AMPHIBIAN SPECIES RICHNESS AND DISTRIBUTION IN NORTHWESTERN ONTARIO: THE IMPORTANCE OF HYDROPERIOD

by

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Abstract

The preservation of biodiversity has become a fundamental ecological goal in recent years. If we wish to prevent or reverse worldwide amphibian declines it is imperative that we understand patterns of abundance and distribution and the causal factors. Virtually every aspect of the amphibian life cycle depends on water, and therefore wetland hydroperiod plays an important part in amphibian species richness and the distribution of individual species, particulary since two major perceived stresses on amphibians are desiccation stress and predation by fish. I used repeated surveys (breeding call and visual surveys) to investigate amphibian species richness and incidence of 93 wetlands (31 each of permanent, semi-permanent and temporary) in Northwestern Ontario in relation to hydroperiod and a number of other wetland characteristics. Amphibian species richness and incidence differed among hydroperiod categories. Species richness peaked in semi-permanent wetlands and was higher in permanent than temporary wetlands, despite presence of predatory fish. Some species, even those considered 'temporary' occurred equally among all wetland types while others were more likely to be found in one or two hydroperiod categories. Species that I found to be rare in the study region may be affected negatively by the amount of roads on the landscape. Salamanders appeared very susceptible to alterations of the landscape. Percent forest cover does not appear to be a factor in determining patterns of species richness or distribution, as it is in other areas. There may be a minimum 'threshold' of forest cover, below which amphibian species decline rapidly, that has not yet been reached in my study region. Permanent bodies of water offer suitable amphibian habitat, despite potential predation by fish. Amphibian species richness was equal among lakes with or without predatory fish present. The availability of refuge habitat significantly increased amphibian species richness in lakes. I suggest that lakes should not be overlooked as amphibian habitat and as conservation areas. Lakes are suitable habitat for wetland-dependent organisms like amphibians, and being permanent, are available for use even during times of drought when other less permanent wetlands are not.

Table of Contents

List of Tables

List of Figures

GENERAL INTRODUCTION

Amphibians have become the target of increasing conservation concern in recent years. Many amphibian populations are declining worldwide and may continue to do so (Blaustein & Wake, 1990; Blaustein, Wake & Sousa, 1994; Blaustein & Wake, 1995; Alford & Richards, 1999; Houlahan et al., 2000; Collins & Storfer, 2003). There are many suspected causes of these declines including increased ultraviolet radiation, introductions of predatory fish to historically fish-free areas, habitat modification or destruction, toxins, and disease (Alford & Richards, 1999). If we wish to understand amphibian declines, we must document and explain amphibian species' distributions. Understanding amphibian distributions is particularly important in the boreal forest regions of North America where little is known about them (Elmberg, 1993). The boreal forest biome (North America and Eurasia) contains the largest expanse of wetlands in the world (Schindler, 1998) and therefore it contains important habitat for numerous amphibian species.

Climate change through global warming is linked with increasingly drier conditions in some North American regions including the boreal forest (Hengeveld, 1994; Schindler, 1998). Drier conditions in this region will likely affect the persistence of the wetlands that are so prevalent. There are other potential threats to amphibians that relate to land use in this region. Forestry is a major industry in the region and the loss or alteration of woodland habitat is likely to affect amphibian species (deMaynadier and Hunter, 1995). Sport fishing is also continually increasing in popularity. To keep up with demand, many lakes are stocked with predatory fish. Not only are predatory fish being introduced into wetlands where they were historically absent, but the possibility of introducing fish-borne disease also exists (Blaustein, Hokit & O'Hara, 1994). Each of these factors can potentially harm amphibian populations.

It is important to determine which characteristics of wetland habitats affect amphibian distribution. Most amphibians have permeable skin, requiring them to live in moist environments and many also have an aquatic larval stage (Behler & King, 1997; Hickman, Roberts & Larsen, 1997; Conant & Collins, 1998). Development time from egg to adult varies among species, from a few weeks to a year or more (Duellman & Trueb, 1986; MacCulloch, 2002). In temperate regions, many species also require deep water for hibernation. Considerable amphibian mortality or even local extinction may occur during hibernation in shallow waters that freeze over (Manion & Cory, 1952; Bradford, 1983). Therefore, the length of time that a wetland continuously holds water (hydroperiod; Pechmann et al., 1989) may be an important factor in determining species distribution.

Consider a hydrological gradient, with temporary water bodies (ephemeral pools) at one end of the scale and the most permanent ones (lakes) at the other. Theoretically, any amphibian breeding site could be placed at some point on this gradient. Numerous studies have demonstrated that the hydroperiod of a wetland can affect amphibian species presence and abundance. (Pechmann et al., 1989; Semlitsch et al., 1996; Skelly, Werner & Cortwright, 1999; Pechmann et al., 2001). The fitness of individuals, and ultimately amphibian abundance, can also be affected by hydroperiod. For instance, drying of ephemeral pools causes increasing competition for food as larval density increases and can result in smaller individual metamorphs (Wilbur, 1984) as well as fewer metamorphosing individuals (Semlitsch & Wilbur, 1988; Pechmann et al., 1989).

Amphibian species are often more successful in wetlands of particular hydroperiod. Larval food requirements, tolerance of temperature, ability to avoid predators and metamorphosis time all determine which species are most successful at a given point on the hydrological gradient (Smith 1983, Semlitsch et al., 1996).

One of my research goals was to contribute to the construction of accurate amphibian species lists for a sample of wetlands in Northwestern Ontario, an area where very little is known about amphibian species distribution. Specifically, my goal was to identify the importance of hydroperiod to amphibian species distributions in the Thunder Bay region of the Boreal/Great Lakes - St. Lawrence forest biome. I examined amphibian species richness and distribution, as well as the relative importance of hydroperiod compared with other environmental factors that may structure amphibian communities in the study region. Because lakes are usually not considered amphibian habitat, I also assessed their potential as such, despite the potential negative effects of predatory fish. My research will help to clarify some of the factors affecting boreal amphibian assemblages, which can assist in their conservation.

GENERAL MATERIALS AND METHODS

STUDY AREA

The study area was located in Northwestern Ontario, within a 100 km radius of the city of Thunder Bay (48' 27"N, 89' 12"W), in the Boreal / Great Lakes-St. Lawrence forest biomes (OMNR, 1974). The forests are dominated by a few conifer and deciduous tree species, most notably *Picea mariana* (black spruce), *Picea glauca* (white spruce), *Abies balsamea* (balsam fir), *Populus tremuloides* (trembling aspen) and *Betula papyrifera* (white birch) (Zoladeski & Maycock, 1990). The region is situated on the Canadian Shield, underlain by volcanic sedimentary and metamorphic rock formed in the Precambrian era (OMNR, 1974; Botts & Krushelnicki, 1988). The climate consists of relatively cool summers and cold winters with an average of 700 to 800 mm of precipitation annually (Botts & Krushelnicki, 1988). The major industry is forestry, dominated by pulp and paper production, but there are also a number of sawmills that operate in the region. Northwestern Ontario is home to a vast number of freshwater wetlands. These wetlands cover an estimated 25 – 50% of the landscape (National Wetlands Working Group, 1988).

STUDY DESIGN

From May to August in 2001 and 2002, I studied 93 wetlands located in the study region. I selected these sites by studying topographic maps of the study area, consulting with the local conservation authority and by searching visually from a vehicle. To investigate differences in amphibian species richness in relation to hydroperiod, I categorized these 93 water bodies into 31 temporary, 31 semi-permanent and 31 permanent wetlands. Temporary sites were generally ditches and other relatively small, shallow and ephemeral bodies of water (area 0.15 ± 0.100 ha, max. depth 0.52 ± 0.040 m). Semi-permanent sites were composed mainly of ponds, both natural and anthropogenic in origin (area 0.54 ± 0.150 ha, max. depth 1.97 ± 0.221 m). The permanent sites were all relatively small lakes (area 27.14 ± 6.248 ha, max. depth 8.12 ± 1.252 m).

FIELD METHODS

Because of the large number of study sites, I was unable to do the fieldwork at every study site myself. With the help of a field assistant, I performed all of the fieldwork at each of the permanent and temporary sites. I obtained data from a random sample of ponds (semi-permanent category) from the study site list of a fellow graduate student, Virginia Abbott.

Regardless of the surveyor(s), all sites were sampled using the same field methods. I used both night (call surveys) and day (visual searching) surveys to obtain an accurate amphibian species list for each site. A typical night visit involved approaching the site and listening for breeding calls of amphibians for about three to five minutes. Three to five minutes is adequate time to hear most of the species that are active on a given visit (Shirose et al., 1997; Crouch & Paton, 2002). During day surveys I searched visually for any amphibian life stage: egg, larvae or adult. I also listened for any breeding calls during these visits. I waded around the temporary and semi-permanent sites and paddled a canoe around the permanent sites, wading wherever possible. During these visits I frequently dipnetted through the aquatic vegetation to find amphibian larvae. I also made note of any fish species observed during these surveys. I identified fish to species level when possible, but I always classified them as either predatory or non-predatory. An amphibian species was considered present at a site if a breeding call was heard or any life stage was visually observed during any visit. In 2001, a minimum of two night and two day visits were made to each site. In 2002, I visited each site a minimum of three times at night and two times during the day.

SPECIES POOL

Based on published range maps, a total of 13 amphibian species potentially occur in the study region (Behler & King, 1997; Conant & Collins, 1998; MacCulloch, 2002; Oldham and Weller 2003) (Table I).

Table I. A list of species that potentially occur in the study region and their traditional classifications as 'temporary' or 'permanent'.

Species	Common Name	Hydroperiod Classification
Order Anura		
Bufo americanus	American toad	Temporary
Pseudacris crucifer	Spring peeper	Temporary
P. maculata	Boreal chorus frog	Temporary
Hyla versicolor	Gray treefrog	Temporary
Rana clamitans	Green frog	Permanent
R. pipiens	Northern leopard frog	Permanent
R. septentrionalis	Mink frog	Permanent
R. sylvatica	Wood frog	Temporary
Order Caudata		
Ambystoma laterale	Blue-spotted salamander	Temporary
A. maculatum	Spotted salamander	Temporary
Necturus maculosus	Mudpuppy	Permanent*
Notophthalmus viridescens	Eastern newt	Permanent
Plethodon cinereus	Eastern red-backed salamander	Terrestrial*

*Note: *N. maculosus* and *P. cinereus* were not observed during this study, likely due to the deep-water habitat of *N. maculosus* and the complete terrestriality of *P. cinereus*.

CHAPTER 1: AMPHIBIAN SPECIES RICHNESS AND INCIDENCE WITH RESPECT TO HYDROPERIOD

Introduction

A central goal in ecology is to determine which factors structure communities. Arguably, more attention in recent decades has focused on biotic processes (i.e. competition, predation) than abiotic processes (Dunson & Travis, 1991). However, the species composition of a community is affected by many factors, both biotic and abiotic. This is true for communities of all organisms, including amphibians. Most temperate-zone amphibian species use wetlands for at least a portion of their life cycle. Because of the importance of wetlands to amphibians, biotic and abiotic wetland characteristics will affect amphibian community composition (Semlitsch, 2000). One important characteristic of a wetland that is likely to affect amphibian species distribution is its hydroperiod (Pechmann et al., 1989; Semlitsch et al., 1996; Skelly, Werner & Cortwright, 1999; Pechmann et al., 2001).

