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**The relative roles of landscape complementation and
metapopulation dynamics in the distribution and abundance
of leopard frogs (*Rana pipiens*) in Ottawa-Carleton.**

Shealagh E. Pope, B.Sc.

**A thesis submitted to the Faculty of Graduate Studies and Research in
partial fulfilment of the requirements for the degree of**

Master of Science

**Department of Biology
Carleton University
Ottawa, Ontario
November 21, 1996**

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in partial fulfilment of the requirements
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Chair, Department of Biology

Thesis Supervisor

Carleton University

ABSTRACT

I evaluated the relative importance of landscape factors at individual and population levels for a species for which landscape complementation is obligate and metapopulation structure likely *Rana pipiens*. I conducted breeding chorus surveys at 34 core ponds and all potential breeding sites within 1.5 km of these ponds around Ottawa, Canada in April-May 1995. Calling from surrounding sites provided an estimate of recolonization and rescue potential (metapopulation effects). Mean pH, amount of spawning habitat, and perimeter length were measured for the core ponds (local effects). From air photos and ground-truthing, I mapped the summer habitat within 1 km of each core pond (landscape complementation effects). The abundance of calling frogs at the core ponds could not be explained by local and metapopulation factors only. The covariate, summer habitat amount, was required to fit a statistically significant model. Density of paved roads also proved a significant factor in depressing calling intensity.

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INTRODUCTION

In landscapes that have been altered by humans, two processes act on the distribution and abundance of resources: habitat fragmentation and habitat loss. Habitat fragmentation is the process of disrupting the continuity within a more-or-less homogeneous landscape (Lord and Norton 1990, Rolstad 1991). In terrestrial systems, fragmentation is necessarily coupled with the loss of a portion of the original habitat and the complementary introduction (or spread) of a replacement habitat type (Rolstad 1991, Saunders et al. 1991). The replacement habitat type is often novel for that landscape.

Habitat fragmentation and loss may oblige animals to move through new habitats or over different ranges of distance to access resources critical to their survival (Taylor 1993, Arnold et al. 1993). If the habitat introduced in the process of fragmentation affects the movement ability of animals differently from the pre-fragmentation habitat, then the connectivity of the landscape may be altered (Merriam 1984, Taylor 1993, Åberg et al. 1995). Impacts of changes in landscape connectivity are particularly evident where new landscape elements constitute barriers to movement, such as heavily-travelled highways for frogs moving between overwintering and breeding sites (Rittschof 1975, Fahrig et al. 1995). As a measure of an organism's ability to move through a particular landscape, connectivity is determined not only by the physical structure of the landscape, but also by the behavioural response of the organism to the habitats it has to move through (Henein and Merriam 1990, Taylor et al. 1993).

Metapopulation theory has advanced our understanding of how populations persist in fragmented habitats (Levins 1969, 1970, Harrison 1991, Hanski 1994, Fahrig and Merriam 1994). A metapopulation is a set of local (patch) populations connected together by dispersal (Laan and Verboom 1990, Merriam 1991). While local populations may go extinct due to stochastic fluctuations in local abundance (Fahrig and Merriam 1994),

metapopulation theory suggests that the larger regional population will be maintained if dispersal results in recolonization of these local extinctions at a rate sufficient to prevent their accumulation into a regional extinction (van Dorp and Opdam 1987, Fahrig and Merriam 1994, Hanski 1994, Hanski and Thomas 1994). Metapopulation theory also predicts that movement will reduce the extinction rate of local populations. This process is known as the "rescue effect" (Brown and Kodric-Brown 1977, Smith 1980, Stacey and Taper 1992). Movement of individuals from larger to smaller populations tends to increase the viability of the regional population (or metapopulation) as smaller populations are more extinction prone than larger ones (Smith 1980, Verboom et al. 1991, Hanski 1994).

There is now evidence for a variety of taxa that the risk of local extinction is influenced not only by the size of the population but also by the degree to which it is isolated from conspecific populations (Smith 1980, Fahrig and Merriam 1985, van Dorp and Opdam 1987, Rolstad 1991, Sjögren 1991, 1994, Kindvall and Ahlén 1992, Dunning et al. 1995). Recolonization and population rescue are both enhanced by shortening the distance to the nearest population (Sjögren 1994) and by increasing the number of sites that may provide dispersers (Lefkovitch and Fahrig 1985, Verboom et al. 1991). These processes are also influenced by the connectivity of the landscape. Conspecific populations that are close in absolute terms may be quite distant when the animal's ability to move between the sites is considered (Taylor et al. 1993).

Metapopulation theory has broadened the scale of inquiry into population dynamics from a focus on local habitat factors to a framework that embeds these local factors in the wider landscape context (Hanski and Thomas 1994). However, much of the theoretical and empirical work on metapopulations has focused on the amount and location of breeding habitat and the capacity of the study organism to move between

patches of habitat deemed suitable for reproduction (Fahrig and Merriam 1985, Fahrig and Palacheimo 1988, Harrison 1991, Lamberson et al. 1994, Sjögren 1994, Andren 1994, Dunning et al. 1995). Essentially, we have been looking at the landscape through a dichotomous filter: "breeding habitat/non-breeding habitat". 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). Such a "black and white" classification may provide sufficient detail for those species that can meet all their resource needs in the breeding habitat. For example, Sjögren (1994) successfully partitioned the variability in population abundance of *Rana lessonae*, the Swedish pool frog, between local pond factors and regional metapopulation factors. The pool frog remains at the pond after breeding (Sjögren 1994) suggesting that only one habitat is required for this species to complete its life cycle. However, many species cannot meet all their resource needs in the breeding habitat.

Dunning et al. (1992) coined the term "landscape complementation" to highlight the requirement for certain 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). Wiklund (1977) characterized the required habitat types for butterflies in functional terms: a mating habitat, a breeding habitat, and a foraging habitat. He noted that these types may be spatially separated or overlapped and that the greater the mobility of the species in question, the greater the capacity to tolerate spatial separation of these functional habitat types (Wiklund 1977).

For organisms that require more than one habitat type, an appropriate landscape is necessarily heterogeneous. In fact, defining an "unfragmented" landscape may be difficult

for such species. Lann and Verboom (1990) described a habitat patch for an amphibian subpopulation as "one or more ponds and parts of the surrounding landscape [that provide] summer and winter habitat". Movement is required if species with complementary resource needs are to persist in a landscape (Arnold et al. 1993). For these species, the landscape context affects persistence at the individual level as well as at the population level. The breeding/non breeding habitat classification common to current metapopulation analyses may result in an underestimate of the importance of metapopulation structure to species that require more than breeding habitat to complete their life cycles. Variation due to landscape constraints at the individual level, if unaccounted for, may mask landscape effects at the metapopulation level.

In this study, I evaluated the relative importance of landscape level factors at the individual and population levels for a species for which landscape complementation is obligate and metapopulation structure 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 mid-summer by the tadpoles, grassy meadows or fields for summer foraging, and a stream or lake for overwintering (Rittschof 1975, Merrell 1977). I considered the influence of two of these three habitat types in this study: the breeding pond and the 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 1993).

I used breeding chorus surveys to assess the relative importance of the need for individual frogs to link breeding ponds and summer foraging habitat versus the population level need for rescue and recolonization from adjacent populations. I hypothesized that local population abundances would be more strongly determined by the availability and

juxtaposition of summer habitat than by the number and proximity of other breeding populations. To operationalize this hypothesis, consider the case where distance from the core, or focal, ponds to summer habitat and to adjacent breeding populations is constant between ponds but the amount of these landscape components varies. The hypothesis then can be written schematically as follows.

	Predicted abundance at the core pond
1) no summer habitat, adjacent ponds many,	NONE
2) summer habitat low, no adjacent ponds,	FEW
3) summer habitat low, adjacent ponds few,	
4) summer habitat low, adjacent ponds many,	
5) summer habitat high, adjacent ponds few,	
6) summer habitat high, adjacent ponds many	MANY

The hypothesis could also be framed in terms of variation in the distance to summer habitat and adjacent breeding ponds, amount being held constant. In reality, of course, both distance and amount may vary. However, it follows from this hypothesis that the ability to detect an effect at the metapopulation level will depend on summer habitat being included in the analysis. As local factors may also determine population levels, I also included characteristics of the pond habitat in all analyses

I addressed these questions by studying a range of landscapes centered on 34 ponds in a region that has been considerably altered from its pre-settlement state by human activities. The study landscapes varied in the amount of summer habitat for leopard frogs and in the number of potential breeding sites for conspecific populations in the area

surrounding each pond. The landscapes were situated along a gradient of urban development from highly developed city sites through to rural, agricultural locations. McDonnell and Pickett (1990) noted that urbanization constituted a massive, unplanned experiment and that the urban-rural gradient provided an unprecedented suite of "experimental manipulations". I substituted an experiment in time with an observational comparison in space that took advantage of this urban-rural gradient (Taylor 1993, Fahrig et al 1995). By comparing the abundance of leopard frogs at the different study ponds, I inferred effects caused by changes in the landscape structure over time from those evident at locations with different landscape structures at one time.

Paving and road density typically decrease from the urban centre to the rural periphery. Increased traffic intensity has been shown to have a negative impact on anuran populations adjacent to roadways (Fahrig et al. 1995). Herptile species richness decreases with increasing road density within 2 km of wetlands (Findlay and Houlihan in press). Since movement is central to the ecology of leopard frogs both at the individual and population levels (Rittschof 1975), I hypothesized that leopard frog abundance at the study ponds would decrease with increasing road density in the surrounding landscapes. I assumed that other connectivity factors varied randomly with respect to road density and the other treatments considered.

It was my intention in conducting this study to elucidate the influence of landscape heterogeneity on the distribution and abundance of organisms that require more than one kind of habitat and likely exhibit metapopulation structure. Constraints imposed by the physiognomy of the landscape at the level of individual resource needs ("the individual level") are hypothesized to limit our ability to detect the influence of the landscape context

on the regional population ("the metapopulation level") when we evaluate that influence from within a framework that classifies the landscape dichotomously

NATURAL HISTORY

The leopard frog (*Rana pipiens*) is the most widely distributed anuran species in North America (McMurray 1984, Dole 1965a). They are often called "grass" or "meadow" frogs because they are commonly found at marsh margins or in wet meadows or fields during the summer months - often quite a distance from any permanent water (Gilhen 1984).

North of the line separating ice-free from ice-covered ponds in winter, post-metamorphic *R. pipiens* exhibit four behavioural states associated with particular seasons (Rittschof 1975) (Figure 1). In the winter, they are aquatic (Merrell 1968ab) and do not feed (Rittschof 1975). For a brief period in the spring, adult *R. pipiens* congregate in breeding ponds; typically, these are not the same water bodies used for overwintering (Merrell 1970, 1977; Hine et al 1981). In instances in which overwintering sites (or hibernacula) are used for breeding, it is not known whether the animals that hibernate there are the same individuals found breeding there (Rittschof 1975). In the summer, leopard frogs are terrestrial, establishing home areas in which they forage (Merrell 1968ab, Dole 1965a). In both the spring and fall, leopard frogs are migratory, undertaking what can be extensive movements between the spring, summer, and winter areas (BM, SM, and FM in Figure 1) (Merrell 1968ab, Rittschof 1975).

