LANDSCAPE COMPLEMENTATION AND METAPOPULATION EFFECTS ON LEOPARD FROG POPULATIONS

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Abstract. For many species, not all required resources are contained in breeding habitat. Such species depend on landscape complementation, i.e., linking together different landscape elements through movement, to complete their life cycles. We suggest that the dichotomous habitat classification of many metapopulation analyses (habitat vs. nonhabitat) masks our ability to detect metapopulation effects for such species. We tested this using a species for which landscape complementation is obligate and metapopulation structure is likely: *Rana pipiens,* the northern leopard frog. We used breeding chorus survey data to index relative abundance of leopard frogs in 34 "core" ponds and conducted Poisson regression analysis to determine the effects on frog density of local pond habitat, availability of summer habitat (landscape complementation), and number of occupied ponds in the surrounding landscapes (metapopulation structure). All of these factors had statistically significant effects on frog density. However, when summer habitat was not included in the statistical model, the metapopulation structure was no longer significant; i.e., its effect was masked. Our results suggest that one must be cautious in applying the results of metapopulation analyses to species for which the habitat vs. nonhabitat categorization of the landscape is not appropriate. The potential for rescue and recolonization to maintain a regional population must be assessed within the constraints of the entire landscape.

Key words: amphibian decline; dispersal; landscape complementation; landscape connectivity; landscape structure; leopard frog; metapopulation dynamics; multiscale analysis; patch isolation; Rana pipiens; recolonization; rescue effect.

INTRODUCTION

Much work on metapopulations has focused on the number and locations of patches of breeding habitat (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988, Harrison 1991, Andrén 1994, Lamberson et al. 1994, Sjögren 1994, Dunning et al. 1995, McCullough 1996). As Wiens (1996) notes, "metapopulation theory assumes that the matrix separating subpopulations is homogeneous and featureless." Such a simple classification may be appropriate for species that meet all of their resource needs in the breeding habitat. For many species, however, not all required resources are contained in the breeding habitat (Law and Dickman 1998).

Dunning et al. (1992) coined the term "landscape complementation" to highlight the requirement for many species to link together different habitat types to complete their life cycles. Landscape complementation is a measure of the proximity of critical habitat types (Dunning et al. 1992) and the degree to which organisms can move between them (Taylor et al. 1993).

We suggest that the usual dichotomous habitat classification of metapopulation analyses (habitat vs. nonhabitat) masks their ability to detect metapopulation effects. Variation in population densities due to variation in landscape complementation is not included in such analyses. We tested this using a species for which landscape complementation is obligate and metapopulation structure is likely: *Rana pipiens,* the northern leopard frog.

Leopard frogs require three distinct habitats: a breeding pond used in the spring by the adults and through to midsummer by the tadpoles, grassy meadows or fields for summer foraging, and a stream or lake for overwintering (Rittschof 1975, Merrell 1977). In this study, we considered the influence of two of these three habitat types: breeding ponds and summer habitat. Leopard frogs appear to operate as metapopulations in other areas of their range (Rittschof 1975, Roberts 1992). Also, the population dynamics of other amphibian species have been elucidated effectively using a metapopulation framework (Gill 1978, Sjögren 1991, 1994, Bradford et al. 1993).

We tested the hypothesis that our ability to detect effects of metapopulation structure on leopard frog density within ponds depends on summer habitat being included in the analysis. In other words, we tested the hypothesis that landscape complementation masks metapopulation effects. We addressed this by studying 34 landscapes centered on 34 ponds in the region surrounding Ottawa, Canada. The study landscapes varied in the amount of summer habitat for leopard frogs and in the number of potential breeding areas for *R. pipiens* populations.

METHODS

We selected 34 permanent "core" ponds, ranging in size from 0.04 ha to 29.1 ha. In addition to the 34 core ponds, all other potential leopard frog breeding sites (ponds, large drainage ditches, and streams) within 1.5 km of the core ponds were surveyed for leopard frogs. This gave a total of 107 survey sites, including the core ponds. We chose a 1.5 km radius because it was the shortest distance for which all 34 core ponds had at least one adjacent site that could potentially supply dispersers to the core pond. The sites within 1.5 km of each core pond constituted the "listen" sites for that pond. Because leopard frogs may move as much as 1–2 km between different habitats in a year (Rittschof 1975, Merrell 1977), the listen sites were all within the movement range of the species. All core ponds and listen sites were identified originally from color aerial photos taken in 1993 at a scale of 1:15 000, and were ground-truthed in the spring of 1995.

The 34 landscapes were not randomly sampled from the region, but were chosen to minimize possible correlation between the density of breeding sites and the amount of summer forage habitat. We selected ponds in four general categories: (1) other ponds near, summer habitat near ($n = 10$ ponds); (2) other ponds near, summer habitat far ($n = 9$ ponds); (3) other ponds far, summer habitat near ($n = 10$ ponds); and (4) other ponds far, summer habitat far ($n = 5$ ponds). Our sample size of 34 landscapes was the largest possible, given our logistical constraints.