Amphibian life histories are diverse and range from totally aquatic to completely terrestrial species (Hecnar, 2003, in press). Amphibian species are often classified as 'temporary' or 'permanent' wetland species, depending upon their life history traits (larval development time, conspicuous vs. cryptic feeding, hibernation requirements) and where they are more likely to breed (Leips, McManus & Travis, 2000; Snodgrass et al., 2000). 'Permanent' water species, such as *Rana clamitans*, cannot persist in ephemeral water bodies, because their larvae require two seasons to develop and adults must hibernate underwater (MacCulloch, 2002). However, a typical 'temporary' species, such as *Pseudacris* *maculata*, has a short larval development time (4 – 6 wks from egg to metamorphosis) and adults hibernate on land (Whitaker, 1971; MacCulloch, 2002). These characteristics may allow 'temporary' species to occupy either temporary or more permanent bodies of water. However, the boreal chorus frog appears to prefer temporary or semi-permanent sites and large numbers call in relatively small bodies of water only metres away from permanent water bodies where no calls are heard (personal observation). Snodgrass et al. (2000), suggested that temporary wetlands have unique amphibian communities, rather than being composed of a subset of species found in more permanent water bodies. Amphibian species characteristics such as larval food requirements and feeding methods, temperature tolerance, anti-predator defenses, and length of development time all play a part in determining which amphibian species will be most successful at any point along the hydrological gradient (Smith, 1983; Semlitsch et al., 1996). It is likely then, that amphibian species differ from one another in terms of suitable wetland habitats, on the basis of hydroperiod.

One proposed theory that explains patterns of amphibian species richness in relation to hydroperiod is discussed in parts in Heyer, McDiarmid & Weigmann (1975), Wilbur (1984), Skelly, Werner & Cortwright (1999) and Semlitsch (2000). It is widely held that the two major stresses on amphibians are desiccation and predation. Desiccation stress is likely to be greatest at the temporary end of the hydrological gradient and lowest at the permanent end. Wetlands with a short hydroperiod may not provide enough time for larvae to develop and metamorphose. Species that hibernate underwater cannot survive a period of drying. Predation stress by fish would be greatest at the permanent end of the hydrological gradient. Fish are known to be important predators of amphibians and are capable of limiting amphibian activity, distribution, or even eliminating them from some water bodies (Sexton & Phillips, 1986; Wellborn, Skelly & Werner, 1996; Hecnar & M'Closkey, 1997; Smith et al., 1999). Invertebrate predators, assuming that they are able to colonize ephemeral sites, may occur over a wide hydrological gradient. Therefore, total predation stress is thought to increase as hydroperiod increases. Because desiccation and predation stresses are opposing, species richness should be maximized where the combined stress is at a minimum. Thus, amphibian species richness should be greatest in the middle range of the hydrological gradient, in semi-permanent water bodies (Figure 1.1).

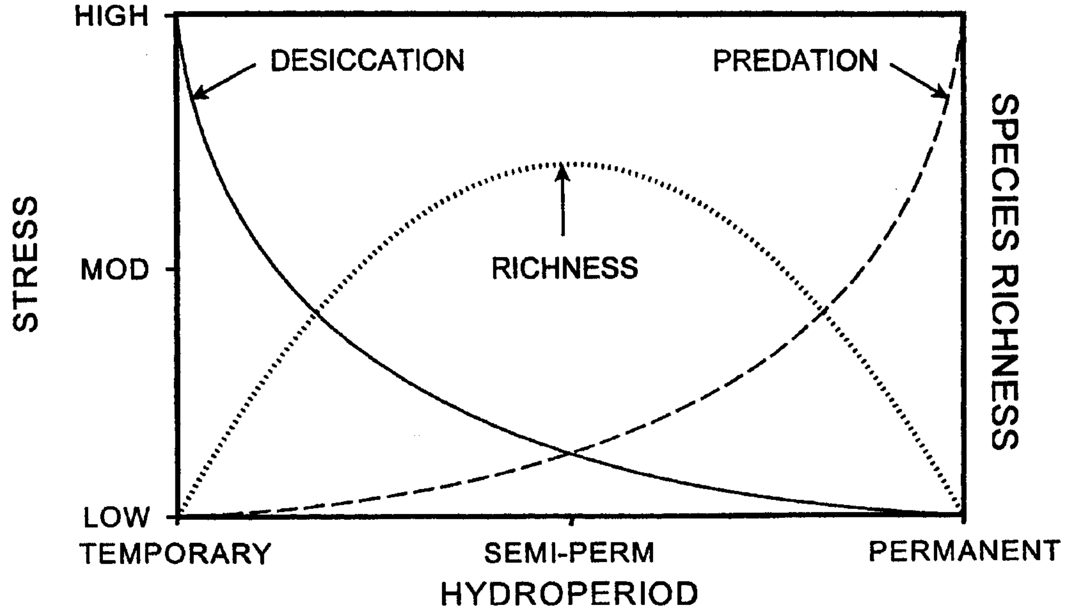

Figure 1.1. A proposed model representing amphibian species richness with respect to hydroperiod, desiccation and predation stresses. Amphibian species richness peaks where the combined stresses of predation and desiccation are at a minimum, in the semi-permanent range on the hydroperiod gradient.

Although various aspects of hydroperiod effects have been studied and the hydroperiod-stress model has become a major tenet of amphibian ecology, it has never been tested directly. It is important to note that Figure 1.1 is a conceptual model and therefore the exact shapes of the curves are not known. It is likely that predation stress reaches a maximum at some level of wetland permanence. However, this plateau should occur at the lake level, and I didn't study any water bodies beyond lakes on the hydrological gradient.

Another theory about how amphibian species are distributed across the hydrological gradient relates to source-sink (Pulliam, 1988) and metapopulation dynamics (Hanski & Gilpin, 1991). Amphibian species are known to exhibit metapopulation dynamics (Gill, 1978; Sjögren, 1991; Blaustein, Wake & Sousa, 1994; Skelly, Werner & Cortwright, 1999; Pope, Fahrig & Merriam, 2000), and a high density of wetlands interspersed over the landscape is important in terms of amphibian dispersal (Gibbs, 1993; Semlitsch, 2000). In this type of a scenario, wetlands nearer to the permanent end of the hydrological gradient should have lower extinction rates and act as sources, 'supplying' surplus individuals to less permanent wetlands when conditions are favourable. Species that are considered 'temporary' may prefer to inhabit wetlands at the temporary end of the gradient, but it is likely that they are also capable of breeding in more permanent water bodies, although possibly with reduced success. If the dynamics of amphibian species operate in this manner, one would expect to find the highest species richness in more permanent water bodies and temporary wetlands would have the lowest number of species.

Another alternative is based on the perceived trend of increasing terrestriality in amphibian evolution (Duellman, 1985). Under this scenario, richness should be greatest at the temporary end of the hydroperiod gradient due to amphibian species' decreasing dependence on water.

My main objective was to compare amphibian species richness and incidence of wetlands with respect to hydroperiod. My interest is in determining if there is a pattern to amphibian species richness between sites in different hydroperiod categories. From a conservation standpoint, it is important to understand which wetlands on a hydroperiod gradient are most suitable for amphibians. Considering recent concerns of drought in the boreal forest, I have particular interest in how amphibians use the more permanent wetlands.

Material and Methods

To determine species richness among the three hydroperiod categories (temporary, semi-permanent and permanent), I studied a total of 93 wetlands (31 per category) in 2001 and 2002. My field methods are outlined in detail in the General Materials and Methods section of this paper.

I performed most statistical calculations using Systat, (version 9). The exception is the heterogeneity G-test, performed using BIOMstat, (version 3.3). I used heterogeneity G-tests to determine any differences between amphibian communities among the three hydroperiod categories. I also used this method to determine if species incidence differed among hydroperiod categories. I used analysis of variance (ANOVA) with Tukey HSD multiple comparisons to determine if mean amphibian species richness differed among hydroperiod categories. Since the possibility exists that any relationship between hydroperiod category and species richness could be due to an area effect (species richness increases with area), I used analysis of covariance (ANCOVA) (with wetland area as a covariate) to compare species richness among hydroperiod categories, while factoring out the influence of area.

Results

In 2001 and 2002, I observed 11 of 13 species that potentially occur in the study area (Table I; Figure 1.2). Incidence values (2001 and 2002 combined) among all three hydroperiod categories (n = 93) ranged from 90 (97%; *Pseudacris crucifer*) to 1 (1%; *Ambystoma laterale*) (Figure 1.2).

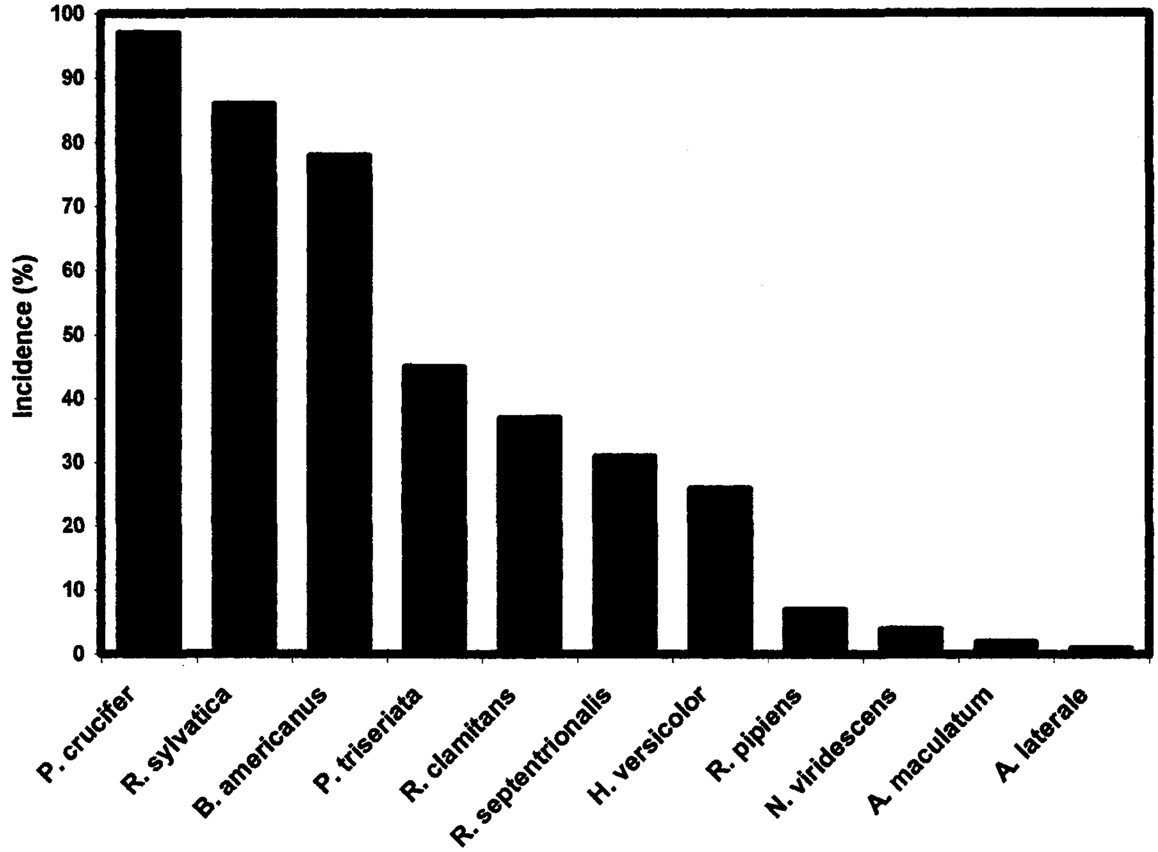

Figure 1.2. Amphibian species incidence (% of sites occupied) of all 93 wetlands, regardless of hydroperiod, for 2001 and 2002 combined.