Overwintering habitat

The choice of an appropriate overwintering site is crucial to survival of frogs (Merrell 1977). However, what makes an 'appropriate' overwintering site one year may constitute an inappropriate choice the next year, depending on various factors including fall rainfall and the severity of the winter (Schueler pers. comm.). Three types of overwintering sites for *R. pipiens* have been observed: lakes, spillways below dams at the

outlet of lakes, and along the shore or the bottom of streams (Merrell 1970, Emery et al 1972, Cunjak 1986). Water or drainage systems have to be permanent and deep enough to not freeze solid to function as hibernacula (Merrell 1977, Hine et al. 1981). An adequate oxygen supply also appears to be a crucial factor in overwinter survival (Merrell 1977, Licht 1991)

Breeding pond

Merrell (1968a) suggested that breeding ponds used by leopard frogs are temporary, drying up periodically in times of drought and thus lacking fish. In contrast, Pace (1974), Collins and Wilbur (1979), and Mount (1975 cited in Noland and Ultsch 1981) suggested that leopard frogs can use either temporary or permanent ponds for breeding. Collins and Wilbur (1979) also suggested that the presence of fish did not preclude successful breeding. In 1994 field surveys, I found metamorphs at 3 ponds which were permanent and also supported fish. Nonetheless, a pond that dries up every decade or so (thus eliminating fish) probably supports a larger leopard frog population than a permanent water body as predation by fish can substantially reduce a frog population (Hine et al. 1981).

In Gatineau park just north of the study area, leopard frogs were found breeding in shallow ponds (<1 m deep) especially where grasses extended the first 0.66-1 m into the pond (McMurray 1984). Hine et al. (1981) suggested that a depth in the spring of at least 1.5 m, preferably greater, led to a better ratio of open water to vegetation cover, they concluded that overall depth was more important than area in determining the appropriateness of a pond for breeding. Merrell (1977) suggested that large ponds were not selected by *R. pipiens* as they warmed too slowly. However, he also noted that small ponds were avoided as they warmed quickly during the day but cooled too quickly at

night In his study area, ponds with breeding ranged from 30-60 m in diameter (Merrell 1977)

In addition to influencing pond choice, water temperature is also a factor in the selection of spawning sites within a pond. Ponds and areas of ponds that warm first usually have the most calling and breeding activity (Pace 1974, Merrell 1977, Hine et al. 1981, Gilbert et al. 1994); often this activity is concentrated at only one site in the pond (Merrell 1977). As a result, egg masses tend to be highly aggregated in sites that are well exposed to sunlight (Hine et al. 1981, Merrell 1977, Gilbert et al. 1994), usually on the north side of the pond (Merrell 1977).

Vegetation

Ponds devoid of vegetation have little value for frogs (Dumas 1964, Hine et al. 1981). Leopard frogs prefer breeding habitats with a strong predominance of narrow-leaved plants such as *Phalaris arundinacea* (canary reed grass) and robust emergent forms such as *Lythrum salicaria* (purple loosestrife) and *Cornus stolonifera* (red osier dogwood) (Leclair 1983, Gilbert et al. 1994). Emergent narrow-leaved vegetation provides cover from predators and attachment for egg masses; submergent vegetation provides further cover, substrate for egg mass attachment, and food for tadpoles (Hine et al. 1981). The area of the pond that supports emergent vegetation, and therefore potentially eggs and tadpoles, is increased if the slope of the pond shoreline is gradual (Hine et al. 1981, Gilbert et al. 1994). Habitats dominated by large-leaved emergent forms such as *Sagittaria latifolia* (common arrow head) and *Pontederia cordata* (pickeral weed) are not used (Gilbert et al. 1994).

Spawning habitat

Egg masses are attached to standing or fallen vegetation - a firm twig, sedge, or dead cattail - typically near the shore (Eddy 1976, Merrell 1977, Hine et al 1981). Plants most often used for support are *Phalaris arundinacea*, *Cornus stolonifera*, *Lythrum salicaria*, *Spartina pectinata* (prairie cordgrass), and *Salix sp.* (willows) (Gilbert et al 1994). Eggs are typically deposited at, or just below, the surface in water 10-65 cm deep (Merrell 1977, Gilbert et al 1994).

Combining water depth and sunlight incidence characteristics with vegetation characteristics leads to the following characterization of preferred spawning habitat: water 10-65 cm deep in full sun with emergent, non-broad-leafed vegetation for attachment of egg masses (Eddy 1976, Merrell 1977, Hine et al. 1981, Gilbert et al. 1994).

Water chemistry

R. pipiens has been shown to be highly sensitive to acidic water (Gosner and Black 1957). pH below 4.5-5.0 is known to have important physiological effects on leopard frogs including reduced hatching success and reduced growth of tadpoles (Gosner and Black 1957, Freda and Dunson 1985, Dale et al. 1985).

Timing of breeding

Adult males of most frog species chorus with distinctive, species-specific calls to attract females for breeding (Zimmerman 1994). *R. pipiens* choruses and breeding begin when the water temperature reaches 8-10°C (Hine et al 1981, Gilbert et al 1994). This coincides with the 8.4°C given by Moore (1939 cited in Gilbert et al. 1994) for normal development of *R. pipiens* eggs in vitro. When water temperatures fall below 8-10°C

breeding stops, although it will resume when the temperature rises again (Gilbert et al. 1994). Air temperature also plays a role, cool (below 10°C), dry nights depress breeding activity (Rittschof 1975, Hine et al. 1981). Data collected by Cook (1992) over the period 1971-1991 indicate that the beginning of calling ranges from 4-28 April while the end of calling falls between 2-27 May for this species in the Ottawa area.

Chorusing begins as soon as males reach the breeding area (Rittschof 1975); however, as females may lag behind males in reaching the breeding pond, the reproductive period may comprise only a subset of the calling period (Hine et al. 1981). The duration of the breeding season is variable although typically highly concentrated; it may range from a few days to a few weeks (Pace 1974, Rittschof 1975, Merrell 1977, Gilbert et al. 1994).

Summer habitat

In 52 observations of leopard frogs (not including young-of-the-year - YOY) over the summer period, McAlpine and Dilworth (1989) found that 96% of these were terrestrial. *R. pipiens* may range as much as a mile or two from the nearest body of water during the summer months (Merrell 1977). Nonetheless, available moisture is a key factor in the distribution and movements of these amphibians (Dole 1967b, 1971, Rittschof 1975, Tracy 1976, Merrell 1977, Beauregard 1988), and leopard frogs are usually confined to moist places (Dole 1967b). Their preferred summer habitats, therefore, are pond and marsh borders, wet meadows, and open fields with dense vegetation cover including hay fields in cultivated areas and unmowed pastures (Wright and Wright 1949, Whitaker 1961, Dole 1965a, Merrell 1977, Hine et al. 1981, Degraaf and Rudis 1983, McMurray 1984, Beauregard 1988). These habitat types are characterized by dense herbaceous vegetation, particularly grasses, with a high moisture content. These conditions provide ideal cover and feeding opportunities for leopard frogs (Tracy 1976, Hine et al. 1981). While

continuous herbaceous vegetation cover would seem to be preferred (Whitaker 1961), leopard frogs are also reported to use clumps of grasses or sedges left in grazed pastures (Dole 1965a, Merrell 1977). *R. pipiens* 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 1965a, Hine et al. 1981, Beauregard 1988); in heavily grazed pastures (Dole 1965a, Merrell 1977); or on closely mowed lawns (Merrell 1977, Hine et al 1981)

Beauregard (1988) found that an open shrub layer, as in wooded swamps, favoured higher populations than purely herbaceous meadows and that wet forests were used (Whitaker 1961, Dole 1965a, Degraaf and Rudis 1983). Whitaker (1961) noted, however, that the forest sites at which leopard frogs were trapped in his study were very close to swamps, and in Wisconsin, *R. pipiens* populations were particularly low in heavily forested areas (Hine et al 1981).

Movement

Adults

Movement is central to the ecology of *R. pipiens* (Rittschof 1975, Merrell 1977). There is often as much as 1-2 km between the different required habitats (Figure 1) (Merrell 1970, 1977, Hine et al 1981). Therefore, over the course of single year an individual adult *R. pipiens* moves, on average, 3 to 6 km and may move substantially farther (Rittschof 1975, Merrell 1977). Rittschof (1975) recorded a case in which the distance between two of the three required habitat types, overwintering and summer habitat, was 8 km.

Long distance movements are highly seasonal in leopard frogs, as they are for many other amphibians, and are often limited to relatively short intervals during the annual activity period (Sinsch 1988, Blaustein et al 1994). *R. pipiens* cover great distances between the habitats required for each phase of the year, but become quite sedentary while in the habitat appropriate to the season (Figure 1). During hibernation, they move if disturbed or perhaps to follow an oxygen gradient, but otherwise remain motionless on the bottom of the pond, lake, or stream (Merrell 1970, Rittschof 1975). There is no evidence of movement between nearby ponds during the brief breeding period (Merrell 1968a, 1970). Dole (1967a) recaptured seven frogs in one pond originally captured at another. However, his surveys occurred at the end of, or after, the breeding period, the four females recaptured had all laid their eggs by the time of their second capture. Over the course of a summer, adult leopard frogs only infrequently change locations (Merrell 1977, Beauregard 1988) and then seldom move more than 5-10 m to a new foraging site (Dole 1965a). Dole (1965b) was thus able to define "summer home ranges" based on the small focal area used by each frog within the overall summer habitat and the infrequent forays made out from these areas. He noted high fidelity not only to a particular summer habitat patch but also to individual summer home ranges for juveniles recaptured as adults in the subsequent year and for adults caught in successive years.

Juveniles

Movement to new breeding sites, like movement to new summer habitat, occurs mainly through juvenile leopard frogs. Dole (1971) and Rittschof (1975) contended that most exchange of individuals, or gene flow, between populations is the result of movements soon after metamorphosis. In summer surveys around a group of ponds, Rittschof (1975) recorded that 61% of the juveniles using the area for summer habitat had not metamorphosed there, indicating a high level of dispersal from the natal pond. This pattern is consistent with the central role of juveniles of other amphibian species in the

colonization of new breeding sites or the recolonization of local extinctions (Gill 1978, Berven and Grudzien 1990, Sjogren 1996)

Juveniles disperse from their natal ponds in three stages. During the first stage, the new metamorphs, or YOY, leave the area adjacent to their natal ponds (Figure 1, YOYD) and seek out a hibernation site in the late summer and early fall (FM) (Bovbjerg and Bovbjerg 1964, Merrell 1970). In the second stage the following spring, these frogs, now juveniles, seek out summer habitat (SM1) (Dole 1965a, Rittschof 1975). While some males may be ready for breeding at one year old (their first spring as frogs), it is not until their second spring that most leopard frogs complete the third stage of juvenile dispersal and seek out a pond in which to reproduce (BM2) (Rittschof 1975, Merrell 1977, Hine et al. 1981, Leclair and Castenet 1987, Gilbert et al. 1994).

