* L.; cf. Ahlén and Berglund 1980); (C) temperature has a major impact on the reproductive success and behavior of the pool frog (Sjögren et al. 1988, Sjögren 1991*a*), and its presence/absence pattern may thus reflect differences in local climate with warmer ponds being more suitable for the species (Forselius 1948, 1962; cf. Ahlén 1984). Alternatively, (D) the presence/absence pattern may reflect random local extinctions, which are impossible to characterize on the basis of habitat variables (cf. Levins 1969, 1970).

To test these hypotheses, repeated censuses were carried out in 1983 and 1987 to assess: (1) changes in local distribution since the 1960s, (2) short-term changes from 1983 to 1987, and (3) environmental characteristics of occupied ponds in comparison with unoccupied ones and extinction sites, respectively. I briefly

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evaluate the applicability of my results for other patch-ily distributed populations.

MATERIALS AND METHODS

The natural history of the Swedish pool frogs is sum-marized by Sjögren (1991b); they are pond-dwelling water frogs (Berger 1977) with an average life-span of ≈2.5 yr (maximum = 8 yr) and a generation time of ≈3.7–3.9 yr (Sjögren 1988, 1991a, b). The postbreed-ing season is spent at the water's edge, and adult frogs are highly faithful to their breeding pond (emigration rate < 1%) whereas emigration is more common among juveniles (35%; P. Sjögren Gulve, unpublished manu-script; cf. Gill 1978). This species' territorial calling behavior and striking preference for higher tempera-tures (Brzoska 1982, Sinsch 1984, Radwan and Schnei-der 1988, Sjögren et al. 1988) make it highly suitable for population turnover studies; playback or imitation calls will prompt even a single male to respond and reveal his presence (P. Sjögren Gulve, personal obser-vations), and conspicuous basking characterizes both the frogs and their larvae (cf. Bradford 1984). Because high water temperatures are required to initiate breed-ing (Sjögren et al. 1988), the pool frog starts spawning 3–5 wk later in spring than do the other anurans along the Baltic coast. Consequently, its reproductive success at 60° N is highly weather dependent and variable. In cold years, breeding is delayed and reproduction fails because few or no larvae complete metamorphosis (Sjögren 1988, 1991a).

In 1983, nearly 200 ponds (including lakes and tem-porary ponds) between Gårdskär (60°38' N, 17°37' E) and Väddö (60°06' N, 18°48' E) were censused, cov-ering all except one of the previously reported localities (see Introduction). The majority of them were censused at least twice during optimal (warm) weather condi-tions: (1) day and night visits between mid-May and the end of June when the pool frogs breed, and (2) day visits in August–September when metamorphosing lar-vae (5–7 cm long) and juveniles (3 cm) easily can be observed/caught in sunny and shallow parts of a breed-ing pond, verifying successful reproduction. If frogs or larvae were not observed in a habitat, the visit was repeated, searching intensified, and known reproduc-tion sites were visited on the same day to check the reliability of the observations.

The ponds were classified according to their pool frog status: (0) not occupied by pool frogs, (1) with calling male(s) present during the breeding season but without reproduction, (2) with a reproducing pool-frog population, or (E) with previously reported occurrence but population now extinct.

At each pond, the presence or absence of other am-phibians, fish (e.g., PIKE) and invertebrate predators (dragonflies, diving beetles) was noted as part of a gen-eral environmental description. The pond's degree of exposure to sun and wind (EXP) was ranked on a scale from 1 (totally surrounded by dense forest and bush

vegetation) to 5 (totally open, i.e., no surrounding bush and tree vegetation). In August–September, the per-manence of the water was assessed.

In 1987, the census was repeated for all permanent ponds. Environmental changes were noted and water samples taken ≈15 cm subsurface, 1–2 m out from the shoreline, to measure alkalinity (ALK) and calcium (lime) content ([Ca^{2+}]: CAL). Alkalinity was consid-ered a more reliable measure of water acidity than pH. Pond area was measured using an ALTEK Digitizer (Board ATC 46-2) from maps or photos with a scale of 1:10 000. A mean (= AREA) was calculated from three to four repeated measurements of each water surface. Distances from each pond to the Baltic Sea (Dsea), to the closest pool-frog pond (status 2; Dloc), and to the closest other habitat with local extinction of the species recorded (Dext) were measured from maps (scale 1:50 000 or 1:10 000).

Temperature measurements and calculation of TEXP

Local climate was measured as mean water temper-atures, ≈15 cm subsurface, in 17 permanent ponds from 1 May to 15 October 1987. Eight of these ponds were inhabited by pool frogs, seven of them were not inhabited by the species in 1983 and 1987 (status 0 above), and two had occurrences of unknown status in the 1950s (Forselius 1962) but were now unoccupied (status E in 1983 and 1987).

In 4 of the 17 ponds, water temperatures were mea-sured each hour at 10 fixed positions using Aanderaa loggers, intercalibrated at the Swedish Meteorological and Hydrological Institute (SMHI). In 15 of the ponds, mean water temperatures were measured at four fixed positions at each pond with pH-buffered sucrose so-lutions (pH 1.21 and 2.3) according to Berthet (1960) and Ryrholm (1988). Thus, two ponds had four sucrose solutions running right beside thermistors from Aan-deraa units, which allowed a direct calibration of the sucrose system. With this methodology, the mean tem-perature values from the sucrose solutions on average deviated 0.1°C from those of the Aanderaa units, and the maximum absolute deviation recorded was 0.3°C.