Certain species were common or rare in all site types; for example, *Pseudacris crucifer* was almost ubiquitous among all sites that I surveyed, while *Ambystoma laterale*, *A. maculatum*, *Notophthalmus viridescens* and *Rana pipiens* occupied relatively low numbers of sites, regardless of hydroperiod category (Figure 1.2). However, incidence for individual species varied among the site categories, in some cases quite dramatically. For example, *Rana clamitans* was absent from the temporary sites, occurred in only 8 (26%) semi-permanent sites, but it was found in 26 (84%) of the permanent sites (Figure 1.3). On the other hand, *Pseudacris maculata* was found in 18 (58%) temporary sites, 23 (74%) semi-permanent sites, but only 1 (3%) permanent site (Figure 1.3). Heterogeneity G-tests revealed significant differences in amphibian communities between hydroperiod categories (Table 1.1). Note that expected values for *Rana pipiens*, *Notophthalmus viridescens*, *Ambystoma laterale* and *Ambystoma maculatum* are below five and therefore the results should be considered with some caution.

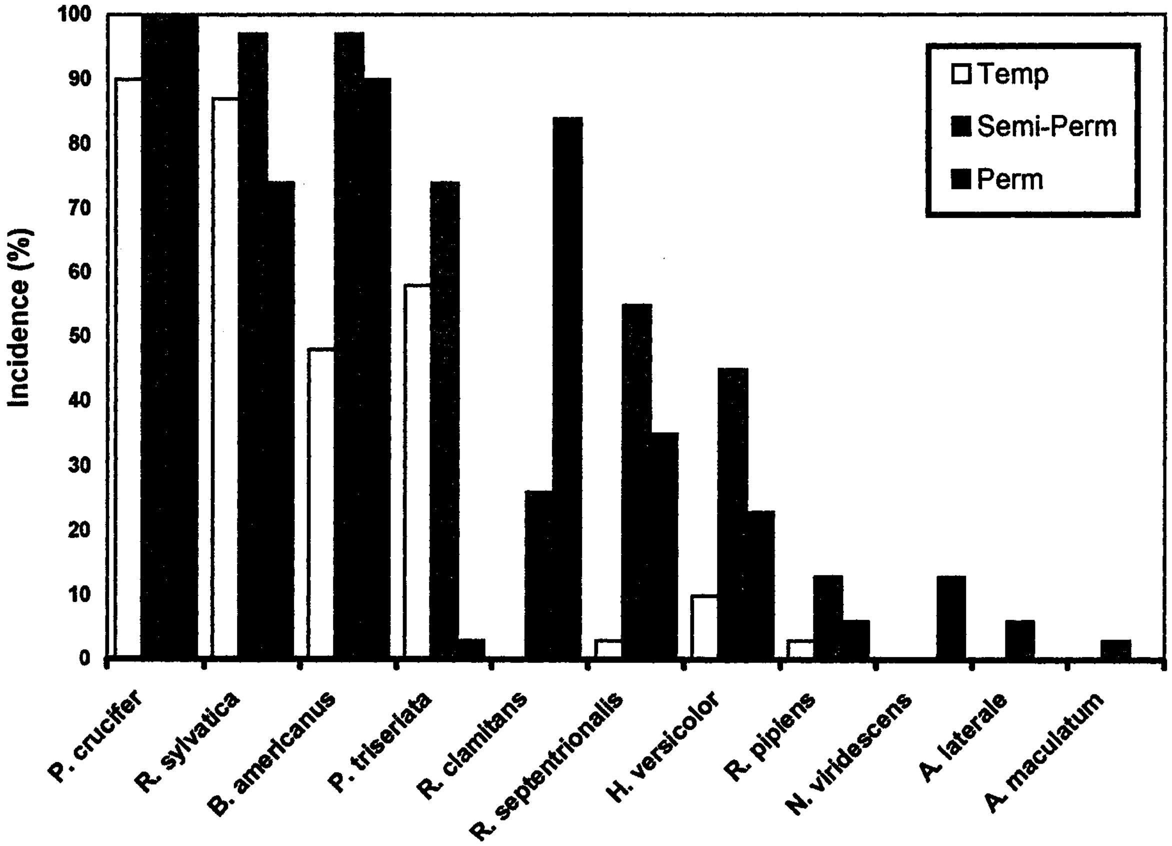

Figure 1.3. Amphibian species incidence (% of sites occupied) in relation to wetland hydroperiod for 2001 and 2002 combined. The sample size of each category (temporary, semi-permanent and permanent) is 31.

Table 1.1. The results of amphibian species by hydroperiod category heterogeneity G-tests. The hydrological gradient is divided into temporary (T), semi-permanent (S) and permanent (P) categories. The overall heterogeneity G = 82.8, 20df, p < 0.001.

	Hydroperiod Category				
Species	T	S	P	G	**Distribution**
Pseudacris crucifer	28	31	31	2.01 ns	P, S, T
Pseudacris maculata	18	23	1	26.19***	S, T
Hyla versicolor	4	14	7	6.05*	S
Rana clamitans	0	8	26	36.88***	P
Rana septentrionalis	1	17	11	17.11***	S, P
Rana sylvatica	27	30	23	0.93 ns	S, T, P
Rana pipiens	1	4	2	1.83 ns	S
Bufo americanus	15	30	28	5.85 ns	S, P, T
Notophthalmus viridescens	0	0	4	7.53*	P
Ambystoma maculatum	0	2	0	1.32 ns	S
Ambystoma laterale	0	1	0	3.30 ns	S

*p < 0.05, **p < 0.01, ***p < 0.001, ns = not significant

Amphibian species richness ranged from 0 to 7 in 2001 and 2002 individually, and 0 to 8 in both years combined. Species richness differed significantly among hydroperiod categories in 2001 (ANOVA; F = 13.67, 2df, $p < 0.001$, $R^2 = 0.23$), 2002 (ANOVA; F = 46.00, 2df, $p < 0.001$, $R^2 = 0.51$), and both years combined (ANOVA; F = 26.47, 2df, $p < 0.001$, $R^2 = 0.37$). Species richness was highest in semi-permanent wetlands (2001 = 4.4 ± 0.23, 2002 = 4.8 ± 0.21, 2001 & 2001 = 5.19 ± 0.22), lowest in temporary wetlands (2001 = 2.9 ± 0.21, 2002 = 1.8 ± 0.28, 2001 & 2002 = 3.0 ± 0.23) and intermediate in permanent wetlands (2001 = 3.7 ± 0.16, 2002 = 3.7 ± 0.19, 2001 & 2002 = 4.3 ± 0.17) (Figure 1.4).

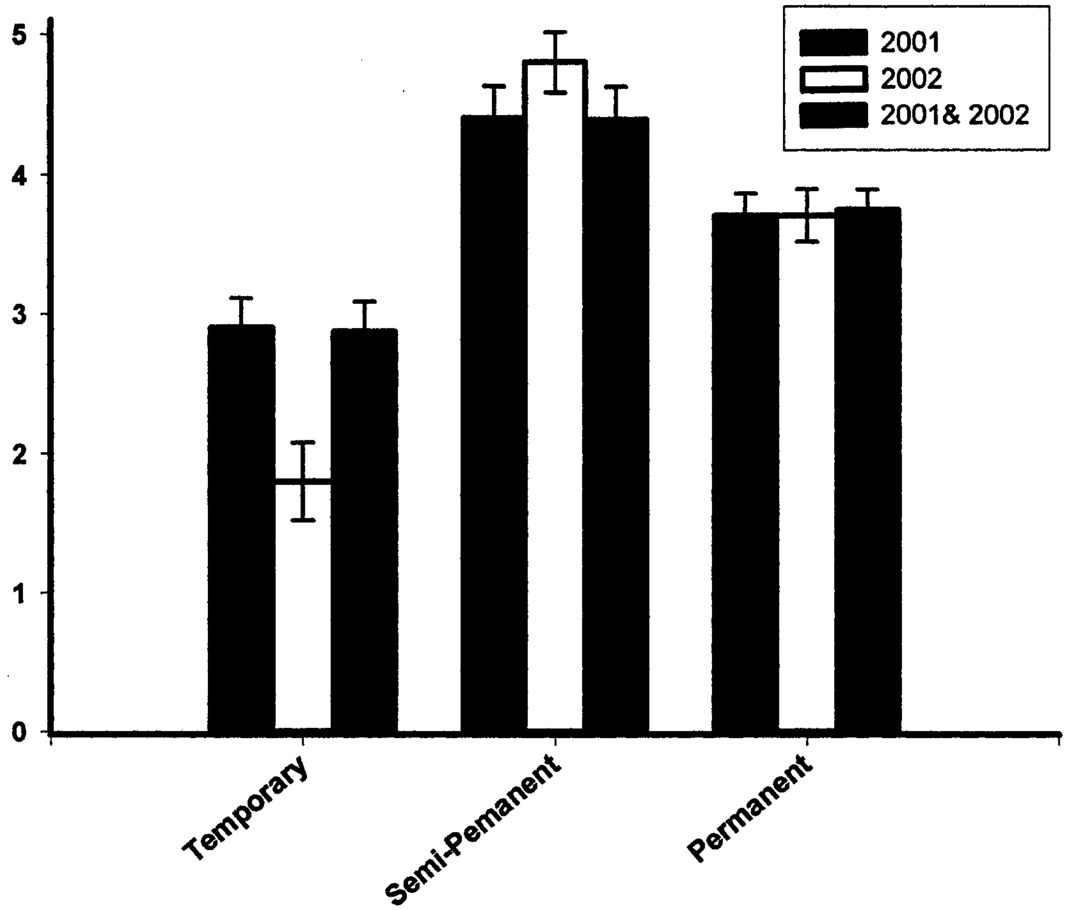

Figure 1.4. Comparison of mean amphibian species richness (± standard error) for 2001, 2002, and both years combined between wetland hydroperiod categories.

Mean amphibian species richness was lower in temporary wetlands than semi-permanent wetlands in 2001 ($p < 0.001$), 2002 ($p < 0.001$), and both years combined ($p < 0.001$). Mean species richness was also lower in temporary wetlands than permanent wetlands in 2001 ($p = 0.011$), 2002 ($p < 0.001$), and both years combined ($p < 0.001$). Mean species richness was significantly lower in permanent wetlands than semi-permanent wetlands in 2002 ($p = 0.003$), and both years combined ($p = 0.009$), however this difference was marginally non-significant in 2001 ($p = 0.066$).

ANCOVA with species richness as the dependent variable, hydroperiod category as the independent variable, and area of the study site as a covariate, revealed significant models in 2001 ($F = 13.46$, 2df, $p < 0.001$, $R^2 = 0.23$), 2002 ($F = 45.67$, 2df, $p < 0.001$, $R^2 = 0.51$) and for both years combined ($F = 26.42$, 2 df, $p < 0.001$, $R^2 = 0.37$). No significant area interactions were observed in any of the models (2001 $p = 0.892$; 2002 $p = 0.591$; combined $p = 0.577$).