Juveniles may cover large distances in the shift from their natal ponds to their adult range (Dole 1971). Dole (1971) recaptured 3 juveniles more than 5 km from their natal pond. Seburn et al. (in press) caught YOY that had moved up to 2.1 km in less than 6 weeks after metamorphosis. One frog marked in their study was captured the following spring 8 km away (Seburn et al. in press).

The influence of connectivity

Like many amphibians, *R. pipiens* are influenced by habitat characteristics as well as weather conditions, particularly rainfall and humidity, when moving through the landscape (Gibbons and Bennett 1974, Blaustein et al. 1994). Their willingness to move through different habitat types and under different weather conditions is related to the type of movement they are undertaking (Rittschof 1975). The connectivity of the landscape, therefore, is not static through time but rather varies with the behavioural state of the frog and the weather conditions at the time that movement is undertaken.

The migration away from the breeding pond (SM, Figure 1) and the fall migration (FM) both tend to be limited to evening and night time movements; rainy conditions are required, and movement tends to be through preferred summer habitat (Rittschof 1975, Merrell 1977). In contrast, leopard frogs have been recorded moving during daylight under dry, even dusty, conditions during the breeding migration (BM) (Bovbjerg and Bovbjerg 1964, Dole 1967a, Merrell 1977). The breeding migration is fast and concentrated (Eddy 1976); it may take as few as six days and nights for all the sexually mature adults to reach breeding ponds in an area (Rittschof 1975). Leopard frogs will move both day and night for the breeding migration; they do not require rain, although it increases movement probability; and they do not limit their movements to preferred summer habitat types (Rittschof 1975).

The age of the frog also influences movement behaviour and, therefore, the connectivity of the landscape as smaller frogs lose moisture at a greater rate than do larger ones (Thorson 1955, Schmid 1965). For YOY frogs, dispersal away from the natal pond usually occurs on warm, rainy nights (Dole 1971). The presence of a ditch or a stream enhances movement ability of YOY frogs (Seburn et al. in press). While Hine et al. (1981), Rittschof (1975) and Dole (1971) noted that movements away from the natal pond by YOY tended to be directed into areas of wet grass and not into wooded or otherwise unfavourable habitat, YOY will move through normally drier areas such as upland woods given warm, rainy conditions (Dole 1971, Rittschof 1975).

Figure 1 Schematic representation of habitat use and movement between habitats by leopard frogs. Adapted from Rittschof (1975). Lomon (1990) presents a generic version of this diagram.

METHOD

The study was based on 34 permanent "core" ponds within a 30 km radius west, south, and east of Ottawa, Ontario. They ranged in size from 0.04 ha to 29.1 ha. The habitats immediately surrounding the ponds varied from pasture fields, corn fields, and old fields to golf courses and urban parks. In addition to the 34 core ponds, all other potential leopard frog breeding sites (ponds, large drainage ditches, streams) within 1.5 km of the core ponds were surveyed for a total of 107 survey sites. 1.5 km was the shortest distance for which all 34 core ponds had at least one adjacent site which 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 and may have included other core ponds as well as non-core sites. Since leopard frogs may move as much as 1-2 km between different habitats in a year, the listen sites were all within the movement range of the species. All core ponds and listen sites were identified originally from colour air photos taken in 1993 at a scale of 1:15,000, and all were ground-truthed in the spring of 1995.

Selecting the core ponds

Selected ponds were distinct, i.e. either not connected to other ponds or not so amorphous as to make defining the boundaries of the study site difficult. I chose only ponds that were permanent since these would hold water long enough for the tadpoles to complete metamorphosis.

The ponds fell roughly into four classes:

- (1) other ponds near, summer habitat near - 10 ponds;
- (2) other ponds near, summer habitat far - 9 ponds;
- (3) other ponds far, summer habitat near - 10 ponds; and
- (4) other ponds far, summer habitat far - 5 ponds.

"Far" for other ponds was defined as greater than 1 km (Rittschof 1975). While 1 km is well within the movement range of the species, there is no evidence for movement of breeding animals between ponds during the breeding season (Dole 1967a, Merrell 1968a, 1970). Thus, at least within any one year, the breeding populations are distinct. For summer habitat, the "far" category was defined as the pond not being adjacent to leopard frog summer habitat, i.e. individuals would have to leave the immediate pond vicinity to find summer habitat (Taylor 1993). For the "near" category, summer habitat was contiguous with the pond edge.

Chorus Surveys

With the help of 34 volunteers, I conducted breeding chorus surveys over five census periods between April 12 - May 9, 1995. Such surveys of breeding choruses can provide estimates of species richness or abundances for across-site comparisons (Scott and Woodward 1994). The basic assumptions of breeding-site studies of a single species are that calling males are equally available for sampling at each site (Scott and Woodward 1994) and that they represent a consistent subset of the population between sites, i.e. that calling males do not constitute a larger proportion of the total population at one site than at another (Zimmerman 1994). I 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 question of whether or not calling males represented a consistent subset of the population between sites was not addressed in this study.

The core and listen sites were divided among 10 routes with roughly 11 sites per route. Each route had a mixture of core and listen sites. The intent was to cover all 107 sites - both core and listen - in one night. However, volunteer availability did not permit this on all the survey nights. Routes were covered in one to three days. The surveys were

initiated when water temperature was 8°C or greater at 5 cm below the water surface (Gilbert et al. 1994) and evening air temperature at sunset was 8-10°C (Hine et al. 1981, Marsh Monitoring Program).

Five surveys were conducted over the following dates: April 12, 23, and 27-28, and May 2-4 and 8-9, 1995. 32 of the core ponds and all listen sites were checked April 12. All 34 core ponds and the 73 listen sites were surveyed April 23, 27/28 and May 8/9. For the May 2-4 survey, 30 core ponds and 57 listen sites were censused. All sites were censused at least four times over the sampling period. Hine et al. (1981) suggested that four chorus surveys were sufficient to detect the presence of calling male leopard frogs.

Whenever possible, routes were surveyed by two people for safety and to increase the accuracy of the survey. There was a substantial time investment in learning a route, so routes were not changed between surveys, and surveyors were not required to learn a new route every night. Instead, I rotated the surveyors so that once a surveyor had done a route he/she was paired with a novice (with respect to that particular route) for subsequent surveys to the extent that volunteer availability permitted.

The length of the route and, therefore, the possible combinations of sites, were limited by time. It is recommended that amphibian chorus censuses be conducted between half an hour after sunset and midnight (van der Ham and Schueler 1992). To vary the survey time of each pond between nights, the routes were driven in different directions - forwards, backwards, and from a starting point in the middle of the route.

Ideal weather conditions for chorus surveys of the early spring breeding frogs, which include leopard frogs, are seasonably warm air temperatures, light rain, and light winds (van der Ham and Schueler 1992). In scheduling the censuses, I endeavoured to choose nights with these conditions. However, coordinating the activities of up to 20

people required advanced notice, and I had to rely on the weather forecasts. The forecast conditions were not always realized.

Surveyors were issued copies of a tape of chorus calls of frogs of the Great Lakes Basin produced by the Canadian Wildlife Service for their "Backyard Frog Surveys". All anurans that call in the Ottawa area are included on this tape. I paired people familiar with the calls with people unfamiliar with them, and I covered 6 of the 10 routes over the 5 surveys myself. Validation surveys comparing inter-observer agreement among experienced and novice surveyors found that novice surveyors trained with the tape agreed with experienced surveyors on species presence/absence in 76-95% of cases and on calling intensity (detailed below) in 56-90% of the cases (Shirose 1995, Bishop et al. in press).

With the exception of leopard frogs and pickerel frogs (*R. palustris*), all the local frogs and toads are easily distinguished on the basis of their calls. Pickerel and leopard frogs call over the same period. However, pickerel frogs are rare in the Ottawa region (Cook 1981). They were not recorded in surveys by Cook over the period 1971-1991 (Cook 1992); nor were they reported in this area in surveys conducted for the Ontario Herpetofaunal Summary over the period 1984-1986 (Weller and Oldham 1988)

Surveyors listened for 5 minutes at each site to determine the intensity of leopard frog breeding choruses (van der Ham and Schueler 1992; Wisconsin Frog and Toad Survey - field data sheet no date in Scott and Woodward 1994) Where traffic or background noise levels were high, but intermittent, the 5 minutes were the sum of pauses in the background noise (Fahrig et al. 1995) For each site surveyors recorded an index of

abundance for each species calling. The calling index was specified originally as follows:

- 0 - no individuals calling,
- 1 - individual(s) can be counted, calls are not overlapping,
- 2 - calls of individuals can be distinguished, but there is some overlapping. and
- 3 - full chorus; calls are constant, continuous and overlapping

(van der Ham and Schueler no date; Wisconsin Frog and Toad Survey - field data sheet no date in Scott and Woodward 1994, Fahrig et al. 1995, Green in press).

However, *R. pipiens* did not prove abundant in the study area. I adjusted the index of calling intensities accordingly. Rather than index level 3 (the highest value in the scale) indicating saturated calling, it was used to denote the maximum number heard - 15-20 leopard frogs calling at once. The calling index, therefore, became

- 0 - no individuals calling,
- 1 - individual(s) can be counted, calls are not overlapping,
- 2 - calls of less than 15 individuals can be distinguished, but there is some overlapping, and
- 3 - calls of 15 or more individuals can be distinguished although there is overlapping.

Characterizing the pond habitat of the core ponds

To account for the possible effects of local habitat factors on the calling intensity of leopard frogs, I characterized the pond habitat for each of the 34 core ponds during

June 1995. For each pond, I noted at each sampling point

- the percent cover of each plant species along a line transect extending out 2 metres at right angles from the shoreline (Figure 2),
- 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 water depth (at 1 and 2 m from the water's edge)

Measurements were taken at equally-spaced sample points around the perimeter of the core ponds. The minimum number of samples per pond was seven, the maximum 25, with spacing based on the total length of the perimeter of the pond as follows

- <166 m - sampled on 19 m,
- <344 m - sampled on 26 m or fewer,
- <561 m - sampled on 38 m or fewer,
- <893 m - sampled on 64 m or fewer, and
- >1275 m - sampled on 96 m.

I was able to sample 31 of the core ponds by pacing the shoreline. For two of these ponds the entire perimeter could not be sampled. In both cases the shallow, northern shoreline area was included in the sampling. Three core ponds had impenetrable, shrubby shorelines which could not be paced. Vegetation, insolation, and depth measurements were taken from the inner line of the vegetation back toward the water's edge. Two of these ponds were sampled by canoe and the third by wading through the water. Perimeter measurements were estimated from the air photos for these five ponds.

The total perimeter (or the total length sampled) was converted to metres from paces and then multiplied by the proportion of samples with full sun and narrow-leafed

emergent vegetation in water of 65 cm or less. In this way, I converted the point samples into estimates of the total length of shoreline with the characteristics preferred by leopard frogs for spawning. Loman (1988) working on *R. temporaria* in Sweden found that the length of shallow, non-shaded shoreline provided the best distinction at the pond level between ponds with and without breeding over measurements of area, perimeter, total shallow shoreline, and total non-shaded shoreline. Similarly, Sjögren (1994) working on *R. lessonae* in Sweden found that area was not useful in discriminating between presence/absence of that species.