For the remaining 98 ponds, where local climate was not measured directly, a calculated mean water tem-perature during 25–31 May 1987 (TEXP) was used as a local climate estimate in the habitat analyses. TEXP was calculated from the pond's surface area (AREA) and its degree of exposure to wind and sun (EXP) using an equation fitted to the temperature data from the 17 ponds above. With $x = \ln(EXP \cdot AREA)$:

$$TEXP = 10.0 + 3.65 \cdot e^{-[(0.127 - 0.022x) \cdot (0.096 + x)^2]}$$

($r^2 = 0.739$, $F_{5,12} = 9 929.6$, $P < 0.0001$; PROC NLIN: SAS 1988), a function which is maximized at $x = -0.1$. For the 17 ponds with temperature data, their respec-tive mean water temperature measured during 25–31 May was used as TEXP.
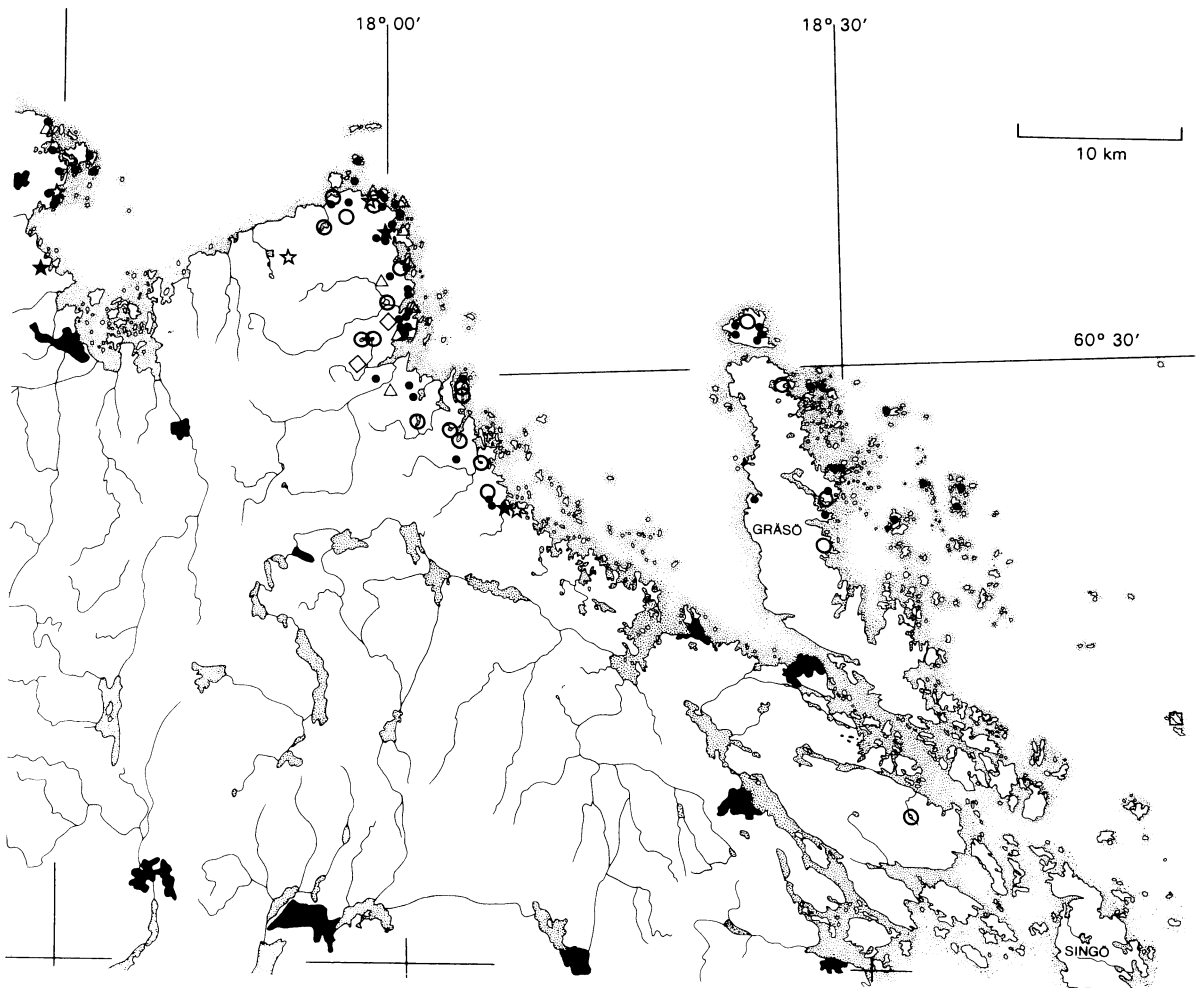
FIG. 1. The regional distribution of the pool frog (*Rana lessonae*) along the Baltic coast of east–central Sweden in 1983–1987. ● = reproducing population (status 2); △ = locality with calling male(s) but without reproduction (status 1); ○ = extinction(s) between 1962 and 1983 (status E); ☆ = extinction(s) between 1983 and 1987 (status E); ★ = declining population with status 2 in 1983 and status 1 in 1987; ◇ = population with status 1 in 1983 and status 2 in 1987; □ = locality reported by Forselius (1962) not visited in 1983 or 1987; four observations are hidden. Black areas other than dots show villages.

Analysis of habitat characteristics

The ponds were grouped according to their status in 1987, with habitats of status 1 and 2 pooled as "occupied" in the statistical analyses. Only ponds from the most thoroughly surveyed areas were included (n = 115); Gräsö and the northern part of its archipelago were excluded.