Chorus surveys

With the help of 34 volunteers, we conducted breeding chorus surveys over four census periods (Hine et al. 1981) between 12 April and 9 May 1995, during the leopard frog breeding period in the Ottawa area (Cook 1992). Such surveys of breeding choruses can provide relative estimates of abundances for across-site comparisons (Scott and Woodward 1994), if calling males are equally available for sampling at each site (Scott and Woodward 1994) and they represent a consistent subset of the population across sites (Zimmerman 1994). We addressed the first criterion by having the surveyors listen at the most likely site for calling at each pond, a shallow-water section on the north side of the pond (Merrell 1977), if accessible. The second criterion was not addressed.

The core and listen sites were divided among 10 routes with roughly 11 sites per route. Routes were designed to allow surveys to be conducted between half an hour after sunset and midnight (van der Ham and Schueler 1992). Routes were surveyed by two people, and surveyors were rotated among routes. To avoid observer bias, the listen sites associated with a particular core site were distributed among as many routes as logistically possible. To vary the sample time for each pond between censuses, the routes were driven in different directions: forward, backward, and from a starting point in the middle of the route. For each census, the routes were covered in as few evenings as volunteer availability permitted (from one to three evenings). The surveys were initiated when water temperature was $\geq 8°C$ at 5 cm below the water surface (Hine et al. 1981, Gilbert et al. 1994) and evening air temperature at sunset was 8–10°C (Hine et al. 1981, Canadian Wildlife Service).

Surveyors listened for 5 min at each site to determine the intensity of leopard frog breeding choruses (van der Ham and Schueler 1992, Scott and Woodward 1994). Where traffic noise interfered with the listener's ability to hear frogs, the 5 min were the sum of pauses in the background noise (Fahrig et al. 1995). For each site, surveyors recorded an index of abundance: 0, no individuals calling; 1, individual(s) can be counted, calls are not overlapping; 2, calls of <15 individuals can be distinguished, but there is some overlapping; and 3, calls of ≥ 15 individuals.

Core pond habitat

We included characteristics of the pond habitat in the analyses, to control for their effects on population levels. Combining all available information leads to the following characterization of preferred spawning habitat for leopard frogs: non-acidic water, 10–65 cm deep in full sun, usually on the north side of the pond, with emergent, non-broad-leaved vegetation for attachment of egg masses (Gosner and Black 1957, Pace 1974, Eddy 1976, Merrell 1977, Hine et al. 1981, Leclair 1983, Dale et al. 1985, Freda and Dunson 1985, Gilbert et al. 1994).

We characterized the pond habitat for each of the 34 core ponds during June 1995. We measured the total perimeter of the pond, the pH, the water depth at 1 m and 2 m from the pond's edge, the degree of insolation in the first 2 m from the shore (full sun all day, shaded part of the day, shaded all day), and the percent cover of each plant species along a line transect extending out 2 m at right angles from the shoreline (Fig. 1). Measurements were taken at equally spaced sample points around the perimeter of the core ponds. For two ponds, the entire perimeter could not be sampled. In both cases, the shallow, northern shoreline area was included in the sampling. Total perimeter measurements were estimated from the aerial photos for these ponds.

The total perimeter was converted to meters from paces and then was multiplied by the proportion of samples with full sun and narrow-leafed emergent vegetation in water ≤ 65 cm deep. In this way, we converted the point samples into estimates of the total length of shoreline with the characteristics preferred by leopard frogs for spawning.