The pH of the water in each pond was determined from samples taken at a depth of 5 cm (Freda and Dunson 1985) 1 m out from shore (Sjögren 1994). I took 4 water samples, approximately evenly spaced around the perimeter of the pond for all ponds except for 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 stored for no longer than 7 days in a refrigerator at 6.5° C. The pH was measured twice for each sample using a Corning Model 5 pH meter. Mean pH values for each pond were calculated using the hydrogen ion concentrations.

Characterizing the landscape surrounding the core ponds

I quantified the habitat within 1 km of the centre of each of the core ponds based on colour air photos taken in August and September 1993 at a scale of 1:15000 (National Air Photo Library). A 1 km radius was chosen to provide a sample of the habitats around the pond that were within the potential dispersal distance of leopard frogs. By visual interpretation, I traced the boundaries of the different fields and/or habitat types evident on the air photos onto acetate overlays. I then ground-truthed the air photo tracings over the course of my other field work in the summer and early fall of 1995. Ground-truthing comprised noting habitat types from the side of the road, walking back from the road

when a patch was not visible from the road, and asking landowners to identify their field types. Where a habitat had changed over the course of the summer (e.g. summer crops that were harvested early in the fall), I noted the summer use.

The tracings were scanned at 200 dpi and imported into a paint program (Corel Photo-paint). With the help of an assistant, I coded them into 22 habitat types according to the results of the ground-truthing (Appendix 1). The coded images then were transferred as TIFF files to a geographic information system program (EPPL). Using the EPPL package, I calculated the amount of each habitat type in pixels within 4 landscape bands 0-0.25, 0.25-0.50, 0.50-0.75, and 0.75-1.00 km from the centre of each core pond. These values were converted to hectares. The bands provided a means of assessing the spatial extent of the landscape influence on leopard frog abundance at the core ponds (Figure 3) (Pearson 1993).

Because each landscape was scanned from a tracing on acetate, the outlines of the different habitat patches constituted a undesired 23rd habitat patch. The amount of outline varied substantially between landscapes depending on the diversity of habitat types and the average patch size. To remove the varying contribution of the outlines, I multiplied the area of each of the 22 desired habitat types in a band by the ratio of the total area including the outlines for that band to the total area not including the outlines for that band.

Statistical Analysis

Variables used in the analyses

Table 1 lists the variables used in the analysis and provides a brief description of each. All variables derived from the breeding chorus surveys were based on the calling indices for 4

out of a maximum of 5 nights. When a site had been surveyed all 5 nights in the chorus census, the 4 indices for inclusion in the study were chosen randomly. This accounts for the possibility of a high calling index on the fifth night for the sites surveyed only four times.

Dependent variable

A measure of the calling intensity at each of the 34 core ponds, **calling.rank**, was used as the response variable in all statistical analyses. Calling intensity was assumed to correlate with population abundance. **Calling.rank** was calculated by summing the 4 calling indices included in the study for each core pond. I used this composite index rather than simply the maximum calling index recorded for each site as **calling.rank** gave a metric with greater range. Unlike the maximum, **calling.rank** gave weight to sites with persistent calling as well as to those with high calling intensity.

Independent variables

The independent variables fell into four categories: local pond characteristics, landscape complementation factors, metapopulation factors, and road density (Table 1). I accounted for possible local habitat effects by including the local pond variables: mean pH (**meanph**), length of the pond perimeter in metres (**perimeter**), and the length of the perimeter that constituted preferred spawning habitat (**spawning.habitat**). I included both **perimeter** and **spawning.habitat** as these two variables could act in opposite directions on the abundance of calling frogs for larger ponds (Merrell 1977).

As I was interested in the contrast between ponds with potential summer habitat and those without and not in what type of habitat provided the best quality summer habitat

to leopard frogs, I aggregated the area of all possible summer habitats into one measure, **summer.habitat**, to assess the contribution of landscape complementation. Of the human-altered habitats in the landscapes surrounding the core ponds, perennial forage crops (e.g. grass, alfalfa, and clover), and pasture constituted potential leopard frog summer habitat. Among the more natural habitats, old fields, scrub, and sedges could serve the same function (Wright and Wright 1949, Whitaker 1961, Dole 1965a, Merrell 1977, Hine et al. 1981, Degraaf and Rudis 1983, McMurray 1984, Beauregard 1988). Since the landscape surrounding each pond was divided into 4 bands (within 0-0.25, 0.25-0.50, 0.50-0.75, and 0.75-1.00 km of the centre of the pond), there were four measures of the amount of **summer.habitat** for each pond.

The possible effects of metapopulation level factors were included in the analyses using three variables: **total.listen**, **number.with.calling**, and **sum.calling.rank** (Figure 4). **Total.listen** was a tally of the number of possible breeding sites within 1.5 km of centre of the core pond in question. **Number.with.calling** indexed the number of these sites for which calling frogs had been recorded at least once. Like the independent variable, **calling.rank**, **sum.calling.rank** was based on the sum of calling indices. However, whereas **calling.rank** summed the four indices at the core pond in question, **sum.calling.rank** summed the sum of the four indices for all of the sites within 1.5 km of the core pond in question.

Lastly, I was interested in whether or not road density might influence calling at the core ponds. **Area.roads** was a measure of the area of roads (paved or dirt) and pavement within the landscape. Since roads in residential and urban areas were not coded separately from housing and buildings, I included 25% of the total residential area as a measure of road cover in these areas (Lovelace 1949). As for **summer.habitat**, there

were four possible measures for **area.roads** related to each of the bands surrounding the centre of the pond.

Analyses

I computed Pearson's product moment correlation coefficients for each pair of the independent variables (Statsci 1991, cor.test) to assess the degree to which each variable provided independent information.

I conducted Poisson regression, a form of generalized linear modelling, since the response variable was comprised of a discrete index of the intensity of frogs calling with no estimate of the number not calling (count data - Crawley 1993) and exhibited a high proportion of zeros (14/34) (Nicholls 1989, Lindenmayer et al. 1991). 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).

The equation that results from Poisson regression analysis takes the form of

$$y = e^{\eta}$$

where y is the response variable and η is the linear predictor, a function of the significant variables in the equation (Lindenmayer et al. 1991). η takes the form

$$a + b_1x_1 + b_2x_2 + b_3x_3 \text{ etc.}$$

The constant (a) and the coefficients (b_i) of the variables (x_i) in the linear predictor are obtained from the regression analysis (Bennett et al. 1994). In the case of Poisson

regression, the link function between the mean value of the response variable (μ) and the linear predictor (η) is the log link, i.e. $\eta = \log(\mu)$ (Crawley 1993). In this way, the expected responses are constrained to positive values.

The calling data (**calling.rank**), however, did not meet the assumptions of Poisson regression completely. Each datum, in this case the calling of a frog, is assumed to be an independent event. Calling in breeding amphibians tends to be contagious: vocalization by one frog may induce vocalization of others in the vicinity (Stebbins and Cohen 1995). This causes clumping, or overdispersion, of the calling and increases the variance relative to a Poisson process.

The degree to which any overdispersion of the data is accounted for by the explanatory variables can be assessed using the dispersion parameter, ϕ . This parameter is estimated by dividing the Pearson Chi-squared statistic by the residual degrees of freedom for the fitted model (McCullagh and Nelder 1991, Crawley 1993). Models meeting the expectations of the Poisson distribution have a dispersion parameter of 1. Models that result in a value greater than 1 for the dispersion parameter suggest either that the response variable is overdispersed and does not derive from a Poisson process or that appropriate explanatory variables are lacking (Beinett et al. 1994).

Poisson regression is reasonably robust to overdispersion if the assumption of mean/variance equality is relaxed to an assumption of mean/variance proportionality (McCullagh and Nelder 1991). Typically, even relatively substantial errors in the assumed functional form of the variance of the response variable generally have only a small effect on the conclusions of a study (McCullagh and Nelder 1991). Hastie and Pregibon (1992) recommended using F-tests for determining parameter significance in over-dispersed models over the Chi-squared statistics usually calculated for Poisson regression. While

corrections to the significance levels for the parameters are required, the parameter estimates themselves are not affected (McCullagh and Nelder 1991, Crawley 1993).

As the contagious nature of breeding choruses suggested that the response variable might not conform to a Poisson series, I repeated all the statistical analyses using linear regression and the square-root transformation recommended for count data (Crawley 1993). Since any one data set can be described typically by many models (McCullagh and Nelder 1991, Crawley 1993), exploring alternative possible models may better illuminate the biological processes at work. Where alternative models concur, they strengthen the conclusions reached. Where they differ, they may suggest avenues for further exploration.

The statistical analyses proceeded in three stages. In all three stages, the possible effects of local pond factors were accounted for by including the pond variables **meanph**, **perimeter**, and **spawning.habitat** in the analyses. To determine the relative importance of the need for individual frogs to link breeding ponds and summer foraging habitat versus the population level need for rescue and recolonization from adjacent populations, I first built a statistical model that related landscape complementation and metapopulation level factors to the calling intensity of leopard frogs. I then assessed the degree to which calling intensity could be accounted for by metapopulation level variables without landscape complementation variables being entered into the model. Lastly, I considered the possible impact of paving density on calling intensity in addition to landscape complementation and metapopulation level variables.

All models were built using forward and backward stepwise regression. The stepwise function in Splus uses the AIC criterion for adding terms to, or dropping terms from, a Poisson regression model (Hastie and Pregibon 1992). The AIC criterion accounts for the change in deviance caused by the step while exacting a penalty for the degrees of freedom associated with that step. I confirmed the significance of each term in

the final model from the stepwise procedure 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. This had proven to be a more stringent test than the AIC criterion in some of my preliminary analyses.

In the first stage of the statistical analyses, I regressed all the pond variables, the summer habitat measures, and all the metapopulation variables onto **calling.rank** (**Splus**, **step.glm**). To determine the appropriate scale for considering the effect of summer habitat, the change in residual deviance was compared for each band of **summer.habitat** substituted individually into the final model for Poisson regression. For the linear regression, the sigma-restricted significance levels for each term substituted individually into the final model were compared. I then tested for possible interactions between significant metapopulation and summer habitat factors.

The second set of regression models did not include the landscape complementation variables in the roster of possible independent variables to be fit. This allowed me to assess the extent to which local and metapopulation level factors could explain the abundance and distribution of leopard frogs independent of the landscape complementation measure, **summer.habitat**.

Finally, the possible effect of roads on the calling intensity at the core ponds was considered. I ran regressions adding **area.roads** to the full suite of independent variables (Table 1). As above, the appropriate scale for considering the effect of road density was determined by comparing the change in residual deviance for each band of **area.roads** substituted individually into the final Poisson model. For the linear regression, the sigma-

restricted significance levels for each term substituted individually into the final model were compared.