With respect to the presented hypotheses, seven variables were analyzed using stepwise logistic regression (BMDPLR: Dixon 1988), i.e., *ALK, CAL, Dloc, Dsea,* ln(*AREA*), *TEXP,* and *PIKE.* In the comparisons of habitats of extinct and extant populations, *Dext* was also included. All variables and the regression constant started out of the logistic model; the critical P values for entering or removing a variable or the constant were 0.05, and step selections were based on a maximum likelihood ratio. Corresponding stepwise discriminant analyses (PROC STEPDISC: SAS 1988), with all vari-

ables except *PIKE*, were also performed to examine possible differences in results after making sure that each variable was normally distributed within each habitat group (PROCs UNIVARIATE and RANK Normal=Blom: SAS 1988). The results were concordant, so the results from discriminant analyses are only shown where the convergence criteria for logistic regression (see Dixon 1988) were not satisfied. Finally, spatial autocorrelation of *TEXP* was examined using the SAAP program by Wartenberg (1989).

RESULTS

The censuses

The results of the censuses in 1983 and 1987 are compiled in Fig. 1. Reproducing pool-frog populations only occurred in permanent ponds ($\approx 70\%$ of the examined localities). Other amphibians and invertebrate predators were also far more abundant at these local-

TABLE 1. Changes in status of pool-frog (*Rana lessonae*) localities from 1983 ($S_1 \rightarrow$) to 1987 ($\rightarrow S_2$): 0 = absence, E = local extinction (no frogs nor larvae present during 1987–1988), 1 = calling locality without reproduction, 2 = reproducing pool-frog population.

	$0 \rightarrow 1$ Coloni-zation	$1 \rightarrow E$ Extinc-tion	$1 \rightarrow 2$	$2 \rightarrow 1$	$1 \rightarrow 1$ $2 \rightarrow 2$
Number of localities	3	6	2	3	6 54

ities than at other ponds in the area. Apart from the permanent ponds of status 2 (reproducing populations) and 0 or E (without pool frogs), some ponds had calling males during the breeding period although no reproduction occurred there (status 1). Such ponds located <300 m from breeding ponds (status 2) were labeled "satellite ponds" since they contain opportunistic males that call early in the breeding season but later often join the neighboring reproducing population (P. Sjögren Gulve, *personal observations*).

Eighteen of the 50 localities reported by Forselius (1962), and 1 of the 5 localities reported by Haglund (1972), did not support any pool frogs in 1983. Another two local extinctions were observed between 1969 and 1983 (K. Elmquist, *personal observations*). Prior to 1983, localities with status 1 unfortunately were not separated from reproduction localities (status 2). Furthermore, none of the extinction localities from 1983 was recolonized in 1984–1988 (P. Sjögren Gulve, *personal observations*).

In 1983, we found 27 new localities with reproducing pool-frog populations (status 2) and 10 new calling localities without reproduction (status 1). The change in status of 14 permanent ponds between 1983 and 1987 is shown in Table 1. The three observed colonizations occurred ≈300 m from reproducing source populations (status 2). Note that two ponds with status 1 in 1983 supported reproducing populations in 1987.

Local climate—mean water temperature

The spring and summer of 1987 were cold. At 60°32' N (Örskär Meteorological Station, SMHI), the monthly mean air temperatures of May, June, July, and August 1987 were 2.0°, 1.7°, 1.2°, and 3.1°C, respectively, below the normal mean monthly values.

The mean water temperatures of the eight pool-frog ponds and nine unoccupied permanent ponds in May–October 1987 are shown in Table 2. The temperatures of the occupied ponds were significantly higher than those of the unoccupied ponds (two-way ANOVA: $F_{1,116}$ = 57.46, $P < 0.0001$). This difference in temperature peaked during 25–31 May (1.4°C), when the pool frogs normally initiate spawning, but changed significantly with time, resulting in minor differences from July to October (Table 2).

Comparing the eight pool-frog ponds with the nine

unoccupied ones in a stepwise discriminant analysis (including *ALK, CAL*, ln[*AREA*], *Dloc, Dsea*, and mean water temperatures during 25–31 May and 1 June–1 July, respectively), only the mean water temperature during 25–31 May was entered into the discriminant model (partial r^2 = 0.62, $F_{1,15}$ = 24.0, P = 0.0002: PROC STEPDISC, SAS 1988). After removing the effect of this factor, no other variable differed significantly between the groups ($P > 0.18$).

Analysis of occupancy pattern (status 0 vs. 1 + 2)

Since data on *ALK, CAL*, and *PIKE* were not available for all visited ponds, the stepwise logistic regression analyses were carried out in three steps. Analysis number 1 included six variables (*ALK, CAL*, ln[*AREA*], *Dloc, Dsea*, and *TEXP*). A second analysis (number 2) included *PIKE, Dloc, Dsea, TEXP*, and ln(*AREA*), but excluded *ALK* and *CAL* which proved insignificant in analysis number 1. Finally, analysis number 3 included only *Dloc, Dsea, TEXP*, and ln(*AREA*). In all analyses, distance to the closest pool-frog habitat (*Dloc*) was greater for unoccupied ponds than for occupied habitats (number 3: χ^2 = 51.14, df = 1, $P < 0.0001$, Table 3). Secondly, the local climate (*TEXP*) of the unoccupied ponds was on average colder than that of the inhabited ones (number 3: χ^2 = 21.54, df = 1, $P < 0.0001$, Table 3). Analysis number 3 included 49 of the 68 current pool-frog localities, and all analyses (1–3) concurred in their ranking order of the significant variables; an intercorrelation matrix is shown in Table 6.