Discussion

The species incidence curve for all 93 wetlands, regardless of hydroperiod (Figure 1.2), was a typical hollow curve, indicating that some species (*Pseudacris crucifer*, *Rana sylvatica*) were common in all wetlands, while others (*Rana pipiens* and the salamander species) were rare, irrespective of hydroperiod. However, certain species are more common in a particular range on the hydrological gradient (Figure 1.3). For example, *Rana clamitans* was not observed in any temporary sites and *Rana septentrionalis* was only observed in one temporary wetland. Each of these species occurs at much higher frequencies in the more permanent wetlands. This is not surprising, due to the obligate over-wintering nature of their larvae in northern areas (Conant & Collins, 1998; MacCulloch, 2002). What is perhaps more interesting is the distribution of a species such as *Pseudacris maculata*, which is present in rather high proportions of semi-permanent and temporary wetlands, but only present in one of the 31 permanent sites that I surveyed. Heterogeneity G-tests indicate that amphibian communities at sites on varying points along the hydrological gradient differ and also that certain species are much more likely to utilize one or two site types more frequently or even exclusively (Table 1.1). Differences in community structure with respect to hydroperiod are due to the unique life-history requirements of each amphibian species, and the differences between ‘temporary’ and ‘permanent’ wetland amphibians. I suspect that most of the variation can be attributed to ‘permanent’ species (*Rana clamitans*, *Rana septentrionalis* etc.; see Table I) being incapable of utilizing temporary wetlands, as many of the ‘temporary’ species were observed along the entire hydrological gradient (Figure 1.3).

Not only did species incidence differ in terms of hydroperiod, but species richness did also (Figure 1.4). Amphibian species richness differed between the sites at the temporary end of the hydrological gradient and the two more permanent wetland categories. Tukey HSD post hoc tests revealed a significant difference in mean species richness between permanent and semi-permanent wetlands in 2002 and both years combined, however, in 2001 this association was marginally non-significant. Upon examination of Figure 1.4, it is evident that species richness does differ between the hydroperiod categories. Furthermore, the highest species richness values occurred in the semi-permanent sites and the species richness values are lower in the temporary and permanent wetlands. This concurs with the predictions of the hydroperiod-stress model that I presented earlier (Figure 1.1). Presumably, desiccation stresses are limiting the number of species that can use the temporary wetlands, allowing only ‘temporary’ species with relatively fast metamorphosis times to be successful in these locations. Support is seen in Figure 1.3, as *Pseudacris crucifer*, *Rana sylvatica*, *Pseudacris maculata* and *Bufo americanus* are all present in over 50 percent of the temporary sites. However, the support is weakened by the fact that three of these four species *(P. crucifer*, *R. sylvatica* and *B. americanus*) are relatively common in all three wetland types in my study area. In fact, *B. americanus* is actually much more common in both the semi-permanent and permanent sites. This is not surprising as the larvae of this species are unpalatable to predatory fish (Kats, Petranka & Sih, 1988) and can therefore coexist with them.

Recall that the temporary sites are, on average, much smaller than the other two site types. The species-area effect, which is widely documented (Brown, 1971; Barbour & Brown, 1974; Bolger, Alberts & Soulé, 1991; Oertli et al., 2002), predicts that larger areas can support more species and therefore, the pattern of species distributions I observed may be related to this phenomenon. However, when area was corrected for (ANCOVA) the qualitative results changed very little. This indicates that amphibian species richness was still different between hydroperiod categories, even after area was controlled.

The pattern of amphibian species richness in relation to hydroperiod is similar to the model presented in Figure 1.1 and discussed in part in the works of others (Heyer, McDiarmid & Weigmann, 1975; Wilbur, 1984; Skelly, Werner & Cortwright, 1999; Semlitsch, 2000). This model assumes that the greatest number of amphibian species will be found in sites near the middle of the hydrological gradient due to increasing desiccation and predation stresses as the sites become more temporary and more permanent, respectively. The model also suggests that species richness values in permanent sites should be approximately equal to those in the temporary sites. However, I found that the mean species richness of permanent wetlands was significantly higher than that of the temporary sites, and in fact almost equal to the values observed for semi-permanent sites. This suggests that the predation stress by fish is not equal to the desiccation stress that species at the temporary end of the scale are facing; or that the nature of the permanent sites is making fish predation less of a factor than it would otherwise be.

It is widely known that habitat complexity can influence species diversity (Ricklefs, 1990). In wetlands of relatively large size such as the permanent water bodies I examined, the habitat can be very heterogeneous and can be beneficial to amphibians in two ways: a more diverse habitat is able to support a greater diversity of species, and among these different habitat types there are likely to be refuge habitats. Shallow areas with extensive emergent and/or submerged vegetation and areas with muddy or leafy bottoms that offer hiding places are all examples of suitable amphibian refuge habitats. Amphibian use of refuge habitats and their subsequent coexistence with predators has been noted in other studies (Sih, Kats & Moore, 1992; Walls, 1995; Hecnar & M'Closkey, 1997).

In addition to supporting the hydroperiod-stress model, the pattern of greater amphibian species richness towards the permanent end of the hydrological scale also supports a source-sink or metapopulation hypothesis. 'Temporary' species can and do occur in more permanent wetlands as well as the temporary ones. As temporary wetlands become less available, these species can shift their occupancy to more permanent bodies of water, although with potentially reduced success. As environmental conditions change from year to year, populations of these species can colonize temporary sites when available. The richness pattern in this study does not support the idea of an evolutionary trend towards greater terrestriality in amphibians, at least with this fauna.

In summary, amphibian species richness of wetlands in Northwestern Ontario does differ with respect to hydroperiod. Mean species richness is highest in the sites at the semi-permanent to permanent range on the hydrological gradient, which is consistent with a hydroperiod-stress or source-sink explanation. 'Temporary' wetland species are also found in more permanent bodies of water, although 'permanent' wetland species are rarely found in temporary water bodies. This has conservation implications because drought conditions in the boreal forest are likely reducing the number of temporary wetlands that are available to amphibian species. However, it appears that more permanent water bodies, despite potential predation pressure from fish, can be suitable habitat for even for the 'temporary' amphibian species, perhaps due to the availability of refuge habitats. The fact that amphibian species appear able to survive in permanent wetlands, despite the potential predation risk, provides hope for their future in the boreal forest regions of the world. As amphibian species continue to decline worldwide (Blaustein & Wake, 1990; Elmberg, 1993; Blaustein & Wake, 1995; Houlahan et al., 2000), and drought being one of the major contributors to these declines, amphibians may become more reliant on these permanent water bodies as the temporary ones continue to disappear.

CHAPTER 2: IMPORTANCE OF WETLAND CHARACTERISTICS TO AMPHIBIAN SPECIES RICHNESS AND DISTRIBUTION

Introduction

A primary goal of ecologists is to learn how biotic and abiotic aspects of the environment interact to determine community composition. In recent years, much research has focused on biotic processes, but the importance of abiotic factors to community composition should not be overlooked (Dunson & Travis, 1991). It is also important to consider multiple spatial scales when attempting to explain community structure. Earlier studies have focused on the importance of local scale variables to community compostition (Pavignano, Giacoma & Castellano, 1990), but in recent years the importance of landscape scale variables has been recognized. Amphibian community structure may be driven by landscape scale processes (Storfer, 2003), and therefore it is important to consider multiple spatial scales when explaining amphibian communities (Knutson et al., 1999).

Amphibian species are declining worldwide, but the cause(s) of these declines remain unclear. A number of hypotheses have been suggested including increased ultraviolet radiation, introductions of predatory fish to historically fish-free areas, habitat modification or destruction, toxins, and disease (Blaustein, Wake & Sousa, 1994; Alford & Richards, 1999; Collins & Storfer, 2003).

It is of fundamental importance to understand the patterns of distribution of amphibian species, particularly in areas like Northwestern Ontario where there is little knowledge on this subject. For conservation purposes, we need to know how amphibian species are distributed and what factors affect their distributions. With this knowledge, we can work to reverse existing declines and prevent future ones by altering land use practices as well as focusing conservation efforts on areas where they are most needed or will be most effective.

We must learn about the patterns of amphibian species richness and distribution in areas that are often considered "pristine", such as the forests of Northwestern Ontario. An area of this type may be used as a benchmark to compare with other more disturbed areas. If links can be established between amphibian species and particular aspects of their habitat (the presence or absence of a certain variable), it may be possible to relate to other areas where declines are obviously occurring,

Situated on the boundary between the Boreal/Great Lakes-St. Lawrence forest biomes, the forest of Northwestern Ontario is important habitat for amphibians, as it contains millions of wetlands and much of the landscape is relatively undisturbed. The world's boreal forest regions are home to the largest expanse of wetlands on earth (Schindler, 1998) as well as a large proportion of the world's freshwater. Land use in this region is primarily forestry related, unlike other areas with a similar species pool, such as southern Ontario, where agriculture is the primary land use. Comparisons of species distribution patterns between the two regions are difficult, however, as there are many more recorded observations in southern regions of the province (Hecnar & M'Closkey, 1996; King et al., 1997; Hecnar & M'Closkey, 1998; Oldham & Weller, 2003).

As I demonstrated in Chapter 1, wetland hydroperiod appears to be important in determining amphibian species richness and distributions. However, the hydrological gradient may be only one of any number of gradients that amphibian species are distributed along. The goal of this chapter is to examine amphibian species richness and individual species distributions in relation to a number of variables that reflect the properties of their breeding habitats and the surrounding landscapes. I hope to determine the importance of these variables in explaining the distribution of individual amphibian species as well as determining how they affect amphibian species richness in the study region. These findings can be useful in gaining further insight into how land-use practices and conservation efforts can be altered to be more effective at preserving amphibian species. It is also possible that one or more wetland variables may affect the distribution of multiple species and these variables are the most important to identify, as they are ones that it would be most beneficial to focus on in conservation practices. Finding a “common thread” among species makes it possible to avoid using species-specific conservation strategies. Conservation areas are most effective when they provide suitable habitat for many species rather than only one or two.

There are a number of variables that are likely to affect the distribution of amphibian species among wetlands in a region. Traditionally, many studies have focused on local scale variables, when attempting to describe species assemblages (Pavignano, Giacoma & Castellano, 1990). However, while the majority of amphibian species use wetlands for breeding purposes, other aspects of the landscape around these sites must be suitable for foraging and hibernating purposes. Pope, Fahrig & Merriam (2000) refer to *Rana pipiens* (northern leopard frog) as an example of this phenomenon, which is termed landscape complementation. Recent studies have shown that amphibian populations and distributions respond to characteristics of the landscape around their breeding sites (Laan & Verboom, 1990; Hecnar & M'Closkey, 1998; Kolozsvary & Swihart, 1999; Lehtinen, Galatowitsch & Tester, 1999; Adams & Bury, 2002). It has been demonstrated that a number of properties of the landscape surrounding amphibian breeding sites may influence the distribution of these organisms. Specifically, the area of forest cover, amount of roads, number of other wetlands, amount of rivers and streams and the heterogeneity of the landscape around amphibian breeding sites may be important in determining which species (as well as how many) breed at a wetland. A number of these variables are likely related to human interference on the landscape and may therefore indicate how human activities affect amphibian populations. Storfer (2003) recommended that since amphibian population dynamics are controlled by landscape scale processes, more research should be focused at larger spatial scales. Although predictive models can be constructed based only on landscape scale variables, local scale variables are also likely to play a part in determining amphibian species presence at a particular wetland (Knutson et al., 1999). More predictive power is possible if we consider multiple spatial scales when discussing amphibian species distributions.

Numerous authors have recently established that amphibian species richness, diversity and abundance values may be positively correlated with forested areas surrounding breeding sites. (Hecnar & M'Closkey, 1998; Guerry & Hunter, 2002; Russell, Guynn & Hanlin, 2002). However, it should be noted that some amphibian species might also be negatively associated with these forested areas (Guerry and Hunter, 2002). Forest harvesting practices can also negatively impact amphibian species (deMaynadier & Hunter, 1995). Regardless of the type of association, these findings stress the potential importance of forest cover when considering amphibian conservation.