To assess the fit of the Poisson models, the Pearson residuals were plotted against the values of the linear predictor, the fitted values, and against each of the independent variables in the model to check for homogeneity of variance and lack of pattern (Nicolls 1989, Crawley 1993, McCullagh and Nelder 1991). They were also plotted against quantiles of the standard normal distribution to examine the degree to which they conformed to that distribution (Statsci 1991 - qqnorm, qqline) (Crawley 1993). Pearson residuals are standardized to achieve constant variance (McCullagh and Nelder 1991).

For the linear regressions, the residuals were plotted against fitted values and against each of the continuous independent variables to check for homogeneity of variance and lack of pattern. They were also plotted against quantiles of the standard normal distribution to examine the degree to which they conformed to that distribution (Statsci 1991 - qqnorm, qqline) (Crawley 1993).

Table 1 Variables used in the statistical analyses

Variable	Level of influence	Description
<i>Dependent</i>		
calling.rank		sum of the calling indices from a maximum of 4 out of 5 surveys
<i>Independent</i>		
meanph	local	mean pH of the water samples taken at each pond
perimeter	local	length of the pond perimeter in metres
spawning.habitat	local	the length of the perimeter that constituted preferred spawning habitat in metres
summer.habitat	landscape complementation	aggregation of all possible summer habitats (grass, alfalfa, and clover fields; pasture, old fields, scrub, and sedges)
total.listen	metapopulation	tally of the number of possible breeding sites within 1.5 km of the centre of the core pond in question
number.with.calling	metapopulation	the number of possible breeding sites within 1.5 km of the centre of the core pond in question for which calling leopard frogs had been recorded at least once
sum.calling.rank	metapopulation	the sum of the calling.rank for all of the sites within 1.5 km of the core pond in question
area.roads	landscape complementation/ metapopulation	the amount of roads (paved or dirt) and pavement within the landscape - includes 25% of the total residential area

Figure 2 Vegetation transect. 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.

Figure 3 A landscape showing the division into bands 0-0.25, 0.25-0.50, 0.50-0.75, and 0.75-1.0 km from the centre of the pond

RESULTS

Chorus surveys

Calling was recorded at only one pond the first census night (April 12) although the conditions were ideal - air temperature of 9°C for the survey period with light rain (van der Ham and Schueler 1992). For the second census, air temperature dropped from 4.3° to -0.4°C, it was windy, and there had been no precipitation within the previous 24 hours. Nonetheless, calling was heard at 12 ponds (Table 2). Weather conditions for the third census on April 27-28 were cool (7.4-6.1°C) but winds were light and it was raining. For the censuses on May 2-4 and May 8-9, temperature and wind conditions were good (19-11°C, 6-20 km/h), and although there was no rain, it was partly cloudy. Calling was the highest for these two nights.

The proportion of sites with calling increased over the first four survey nights and then dropped on the last night (Table 2). The proportion of sites for which calling was recorded for the first time in the series dropped steadily over the last four sample periods.

Habitat measures

Pond characteristics

Pond perimeter measurements ranged from 139 m to 2328 m, with a mean of 476 m but a median of only 308 m (Table 3). On average, 42.6% of the sampled shoreline of the study ponds afforded good spawning habitat. Five of the study ponds had no preferred spawning habitat as emergent vegetation was lacking. A sixth pond did not have any emergent vegetation in full sun. Calling was not recorded at these ponds. In contrast,

for 3 ponds the entire perimeter offered good opportunity for spawning, and calling was recorded.

Mean pH ranged from slightly below neutral to quite basic in the study ponds. The mean was 7.05, while the extremes were 6.00 and 9.39 (Table 3).

Summer habitat

The mean proportion of summer habitat in each of the 0.25 km wide bands surrounding the core ponds was constant although the coefficient of variation (CV) decreased with increasing distance out from the ponds (Table 4). Five core ponds had no suitable summer habitat within 0.25 km. Calling was heard at only one of these five ponds. Another pond lacked summer habitat in the 0.25-0.5 km band, no calling was recorded.

Paving

The mean percentage of roads and paved surfaces in each of the 0.25 km wide bands increased with increasing distance from the ponds as did the coefficient of variation (Table 5).

Statistical analyses

Correlation analysis

MeanpH was not correlated significantly with any of the other variables entered into the statistical models (Table 6). **Perimeter** and **spawning.habitat** were highly

positively correlated (0.781, $p < 0.001$, Table 6). In addition to being correlated with **perimeter**, **spawning.habitat** was also positively correlated with **area.roads100**.

Strong positive correlations existed between the four summer habitat variables. There were also strong negative correlations between these and all the paving variables. The summer habitat variables correlated most strongly with the amount of roads and paving in the two outermost bands (0.50-0.75 and 0.75-1.0 km). All four paving variables were highly positively correlated.

The metapopulation variables were strongly positively correlated with each other. **Number.with.calling** and **sum.calling.rank** both were correlated negatively with the amount of roads and pavement in the last 0.25 km band (0.75-1.0 km) at the 0.05 level. A significant negative correlation also existed between **number.with.calling** and **area.roads75**, while the negative correlation between **sum.calling.rank** and **area.roads75** was nearly significant at the $\alpha=0.05$ significance level.

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

Model results

For all results reported, significance levels are given for sigma-restricted deviances. These are derived by comparing the residual deviance from the final model to that of the final model less each term (Nicholls 1989, Crawley 1993).

Landscape complementation and metapopulation variables included

Mean pH, the amount of spawning habitat, the amount of summer habitat within 0.5-0.75 km of the centre of the core pond, and the number of sites with calling within 1.5 km of the core pond all contributed significantly to explaining the observed variation in calling intensity at the core ponds using Poisson regression. However, this model proved slightly overdispersed ($\phi = 1.219$; Table 7a), and I, therefore, used F-tests rather than Chi-squared tests to determine significance levels. Inspection of the residuals suggested that the Poisson model provided a reasonable description of the data despite the slight overdispersion observed.

Decreases in mean pH related to increases in the calling at the core ponds. More spawning habitat, more summer habitat, and more surrounding sites with calling all led to greater calling intensity at the core pond. The model explained roughly 37% of the variation observed ($[1 - (\text{residual deviance} / \text{null deviance})] * 100$, Crawley 1993). Comparing the relative contribution of the best-fitting landscape and metapopulation level variables, **summer.habitat75** was shown to have a similar effect to **number.with.calling** as measured using standardized partial regression coefficients (B_k) (Neter et al. 1983) (Table 7a). Exponents were taken after the standardization.

The three metapopulation level variables did not prove equivalent in terms of their significance in the four-term model despite high correlations (Table 6). **Sum.calling.rank**, the sum of the calling ranks from all of the ponds within 1.5 km of the core pond, could be substituted for **number.with.calling**, the number of sites with calling within 1.5 km of each core pond. However, the significance level was slightly lower for this variable at $p=0.0287$ (Table 7b). The parameter estimate for **total.listen**, the number

of sites surveyed within 1.5 km of each core pond, when substituted for **number.with.calling** did not differ significantly from zero (Table 7c).

Of the four possible summer habitat measures, the 0.50 - 0.75 km band proved the most significant in this four-term Poisson model. The last band (0.75 - 1.00 km) could be substituted for **summer.habitat75**; however, it proved less significant (Table 7d). Neither of the two bands closest to the core ponds offered significant explanatory power when substituted into the four-term Poisson model.

I ran another stepwise Poisson regression including the interaction between **summer.habitat75** and the metapopulation level factor **number.with.calling** as one of the possible terms to be fit. The interaction term did not contribute significantly to the model ($p=0.357$), and the parameter estimate did not differ significantly from zero.

For the linear regression model with the square-root transformed dependent variable, **sqrt.calling.rank**, the data were best described by the single-term model of **meanph** although this term was barely significant at the $\alpha=0.05$ level (Table 8). Decreases in mean pH were correlated with increases in calling intensity at the core pond. The residuals from this model were reasonably homogeneous, without pattern, and normally distributed.

For comparison, I fit the four independent terms which comprised the best Poisson regression against the transformed dependent variable in a linear regression (Table 9). The rank of the terms with respect to significance level was the same between the Poisson and linear models although only the spawning habitat was significant at the $\alpha=0.05$ level in the latter model. As for the Poisson model, addition of the interaction term,

summer.habitat75*number.with.calling, did not improve the fit of the model significantly. Again, the parameter estimate did not differ significantly from zero

Landscape complementation variables not included

I could not fit a Poisson model to explain the distribution and abundance of leopard frogs in my study area with all terms significant at the $\alpha = 0.05$ level including only local level factors (characteristics of the breeding pond) and metapopulation level factors (potential for population rescue and recolonization). **Meanph** was the parameter closest to significance at $p=0.068$.

Stepwise linear regression produced similar results. The best-fitting model contained only the single term **meanph**. As noted above, this term proved barely significant at $p=0.0496$ (See Table 8).

Landscape complementation, metapopulation, and paving variables included

When the amount of pavement was added to the full Poisson model, the model reduced to include only **meanph**, **spawning.habitat**, and **area.roads75** as significant independent variables (Table 10). Again, **meanph** was negatively correlated with calling intensity at the core pond, and spawning habitat contributed positively. The amount of pavement was negatively related to calling intensity. This model accounted for roughly 38.1% of the observed variation.

The model was slightly over-dispersed with respect to the Poisson process ($\phi = 1.171$). F-tests were used therefore to assess the significance of explanatory variables.

Inspection of the residuals suggested that the Poisson model provided a reasonable description of the data despite the slight overdispersion observed.

Like the summer habitat in the previous model, the amount of roads and paving in the first 0.25 km band (0 - 0.25 km) did not contribute significantly to the model. The other three bands could each be substituted for the other at the $\alpha=0.05$ level. **Area.roads** within 0.50 - 0.75 km from the centre of the core pond proved the most significant. **Area.roads75** was significantly correlated with the dropped explanatory variables from the 4 term Poisson model: **summer.habitat75** and **number.with.calling** (Table 6). The F-test probabilities for **summer.habitat75** and **number.with.calling** as single term additions to the fitted model were 0.912 and 0.112 respectively.

The stepwise linear regression of the square-root transformed dependent variable, **sqrt.calling.rank**, against the full suite of possible explanatory variables including the paving variables confirmed the results of the Poisson regression (Table 11). The best-fitting explanatory variables were the same. The most significant of the bands in terms of paving also proved to be the 0.50 - 0.75 km band. The order of the terms by significance also agreed between the two models. The residuals for the linear model were homogeneous, showed no pattern, and were reasonably normal.

Summary of results

Mean pH, the amount of spawning habitat, the amount of summer habitat within 0.5-0.75 km of the centre of the core pond, and the number of sites with calling within 1.5 km of the core pond all contributed significantly to explaining the observed variation in calling intensity at the core ponds using Poisson regression. Only mean pH was significant according to linear regression of the square-root transformed dependent variable. If the

landscape complementation measure, amount of summer habitat, was not included in the Poisson model, neither the pond variables nor the metapopulation variables could be fit at the $\alpha=0.05$ level. Adding the paving variable, **area.roads**, produced equivalent results from the Poisson and linear regressions. Mean pH, the amount of spawning habitat, and the area of paving within 0.5-0.75 km of the centre of the core pond all contributed significantly to explaining the observed variation in calling intensity at the core ponds.

Table 2 Changes in calling frequencies over the survey period.