Fig. 2 depicts the status of each surveyed permanent

TABLE 2. Means of mean water temperature at eight pool-frog (*Rana lessonae*) ponds and nine ponds/lakes without pool frogs during eight measurement periods in 1987.*

	Mean water temperature (°C [mean ± 1 SD])	
Period	A) Pool-frog ponds	B) Unoccupied ponds
1–13 May	10.9 ± 0.3	9.9 ± 0.7
14–24 May	12.0 ± 0.3	11.1 ± 0.7
25–31 May†	13.5 ± 0.3	12.1 ± 0.8
1 Jun–1 Jul†	14.8 ± 0.4	13.8 ± 0.7
2 Jul–2 Aug‡	20.5 ± 0.6	19.8 ± 0.9
3 Aug–15 Sep‡	15.0 ± 0.4	14.4 ± 0.7
16–28 Sep‡	9.9 ± 0.2	9.5 ± 0.4
29 Sep–15 Oct‡	8.3 ± 0.2	8.2 ± 0.5

* Differences in mean water temperatures were tested using a two-way ANOVA (PROC GLM: SAS 1988) with pond group (A or B) and measurement period as class variables. The water temperatures differed significantly both between occupied and unoccupied ponds ($F_{1, 116}$ = 57.46, $P < 0.0001$) and over the measurement periods ($F_{7, 116}$ = 728.98, $P < 0.0001$); the group × period interaction is significant ($F_{7, 116}$ = 2.35, P = 0.0280).

† Choruses were initiated during 25–31 May in the breeding populations; spawning commenced on 5 June. Breeding/calling ceased on 26 June.

‡ From 2 July to 15 October: $N_B = N_A = 8$.

TABLE 3. Differences in seven environmental variables between pool-frog (*Rana lessonae*) ponds (status 1+2: Table 1) and unoccupied permanent ponds (status 0) in 1987 using stepwise logistic regression (BMDPLR: Dixon 1988).* Step selections were based on maximum likelihood ratio; regression coefficients shown are significant at $P < 0.05$. Goodness of fit of the resulting model: $\chi^2 = 77.21$ df = 102, $P = 0.968$.

| Variable | Pond occupation status ($\bar{X} \pm 1$ SD) | | Regression coefficient, β | | | |
	1+2	0	Mean	SE	χ^2	P
Entered						
0 Constant			−22.43	6.65	18.66	<0.0001
1 *Dloc* (km)	0.74 ± 0.90	4.08 ± 3.36	−0.976	0.234	51.14	<0.0001
2 *TEXP* (°C)	13.3 ± 0.5	12.7 ± 0.9	1.844	0.516	21.54	<0.0001
Not entered	-					
a *CAL†* (g/m³)	38.79 ± 18.35	46.14 ± 19.89	...	...	3.43	0.0642
b *Dsea* (km)	0.39 ± 0.46	0.47 ± 0.71	...	...	2.99	0.0838
c *PIKE‡*	...	...	...	...	1.87	0.1711
d *ALK†* (HCO₃⁻, mol/m³)	2.14 ± 0.95	2.13 ± 0.95	...	...	0.05	0.8168
e Ln(*AREA*) (ha)	−1.03 ± 0.95	−0.96 ± 1.56	...	...	0.02	0.8925
N =	49	56				

* *ALK* = water alkalinity; *AREA* = water surface area; *CAL* = [Ca²⁺]; *Dloc* = distance to closest pool-frog locality; *Dsea* = distance to the Baltic sea; *PIKE* = presence or absence of pike (*Esox lucius*); *TEXP* = estimated mean water temperature in late May 1987.

† $N_{1+2} = 22$, $N_0 = 33$, χ^2 given with effects of variables 1 and 2 removed.

‡ $N_{1+2} = 36$, $N_0 = 40$, χ^2 given with effects of variables 1 and 2 removed.

pond in relation to the variables *Dloc* and *TEXP*. It suggests that *TEXP* can be regarded as a reliable measure of habitat quality. Close to pool-frog localities (*Dloc* < 1.0 km), virtually all warm ponds were occupied but the proportion of ponds being occupied declined with increasing *Dloc*. Defining ponds with *TEXP* ≥ 12.3 as suitable for the pool frog (Fig. 2), the

average occupancy (*P* of Levins [1970]) was 0.867 at *Dloc* ≤ 1.0 km, 0.385 at 1–2 km, 0.167 at 2–3 km, 0.333 at 3–4 km, and 0.00 at *Dloc* > 4.0 km. This decline (Spearman $r_s = -0.928$, $n = 6$, $P = 0.008$) was not caused by spatial autocorrelation of local climate (*TEXP*; Moran's $I = -0.008$, $P = 0.497$; all 115 ponds included).
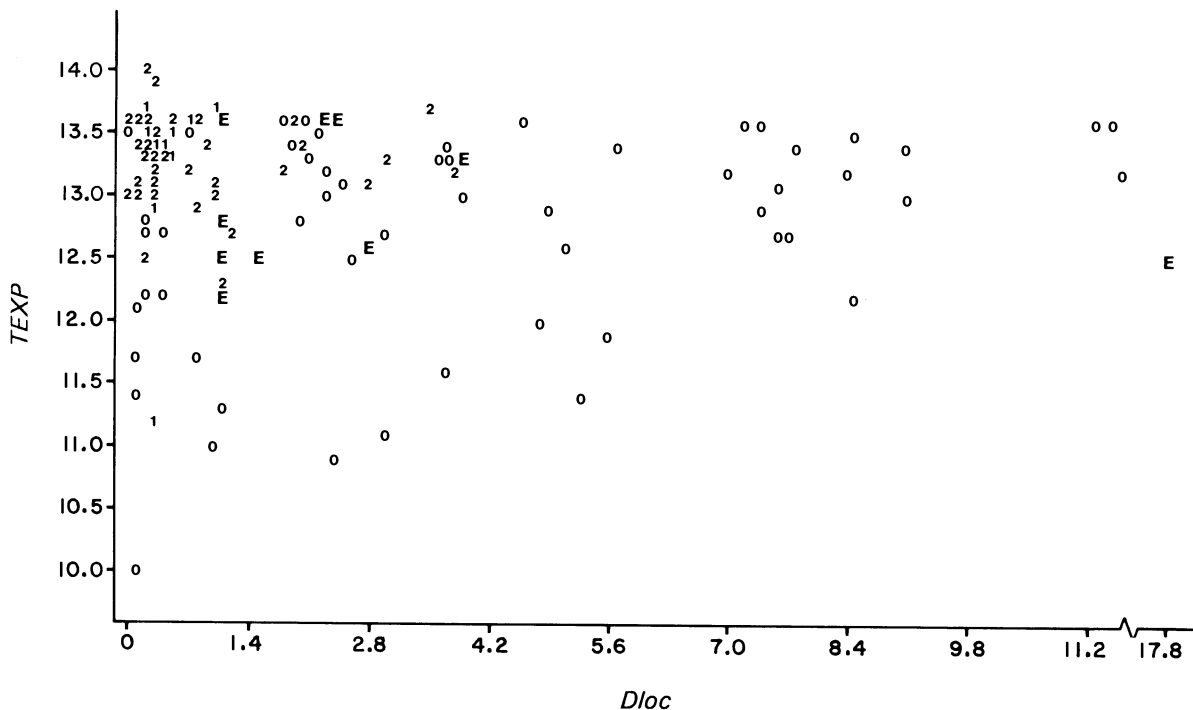