Amphibians are known to exhibit metapopulation dynamics (Gill, 1978; Hecnar & M'Closkey, 1996; Semlitsch, 2000; Skelly, 2001) and also to migrate among habitats to complete their life cycle (i.e. reproducing, foraging, hibernating) (Sinsch, 1990; Pope, Fahrig & Merriam, 2002). A higher density of wetlands on a landscape increases the probability of amphibian species persistence by increasing the amount of source areas available and the probability of successful dispersal (Gibbs, 1993). Therefore, the number of other wetlands and the total length of rivers and streams around a potential amphibian breeding site will likely play a role in determining which species are present.

Roads are another feature on the landscape known to affect amphibian species. It is well-documented that roadways fragment habitats and impose barriers to dispersal for many forms of wildlife. High road densities are correlated with lower amphibian species richness and abundance (Findlay, Lenton & Zheng, 2001). Significant mortality of migrating amphibians occurs on roadways (Ashley

& Robinson, 1996) mortality is correlated with traffic density (Fahrig et al., 1995). Species are affected differently, however. More vagile species appear to be affected more seriously than those that are less vagile (Carr & Fahrig, 2001). Paved roads are likely to be wider and have a much heavier traffic flow than unpaved ones, and there is likely a difference in the effects that amphibians may experience between the two types. It is also theoretically possible that roads with little traffic flow can be beneficial to amphibians. They may provide dispersal routes, and ditches and borrow pits associated with roads may also provide beneficial amphibian habitat.

Amphibian diversity may increase with increasing landscape heterogeneity (Atauri & de Lucio, 2001; Kretzer and Cully, 2001). The term landscape heterogeneity refers to the complexity of the mosaic of habitats on the landscape (Atauri & de Lucio, 2001). At a large spatial scale, landscape heterogeneity is likely reflected by changes in elevation around an amphibian breeding site. A higher number of elevation changes should reflect a greater abundance of micro- and mesohabitats and this can be inferred as an increase in the habitat heterogeneity of the landscape.

There are also a number of variables at a smaller, local scale that are likely to affect amphibian species distributions including the elevation, area, perimeter, maximum depth, volume and hydroperiod of a wetland as well as its distance from urban areas and whether or not it contains fish.

As elevation changes, the natural moisture gradient will also change. Amphibian species have been observed to respond to this change. Two similar studies in Texas (Fleet & Autrey, 1999; Lewis, Fleet & Rainwater, 2000) found that amphibian species distributions differed among forest types along the elevation-moisture gradient. Wetlands at lower elevations are likely to be associated with a greater number of other wetlands and a more even landscape which makes movement easier for amphibians. It is also likely that wetlands of differing elevation will experience individual microclimatic effects, which might also play a role in determining their suitability for amphibian breeding.

The species-area effect is a well-documented phenomenon among many taxa (Brown, 1971; Barbour & Brown, 1974; Bolger, Alberts & Soulé, 1991; Oertli et al., 2002). As area increases, so does the number of species that can occur in that area. When considering amphibian breeding sites, I must consider not only the area of these wetlands but also other parameters related to area, including the wetland's maximum depth, perimeter and volume. Amphibians are likely most affected by the maximum depth of a wetland and its perimeter. Many amphibian species require a relatively deep water body in which to hibernate (MacCulloch, 2002) and depth is also potentially related to other factors of importance to amphibians, such as water permanence (desiccation stress) and vegetation cover and type. The interface between the water and land is the area that amphibians are likely to utilize the most in normal daily activities such as basking and foraging, and larvae also prefer shallower shorelines to deeper water. Therefore it is better to examine the perimeter of a wetland than the area or volume of water present.

Urbanization of the landscape has been suggested to affect amphibian species richness and their distributions (Minton, 1968; Cochran, 1989). Draining of wetlands and clearing of forest and grassland areas for urban land use results in the loss of amphibian breeding sites or it inhibits amphibians from moving to these sites (Semlitsch, 2000). The metapopulation dynamics that are exhibited by amphibians can be disturbed as the landscape becomes more and more fragmented with increased urbanization (Lehtinen, Galatowitsch & Tester, 1999). My region of study is somewhat unique in that it is situated around the only major urban area for a great distance in any direction. This makes it possible to quantify any effects that urbanization has on amphibian species by using distance to represent an urbanization gradient. Wetlands that are farther away from the City of Thunder Bay will be affected less by any impact that urbanization may have on amphibian breeding sites.

Another property of a wetland that is likely to affect the amphibian species that are found there is whether or not it contains predatory fish. Ponds containing predatory fish have been shown to have lower amphibian species richness than non-predatory or fish free ponds (Hecnar and M'Closkey, 1997). Abundance of amphibians can also be altered by predatory fish presence (Smith et al., 1999). Furthermore, amphibian distributions can be altered when traditionally fishless wetlands receive spillover water (and presumably fish) from wetlands that contain fish (Babbitt & Tanner, 2000). Not all species are affected the same way by the presence of fish. While some species decline or are not found in the presence of fish, others are more abundant (Hecnar & M'Closkey, 1997; Smith et al., 1999).

Methods

FIELD METHODS

I surveyed 93 wetlands of varying hydroperiod (temporary, semi-permanent or permanent) in spring and summer of 2001 and 2002 to construct accurate amphibian species lists for each. Surveys involved both night and day sampling visits.

I conducted night surveys from early May to late June to cover the breeding season of all amphibian species in the study region (MacCulloch, 2002). Night surveys involved quietly approaching the site and listening for 3-5 minutes to identify the breeding calls of anurans. This time period is sufficient to provide a margin against both surveyor inexperience and less than optimal surveying conditions (Shirose et al., 1997). I also recorded any amphibians that were observed during these visits. A minimum of two night visits were made to each study site in 2001 and at least three were made in 2002.

I conducted day surveys throughout the entire sampling period (May – August) in both years. Day visits consisted of wading/paddling around the wetland, searching for any amphibian life stage: eggs, larvae or adults. I frequently dipnetted through submerged vegetation to detect larvae. It was possible to wade around the majority of the semi-permanent and temporary sites. I used a canoe to paddle through deep areas of permanent sites, but waded wherever possible. I also recorded any calls heard at any site during day visits. A minimum of two day visits were made to each site in each year.

VARIABLE DETERMINATION

I examined 15 habitat variables including both physical properties of wetlands and properties of the surrounding landscape. The variables I measured were: distance from the City of Thunder Bay (I used Lakehead University as the approximate center of the city) for an urban gradient, elevation above mean sea level, area, perimeter, maximum depth, volume, presence or absence of fish, and hydroperiod (temporary, semi-permanent or permanent) of each site as well as the spatial heterogeneity (changes in elevation), percent forest cover, number of wetlands, and length (km) of rivers and streams, paved roads, unpaved roads, and total km of all roads within 2km of the perimeter of each wetland.

Physical variables of each wetland were obtained from topographic maps (NAD 27, 1:50,000), measured and /or calculated. I used a distance calculator (**www.indo.com/distance**) to obtain the direct linear distance of each site from Lakehead University. This tool allows the user to enter two sets of co-ordinates (latitude and longitude) and the straight-line distance between the two points is calculated. I determined presence or absence of fish in each wetland through personal observations, communication with landowners or government personnel (Ontario Ministry of Natural Resources and Center for Northern Forest Ecosystem Research) and from relevant publications (Hartviksen & Momot, 1989; Stephenson & Momot, 1994; Momot & Stephenson, 1996). Due to the variability of available information, I chose to use presence or absence of fish as the variable. Prior to the study, hydroperiod was classified as temporary, semi-permanent or permanent for each wetland.

I measured the other physical variables of each wetland (area, perimeter, maximum depth and volume) in a numerous ways, depending on the site type. Areas and perimeters of permanent sites were calculated by scanning map images of each lake into a computer and using image analysis software (Sigma Scan Pro, version 5). For temporary and semi-permanent sites, I used a compass and an optical range finder to hand-draw maps and then scanned these drawings into the computer using the same methods listed above. I measured the maximum depths of the temporary sites using a meter stick. In semi-permanent sites I used a weight attached to a marked rope to sound the depth from an inflatable boat. At permanent sites, I used an Eagle Portable 120 fish finder mounted on a canoe to determine maximum depth. I calculated wetland volume by the formula: V=0.467*(max depth)*(area) (Wetzel, 2001).

Each of the variables pertaining to the area surrounding a wetland was measured within an area encompassing 2 km from the site's perimeter. I chose this distance to ensure that all of the landscape that would potentially be encountered by an individual amphibian in its normal annual movements was included. Most frogs and toads do not travel >1km from their natal wetland (Sinsch, 1990), so doubling this distance should include even the most exceptional migrations. Each of these variables (except the percentage of forest cover) were standardized to a measurement per km^2 and were obtained from topographic maps (NAD 27; 1: 50,000) of the study area.

To measure spatial heterogeneity, percent forest cover, number of wetlands, and length (km) of rivers and streams, paved roads, unpaved roads, and total km of all road surrounding each wetland, I used grid-lined transparency sheet overlays and a mechanical curvimeter. The temporary and semi-permanent wetlands are small enough that I was able to draw a circle of appropriate radius (4 cm which represents 2 km) on the overlay with an individual site at the center. For permanent sites, I traced each lake using a compass set at 4 cm (representing 2 km), to obtain an area representing the wetland itself plus 2 km from any point on its perimeter (Figure 2.1).

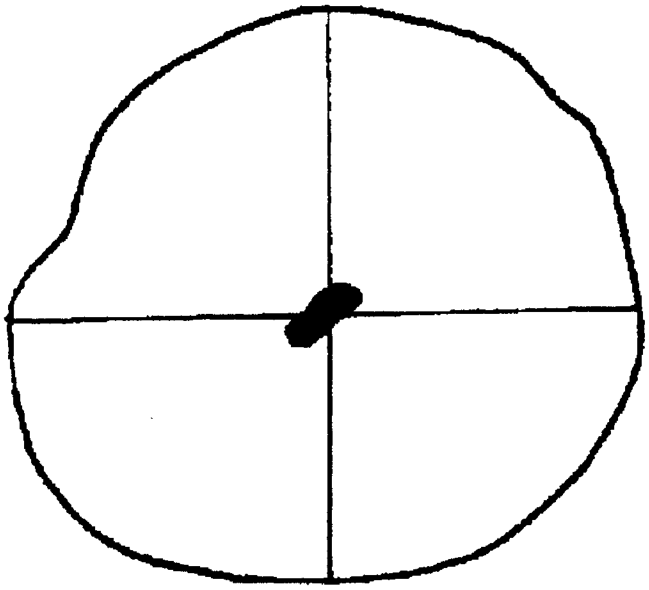

Figure 2.1. An illustration representing the methods used to calculate the landscape scale variables examined in this chapter. The shaded region represents the area of the wetland and the outer line is the perimeter of the area encompassing a two kilometer distance from the wetland's edge. The unshaded region in between represents the area in which I measured variables. The perpendicular lines were used as axes to determine the spatial heterogeneity of the landscape.

I determined spatial heterogeneity of the surrounding landscape of each wetland by quantifying the changes in elevation. I did this by overlaying a transparency having a pair of perpendicular lines centered on the target site. I rotated this transparency until one of the lines crossed a maximum number of contour lines. I recorded this number within the 2 km area and then counted the number of contour lines that crossed the perpendicular line. I used the total number of contour lines crossed by the two perpendicular transects as a measure of the spatial heterogeneity of the landscape (Figure 2.1). A relatively large number indicates a very heterogeneous landscape, while a smaller number reflects relatively flat terrain. I used the sum of the two transects rather than an average because it has a larger range of values.