Date	total # sites surveyed	# sites with calling	% sites with calling	# sites with calling for the first time	% sites with calling that were calling for the first time
April 12	105	1	0.9	1	100
April 23	107	12	11.2	12	100
April 27-28	107	15	14.0	10	66.7
May 2-4	87	28	32.2	16	57
May 8-9	107	25	23.4	11	44

Table 3 Data used in the analyses.

Core pond	calling rank	mean pH	perimeter (m)	spawning habitat (m)	summer habitat25 (ha)	summer habitat50 (ha)	summer habitat75 (ha)	summer habitat 100 (ha)
BAASW	1	9.4	165.8	94.5	18.39	44.97	59.96	106.28
BAASN	5	6.8	320.0	115.2	7.55	34.40	81.01	97.88
BOWES	2	7.1	153.0	153.0	14.06	46.62	75.47	103.41
SPTRR	0	7.2	235.2	0.0	12.53	43.12	65.71	95.41
FICKO	0	8.5	164.5	54.3	9.43	46.75	70.08	98.25
SPTSH	1	6.0	413.1	49.6	18.44	54.22	72.84	82.36
SPTAN	0	7.0	269.0	96.8	19.59	50.20	76.46	116.04
SPTAS	0	9.1	196.4	122.7	18.53	56.60	91.37	107.11
PATTE	2	8.2	256.3	128.1	7.71	29.53	38.36	73.88
BREWR	1	7.0	869.6	869.6	0.06	0.73	1.35	5.08
FRISB	4	6.9	345.5	307.5	12.31	41.32	74.78	111.88
BIMIN	2	7.0	260.7	234.7	12.80	26.31	49.86	78.96
BOUND	1	6.9	173.4	135.3	12.14	6.90	47.26	56.01
BELSW	7	7.3	802.0	585.4	8.16	20.59	34.01	50.25
NELS	1	7.9	520.2	296.5	11.02	32.30	61.21	60.34
BERGE	2	7.1	224.4	125.7	11.40	38.10	52.45	75.29
CLEMT	1	6.8	265.2	238.7	16.06	47.88	66.25	88.64
BELCR	1	7.9	2328.2	1024.4	10.25	33.16	23.81	30.50
AVIAT	1	6.6	314.9	299.2	3.59	2.19	5.36	4.36
PATTW	4	7.0	198.9	59.7	5.64	25.86	37.53	49.57
METCC	2	8.6	612.0	153.0	0.00	15.16	37.95	54.71
METCB	2	7.3	204.0	36.7	2.49	13.52	27.66	55.04
METCA	0	7.2	229.5	0.0	1.49	5.82	19.10	56.72
ELWST	1	8.2	606.9	121.4	3.74	27.32	50.25	32.90
ELNE	0	8.0	983.0	324.4	0.35	14.47	31.57	32.79
ELSE	0	9.2	693.6	187.3	4.74	6.20	18.97	35.63
ELMO	0	7.2	331.5	0.0	9.62	29.13	42.86	61.46
HUNTN	0	8.2	335.3	0.0	0.00	0.00	18.39	49.85
HUNTS	0	8.0	511.2	0.0	0.00	0.13	11.79	44.10
CRAWF	0	7.8	190.0	95.0	1.70	1.00	4.49	25.18
BARNS	0	8.9	139.0	69.5	1.52	8.61	10.57	15.27
VALLS	0	6.8	301.2	0.0	0.00	0.73	18.05	18.31
MACKA	1	7.3	1775.1	84.8	0.00	0.39	6.90	3.22
BEECH	0	7.3	748.4	187.1	3.73	4.97	5.70	9.71

Table 3 (con't)

Core pond	number with calling	total listen	sum. calling rank	area roads25 (ha)	area. roads50 (ha)	area roads75 (ha)	area roads 100 (ha)
BAASW	2	5	7	0.26	1.08	3.28	5.66
BAASN	2	5	3	0.00	0.14	2.57	5.11
BOWES	2	7	3	0.00	0.09	2.20	5.46
SPTRR	4	10	6	0.27	0.57	2.16	3.67
FICKO	2	6	3	0.73	2.01	3.47	4.87
SPTSH	1	7	2	0.19	0.75	2.18	3.53
SPTAN	2	6	3	0.00	0.00	0.73	1.36
SPTAS	3	9	4	0.27	0.57	1.36	2.28
PATTE	4	7	12	0.23	1.12	3.48	4.63
BREWR	0	7	0	0.89	16.24	52.35	101.07
FRISB	0	1	0	0.00	0.35	1.80	1.64
BIMIN	1	2	1	0.14	0.55	3.16	5.25
BOUND	0	1	0	0.18	1.33	2.66	4.05
BELSW	2	4	5	0.68	1.40	2.27	4.74
NELS	2	5	8	0.92	2.46	3.89	5.40
BERGE	0	4	0	0.13	0.59	2.33	4.26
CLEMT	1	1	1	0.00	1.99	3.34	5.11
BELCR	0	2	0	0.00	1.79	15.70	36.72
AVIAT	0	1	0	2.11	10.30	40.39	92.92
PATTW	5	9	8	0.79	1.30	1.98	3.09
METCC	6	11	8	0.00	0.00	1.10	3.92
METCB	6	12	8	0.00	0.12	2.41	4.26
METCA	7	11	16	0.73	2.09	4.14	5.94
ELWST	1	3	1	1.57	4.94	7.34	9.43
ELNE	1	6	1	0.16	2.68	5.44	9.01
ELSE	0	5	0	0.17	2.69	7.91	13.40
ELMO	1	4	1	1.19	3.74	8.45	11.72
HUNTN	0	4	0	0.29	8.07	23.33	39.08
HUNTS	0	4	0	0.00	8.27	24.07	45.23
CRAWF	1	1	1	0.23	0.49	0.97	1.75
BARNS	1	3	4	0.16	0.55	1.89	3.09
VALLS	3	4	5	2.45	14.57	34.08	64.69
MACKA	0	3	0	2.25	14.10	29.76	53.57
BEECH	1	4	1	3.06	17.12	52.05	91.18

Table 4 Amount of summer habitat in each of the landscape bands.

Band	Mean (ha)	Mean (as % of the total landscape in the band)	CV	Maximum	Minimum
0-0.25 km	7.6	38.9	83.5	100.0	0
0.25-0.50 km	23.8	40.4	78.5	96.1	0
0.50-0.75 km	40.9	41.6	64.5	93.1	1.4
0.75-1.00 km	58.4	42.5	58.6	84.5	2.3

Table 5 Amount of roads and paved surfaces in each of the landscape bands.

Band	Mean (ha)	Mean (as percentage of total landscape in the band)	CV	Maximum	Minimum
0-0.25 km	0.59	3.0	136.3	15.6	0
0.25-0.50 km	3.65	6.2	138.2	29.1	0
0.50-0.75 km	10.4	10.6	141.5	53.3	0.7
0.75-1.00 km	19.4	14.1	147.9	73.6	1.0

Table 6 Correlations among the independent variables.

	Pond variables			Metapopulation variables			Landscape complementation variables				Paving variables			
	meanph	perimeter	spawning habitat	total listen	number with calling	sum calling rank	summer habitat25	summer habitat50	summer habitat75	summer habitat100	area roads25	area roads50	area roads75	area roads100
calling rank	-0.295	0.023	0.266	-0.006	0.131	0.127	0.109	0.172	0.235	0.209	-0.172	-0.28	-0.256	-0.228
meanph	1	0.074	-0.07	0.13	0.059	0.138	-0.122	-0.035	-0.071	-0.008	-0.2	-0.173	-0.191	-0.212
perimeter		1	***0.781	-0.166	-0.288	-0.276	-0.191	-0.149	-0.316	*-0.410	0.071	0.229	0.314	0.332
spawning habitat			1	-0.234	-0.325	-0.262	-0.001	-0.032	-0.187	-0.266	-0.046	0.151	0.292	*0.340
total listen				1	***0.822	***0.688	-0.047	0.159	0.164	0.234	-0.185	-0.21	-0.211	-0.225
number with calling					1	***0.896	-0.074	0.199	0.129	0.222	-0.095	-0.315	*-0.345	*-0.348
sum calling rank						1	-0.027	0.088	0.086	0.204	-0.079	-0.302	-0.338	*0.344
summer habitat25							1	***0.882	***0.825	***0.798	*-0.373	**0.527	**0.486	**0.469
summer habitat50								1	***0.915	***0.850	*-0.411	***0.597	***0.577	***0.564
summer habitat75									1	***0.912	**0.438	***0.618	***0.635	***0.630
summer habitat100										1	***0.583	***0.674	***0.664	**0.6621
area roads25											1	***0.800	***0.717	***0.689
area roads50												1	***0.961	***0.930
area roads75													1	***0.991

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 7 a) Best model from stepwise Poisson regression relating the summed calling index at each of the core ponds (**calling.rank**) to the local pond, metapopulation, and landscape complementation variables. B_k is the standardized partial regression coefficient. b) As for a) with **sum.calling.rank** substituted for **number.with.calling**. c) As for a) with **total.listen** substituted for **number.with.calling**. d) As for a) with **summer.habitat100** substituted for **summer.habitat75**.

a)

	Coefficient	Std. err.	$e^{\text{coefficient}}$	e^{B_k}	df	Deviance	F	Pr(F)
intercept	2.932	1.783			1	2.93	2.396	0.132
spawning. habitat (m)	0.003	0.0008	1.003	1.526	1	12.43	10.187	0.003
meanph	-0.650	0.248	0.52	0.719	1	8.28	6.788	0.014
summer. habitat75 (ha)	0.020	0.007	1.02	1.381	1	7.80	6.396	0.017
number. with.calling	0.279	0.105	1.32	1.391	1	7.33	6.012	0.020

null deviance = 64.403

residual deviance = 40.812

$\phi = 1.219$

b)

	Coefficient	Std. err.	df	Deviance	F	Pr(F)
intercept	3.171	1.782	1	3.42	2.748	0.108
spawning. habitat (m)	0.002	0.0007	1	11.42	8.939	0.006
meanph	-0.651	0.246	1	8.40	6.741	0.015
summer.	0.019	0.007	1	7.46	5.985	0.021
habitat75 (ha)						
sum.calling.rank	0.120	0.045	1	6.60	5.296	0.029

null deviance = 64.403

residual deviance = 41.545

 $\phi = 1.245$

c)

	Coefficient	Std. err	df	Deviance	F	Pr(F)
intercept	2.588	1.686	1	2.49	1.580	0.212
spawning habitat (m)	0.002	0.0006	1	7.35	4.653	0.039
meanph	-0.501	0.219	1	5.76	3.647	0.066
summer	0.016	0.007	1	5.74	3.635	0.066
habitat75 (ha)						
total listen	0.043	0.055	1	0.60	0.378	0.543

null deviance = 64.403

residual deviance = 47.55

 $\phi = 1.580$

d)

	Coefficient	Std err	df	Deviance	F	Pr(F)
intercept	3.075	1.847	1	2.97	2.379	0.134
spawning. habitat (m)	0.002	0.0007	1	11.74	9.385	0.005
meanph	-0.647	0.252	1	8.02	6.412	0.017
summer. habitat100 (ha)	0.014	0.005	1	6.53	5.221	0.030
number. with.calling	0.231	0.093	1	5.84	4.672	0.039

null deviance = 64.403

residual deviance = 42.085

 $\phi = 1.250$

Table 8 Best model from stepwise linear regression relating the summed calling index at each of the core ponds (**calling.rank**) to the local pond, landscape complementation, and metapopulation variables

	Coefficient	Std. error	df	t	Pr(F)
intercept	3.221	1.191	1	2.705	0.0109
meanph	-0.319	0.156	1	-2.041	0.0496

model $r^2 = 0.115$, $p = 0.0496$

Table 9 Linear regression relating the summed calling index at each of the core ponds (**calling.rank**) to the same independent terms as in Table 7a above.