FIG. 2. Plot of distance to the closest pool-frog population (*Dloc*) and local spring climate represented as estimated mean water temperature during 25–31 May 1987 (*TEXP*) of each of the 115 permanent ponds/lakes analyzed in Tables 3 and 5. 0 = pond without pool frogs (status 0); 1 = calling locality without reproduction (status 1); 2 = pond with reproducing pool-frog population; E = pond with local extinction. Six observations are hidden. (Also reproduced in Sjögren [1991*b*].)

TABLE 4. Observed or probable causes of local extinctions of pool-frog populations (*Rana lessonae*) in 1962–1987. Figures show numbers of extinct local populations.

Formerly permanent ponds		Permanent ponds		
Draining	Over-growing/ succession	Satellite ponds	Isolation	
3	6	7	10	Σ26

Analysis of extinction pattern
(status E vs. 1 + 2)

The censuses in 1983 and 1987 detected a total of 26 local extinctions during 1962–1987, the net extinction frequency thus being one per year or four per pool-frog generation (≈ 4 yr) in 1962–1983, and 1.5 per year or six per generation in 1983–1987. Regarding all local occurrences (status 1 + 2) as equal, the extinction probability per occurrence/population and year was 18/(49·21) $\approx$ 1.7%/yr in 1962–1983, and 6/(71·4) $\approx$ 2.1%/yr in 1983–1987. This can be recalculated to 7.0 and 8.5%, respectively, per generation.

Disappearance of formerly permanent water due to natural plant succession (six ponds) or human-engineered draining (three ponds) was responsible for nine of these extinctions; seven of the extinction sites were close to reproducing populations and were probably satellite ponds (status 1: Table 4). (Recent analyses have shown low *TEXP* to be a significant predictor of such "satellite extinctions" [P. Sjögren Gulve, *unpublished data*]). The remaining 10 extinction sites were compared with the currently occupied ponds (status 1 + 2: N = 49) using stepwise logistic regression as above. These 10 ponds were on average larger than the occupied ones (ln[*AREA*], Table 5) and were situated significantly farther away from neighboring pool-frog

localities (*Dloc*, Table 5, Fig. 2). The extinct populations also had a shorter average distance to the closest extinct neighbor than did the extant populations (*Dext*, Table 5); Table 6 shows the intercorrelations of the variables. Furthermore, the 10 extinction sites differed significantly from unoccupied ponds (status 0) in terms of larger *AREA* (χ^2 = 12.97, df = 1, P = 0.0003) and warmer local climate (*TEXP*: χ^2 = 5.72, df = 1, P = 0.0168).

The significant variables in Table 5 were further evaluated in a misclassification analysis using the logistic model and the regression coefficients (see Dixon 1988). In doing so, I found that 4 of the 59 ponds (6.8%) were misclassified. One of them was a vacant pond with extinction recorded in 1983. Interestingly, the others (misclassified as "extinct") were two marginal ponds, which are discussed under *Discussion: Extinction, area, and predation* below, and one pond where extinction occurred in 1992 (P. Sjögren Gulve, *personal observation*). As the habitat analysis totally ignores the demography of the local populations, and with reference to the discussion below, I find the predictive power of the selected variables to be satisfactory; a more objective measure of judgement is provided by the goodness-of-fit statistics (Table 5).

Interpreting the *AREA* effect, pool-frog population size was not correlated with pond area (Sjögren 1991*b*). However, stepwise logistic regression analyses including *Dsea*, *ALK*, *CAL*, *TEXP*, and ln(*AREA*) showed that large *AREA* was the only significant predictor of pike presence (χ^2 = 73.26, df = 1, P < 0.0001). Although eight out of nine extinction sites were pike ponds, the results in Tables 3 and 5, plus the fact that pike were caught with nets in ponds where pool frogs reproduced successfully, indicate that pike predation per se cannot fully explain the extinction pattern (see *Discussion: Extinction, area, and predation*).

TABLE 5. Differences in eight environmental variables between permanent ponds with extant (status 1+2: Table 1) and extinct (status E) pool-frog populations (*Rana lessonae*) in 1987 using stepwise logistic regression (BMDPLR: Dixon 1988). *Dext* = distance to the closest neighboring extinction site. See Table 3 for methodological details and definition of other variables; regression coefficients shown are significant at P < 0.05. (Also reproduced in Sjögren 1991*b*). Goodness of fit of the resulting model: χ^2 = 16.90, df = 56, P = 1.000.