To determine percent forest cover within 2 km of the perimeter of each site I counted the number of squares (on the grid-lined transparency) within the area of interest that indicated forested area (green shading on map). I then used the total area of these squares to calculate percentage. For the total number of other wetlands within the same area, I simply counted the number of wetlands (not including rivers and streams) present on the map within the appropriate area. The total kilometers of rivers/streams, paved roads and unpaved roads were each measured by tracing the mechanical curvimeter over the lines representing each of the respective variables that are within the area of interest. For total kilometers of roads, I summed the respective measurements of paved and unpaved roads in the same area around each wetland.

STATISTICAL METHODS

The area, maximum depth, perimeter and volume of wetlands were highly correlated with one another so I used only maximum depth and perimeter in the analyses. I used stepwise multiple regression analysis to determine potential relationships between amphibian species richness and the remaining 13 variables listed above. I used the default p-value of 0.15 for entry and removal of a variable to/from the model. It is recommended to use p-values slightly higher than the traditional 0.05 to ensure that all variables with coefficients different from zero are included in the model (Tabachnick and Fidell, 1996). After running both the forward and backward stepwise regressions, I chose the significant ($p < 0.15$) variables and ran a final multiple regression using only these variables. This method provided me with a parsimonious model having reasonable explanatory power. It is this parsimonious, "best fitting" model that I report on in the results and discussion.

I followed the same methods as listed above and used stepwise logistic regression analyses to determine potential relationships between the presence or absence of each individual amphibian species and the same 13 variables.

I also produced complete (non-stepwise) models for species richness (multiple regression), and each species individually (logistic regression) which included all 13 variables in each model.

To simplify the analyses, I used combined (2001 and 2002) species richness and incidence data because the same qualitative results were obtained for 2001, 2002, and both years combined for all analyses reported in Chapter 1.

All statistical analyses were performed using Systat, (version 9).

Results

SPECIES RICHNESS

I observed 11 of 13 species that potentially occur in the study area (Table I; Figure 1.2).

Basic statistics for independent variables I used are reported in Table 2.1. There were 31 wetlands in each hydroperiod category (temporary, semi-permanent and permanent) and a total of 52 of these wetlands had fish present in them, while 41 did not.

Table 2.1. Thirteen non-categorical independent variables examined in this study.

Variable*	Mean ± SE	Range
Area	9.4 ± 2.45 ha	$3.0\text{X}10^{-4}$ – 127.0 ha
Maximum depth	3.5 ± 0.54 m	0.2 – 26.9 m
Perimeter	1.0 ± 0.17 km	0.02 – 7.4 km
Volume	$4.2\text{X}10^5 \pm 1.75\text{X}10^5$ m^3	0.28 – $1.42\text{X}10^7$ m^3
Elevation	1053.8 ± 33.91 ft	600 – 1700 ft
Distance from city	27.4 ± 2.14 km	1.0 – 90.0 km
Spatial heterogeneity	24.1 ± 1.11	8.0 – 58.0
% Forest cover	72.5 ± 2.43 %	15.4 – 99.6 %
Wetlands	8.1 ± 0.64	0.0 – 35.0
Rivers	6.9 ± 0.36 km	0.0 – 16.0 km
Paved Roads	3.9 ± 0.54 km	0.0 – 40.0 km
Unpaved Roads	6.5 ± 0.34 km	0.0 – 13.0 km
Total Roads	10.3 ± 0.54 km	0.0 – 40.0 km

*Detailed information regarding each variable, including how it was calculated can be found in the Methods section of this chapter.

The results of the full regression models for species richness and each species individually are in Tables A3 and A4 (Appendix 2), respectively.

The final multiple regression model measuring amphibian species richness against 13 wetland variables contained five variables. The model indicated positive relationships between amphibian species richness and fish presence, unpaved roads and maximum wetland depth. Species richness was also negatively associated with total roads and landscape heterogeneity (Table 2.2).

Table 2.2. Detailed results of the final multiple regression model, including the variables retained and their respective coefficient, tolerance, t- and p-values. Final model $F = 5.91$, $p = 0.0001$, $R^2 = 0.21$.

Variable	Coefficient	Tolerance	t-value	p-value
Constant	6.286	n/a	6.883	<0.001
Fish	0.550	0.570	1.528	0.130
Unpaved roads	0.918	0.836	1.545	0.126
Total roads	-4.696	0.709	-2.733	0.008
Maximum depth	0.888	0.525	2.472	0.015
Landscape heterogeneity	-0.408	0.709	-2.764	0.007

SPECIES ACCOUNTS

Significant logistic regression models were derived for 10 of 11 species and Rho^2 values ranged from 0.224 to 0.999 (Table 2.3). However, nearly ubiquitous and rare species have disproportionate presence:absence ratios. The models for *Pseudacris crucifer*, *Rana pipiens*, *Notophthalmus viridescens*, *Ambystoma laterale* and *Ambystoma maculatum* are not worth discussing and I excluded them.

The final logistic regression model for *Pseudacris maculata* indicated a positive association with semi-permanent wetlands and negative associations with fish presence and landscape heterogeneity (Table 2.3).

Negative effects on *Hyla versicolor* 's presence were indicated for permanent wetlands, paved and unpaved roads, percentage of forest cover, landscape heterogeneity and the presence of fish. Positive effects of total roads, wetland perimeter, maximum depth, and the distance from an urban area were also observed (Table 2.3).

The final model for *Rana clamitans* contained five variables. Elevation, fish presence, total roads and perimeter of wetlands all had positive associations with the presence of *R. clamitans*, while landscape heterogeneity had a negative association (Table 2.3).

The presence of *Rana septentrionalis* was positively associated with permanent and semi-permanent wetlands, fish presence, other wetlands on the landscape, and rivers and streams (Table 2.3).

A total of four variables were included in the final model for *Rana sylvatica*. Its presence was positively associated with semi-permanent wetlands and negatively associated with elevation, rivers and streams and total roads (Table 2.3).

The final model for *Bufo americanus* revealed a positive association with semi-permanent wetlands and wetland perimeter, and negative associations with elevation and paved roads (Table 2.3).

Table 2.3. Detailed information (by species) regarding the variables included in the final logistic regression models. Note that for the categorical variables (Hydroperiod, Fish) that P, S and T denote Permanent, Semi-permanent or Temporary wetlands and Fish refers to fish presence. The number of presences/absences and full model statistics are also included for each species.

Species	Variable*	Estimate	t-ratio	p-value
P. maculata	Constant	6.734	3.595	<0.001
42/51	Hydroperiod (S)	3.091	2.769	0.006
	Fish	-1.880	-1.894	0.058
	Landscape heterogeneity	-1.903	-4.04	<0.001
	Full model	**Rho^2 = 0.563**		**<0.001**
H. versicolor	Constant	-17.145	-1.253	0.210
25/68	Hydroperiod (P)	-52.676	-2.517	0.012
	Paved roads	-76.757	-1.99	0.047
	Unpaved roads	-76.483	-1.926	0.054
	Total roads	253.254	1.832	0.067
	% Forest Cover	-0.001	-1.725	0.085
	Perimeter	14.082	2.389	0.017
	Maximum depth	15.340	2.479	0.013
	Distance from city	10.562	2.529	0.011
	Landscape heterogeneity	-5.563	-2.168	0.030
	Fish	-5.907	-2.113	0.035
	Full model	**Rho^2 = 0.806**		**<0.001**
R. clamitans	Constant	-8.386	-2.358	0.018
34/59	Elevation	0.013	3.347	0.001
	Fish	7.296	2.927	0.003
	Total roads	8.556	1.883	0.060
	Perimeter	2.418	2.227	0.026
	Landscape heterogeneity	-1.077	-1.774	0.076
	Full model	**Rho^2 = 0.798**		**<0.001**
R. septentrionalis	Constant	-4.961	-3.150	0.002
29/64	Hydroperiod (S)	3.220	2.742	0.006
	Fish	1.508	1.919	0.055
	Wetlands	3.852	1.453	0.146
	Rivers/Streams	10.406	2.426	0.015
	Full model	**Rho^2 = 0.316**		**<0.001**
R. sylvatica	Constant	10.301	2.810	0.005
80/13	Elevation	-0.004	-1.944	0.052
	Rivers/Streams	-11.674	-2.090	0.037
	Total roads	-8.527	-1.455	0.146
	Hydroperiod (S)	1.946	1.518	0.129
	Full model	**Rho^2 = 0.224**		**0.005**
B. americanus	Constant	9.241	2.705	0.007
73/20	Hydroperiod (S)	4.157	2.468	0.014
	Elevation	-0.005	-1.572	0.116
	Paved roads	-2.609	-1.910	0.056
	Perimeter	4.220	2.738	0.006
	Full model	**Rho^2 = 0.454**		**<0.001**

*Detailed information regarding each variable, including how it was calculated can be found in the Methods section of this chapter.

Discussion

SPECIES RICHNESS

The positive relationship between amphibian species richness and fish presence is a weak but reasonable one. Although they are not highly correlated, fish presence is likely associated with the maximum depth and permanence of a wetland. A strong positive association is indicated between amphibian species richness and maximum depth and this could be the reason for the weak relationship between amphibian species richness and fish presence. The positive association with maximum depth is likely due to the fact that numerous species would benefit from a wetland with a greater maximum depth. Species such as *R. clamitans*, *R. pipiens* and *R. septentrionalis* require deeper bodies of water for hibernation, and over-wintering larvae (except *R. pipiens*). In addition, other species may find these deeper wetlands suitable for breeding even though the depth is not required. This means that a deeper, more permanent wetland is suitable to a greater number of species and therefore higher species richness is expected at these sites.

The patterns of amphibian species richness being positively associated with unpaved roads but negatively associated with the total km of paved and unpaved roads combined seems contradictory. First of all, the positive relationship observed was not a very strong one, ($p = 0.126$) and also, unpaved roads likely have much less traffic on them and are a much smaller threat in terms of mortality from roadkill. Borrow pits or ditches associated with unpaved roads may actually create suitable breeding habitat or facilitate amphibian movements from one wetland to another or from one habitat type to another (Reh & Seitz, 1990; deMaynadier & Hunter, 1995). Roads also fragment the landscape, creating greater habitat heterogeneity. Both of these factors may increase the species richness at a wetland. It is a bit easier to understand why amphibian species richness is negatively associated with total roads on the landscape. In addition to the increased risk of traffic mortality with increasing roads (Fahrig et al., 1995; Carr & Fahrig, 2001), it is also likely that although some fragmentation of the landscape by roads can be beneficial, too much will have the opposite effect, lowering amphibian species richness and abundance as Findlay, Lenton and Zheng (2001) discovered. In addition to increasing habitat fragmentation, roads also divide populations of organisms into smaller subpopulations and block wildlife corridors (Reh & Seitz, 1990; Forman & Deblinger, 2000; Semlitsch, 2000) and both of these effects will act negatively on amphibian species.

It would be expected that if amphibian species richness were affected by landscape heterogeneity, the effect would be positive, as observed in other studies (Atauri & de Lucio, 2001; Kretzer and Cully, 2001). However the multiple regression model that I produced suggests that amphibian species richness decreases with increasing landscape heterogeneity. This may be due to the method I used to determine landscape heterogeneity. Recall that I used a measure of the changes in elevation around each wetland to come up with an index of landscape heterogeneity. A greater number of changes in elevation should reflect a greater number of habitats and may be associated with higher amphibian species richness. However, a high number of contour lines might also reflect a mountain or some other landscape feature that is unfavourable to amphibian species. A low number of contour lines may also indicate low areas where wetlands occur. I suspect that this is the reason for the negative association that I observed.