	Coefficient	Std. err.	B ₁	df	t	Pr(F)
intercept	2.201	1.146		1	1.920	0.065
spawning. habitat (m)	0.001	0.0006	0.141	1	2.580	0.015
meanph	-0.283	0.144	-0.143	1	-1.970	0.058
summer. habitat75 (ha)	0.0083	0.005	0.134	1	1.813	0.080
number. with calling	0.084	0.0649	0.099	1	1.298	0.204

model $r^2 = 0.328$, $p = 0.018$

Table 10 Best model from stepwise Poisson regression relating the summed calling index at each of the core ponds (**calling.rank**) to the local pond variables, metapopulation variables, landscape complementation variables, and road variables.

	Coefficient	Std. err.	df	Deviance	F	Pr(F)
intercept	5.152	1.712	1	9.906	8.463	0.007
area.roads75 (ha)	-0.054	0.019	1	13.909	11.885	0.002
spawning.habitat (m)	0.002	0.0006	1	10.286	8.789	0.006
meanph	-0.675	0.238	1	9.370	8.007	0.008

null deviance = 64.403

residual deviance = 39.83

$\phi = 1.171$

Table 11 Best model from stepwise linear regression relating the summed calling index at each of the core ponds (**calling.rank**) to the local pond variables, metapopulation variables, landscape complementation variables, and road variables

	Coefficient	Std error	df	t	Pr(F)
intercept	3.555	1.088	1	3.267	0.003
spawning. habitat (m)	0.001	0.0005	1	2.724	0.011
area.roads75 (ha)	0.022	0.008	1	-2.696	0.011
meanph	-0.366	0.140	1	-2.620	0.014

model $r^2 = 0.359$, $p = 0.003$

DISCUSSION

It often has been assumed that ecological processes important to populations operate at local spatial scales (Hansson 1979, Dunning et al. 1992). Until recently, much of the amphibian literature focused on effects local to the breeding pond (Beauregard and Leclair 1988, Dale et al. 1985, Skelly 1996). Metapopulation theory has broadened the research focus to include consideration of the landscape context for local population dynamics (Sjögren 1991, 1994, Gill 1978, Henderson et al. 1985, Berven 1990, Bradford et al. 1993). However, neither breeding site characteristics nor metapopulation factors are sufficient to explain the distribution and abundance of animals that cannot meet all their resource needs at the breeding site. As shown in this study of the leopard frog, such species require that the landscape context at the level of individual resource needs be considered when evaluating the distribution and abundance of local populations.

Of course, the conclusions of this study must be tempered by the fact that, as in all observational work, there is a myriad of unaccounted sources of variation that could have affected the observed abundance and distribution of leopard frogs. The availability of overwintering sites, the quality of the summer habitat, pesticides, and fertilizers are all factors that could have influenced the number of males heard calling. Data on movement and road mortality of *R. pipiens* within the study landscape might have provided a clearer picture of the relative importance of summer habitat, adjacent breeding sites, and road density. These factors were confounded by correlation in the present study. Similarly, metapopulation dynamics are more accurately determined from time series data from which extinctions and recolonizations could be discerned. However, such was not possible within the time frame of this thesis.

Within the constraints of the data collected, I could not fit a model to explain the distribution and abundance of leopard frogs in my study area with all terms significant at

the $\alpha = 0.05$ level including only local level factors (characteristics of the breeding pond) and metapopulation level factors (potential for population rescue and recolonization as measured by possible breeding sites within 1.5 km of the study ponds and calling from these sites). Including a measure of the amount of a second required resource, summer habitat, in the analysis allowed me to fit a model explaining the relative abundance of *R. pipiens* in terms of local pond variables, a landscape complementation variable, and a metapopulation level (Table 7a).

Contrary to my original hypothesis, 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 is consistent with their relative effects as measured by the standardized partial regression coefficients in the model in which they were both fit. It suggests that all levels of influence of landscape structure need to be considered when assessing the distribution and abundance of species with complementary resource needs and possible metapopulation structure.

These results suggest that resources required at the individual level are as important to local population abundance as having adjacent populations that could potentially supply immigrants. Just as the local-level factors (i.e. the pond variables) have been shown to be insufficient to account for variability in the focal population in a number of autoecological and metapopulation studies (Dale et al. 1985, Sjögren 1994), the combined effects of local conditions and regional population factors are insufficient to explain the abundance and distribution of a species for which landscape structure influences survival at the individual level.

There is a two-tiered set of requirements for persistence of a regional population of such species. Firstly, access to resource patches must be appropriate at the individual level and secondly, immigration from potential colonizing populations must be sufficient to

sustain the regional population. Soibreck (1995) documented such a layered effect of habitat structure on 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 while the potential for recolonization from adjacent regions proved critical to the long-term success of the regional population.

Previous studies have considered the possible influence of landscape context in terms of individual resource needs on sites chosen by amphibians for breeding. In Wisconsin, Hine et al. (1981) found that forest accounted for less than 50% of the cover within 300m of ponds in which breeding was observed. Wederkinch (1988) similarly concluded that the distance to forest was significant in explaining the presence/absence of *R. dalmatina* in Denmark. Beebee (1985) found that presence/absence information on terrestrial habitats within 100 m of ponds provided greater explanatory power on the distribution and abundance of five English amphibian species than did pond characteristics. Loman (1988) found that not only pond characteristics (length of shallow shoreline, and length of non-shaded and shallow shoreline) but also the landscape variable "distance to summer habitat" distinguished between breeding and non-breeding ponds for *R. temporaria*. My study confirms the importance of the landscape context at the individual level and further indicates that knowledge at this level may be required to understand the influence of the landscape at the population level for species with complementary resource needs.

Connectivity

Wilbur (1980) coined the term "complex life cycles" to describe life histories that include an abrupt change in an individual's morphology, physiology, and behaviour. This change is usually associated with a shift in habitat. Complex life cycles are thought to have evolved to take advantage of growth potential of the aquatic larval environment and

the dispersal potential available to the terrestrial adult (Wilbur 1980). For an organism to use different habitats for different stages in its life cycle either these habitats must be contiguous or the organism must be able to move between them (Gibbons and Bennett 1974, Schueler 1992). The theory of "complex life cycles" presupposes that any costs associated with moving between the required habitat types are outweighed by the benefits to the organism obtained in the different habitat types. A similar argument is made for species that undertake long-distance migrations to link different habitats (Moore and Simons 1992).

Where the required habitats are contiguous in the landscape, movement distance is minimal, and there is probably little cost in moving between them. As the habitat patches become more dispersed, the distance over which individuals must range to integrate the required resources increases (Taylor 1993). At some point the distance between required patches becomes insurmountable. This maximum distance is determined not only by the distance between the habitat patches but also by the mortality incurred in moving between them and the organism's behavioural response to the intervening habitat (Reh and Seitz 1990, Mader 1989, Mader et al. 1990). Beyond this maximum distance, the situation becomes indistinguishable from absolute resource elimination (Merriam 1991). Effectively, the landscape, considered at the scale of the individual, no longer contains all the resource elements required for that individual's survival.

Middleton and Merriam (1983) suggested that species that had the capacity to cope with heterogeneous landscapes prior to European settlement would be "pre-adapted" to dealing with the heterogeneous landscapes created by humans. However, the presumed benefit of having evolved in a heterogeneous landscape rests on the number of assumptions. It assumes that the distance between habitat patches does not change significantly or that organisms have sufficient behavioural flexibility to move over any

greater distance. Behavioural flexibility is also assumed in the organism's response to novel intervening habitat.

Not all landscape features introduced by humans are hospitable to native species. Fahrig et al. (1995) demonstrated a significant positive relationship between traffic intensity and mortality of anurans on roads. Sjögren (1995), in a 2 year study of amphibians in the city of Stockholm, noted that the presence of a used road 200 m or less from the pond increased the probability of extinction for the common frog (*R. temporaria*) and significantly decreased the probability of colonization in the common newt (*Triturus vulgaris*). In a 1971 study in Michigan, Rittschof (1975) reported that a two-lane road servicing about 70 families killed 50% of the *R. pipiens* population during the fall migration to an overwintering lake. Superhighways intersecting migratory routes in Ann Arbor were 100% effective as barriers during the fall migration of this species (Rittschof 1975). These studies indicate that a significant cost to movement in the form of roads has been added recently - in evolutionary terms - to the suite of landscape-level factors to which organisms must respond.

In this study, roads proved to be a significant negative factor in explaining the abundance of calling leopard frogs at the breeding ponds (Table 10). This accords well with the central role of movement in the life history of *R. pipiens* as argued by Rittschof (1975). Rittschof (1975) suggested that the elimination, or reduction, of successful dispersal would contribute to the destruction of a *R. pipiens* population and that roads, traffic, and the mechanization of agriculture all reduce the dispersal success of leopard frogs (Rittschof 1975, Merrell 1977). For this and other species with complementary resource needs, the reduction in connectivity associated with roads can have an impact at two levels: first, when an individual is moving between the different required habitat types, and second, when it is moving between populations. The consequences of road mortality,

therefore, may be more serious for these species than for species for which one habitat patch serves all their resource needs (Reh and Seitz 1990)

However, in this study, road density was significantly correlated with both summer habitat and the number of listen ponds with calling. Neither the summer habitat nor any of the listen pond measures was significant once road density was considered. It was not possible to determine from this study whether road density measures a reduction in connectivity between the breeding and the summer habitat and between adjacent populations or simply acts as an index of increasing urbanization and the attendant decrease in summer habitat and alternative breeding sites for frogs.

Scale of landscape influence

Pearson (1993) suggested that the spatial extent of the landscape influence on a site could be measured by the distance to the farthest habitat patches that influenced a population at a given site. In this study, the summer habitat was measured in concentric 0.25 km bands around each core pond. In the Poisson regression model of abundance against local pond variables, summer habitat, and metapopulation level variables, the amount of summer habitat in the 0.50-0.75 km band proved to be the most significant (Table 7a; $p = 0.017$). The band 0.75-1.0 km from the centre of the core ponds could be substituted as a measure of summer habitat, but the significance level was lower (Table 7d, $p = 0.03$). No significant fit was obtained when the summer habitat amount in the two bands closest to the pond were substituted in the model. Dole (1971) observed that newly metamorphosed young did not select necessarily the first suitable summer habitat they encountered in moving away from the natal pond. This type of movement behaviour may account for the lack of a significant fit for the 0-0.25 km and 0.25-0.50 km summer habitat bands while the two outer bands proved significant. These results highlight the importance of behavioural studies at the landscape scale (Lima and Zollner 1996)

This study indicates 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 centre of the pond. However, without explicit measures of dispersal from the breeding sites, or studies at even greater spatial extent in landscapes with similar habitat amount, it is not certain whether these results indicate a characteristic of leopard frogs' scale of landscape use or of the distribution and abundance of summer habitat in the study landscape.