Variable	Pond occupation status ($\bar{X} \pm 1$ SD)		Regression coefficient, β		χ^2	P
	1+2	E	Mean	SE		
Entered						
1 Ln(*AREA*) (ha)	−1.03 ± 0.95	0.55 ± 1.25	−2.262	0.838	16.30	0.0001
2 *Dloc* (km)	0.74 ± 0.90	3.50 ± 5.11	−2.193	0.783	24.96	<0.0001
3 *Dext* (km)	2.87 ± 2.08	2.53 ± 4.39	2.654	0.978	29.38	<0.0001
Not entered						
a *Dsea* (km)	0.39 ± 0.46	0.84 ± 0.64	⋯	⋯	3.08	0.0790
0 Constant			⋯	⋯	1.97	0.1608
b *TEXP* (°C)	13.3 ± 0.5	12.9 ± 0.5	⋯	⋯	1.82	0.1776
c *CAL** (g/m³)	38.79 ± 18.35	47.02 ± 20.31	⋯	⋯	1.20	0.2730
d *ALK** (HCO₃⁻, mol/m³)	2.14 ± 0.95	2.34 ± 1.24	⋯	⋯	1.12	0.2904
e *PIKE*†	⋯	⋯	⋯	⋯	0.22	0.6385
N =	49	10				

* N_{1+2} = 22, N_E = 9, χ^2 given with effects of variables 1, 2 and 3 removed.
† N_{1+2} = 36, N_E = 8, χ^2 given with effects of variables 1, 2 and 3 removed.

TABLE 6. Total sample intercorrelations of the variables included in the stepwise logistic regressions presented in Tables 3 and 5. Correlation coefficients are shown with total sample size within parentheses. Habitat groups and variables are defined in Tables 1, 3, and 5; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

A) Extinct vs. extant (status E vs. 1+2)

	Ln(AREA)	TEXP	CAL	ALK	Dsea	Dloc
Dext	−0.100 (59)	0.036 (59)	−0.565*** (31)	−0.492** (31)	−0.067 (59)	0.549*** (59)
Dloc	0.231 (59)	−0.193 (59)	0.024 (31)	−0.167 (31)	0.271* (59)	
Dsea	0.404** (59)	−0.248 (59)	−0.191 (31)	−0.399* (31)		
ALK	−0.200 (31)	−0.081 (31)	0.891*** (31)			
CAL	0.010 (31)	−0.110 (31)				
TEXP	−0.184 (59)					
Ln(AREA)	—					

B) Unoccupied vs. occupied (status 0 vs. 1+2)

	Dloc	Dsea	ALK	CAL	TEXP
Dloc					
Dsea	0.153 (105)				
ALK	0.015 (55)	−0.343* (55)			
CAL	0.199 (55)	−0.300* (55)	0.745*** (55)		
TEXP	0.048 (105)	−0.088 (105)	0.080 (55)	0.200 (55)	
Ln(AREA)	0.178 (105)	0.273** (105)	−0.005 (55)	0.055 (55)	0.115 (105)

The significance of *Dext* in Table 5 indicates a spatial correlation of the local extinctions. This result was not due to correlation between *Dext* and the other variables (Table 6); the significant positive correlation between *Dext* and *Dloc* was caused by one extreme observation (status E: *Dloc* = 17.8 km) and neither *ALK* nor *CAL* entered the regression model if *Dext* were excluded from the analysis. I hypothesize that the significance of *Dext* in the extinction pattern may reflect the great and in some years completely correlated impact of environmental stochasticity on population growth in the metapopulation (Sjögren 1988, 1991a). An analysis of population data (P. Sjögren Gulve, *unpublished data*) showed that 11% of the total variance in pool-frog population size at two ponds 1.4 km apart was partitioned among the populations (F = 0.28, P = 0.626) and 89% among years ($F_{2,3}$ = 16.94, P = 0.023, PROC NESTED, SAS 1988). Moreover, spatially correlated extinctions would be expected over periods of several generations (here: 1962–1987) since the extinction of a neighbor increases *Dloc*, and thus the risk of extinction, for the remaining population.

DISCUSSION

Table 1 shows that local turnover occurs in the pool-frog system as part of regional population dynamics described by Levins' (1969, 1970) theory. Unoccupied ponds are not necessarily unsuitable for the species, and absence of pool frogs or reproduction at a particular pond need not be a static condition. The calling behavior of the males (see *Materials and Methods*) and the fact that even a small adult female will give rise to > 100 conspicuous metamorphosing larvae (clutch > 500 eggs; Sjögren 1991a), suggest these turnover data are reliable.

However, the dynamics of this system also differ from Levins' (1969) general model, which assumes qualitatively identical habitat patches (hypothesis D in the *Introduction*); the probabilities of colonization (occupancy) and extinction differed among the ponds and were correlated with particular environmental parameters (cf. Harrison et al. 1988). Proximity to the closest pool-frog population (i.e., *Dloc*) was significant in both the occupancy and extinction patterns (Tables 3 and 5). Lower water temperatures (*TEXP*) separated unoccupied ponds (status 0) from both currently occupied ones (status 1 + 2: Table 3) and the 10 isolated ponds where local extinctions occurred; the latter was expected since these extinction sites at one time did support pool frogs. The biological significance of pond *AREA* in the extinction analysis (Table 5) is discussed further below.

The significance of *Dloc* in both the occupancy and extinction patterns (Tables 3 and 5) probably reflects the dispersal range and colonization power of the frogs and not spatial autocorrelation of habitat quality (cf. Brown 1984). Fig. 2 shows that distant warm and permanent ponds do exist, and the fact that very few pool frogs disperse >1 km from their native pond per 3-yr period (Sjögren 1988) can explain why the proportion of occupied warm ponds declines so sharply with *Dloc* (Fig. 2). For the same reason, the 10 nonsatellite extinctions are unlikely to have been colonization failures. This distance effect is probably strengthened by the external fertilization of eggs in frogs that prevents colonization by single pregnant females.