Water pH was determined from samples taken at 5 cm depth (Freda and Dunson 1985) 1 m from shore (Sjögren 1994). We took four water samples, approx-
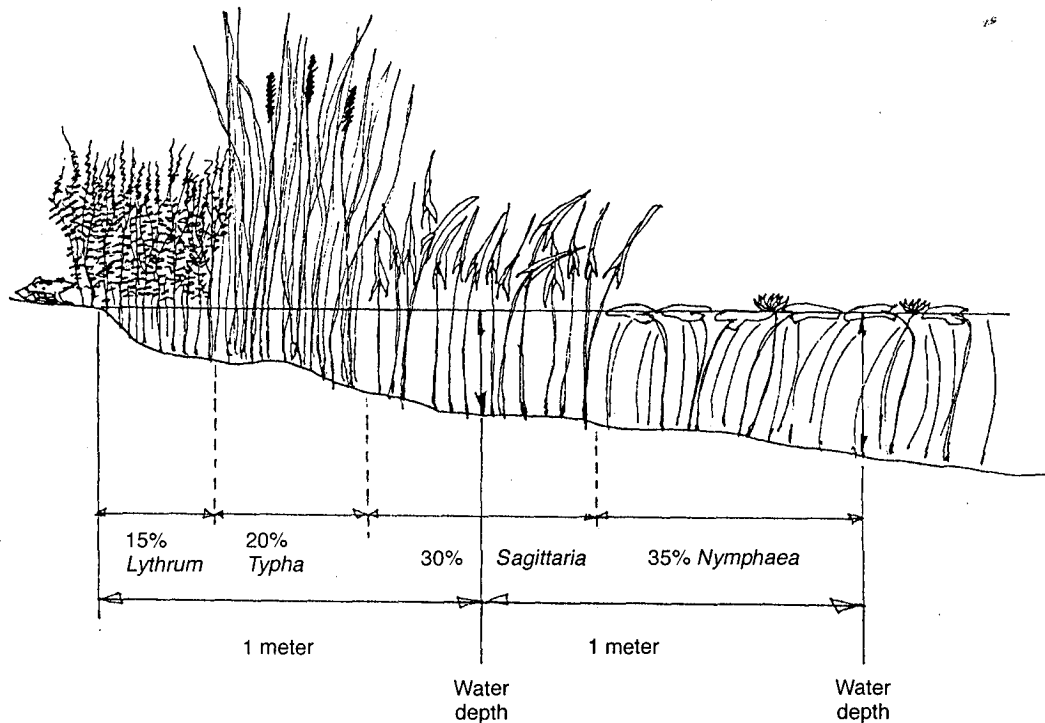
FIG. 1. Vegetation transect of a leopard frog pond. Water depth was measured at 1 and 2 m from the shore. Percent cover was noted for each species for the first 2 m from the shore.

imately evenly spaced around the perimeter of the pond, for all ponds except two for which two samples were taken and one for which three samples were taken. Samples were returned to the lab in a cooler with ice (Freda and Dunson 1985) and were stored for no longer than 7 d in a refrigerator at 6.5°C. The pH was measured twice for each sample using a Corning Model 5 pH meter (Corning, New York, USA). Mean pH values for each pond were calculated using the hydrogen ion concentrations.

Landscape surrounding core ponds

We quantified the habitat within 1 km of the center of each of the core ponds (Fig. 2) based on color aerial photos taken in August and September 1993 at a scale of 1:15 000 (National Air Photo Library). A 1 km radius was chosen to characterize the habitats around the pond that were within the potential dispersal distance of leopard frogs (Merrell 1977). We traced the boundaries of the different fields and/or habitat types evident on the aerial photos onto acetate overlays and ground-truthed the aerial photo tracings.

The tracings were scanned at 200 dpi and imported into a paint program (Corel Photo-paint). They were coded into 22 habitat types according to the results of the ground truthing (Table 1). The coded images were transferred as TIFF files to a geographic information system program (EPPL). Using EPPL, we calculated
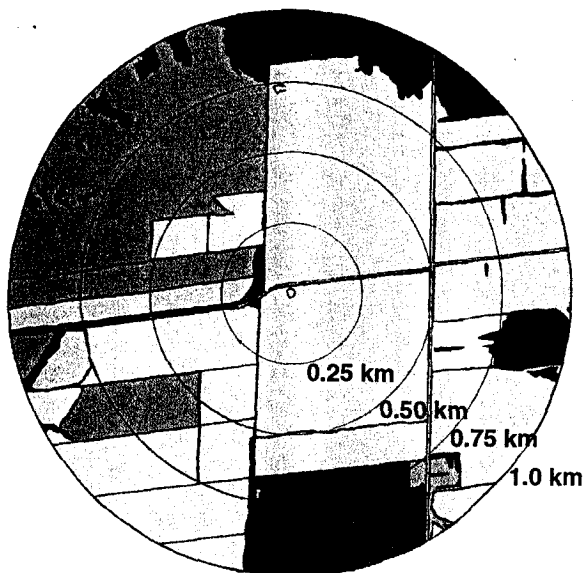

FIG. 2. Classified landscape with perimeters marked for each of the four circular areas used in the analyses (0–0.25, 0–0.5, 0–0.75, and 0–1.0 km radii). The core pond (small white area) is at the center of the central circle.

TABLE 1. Variables used in the statistical analyses of landscape complementation and metapopulation effects on *Rana pipiens* in the Ottawa, Canada, region.