SPECIES ACCOUNTS

The logistic regression models I produced for each species are interesting and should be quite useful in helping to explain amphibian species distributions in Northwestern Ontario. These models may have some predictive power, but they will be better used to indicate which properties of wetlands and the surrounding landscape are important to the distribution of amphibians. Most models had high McFadden's Rho squared values (Table 2.3) indicating that much of the variance in the presence and absence of each species was being explained by only a few variables. My goal was not necessarily to come up with predictive models but more to suggest variables that may be important in the distribution of amphibian species in the study area

It is somewhat puzzling that *Pseudacris maculata* was positively associated with semi-permanent wetlands since it is often classified as a typical 'temporary' wetland species, often associated with breeding in shallow, temporary wetlands (Collins & Wilbur, 1979; Conant & Collins, 1998; Hecnar & Hecnar, 1999). This makes more sense when you consider that it is also negatively associated with fish presence (Hecnar & M'Closkey, 1997). As I've stated in Chapter 1, one theory as to why amphibians may prefer semi-permanent sites is to avoid the stresses of desiccation in temporary wetlands and fish predation in permanent ones. When you take that into consideration, a fishless, semi-permanent wetland is ideal habitat for a 'temporary' species like *P. maculata*. This species is also one that breeds in wetlands, but then moves to meadows and woodlands for the summer (Conant & Collins, 1998; MacCulloch, 2002). It is negatively associated with landscape heterogeneity and this may be because of its movement habits. Even small changes in elevation may impose significant barriers to dispersal for such a small-bodied frog.

Hyla versicolor had by far the most complex model of the 11 species that I studied. Ten of the 13 variables I examined were retained in the final model, all were significant (some marginally) (Table 2.3) and the model had a high McFadden's Rho value (0.806) (Table 2.3). It is negatively associated with both permanent wetlands and fish presence. This makes sense considering that its larvae are palatable to fish (Kats, Petranka & Sih, 1988); they have been demonstrated to decline in the presence of predatory fish (Smith et al., 1999) and all but one permanent site had fish present in them. It is also positively associated with wetland perimeter and maximum depth. This is also probably related to their susceptibility to predation. Although their larvae are susceptible to fish, these species do breed in both temporary and permanent waters (Collins & Wilbur, 1979; Kats, Petranka & Sih, 1988). A deeper wetland with more shoreline is likely to have a higher number of shallow areas that act as refuges from fish predators. The gray treefrog's presence is also negatively associated with forest cover. Although this opposes what you might expect, consider that these frogs prefer to breed in ponds with overhanging shrubs and other similar vegetation and also forage in relatively small trees and shrubs (Conant & Collins, 1998; MacCulloch, 2002). This type of wetland habitat isn't necessarily surrounded by forest. Also, forest cover isn't likely a limiting factor for amphibian distributions in my study region as the mean percentage of forest cover around a wetland is relatively high at 72.5 ± 2.44%. This species was also the only one that was positively associated with the distance from the City of Thunder Bay. However, I am not convinced that this is due to effects of urbanization, but rather it is an effect of the species distribution. The known range of *H. versicolor* is just to the west and south of Thunder Bay, Ontario (Conant & Collins, 1998; MacCulloch, 2002). It appears to be slowly moving into the area from both directions (S. J. Hecnar, personal communication). If it is in fact converging on Thunder Bay from the west and south, you would expect this species to occur at a higher proportion of wetlands further from the city. *H. versicolor* is another species that uses wetlands for breeding purposes but moves into the surrounding landscape to spend the summer and overwinter (Conant & Collins, 1998; MacCulloch, 2002). As with *P. maculata*, this may explain the negative association with landscape heterogeneity that the model predicts. A relatively flat landscape may make movements easier for these frogs. The most contradictory part of this model is that *H. versicolor* was negatively associated with both paved and unpaved roads separately, but its presence was positively associated with total roads. It is easy to explain why a higher amount of roads (paved or unpaved) can have a negative effect on the presence of this species, as I discussed in the introduction. However, it is confusing that this negative association is reversed when the paved and unpaved roads are summed. I suspect that roads can have both positive and negative effects on this species, depending on their density. Negative effects on the gray treefrog are seen at lower road densities through roadkills. However, another thing that we know about roads is that they fragment the landscape and create edge habitats. These types of habitats may be associated with less forest cover and an increased number of wetlands with shrubs around them. Gray treefrogs are often associated with borrow pits and ditches that result from road construction (McAlpine et al., 1991). Perhaps roads have a negative impact on *H. versicolor* until a certain density is reached and then the benefits of the habitat fragmentation outweigh the negatives of mortality through roadkill and a net positive effect is observed.

It is not surprising that *R. clamitans* had positive associations with fish presence and wetland perimeter. Green frogs are considered to be 'permanent' water species as the adults are highly aquatic and the larvae require an entire year to metamorphose (Collins & Wilbur, 1979; MacCulloch, 2002). I did not observe green frogs in any temporary wetlands. In addition, the larvae of these frogs are rather unpalatable (Kats, Petranka & Sih, 1988) and therefore they can coexist with predatory fish, thus avoiding competition with other amphibians that do not have any anti-predator defenses. Permanent wetlands are usually larger and deeper and therefore also have longer perimeters. Male green frogs are also quite territorial during the breeding season (Brode, 1959; Jenssen &

Preston, 1968) and the juveniles will travel long distances after metamorphosis searching for new habitats (MacCulloch, 2002). This may explain the green frog's negative association with elevation. A wetland at a lower elevation is likely to have a higher number of other wetlands nearby making the travel by juveniles easier. This may also be the reason for a positive association with total roads, contrary to what is expected. Although vagile species are more susceptible to road mortality (Carr & Fahrig, 2001) it is also possible that roads can make migrations between wetlands easier and more direct. As I've mentioned for other species, the ability to move easily between wetlands may also be the reason that *R. clamitans* is negatively associated with higher landscape heterogeneity.

It seems contradictory that R. *septentrionalis* was positively associated with both semi-permanent wetlands and fish presence. The mink frog cannot breed in temporary wetlands, as the larvae do not metamorphose until the summer following hatching and the adults hibernate in the same wetland (MacCulloch, 2002). It is typically found in ponds and lakes (Conant and Collins, 1998). As I discussed in Chapter 1, theory states that amphibian species may prefer semi-permanent wetlands to permanent ones to avoid predation by fish. This apparent contradiction may be explained by the fact that this species is found in over half of the semi-permanent wetlands that I examined (Figure 1.3) and many of these wetlands also contained fish. Therefore *R. septentrionalis* may be positively associated with fish, due to a common necessity for a reasonably permanent water body to inhabit but they may prefer semi-permanent wetlands to permanent ones to avoid predatory fish. However, mink frogs do produce a disagreeable odour, which may act as a predator deterrent, thus allowing them to coexist with predatory fish (Duellman & Trueb, 1986). The reason for the positive relationship between the mink frog and both the number of other wetlands on the landscape and the amount of rivers and streams is easy to explain. Mink frogs are one of the most aquatic frog species and a high density of water bodies in the landscape would aid in dispersal.

Although the final logistic regression model and individual variables for *R. sylvatica* were significant, the McFadden's Rho squared value was only 0.224 (Table 2.3). This suggests that much variation in wood frog presence and absence was not explained. The associations that do exist are easy to understand. As with other species that move from their breeding wetlands to other parts of the landscape for the summer, *R. sylvatica* is negatively associated with elevation. Similar to other amphibians, they need to stay moist even though they forage away from water on the forest floor (Conant & Collins, 1998; MacCulloch, 2002) so it makes sense that this species would breed in wetlands of lower elevation. The negative association between wood frogs and total roads on the landscape is also easily understood. Because they do not remain at the breeding site, there is a much greater potential for mortality on roads. Since wood frogs wander into forested uplands for summer foraging, it is not surprising that they are negatively associated with rivers and streams on the landscape. This species was positively associated with semi-permanent wetlands but it was also quite common in both temporary and permanent wetlands (Figure 1.3).

Contrary to findings of Hopey & Petranka (1994), there is nothing in this model to suggest a negative association between wood frogs and fish presence.

B. americanus is another 'temporary wetland' species (like *R. sylvatica* and *P. maculata*) that is positively associated with semi-permanent wetlands. However, like the wood frog, the American toad is also quite common in both temporary and permanent wetlands (Figure 1.3). It is also a species that breeds in wetlands but uses the terrestrial landscape extensively when not breeding (MacCulloch, 2002). As with other species, this explains its negative associations with elevation and paved roads. It is also positively correlated with perimeter, likely because it lays its eggs in shallow water possibly because these areas are inaccessible to predatory fish and are also warmer which speeds growth (Holomuzki, 1995). This aggregation behaviour may also be an act of predator avoidance (Brodie & Formanowicz, 1987). The unpalatable or toxic feature of toad eggs and larvae also explains their coexistence with predatory fish (Kruse & Stone, 1984; Hecnar & M'Closkey, 1997). Wetlands of larger perimeter should have more of this type of habitat available.

GENERAL PATTERNS

One common theme among all the models is that no amphibian species was associated solely with temporary wetlands. Although amphibian species are often classified as 'permanent' or 'temporary' (Leips, McManus & Travis, 2000; Snodgrass et al., 2000), the logistic regression results indicated that there are no true 'temporary' species in the species pool that I studied. Amphibians certainly had success breeding in temporary wetlands during the two years of my study, as I noted larvae and metamorphs at these sites in the latter part of both summers. In addition, certain species (i.e. *P. crucifer*, *R. sylvatica* and *B. americanus*) were much more common at temporary wetlands than other species and they are traditionally considered to be temporary species. However, they were just as common at wetlands closer to the permanent end of the hydrological gradient (Figure 1.3), which indicates no particular preference for temporary breeding sites.

The overall species richness as well as a number of individual species appear to be negatively impacted by roads (Table 2.3). In fact, seven of the eleven species (63.6%; including nearly ubiquitous and rare species) that I observed in the study region show negative associations with roads of some sort (paved, unpaved or total). Roads can have negative effects on the habits and movements of many species (Mader, 1984; Forman & Deblinger, 2000). The negative impact of roads through direct road kills and habitat fragmentation has been the subject of several amphibian studies in recent years (Fahrig et al., 1995; Ashley & Robinson, 1996; Carr & Fahrig, 2001; Hels & Buchwald, 2001). My models suggest that the amount of roads present on the landscape is something that should be considered when creating and/or protecting amphibian habitat. Although the models produced for rare species should be interpreted with great caution, three out of the four rare species in my study area were negatively associated with roads. Both *Ambystoma* species were negatively associated with total roads and a negative association was also observed between *R. pipiens* and paved roads. Declines of *R. pipiens* have been documented in recent years in many areas of North America (Roberts & Lewin, 1979; Clarkson & Rorabaugh, 1989; Arkinstall, 1994; Green, 1997; Kolozvary & Swihart, 1999). Historically, these species were more abundant in my study region (personal communications: S. Hecnar and local landowners). Therefore, although the species are quite rare and the models that I constructed are based on very few presences and many absences, this relationship is still important to notice. A possible link exists between the construction of roads and the declines of these species. Each of these species uses the terrestrial landscape extensively and would therefore encounter roads during their movements (Dole, 1965; Pope, Fahrig & Merriam, 2000; MacCulloch, 2002). Leopard frogs have even been observed foraging on a roadside (Wiggins, 1992).

Another interesting point is that neither species richness nor the presence of any individual species was positively associated with forest cover. This is contrary to the findings of other studies that link amphibian species richness and abundance with forest cover (Hecnar & M'Closkey, 1998; Guerry & Hunter, 2002; Russell, Guynn & Hanlin, 2002). Although initially puzzling, this result seems to make sense when considering the nature of the landscape in Northwestern Ontario. This area is a relatively 'pristine' environment and although the primary industry is forestry, much of the landscape is still forested. I agree with other studies that forest cover on the landscape is important for amphibian species. However, in Northwestern Ontario the forests are still plentiful and are therefore not playing a major role in how amphibian species are distributed. There may be a 'threshold effect' where incidence does not change until a minimum level of forest cover is reached before a precipitous decline. Gibbs (1998) found this type of 'threshold effect' for *R. sylvatica*, *A. maculatum* and *N. viridescens*, with critical percent forest cover values ranging from 30 - 50%.