The temperature-dependent onset of reproduction in the Swedish pool frogs (Forselius 1962, Sjögren et al. 1988; see also Radwan and Schneider 1988) offers a direct explanation for the significant difference in local climate between unoccupied and occupied ponds (i.e., *TEXP* in Table 3). Sjögren et al. (1988) found that although the Swedish pool frogs breed late in spring, their spawning was strongly biased towards the beginning of the breeding period. They interpreted this as a behavioral response to the reproductive time constraint at 60° N; early spawning would mean enhanced chances for the offspring to complete metamorphosis before winter, and thus to survive.

The difference in water temperature between occupied and unoccupied ponds that peaked in May–June (Table 2) suggests a similar phenomenon at the population level. Forselius (1962) noted that the starting date for spawning in the pool frogs could differ by 1–2 wk between ponds 0.5–1 km apart, probably reflecting climatic differences (cf. Fig. 2), and preliminary results from introduction experiments at 14 isolated ponds (P. Sjögren Gulve, *unpublished data*) indicate that a warm local climate (high *TEXP*) is prerequisite for reproduction at a new locality. This effect on local reproductive performance may explain the significance of *TEXP* in the "satellite extinctions," an analysis of which is presented elsewhere (P. Sjögren Gulve, *unpublished manuscript*).

Extinction, area, and predation

The local extinctions in the pool-frog metapopulation exhibited both deterministic and stochastic components (cf. Gilpin and Soulé 1986, Shaffer 1987). With respect to the late metamorphosis of the pool-frog larvae (Sjögren 1988), extinction due to disappearance of permanent water (i.e., overgrowing by natural succession or draining: Table 4) was expected and deterministic. The extinctions at the remaining permanent ponds, however, were probably governed mainly by stochastic population processes, which are treated in more detail by Sjögren (1991*b*).

The 10 extinct nonsatellite populations inhabited larger ponds and were relatively isolated from other local populations (greater *Dloc*; Table 5, Fig. 2). All local extinctions between 1983 and 1987 were preceded by presence of only 1–3 males (status 1; Table 1). This pattern seems due to the fact that female pool frogs experience higher annual mortality than do males, resulting in a male-biased sex ratio (Sjögren 1991*a, b*) which increases the impact of demographic stochasticity in small populations (cf. Ebenhard 1991). Under these circumstances, the pool frog's susceptibility to environmental stochasticity at 60° N (i.e., the environmentally induced variation in reproductive rate: Sjögren 1991*a*) is likely to elevate the risk of extinction significantly in isolated local populations (cf. Leigh 1981, Shaffer 1981, 1987, Karr 1982, Goodman 1987*b*).

Synergistic effects of this kind, which have been documented in other amphibians (e.g., Pechmann et al. 1991), could explain the observations made in two marginal pool-frog populations with *Dloc* = 1.1 and 1.2 km, respectively, known from 1962 when they were less isolated, and which reproduced in 1987 but not in 1983 (Fig. 1; Table 1). Since we easily found basking larvae in ponds with known reproduction on the same days, these observations imply a lack of egg-carrying females at these localities in 1983, which could be expected in small and isolated populations. These ponds were also large and inhabited by pike, thus resembling the 10 nonsatellite extinction sites (Table 5). As pike feed on a wide range of prey and could potentially reduce a pool frog population to a critical size, pike predation may explain the area effect, provided no compensatory immigration occurs. A greater immigration rate could explain why no central pike ponds changed status in this way (a "rescue effect": Brown and Kodric-Brown 1977, Forney and Gilpin 1989).

The above extinction pattern is unlikely to be caused by vagile and omnipresent predators such as mink (*Mustela vison*), Grey Heron (*Ardea cinerea*), and grass snake (*Natrix natrix*). The same pertains to smaller predators such as newts (*Triturus cristatus* and *T. vulgaris*), dragonfly larvae, and diving beetles, which are restricted to small prey items, viz. the eggs and young larvae of the frogs (e.g., Calef 1973, Brodie and Formanowicz 1983, Formanowicz 1986). Since such predation is mitigated in warm ponds by rapid growth in the tadpoles, and furthermore these predators were most abundant in ponds with pool-frog reproduction, I didn't find any apparent pattern relating to the presence or absence of the frogs.

Suggested extinction scenario

The results in Tables 3, 5, and 6 offer a plausible extinction scenario for the pool frogs that in part resembles a metapopulation model proposed for the newt *Notophthalmus viridescens* by Gill (1978).

A special feature of the Baltic coast in the pool-frog region is its continuing post-Pleistocene land uplift of 60–80 cm per century (Åse 1982). New land areas emerge from the shallow sea, and bays are cut off to form ponds and lakes, of which 0.2–2 ha ponds offer

warm and permanent water in which pool frogs can thrive (Fig. 3). Some 100–400 yr later, the shallower ponds will become overgrown due to natural vegetation succession, which causes deterministic extinctions (Table 4), but descendants of the pool-frog populations will have colonized new suitable ponds, provided that these are close enough (Fig. 3). This turnover pattern has been observed both during this study and earlier (Forselius 1962). Consequently, the abundance of suitable pool-frog ponds ($Dloc^{-1}$) will decrease with increasing distance to the Baltic sea ($Dsea$), while the proportion of large permanent ponds (i.e., average $\ln[AREA]$) will increase (Fig. 3; cf. intercorrelations in Tables 5 and 6).