Variable	Mean	Max.	Min.	1 SD	Level of influence	Description
Dependent variable						
Calling rank	1.23	7	1	1.63		sum of calling indices from maximum of four out of five surveys
Independent variables						
Mean pH	7.06	9.39	6.77	0.8287	local pond	mean pH of water samples taken at each pond
Perimeter (m)	444	2328	139	407	local pond	length of pond perimeter
Spawning habitat (m)	184	1024	0	230	local pond	length of perimeter that constituted preferred spawning habitat
Summer habitat (ha)†					landscape complementation	aggregation of all possible summer habitats (hay fields, alfalfa/clover/vetch fields; pasture; old fields; scrub; and sedges)
0–0.25 km	7.62	19.59	0	6.37		
0–0.50 km	31.42	75.13	0	24.48		
0–0.75 km	72.48	166.50	2.15	49.73		
0–1.0 km	130.70	273.60	7.23	82.01		
Total listen	5.12	12	1	3.08	metapopulation	tally of no. possible breeding sites <1.5 km from center of core pond in question
Number with calling	1.79	7	0	1.93	metapopulation	no. of possible breeding sites <1.5 km from center of core pond in question for which calling leopard frogs had been recorded at least once
Sum calling rank	3.29	16	0	3.90	metapopulation	sum of calling rank for all sites <1.5 km from core pond in question

† The listed summer habitats are used only in the summer. Other types classified as "not summer habitat" are: outlines; pavement/railroad/road; corn field; forest/trees/wooded fencerow; lawn/mowed grass/park; housing/farmyard; industrial; construction site; plowed field/dirt/quarry; soya beans/beans; grain field; orchard/tree nursery/berries; annual vegetable crop; canola; water other than core pond; core pond. Core ponds are used in the summer, but are also used in the spring; if large enough, they may be used for overwintering.

the amount of each habitat type within circular areas of radius 0.25, 0.5, 0.75, and 1 km from the center of each core pond, to enable us to assess the spatial extent of the landscape influence on leopard frog abundance in the core ponds (Pearson 1993, Findlay and Houlahan 1997).

Statistical analysis

Variables used in the analyses.—Table 1 lists and describes the variables used in the analyses. The response variable, *calling rank,* was a measure of the calling intensity at each of the 34 core ponds, and was assumed to be correlated with population abundance at the ponds. It was calculated by summing the four calling indices (from the four census periods) for each core pond. Calling rank therefore gave high weight to sites with persistent calling, as well as to those with high calling intensity. The independent variables fell into three categories: local pond characteristics, landscape complementation factors, and metapopulation factors (Table 1).

Local pond factors.—We included the local pond variables: mean pH (*mean pH*), length of the pond perimeter in meters (*perimeter*), and the length of the perimeter that constituted preferred spawning habitat (*spawning habitat*). We included both perimeter and

spawning habitat because these variables could act in opposite directions on the abundance of calling frogs in larger ponds (Merrell 1977).

Landscape complementation factors.—We aggregated the area of all possible summer habitats into one measure, *summer habitat* (Table 1). Summer habitat included perennial forage crops (e.g., grass, alfalfa, and clover), pasture, old fields, scrub, and sedges (Wright and Wright 1949, Whitaker 1961, Dole 1965, Merrell 1977, Hine et al. 1981, Degraaf and Rudis 1983, McMurray 1984, Beauregard 1988). Leopard frogs are seldom found during the summer in heavily wooded areas away from water (Whitaker 1961, Merrell 1977, Hine et al. 1981, Beauregard 1988); on barren ground (Merrell 1977); in open sandy areas (Merrell 1977); in cultivated fields, especially those recently cut (Dole 1965, Hine et al. 1981, Beauregard 1988); in heavily grazed pastures (Dole 1965, Merrell 1977); or on closely mowed lawns (Merrell 1977, Hine et al. 1981). There were four measures of summer habitat for each pond, corresponding to the four circular areas in which the landscapes were characterized.

Metapopulation factors.—*Total listen* was the number of possible breeding sites within 1.5 km of the center of the core pond in question. *Number with calling* was the number of these sites for which calling

Sample calculation of independent
variables used in analyses

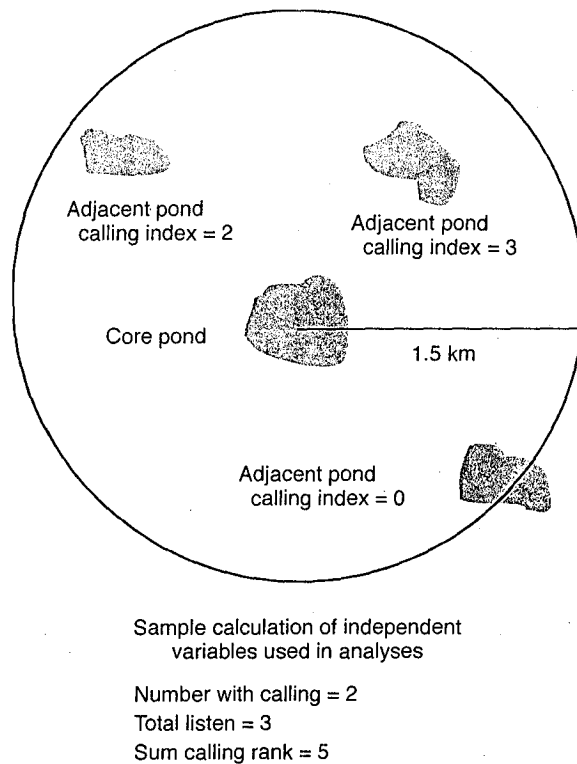Number with calling = 2
Total listen = 3
Sum calling rank = 5

FIG. 3. Explanation of leopard frog calling variables.

leopard frogs were recorded at least once in the four censuses. *Sum calling rank* was the sum of the four census indices for all of the sites within 1.5 km of the core pond in question (Fig. 3).