That the summer habitat exerts its greatest influence at 0.5-0.75 km from the pond suggests that my original selection of the study ponds based on two classes with respect to their contiguity with summer habitat may have under-estimated the movement tendencies of the frogs. Five of the fifteen sites classed as "summer habitat far" (i.e. the habitat at the pond edge did not constitute summer habitat), in fact, did support calling leopard frogs. These results indicate that for leopard frogs, at least, landscape complementation does not require contiguity of the different required habitat types. As long as the organisms can move between the habitat patches, i.e. the landscape connectivity is maintained, the evolved movement range of the species is sufficient to allow it cope with the alteration of the landscape imposed by human activities. These results parallel those of Taylor (1993) for the damselfly *Calopteryx maculata* in forested areas fragmented 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 the local populations.

In the three-term Poisson model of abundance against local pond, summer habitat, metapopulation, and paving variables, the road density measure was also strongest for the 0.5-0.75 km band (Table 10). As discussed above, the strong correlations between summer habitat and road density (Table 6) make it difficult to distinguish the relative effects of these two variables.

Influence of pH

The ponds in this study ranged in pH from slightly acidic at 6.00 to quite basic at 9.39. The mean for the 34 ponds was neutral at 7.05. The soils of the Ottawa area are, for the most part, drift soils derived from superficial deposits of Pleistocene and Recent ages (Patterson 1969). This results in relatively high pH values for surface water in this area as these glacial- and marine-derived deposits are somewhat calcareous (Patterson 1969). pH tends to be high in calcareous soils because the calcium carbonate dissociates to form free carbonate ions. These carbonate ions then combine with free hydrogen ions to form the highly soluble product hydrogen carbonate or bicarbonate (Briggs et al. 1989).

A number of studies have evaluated the effects of acidic water on egg and tadpole development. Gosner and Black (1957) noted the lethal range, critical pH range, and minimum limiting pH value for leopard frog embryos under laboratory conditions for water samples ranging from pH 3.5-5.1. Freda and Dunson (1985) studied survival time at pH 3.0 and growth at pH 4.4 for *R. pipiens* tadpoles compared to controls at pH 5.8. Both studies reported negative effects due to low pH. More generally, Clark and Euler (1982) evaluated the possible effect of pH of breeding ponds on densities of adult amphibians in the Muskoka area of Ontario and noted a positive relationship. pH in their study ranged from 4.55-6.58. Dale et al. (1985) tried to relate the presence/absence of amphibian species to the chemistry of water bodies in Nova Scotia. Using discriminate

function analysis, they were unable to differentiate between sites with and without individuals of the 11 species observed

The results of this study combined with previous work on acid tolerance in *R. pipiens* suggest that the relationship between leopard frog abundance at breeding ponds and pH may be peaked - abundance increasing as pH increases to neutral and decreasing again as the water becomes more basic. This may explain, in part, the inability of Dale et al (1985) to relate pH to presence/absence of particular amphibian species; pH values ranged from 3.88 to 8.95 in their study

Amphibian decline

It has been suggested that we are witnessing a world-wide decline in amphibians (Blaustein and Wake 1990, Fellers and Drost 1993). Both reductions in 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 in press). However, amphibian population dynamics are naturally characterized by wide oscillations in numbers and high spatial heterogeneity (Blaustein and Wake 1990, Travis 1994). Juvenile recruitment can vary by several orders of magnitude from year to year (Pechmann et al. 1991, Berven and Grudzien 1990). The high natural variability and the dearth of long time series makes verifying the putative declines of these species difficult (Pechmann et al 1991, Blaustein et al 1994).

Blaustein et al. (1994) contended that habitat destruction was the major cause for amphibian losses worldwide. In Ontario south of the Canadian Shield, an area that includes the study sites, 75% of wetlands have been lost (Regional Municipality of Ottawa-Carleton 1993). Other possible causes include the introduction of predators and

competitors, (Fellers and Drost 1993, Bradford et al. 1993), pollution from pesticides and/or fertilizers (Hine et al. 1981), mining and logging, acid precipitation, increased levels of ultraviolet radiation, consumption by humans, climate change (Beauregard 1988, Blaustein et al. 1994, Arkinstall 1994), and road mortality (Fahrig et al. 1995)

The common requirement among amphibians for more than one habitat makes this group particularly vulnerable to the impacts of habitat fragmentation and loss. Reduction or removal of any one of the required habitats may render the landscape unsupportive of these species. Equally important, reduction in the connectivity of the landscape between the required resources may reduce greatly 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 semi-arid 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.

Implications for conservation

This study suggests that we must be cautious in applying the results of current metapopulation analyses in conservation for species for which the breeding/non breeding categorization of the landscape does not apply. Considerations of rescue and recolonization potential to maintain a regional population must be framed in the context of the individual-level spatial constraints of the landscape. While 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 breeding ponds. When the habitat surrounding the ponds was restored to grasslands from scrub forests, *R. pipiens* numbers increased dramatically (Mierzwa, pers. comm.)

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* (Pullin, pers. comm.). 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. Both they and Buhlman (1995) contended that this failure to integrate the terrestrial and aquatic habitats could result in the failure of the conservation strategy. Findlay and Houlihan (in press) demonstrated that land use practices extending out as far as 2 km from a wetland may be as important to species richness as the wetland's size. We need to broaden our conservation focus to include all phases of the life cycle and to be mindful of how those different phases play themselves out in different parts of the landscape.

Many species have requirements for distinct habitats for overwintering, foraging, and/or oviposition. These include many reptiles (snakes: Semlitsch et al. 1988; turtles: Bennett et al. 1970, Burke and Gibbons 1995, Buhlman 1995), amphibians (Gill 1978), birds (Wiens 1989), and insects (Wiklund 1977, Wiklund and Åhrberg 1978, Ehrlich and Murphy 1987, Pollard and Hall 1988, Taylor 1993, Solbreck 1995). Like leopard frogs, many of these species exhibit "complex life cycles" (Wilbur 1980). When devising conservation strategies, the appropriateness of the dichotomous classification of the landscape into breeding habitat/non-breeding habitat should be verified for organisms exhibiting these life history patterns. For species such as bull frogs, *R. catesbeiana*, that breed, forage, and overwinter in the same site (Willis et al. 1956), the change from larvae to adult is not accompanied by a change in habitat. The classification of the landscape into

breeding/non-breeding habitat may well provide sufficient detail. However, management based on a dichotomous classification of the landscape relies on chance to supply the other habitat components required by species with complementary resource needs.

Long distance migration is a striking manifestation of the need to link different habitats together to survive. Salmon, gray whales, monarch butterflies, and the Porcupine caribou herd are all dramatic examples of a life history strategy that relies on extensive movement to meet resource needs. However, in trying to understand the distribution and abundance of migratory species, we have often divorced the two end points. Processes in one habitat are treated as independent from those in the other. This disjunction is abetted by geographical distance and also often by shifts between systems. Aquatic and terrestrial ecosystems are usually studied separately, by different sets of researchers, often using different methods and approaches (Willson and Halupka 1995). We have obtained valuable insights on the effects of landscape pattern on population survival from this approach (see Temple and Carey 1988, Donovan et al. 1995, Taper et al. 1995 for examples of the large literature on the effects of breeding habitat availability and configuration on neotropical migrant song-bird populations). However, we have also come to recognize that maintenance of migratory species, like the maintenance of species with complementary resource needs at smaller scales, will require not only preservation of the breeding habitat, but also preservation of the overwintering habitat and of the links between these two end-points.

Conclusions

This study has demonstrated the importance of considering habitat other than that used for breeding to understanding the distribution and abundance of species with complementary resource needs. Just as the local scale has been shown to be insufficient to explain the distribution of species that exhibit metapopulation structure, so too the local

and metapopulation context are insufficient for species with complimentary resource needs

I evaluated the importance of the second habitat type in terms of the amount of this resource in the landscape. This does not address the importance of the spatial pattern of habitat distribution to the organism of question. While I was able to discern an effect of amount on the distribution and abundance of leopard frogs, it is possible that the pattern of the summer habitat relative to the breeding habitat (and, also, the overwintering habitat) may afford further explanatory power. Simulation modelling done within the metapopulation framework and the breeding/non-breeding classification of the landscape suggests that spatial pattern becomes important when less than 30% of the habitat is suitable for the organism under study (Andrén 1994). Given that the landscape context may matter for both individual and population survival for species with complementary resource needs, spatial pattern may be important at habitat levels greater than 30% for these species.

At the individual level the probability of all required habitats being contiguous or, at least, proximate, decreases, on average, as number of habitats required increases. Comparisons of similar species that require different suites of habitat types would allow assessment of the importance of the spatial pattern with increasing numbers of required habitat types. *R. clamitans*, the green frog, uses similar breeding sites to *R. pipiens* but does not require summer habitat away from the breeding pond (Martof 1953). A comparison of these two species in habitats with differing amounts and spatial patterns of habitat may elucidate the interaction between the requirement for landscape complementation and the response to spatial pattern. Based on this type of comparative work, it may be possible to predict a species response to habitat fragmentation and loss according to the number of habitats it requires. Note that it is unlikely that any one

landscape will supply the same amount of habitat (when all required habitats are considered) for these two species.

The metapopulation construct is a useful tool for thinking about populations in fragmented landscapes. However, as construed at present, it reduces the landscape from a full-colour image to a high contrast photograph in black and white. For some organisms, the simplification may provide an adequate understanding of how the landscape pattern affects those species. For others, the dichotomous filter impairs our ability to detect the heterogeneity to which those species are responding and, therefore, diminishes our ability to understand the patterns and processes that effect the distribution and abundance of those species.

APPENDIX 1

Landscape classifications used in determining the amount of summer habitat and paving within 1 km of the centre of each core pond. The classes are denoted as having contributed to the total amount of summer habitat if marked with an "S" and to the total amount of roads if marked with a "P". Note that roads in residential areas were assessed at 25% of the total residential area.

Code	Description	
0	Outlines	
1	Corn	
2	Hay - Alfalfa/clover/vetch	S
3	Forest/trees/wooded fencerow	
4	Hay - Grass	S
5	Pavement/railroad/road	P
6	Old field	S
7	Water - not core pond	
8	Lawn/mowed grass/park	
9	Housing/farmyard	P
10	Industrial	P
11	Construction site	
12	Scrub	S
13	Pasture	S
14	Plowed field/dirt/quarry	
15	Soya beans/beans	
16	Grain	
17	Orchard/tree nursery/berries	
18	Unknown - not classified	
19	Annual vegetable crop	
20	Canola	
21	Sedges	S
22	CORE POND	

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