Assume that, at a given time, pool frogs inhabit a "cohort" of suitable coastal ponds (1 in Fig. 3). Some of these ponds have pike, but the frog populations persist as long as "rescuing" immigrants arrive from neighboring populations. Over time, remaining ponds become farther from the sea and more isolated from neighboring pool-frog populations due to overgrowing of the shallower ponds (2 and 3 in Fig. 3). The proportion of large ponds with pike in the cohort will increase because of their slower succession, but each remaining frog population has become more isolated and extinction prone, and confined to a habitat with status E features (Table 5). Since *Dloc* but not *AREA* has increased with time in this scenario, *Dloc* appears as the key factor. In the light of what has been documented about the effects of isolation on population persistence (see Sjögren 1991*b*) this demographic scenario makes sense; it also offers an explanation for why *Dsea* appears as a nearly significant variable/correlate in Tables 3 and 5. Throughout this scenario, colder "satellite ponds" may have some calling males and in warm years even occasional reproduction, but they have no core function in the system (cf. Gill 1978).

In accordance with metapopulation theory (e.g., Levins 1970, Hanski and Gilpin 1991), this scenario emphasizes the importance of (re)colonization for long-term regional persistence of subdivided populations. In a simulation study, Hanski (1985) documented regional extinction when interpatch migration decreased below a certain rate. Similarly, Fig. 2 and the reduced pond occupancy with increased *Dloc* (0.867 at 0–1 km and 0.385 at 1–2 km) suggest a critical interpopulation distance of ≈ 1 km for regional persistence in the pool frogs (Sjögren 1991*b*).

Conclusions

The pond affinity and the local extinctions and colonizations of the Swedish pool frogs support the idea of a metapopulation structure and a dynamic regional distribution (Levins 1969, 1970; cf. hypothesis D). Occupied ponds were characterized by a warm local climate (hypothesis C) and close proximity to neighboring pool-frog sites, whereas pike presence/absence (hypothesis B) and water alkalinity and lime content (hy-
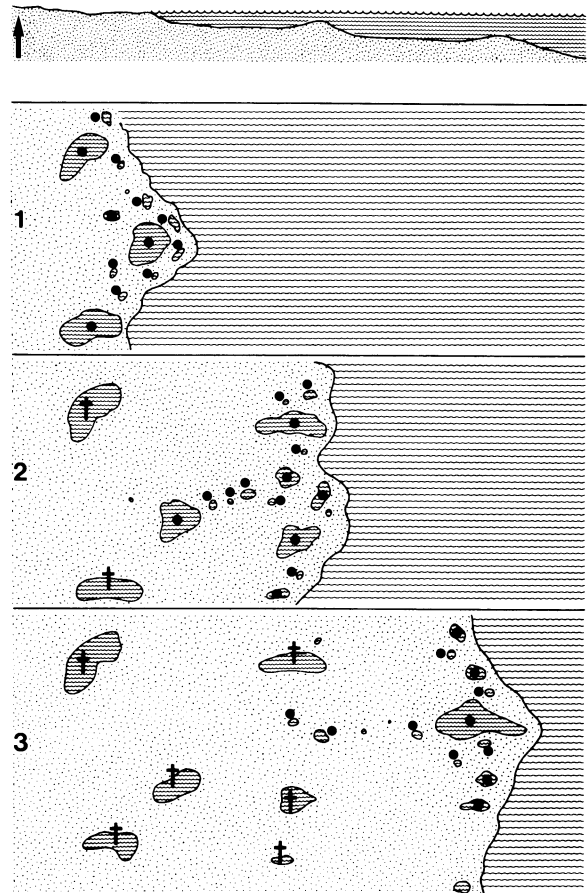

FIG. 3. The successive land uplift (≈ 60 cm/century) and extension of a hypothetical section of the Baltic coast (central Sweden), with long-term changes in the distribution of the pool frog (*Rana lessonae*) as proposed in the text. ● = permanent pond/lake occupied by pool frogs; † = permanent pond where the pool frogs have become extinct. Top shows a vertical cross section of the shallow Baltic coast, from which permanent ponds of different sizes are cut off; (1) shows the initial distribution of pool frogs in warm permanent ponds; (2) and (3) are sequential "snapshots" of the same area 200–400 yr later when new suitable ponds have been cut off from the Baltic Sea and, provided they are close enough, been colonized by pool frogs. The smaller and shallow ponds are overgrown by plant succession, causing deterministic local extinction of the pool frogs. Therefore, the populations at the larger remaining ponds of the original habitat cohort become more and more isolated, and eventually become extinct.

pothesis A) had minor or no significance in the distribution pattern.

This is one of the first studies where metapopulation dynamics have been investigated with a multivariate approach. A major result is that even among the warm ponds qualifying as patches or sites sensu Levins (1969, 1970), distance effects induce significant heterogeneity in the regional dynamics; this has been documented also in other studies (e.g., Kindvall and Ahlén 1992). The pattern that isolated populations are more extinction prone than central populations, even in high-qual-

ity habitats, has been verified for a variety of taxa (see review by Sjögren 1991b). Reported extinction rates range from 2 to 42% per population and year (Fritz 1979, Smith 1980, Pokki 1981, Schoener and Spiller 1987, Bengtsson 1989; this study). All this underlines the importance of considering spatial dynamics in species conservation (Gilpin 1987).

The fact that population proximity (Dloc) stands out as a key factor preventing extinction in a system where local extinctions are spatially correlated may seem like a paradox (cf. Goodman 1987a, Quinn and Hastings 1987). However, in an isolated situation a neighboring reproducing population will enhance local persistence more than a few neighboring males. Moreover, with reference to the results of Harrison and Quinn (1989), the low average extinction rate of the pool frogs (maximum of 8.5%, which is less than the critical 25% in Harrison and Quinn [1989]) suggests that the effect of correlated extinctions on pool-frog persistence would be completely overruled by the great number of interconnected ponds.

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