Analyses

We used stepwise Poisson regression analysis with forward selection and backward elimination (in SPlus) to test our hypothesis. Poisson regression constrains the fitted values to positive values and fits a model for which the error variance is equal to the mean, in keeping with the nature of count data (Crawley 1993) such

as *calling rank*, our response variable. The stepwise procedure in Splus uses AIC (Akaike's information criterion) for adding terms to, or dropping terms from, the model (Hastie and Pregibon 1992). We confirmed the statistical significance of each term in the final model from the stepwise procedure, using sigma-restricted deviances, i.e., by comparing the residual deviance from the final model to that of the final model less each term (Nicholls 1989, Crawley 1993, Trexler and Travis 1993). A term was maintained if its removal from the model resulted in an increase in the residual deviance that was significant at the $\alpha = 0.05$ level.

Analysis I.—We first built a statistical model that related both landscape complementation and metapopulation-level factors to the relative abundance of leopard frogs. We included all of the pond variables, the summer habitat measures, and all of the metapopulation variables in a stepwise Poisson regression analysis on calling rank.

Analysis II.—We then determined the degree to which calling rank could be accounted for by pond and metapopulation variables, without entering landscape complementation variables into the model. By comparing this model with the previous one, we tested the hypothesis that landscape complementation variables mask metapopulation variables.

RESULTS

Correlations among independent variables

The correlations among independent variables are presented in Table 2. Mean ph was not correlated significantly with any of the other independent variables. Perimeter and spawning habitat were highly positively correlated. Strong positive correlations existed between the four summer habitat variables (for the four circles around the core ponds). The metapopulation variables were strongly positively correlated with each other.

There were no significant correlations between the landscape complementation and metapopulation variables, nor between the pond variables and either the

TABLE 2. Correlations among the independent variables (see Table 1 for definitions).

| | Pond variables | | | Landscape complementation variables | | | |
| | | | | Summer habitat (km) | | | |
Variables	Mean pH	Perimeter	Spawning habitat	0–0.25	0–0.5	0–0.75	0–1.0
Mean pH		0.075	−0.0705	−0.122	−0.058	−0.066	−0.044
Perimeter			0.781***	−0.191	−0.164	−0.248	−0.322
Spawning habitat				−0.001	−0.024	−0.111	−0.178
Summer habitat							
0-0.25 km					0.933***	0.897***	0.877***
0–0.5 km						0.976***	0.949***
0–0.75 km							0.984***
0–1.0 km							
Total listen							
Number with calling							

*** $P < 0.001$.

landscape complementation or the metapopulation variables. This suggests that we were successful in selecting ponds that would allow us to distinguish between landscape complementation and metapopulation effects.

Analysis I

Mean pH, the amount of spawning habitat, the amount of summer habitat within 1 km of the center of the core pond, and the number of sites with leopard frogs calling within 1.5 km of the core pond all contributed significantly to explaining the observed variation in relative abundance at the core ponds (Table 3). This model was slightly overdispersed ($\phi = 1.219$); therefore, we used F tests rather than chi-squared tests to determine significance levels (McCullagh and Nelder 1991, Hastie and Pregibon 1992, Crawley 1993). Inspection of the residuals suggested that the Poisson model provided a reasonable description of the data, despite the slight overdispersion observed.

Relative abundance was higher in ponds with lower mean pH. More spawning habitat, more summer habitat, and more surrounding sites with frogs calling all led to greater relative abundance at the core pond. The model explained ~37% of the variation observed ([1 − (residual deviance/null deviance)] × 100; Crawley 1993). Of the four possible summer habitat measures, the 1 km radius area was the most significant. The landscape complementation variable (summer habitat 0–1.0) had a similar magnitude of effect to the metapopulation variable (number with calling) (Fig. 4).

Analysis II

When landscape complementation variables were not included in the stepwise procedure, none of the metapopulation variables entered the model. Only mean pH was marginally significant ($P = 0.05$). This supports our hypothesis that habitat complementation effects mask metapopulation effects in this species. Fig. 5A shows the apparent lack of relationship between calling rank and number with calling. Much of the var-

iation in this relationship is due to the fact that the larger values of calling rank typically occur in ponds that have landscapes with larger summer habitat 0–1.0 values (denoted by squares in Fig. 5A), with one obvious exception.

DISCUSSION

It often has been assumed that ecological processes important to populations operate at local spatial scales (Hansson 1979, Dunning et al. 1992). In keeping with this assumption, much of the amphibian literature has focused on factors local to the breeding pond (Dale et al. 1985, Beauregard and Leclair 1988, Skelly 1996). Recognition that local factors may not be sufficient to explain population dynamics has resulted in two streams of inquiry. The first has evaluated the effect of nonbreeding habitat availability in the surrounding landscape on sites chosen for breeding (Hine et al. 1981, Beebee 1985, Loman 1988, Wederkinch 1988). The second, metapopulation theory, has evaluated the possible influence of the landscape context in terms of population supplementation and recolonization potential on local population dynamics (Gill 1978, Henderson et al. 1985, Berven 1990, Sjögren 1991, 1994, Bradford et al. 1993). Our study links these two streams and demonstrates that knowledge of the landscape context in terms of both breeding habitat and complementary habitat may be required to understand the distribution and abundance of species with complementary resource needs.

When landscape complementation variables were not included in the analysis, none of the metapopulation variables was significant. Including a measure of the amount of a second required resource, summer habitat, in the analysis resulted in a model that explained the relative abundance of *Rana pipiens* in terms of local pond variables, landscape complementation, and metapopulation structure (Table 3).

Interestingly, there was symmetry in the masking effects of the complementary and metapopulation-level factors. Summer habitat was only significant if metapopulation effects were also included in the model. This result suggests that the full landscape structure, not just breeding habitat or just complementary habitat, needs to be considered for predicting local population density (Figs. 4, 5B).

There is a two-tiered set of requirements for the persistence of a regional population of a species with complementary resource needs. First, access to resource patches must be appropriate at the individual level, and second, immigration from potential colonizing populations must be sufficient to sustain the regional population. Solbreck (1995) documented this for the persistence of a regional population of the insect *Lygaeus equestris* (Heteroptera: Lygaeidae) in Sweden. The spatial distribution of breeding and diapause sites was important at the individual level, whereas the potential for recolonization from adjacent regions proved critical

TABLE 2. Extended.

Metapopulation variables		
Total listen	Number with calling	Sum calling rank
0.130	0.059	0.139
−0.166	−0.287	−0.276
−0.234	−0.325	−0.262
−0.047	−0.074	−0.027
0.109	0.056	0.060
0.140	0.096	0.075
0.183	0.151	0.131
	0.822***	0.688***
		0.896***

TABLE 3. Analysis I Poisson regression model relating the summed calling index at each of the core ponds (calling rank) to the local pond, metapopulation, and landscape complementation variables.

Variables	Coefficient	1 SE	Deviance	F	P	e^{Bk}
(Intercept)	3.145	1.798				
Mean pH	−0.6433	0.2474	−8.149	6.431	0.01686	0.7216
Spawning habitat	0.002454	0.0007231	−11.10	8.762	0.006074	1.4130
Number with calling	0.2504	0.097921	−6.485	5.118	0.03135	1.3451
Summer habitat 0–1.0 km	0.005415	0.002342	−5.873	4.635	0.03977	1.3123

Notes: The e^{Bk} values are a measure of the relative importance of the four predictor variables. Bk is the standardized partial regression coefficient; Bk $= b_k$* sqrt(var(x_k)/var(y)), where b_k is the regression coefficient for variable x_k (Neter and Wasserman 1974, Neter et al. 1983). The overall fit of the model is 0.34 as per Crawley (1993) (1 − [residual deviance/null deviance]). For an F test comparing the full model with the full model less a term, df $= 1,29$ ($n = 34$).

to the long-term success of the regional population. Factors not included in our models that might explain the residual variation were the availability of overwintering sites, the quality of summer habitat (rather than just quantity), applications of pesticides or fertilizers, and variation in weather.

Scale of landscape influence

Pearson (1993) suggested that the spatial extent of the influence of landscape structure on a local site could be measured by the distance to the farthest habitat patches that influenced a population at a given site. In Analysis I, the amount of summer habitat in the 1 km radius circle proved to be the most significant. This study suggests that, in the Ottawa-Carleton area, the amount of summer habitat exerts an influence on population abundance at the breeding pond out to at least 1.0 km from the center of the pond.

However, because of the high correlations among landscape circles in summer habitat values (Table 2), we could not unequivocally identify the critical scale of landscape influence for leopard frogs. We attempted to deal with this by also conducting the analyses using summer habitat measured in non-overlapping rings surrounding the core ponds. The results of this analysis were qualitatively identical to the analysis using circles. The most significant summer habitat ring was the 0.5–0.75 km ring, suggesting a slightly smaller scale of landscape influence than that suggested by the analysis using habitat circles. However, as for the circles, the correlations among summer habitat rings were very high, ranging from 0.798 to 0.915, with $P < 0.001$ for all between-ring correlations. The analysis using the 0.75–1.0 km ring was nearly identical to that using the 0.5–0.75 km ring. Therefore, the analysis using rings did not improve our ability to identify the critical scale of landscape influence for leopard frogs.

Dole (1971) observed that newly metamorphosed young did not necessarily select the first suitable summer habitat that they encountered in moving away from the natal pond. This type of movement behavior may account for the lack of a significant fit for the 0.25-km and 0.50-km summer habitat areas, whereas the two larger areas proved significant. These results highlight the importance of behavioral studies at the landscape scale (Lima and Zollner 1996).

This result also suggests that we may have underestimated the movement capabilities of the frogs when
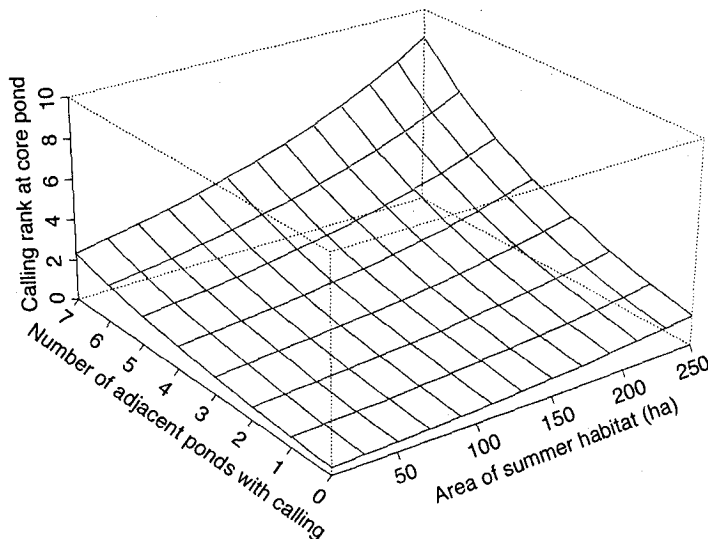

FIG. 4. Predicted values (model in Table 2) for calling rank when pH and spawning habitat are set to mean levels and number with calling and summer habitat 0–1.0 km are varied systematically.
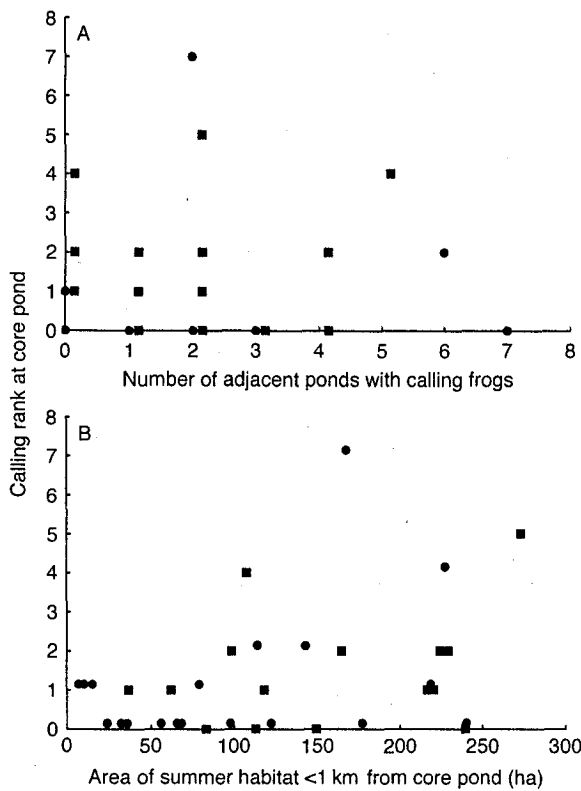
FIG. 5. (A) Relationship between calling rank and number with calling. Circles are calling rank values for ponds in landscapes with less than the median value of summer habitat 0–1.0 km, and squares are calling rank values for ponds in landscapes with greater than the median value of summer habitat 0–1.0 km. (B) Relationship between calling rank and summer habitat 0–1.0 km. Circles are calling rank values for ponds in landscapes with less than the median value of number with calling, and squares are calling rank values for ponds in landscapes with greater than the median value of number with calling.

selecting the study ponds. In fact, five of the 15 sites classed as "summer habitat far" did contain leopard frogs. These results indicate that, for leopard frogs, landscape complementation does not require contiguity of the different required habitat types. As long as the frogs can move between the habitat patches, i.e., the landscape connectivity is maintained, the movement range of the species is sufficient to allow it to cope with some alteration of the landscape by human activities. These results parallel those of Taylor (1993) for the damselfly *Calopteryx maniculata* in forested areas separated by pasture.

The presence of vegetated drainage ditches throughout the study area may enhance the connectivity of the landscape, allowing frogs to use summer habitat farther from the ponds. Reh and Seitz (1990) reported a correlation between the presence of drainage ditches and the measured genetic distances between local populations in their study of *Bufo bufo,* the common toad, in Germany. They hypothesized that the toads used the

ditches as corridors for movement between local populations.

Influence of pH

Several studies have demonstrated negative effects of acidic water on egg and tadpole development (Gosner and Black 1957, Clark and Euler 1982, Freda and Dunson 1985). The results of this study, combined with previous work on acid tolerance in *R. pipiens,* suggest that the relationship between leopard frog abundance and pH may be peaked, with abundance increasing as pH increases to neutral and decreasing again as the water becomes more basic.

Amphibian decline

It has been suggested that we are witnessing a worldwide decline in amphibians (Blaustein and Wake 1990, Fellers and Drost 1993). Reductions in both population size and geographic range have been reported (Blaustein and Wake 1990). Local declines of *R. pipiens* have been recorded across North America (Roberts and Lewin 1979, Hine et al. 1981, Beauregard and Leclair 1988, Roberts 1992, Arkinstall 1994, Green 1997).

Blaustein et al. (1994) contend that habitat destruction is the major cause of amphibian losses worldwide. In Ontario south of the Canadian Shield, an area that includes our study sites, 75% of wetlands have been lost (Regional Municipality of Ottawa-Carleton 1993). The common requirement among amphibians for more than one habitat makes this group particularly vulnerable to the impacts of habitat loss and fragmentation. Reduction or removal of any one of the required habitats may render the landscape unsupportive of these species. Reduction in the connectivity of the landscape between the required resources may also reduce the capacity of the landscape to support species with complementary resource needs (Reh and Seitz 1990). Roberts (1992) hypothesized that surviving populations of leopard frogs in the semiarid landscape of southwestern Alberta may be limited by summer habitat availability and lack of opportunity for dispersal. Fahrig et al. (1995) demonstrated a negative relationship between anuran densities along roadways and increasing traffic intensities, indicating that roads may reduce landscape connectivity for these species. Vos and Chardon (1998) found similar results for the moor frog, *Rana arvalis.*

Implications for conservation

This study suggests that we must be cautious in applying metapopulation analyses to species for which the habitat vs. nonhabitat categorization of the landscape is not appropriate (e.g., Halley et al. 1996). The potential for rescue and recolonization to maintain a regional population must be assessed within the constraints of the entire landscape. Although breeding habitat may be of "primary importance to long term population survival" (Harrison and Fahrig 1995), other habitats may be critical if individuals are to survive to

reproductive maturity. For example, leopard frog abundances were low in an area outside of Chicago, despite numerous potential breeding ponds. When the habitat surrounding the ponds was restored to grasslands from scrub forests, *R. pipiens* numbers increased dramatically (K. S. Mierzwa, *personal communication*). Similarly, fenland restoration in Britain to augment populations of the endangered butterfly, *Lycaena dispar*, was unsuccessful until the male territories in the fen meadows were complemented with areas of high densities of the larval food plant *Rumex hydrolapathum* (A. S. Pullin, *personal communication*). In focusing on the breeding habitat, we risk overestimating the potential of a landscape to maintain species that require more than breeding habitat to complete their life cycles.

Burke and Gibbons (1995) noted that legislation intended to address conservation goals in wetlands protected the wetland itself, but afforded no protection to the upland habitat required by some wetland organisms. Findlay and Houlahan (1997) demonstrated strong effects of landscape composition on wetland species richness out to ≥2 km in the landscape surrounding wetlands. Failure to integrate terrestrial and aquatic habitats will result in the failure of wetland conservation strategies (Buhlman 1995).

Many species require distinct habitats for overwintering, foraging, and/or oviposition. These include many reptiles (snakes, Semlitsch et al. 1988; turtles, Bennett et al. 1970, Buhlman 1995, Burke and Gibbons 1995), amphibians (Gill 1978), birds (Wiens 1989), and insects (Wiklund 1977, Wiklund and Åhrberg 1978, Pollard and Hall 1980, Ehrlich and Murphy 1987, Taylor 1993, Solbreck 1995). Like leopard frogs, many of these species exhibit "complex life cycles" (Wilbur 1980). When devising conservation strategies, the appropriateness of focusing solely on breeding habitat should be verified for organisms exhibiting these life history patterns. Otherwise, management based on a breeding/nonbreeding habitat classification of the landscape relies on chance to supply the other habitat components required by species with complementary resource needs.

The metapopulation construct is a useful tool for thinking about populations in fragmented landscapes. However, as usually implemented, it reduces the landscape from a full-color image to a high-contrast photograph in black and white. This two-phase classification is perhaps a relict of the island/sea dichotomy of the *Theory of Island Biogeography* (MacArthur and Wilson 1967), a precursor to metapopulation theory (Middleton and Merriam 1983, Wiens 1995). For some organisms, the simplification may provide an adequate understanding of how the landscape pattern affects those species. For others, the breeding/nonbreeding habitat filter impairs our ability to detect the heterogeneity to which those species respond and, therefore, diminishes our ability to understand the processes that determine the distribution and abundance of those species.

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