Although Northwestern Ontario is largely forested, much of the area has been logged in the past and the current forest is relatively young. Salamander species in particular are sensitive to this type of change. Salamanders are less likely to be found in forested but recently cut areas than anurans (deMaynadier & Hunter, 1995) and are more often associated with old, natural forest stands due to the presence of coarse woody debris (deMaynadier & Hunter, 1995; Waldick, Freedman & Wassersug, 1999). This is a very plausible explanation for the notable lack of salamanders at most of my study sites.

Numerous species were positively associated with semi-permanent wetlands (Table 2.3). This agrees with the theory that I examined in Chapter 1, that amphibian species respond to the opposing stresses of desiccation and fish predation by preferring semi-permanent wetlands, where these two stresses are at a minimum. Although the final multiple regression model for amphibian species richness did not indicate any relationship (positive or negative) with hydroperiod, maximum depth was an important contributor to the model (Table 2.2). Increasing maximum depth parallels an increase in hydroperiod and the differences in amphibian species richness with hydroperiod are likely being reflected in maximum depth. These differences are not clear-cut, however and other factors are also contributing to the amphibian species richness of wetlands in Northwestern Ontario.

In summary, there appears to be much variation in the factors affecting the individual species distributions in Northwestern Ontario. There are not one or two variables having similar effects on all amphibian species in the region. This makes it difficult to choose suitable habitat or alter land use practices to conserve all amphibian species in the region. However, it does appear that roads may be having a negative impact on a high proportion of amphibian species in the study area, particularly those that are not as common as they once were. More research is needed to assess whether relationships exist between a decline in amphibian species distributions and the construction of roads. It seems that there may be a minimum amount of forest cover necessary to support amphibian species and in Northwestern Ontario forest levels are still higher than these critical values. However, forestry still has an effect on the amphibians in the region. This effect is reflected in the rarity of salamander species, likely due to a lack of coarse woody debris, which is an important microhabitat requirement for these species (deMaynadier and Hunter, 1995). The forest may be present in sufficient quantity, but the quality may not be what is required by all species.

It appears that no amphibian species, even those considered to be 'temporary' are positively associated with temporary wetlands. This is very important as it demonstrates that they are capable of breeding in more permanent bodies of water. In a time of global warming and drought conditions, it is reassuring to know that these species may not be severely affected by the loss of temporary wetland habitats.

CHAPTER 3: LAKES AS AMPHIBIAN HABITAT

Introduction

Understanding the distribution of organisms is a fundamental goal of ecology. Historically, early naturalists explained distribution in terms of minimum resource requirements (Liebig, 1840) or a range of tolerance along environmental gradients (Shelford, 1913). Water influences virtually every aspect of amphibian biology (Stebbins & Cohen, 1995). Not surprisingly, much attention in the amphibian literature has focused on hydroperiod (Pechmann et al., 1989; Semlitsch et al., 1996; Skelly, Werner & Cortwright, 1999; Pechmann et al., 2001). However, it can be argued that disproportionate attention has been given to the temporary end of the hydrological gradient. Amphibians are often viewed as being restricted or even eliminated from large permanent bodies of water by fish predation (Heyer, McDiarmid & Weigmann, 1975; Wilbur, 1984; Sexton & Phillips, 1986; Wellborn, Skelly & Werner, 1996; Hecnar & M'Closkey, 1997; Smith et al., 1999). For this reason, lakes are often overlooked in amphibian studies.

However, many amphibian species in Northwestern Ontario, even those considered 'temporary' pond species, use permanent water bodies to breed (Chapters 1 & 2). These observations offer hope that amphibian populations declining due to drought caused by climate change are not doomed. As I've demonstrated (Figure 1.3), many amphibian species are as common in permanent wetlands as they are in other less permanent water bodies, indicating that the influence of predatory fish may not be as important as originally thought, at least in lakes of Northwestern Ontario.

Amphibians demonstrate a number of different anti-predator adaptations. Many have cryptic colouration and behaviours to avoid detection (Duellman & Trueb, 1986). Nearly all amphibian species secrete toxic substances of varying strengths through their skin and many larvae are unpalatable or toxic (Duellman & Trueb, 1986; Stebbins & Cohen, 1985). Another defense, particularly for those that are less toxic and therefore more susceptible to predation, is the use of chemical cues to detect fish presence and subsequent increased use of refuges, where predators are unable to access their prey (Petranka, Kats & Sih, 1987; Holomuzki, 1989; Olson, 1989; Sih, Kats & Moore, 1992; Jackson & Semlitsch, 1993; Holomuzki, 1995; Walls, 1995). Although some species breed in temporary water bodies to avoid predation by fish, these species will also breed in water bodies that contain fish (Petranka, Kats & Sih, 1987). Larvae often aggregate in large groups providing a dilution effect against predation (Macan, 1966; Stebbins & Cohen, 1995). It also appears that larvae don't spend any less time feeding in favour of more time in refuge in the presence of a predator (Bridges, 2002). Although feeding as often as they would in absence of predators, amphibian larvae may suffer decreased fitness in a water body containing predators if they spend less time swimming and settle for a sub-par food patch or an environment of undesirable temperature (Bridges, 2002). Ideally, amphibian larvae will select microhabitats that offer both refuge from predators and the ability to forage for food, allowing them to forage both day and night to maximize their growth and development (Holomuzki, 1989). Adults of permanent species like *Rana clamitans* also behave differently in the presence of predatory fish. When disturbed on shore, green frogs jump into the water to escape, but if the threat of fish predation exists, they quickly swim back to shore (Macan, 1966; S. Hecnar, pers. comm.; personal observation). Lakes are often larger and structurally more complex than other water bodies. They provide different habitats, some of which are likely suitable for amphibians to use and avoid fish predation while still experiencing successful breeding and foraging opportunities.

Amphibian species richness values in predatory fish lakes may not be different from those in fishless lakes, because of a refuge effect. If this is true, then the lowest amphibian species richness would be in lakes that lack refuge habitat and contain predatory fish. Lakes with no predatory fish or refuge habitat and those without predatory fish but with refuge habitat may have approximately equal but higher species richness values.

Lakes have a number of properties not shared with wetlands closer to the temporary end of the hydrological gradient. Any potential benefit of refuge habitat on amphibian species is likely increased as the amount of this beneficial habitat increases. In addition, different amphibian species will have different microhabitat requirements and thus the number of different habitats surrounding a lake may also be important in determining the number of species found there. Local habitat heterogeneity has been positively linked with amphibian species richness (Burbrink, Phillips & Heske, 1998).

The intensity of potential human disturbance is another factor likely to affect the species richness of amphibians in a lake, as lakes are used by humans to a much larger extent than other less permanent wetlands. Many of the lakes I studied have cottages with private water access and shorelines that have been altered by the installation of docks or creation of beaches etc. Woodford and Meyer (2003) found that the abundance of *R. clamitans* declined with increased shoreline development by landowners.

My goal in this chapter was to assess the potential of lakes as suitable amphibian habitat. Specifically, I compared the amphibian species richness and incidence in lakes to other less permanent water bodies. I assessed the patterns of coexistence of predatory fish with amphibian species richness in the presence and absence of predatory fish. I also investigated amphibian species richness and distribution in relation to unique characteristics of lakes.

Methods

FIELD METHODS

In 2001, I made two night visits and two day visits to each lake (n = 31). In 2002, I increased the number of night visits to three and still made two day visits. I used the same methods for night visits as described earlier (General Methods), with one exception. Where possible on larger lakes, I would listen at two different places on the lake, to ensure that I was able to hear any amphibians that were calling from any point around the lake.

The methods I used during day surveys are slightly different for lakes than for less permanent water bodies. Because of their relatively large size, I used a canoe for surveys. Canoe surveys are an effective way to survey for amphibians (Jung et al., 2002). There were a large number of instances where I spotted a frog or toad sitting on a log or rock from the canoe that I may not have seen if I attempted to wade through the deep water. I waded and dipnetted through the submerged vegetation and shallow areas, using the 'traditional' methods whenever possible.

PREDATORY FISH

While searching for amphibians during day surveys, I identified fish species I observed (where possible) and always noted whether it was a predatory species. I did not use special methods to observe or capture fish; all observations were coincidental to the amphibian surveys. I used only my observations in further analyses rather than what is available in the literature (Hartviksen & Momot, 1989; Stephenson & Momot, 1994) and information that I obtained through both the Ontario Ministry of Natural Resources and Centre For Northern Ecosystem Research for two reasons. First, I was unable to obtain data from these sources for all 31 lakes and there are some inconsistencies between the sources that I examined (i.e. one source indicated the presence of a particular species while another did not). Second, the most recent literature source that is available was published in 1994, which is quite a bit earlier than the beginning of my study. Some studies from the OMNR were dated into the 1950's. It is quite probable that fish populations in these lakes may have changed considerably over this time period. My personal observations were of fish present during the same time period that I obtained the amphibian data.

While it is possible that there were predatory fish species present in some lakes that I did not observe during my surveys, they are likely in small enough numbers as not to affect the amphibian populations or do not forage in the shallow areas where the amphibians are most likely to be located. Table A2 (Appendix 1) contains all information I obtained regarding predatory fish in the lakes of interest.

HABITAT VARIABLES

During one of the two day visits in 2002, I used a GPS unit (Garmin eTrex Venture) to ‘map’ the entire perimeter of each lake as I paddled around it. When I encountered a significant change in the shoreline habitat I marked the location on the GPS unit. I also recorded a brief description of the habitat (i.e. rocky shoreline, sandy beach, forest to edge, shallows with abundant emergent vegetation), which enabled me to upload the points to a computer and use software to produce a map of each lake. From these maps I was able to calculate the length (and approximate area) of each habitat type and the number of different habitat types on each lake.

I also counted the number of areas of shoreline subject to human use and potential disturbance. These areas include cottages with private water access, public boat launches, as well as camping and swimming areas. The total number of these areas around a single lake represents the intensity of human use and potential disturbance.

STATISTICAL ANALYSES

I used combined species richness (2001 and 2002) data for analyses as I found the results in Chapter 1 to be qualitatively the same for 2001, 2002 and both years combined and also because the predatory fish data was combined over both years of the study to ensure a more accurate list.

I used ANOVA to determine differences between the amphibian species richness of lakes with and without predatory fish as well as lakes with and without refuge habitats. I also used ANOVA to determine differences in mean amphibian species richness values for lakes that have refuge habitat and no predatory fish, predatory fish and refuge habitat, no predatory fish or refuge habitat and predatory fish and no refuge habitat.

I used stepwise multiple regression analysis to determine the importance of local and landscape factors to amphibian species richness for lakes alone. I also produced a full (non-stepwise) model including all variables.

I used the same variables in these analyses as I did in Chapter 2 with the following exceptions: I did not include the hydroperiod variable as all wetlands in these analyses are permanent; and I used the presence or absence of predatory fish instead of the presence or absence of fish species in general. I also included variables representing the number of different habitats on the shoreline of each lake, the area of potentially suitable amphibian habitat on each lake (shallow bays with lots of emergent vegetation, floating vegetation mats, cattail mats; areas that typically have a lot of submerged vegetation and muddy bottoms, suitable for amphibians to hide from predators and forage for food), presence or absence of refuge habitat, and the number of cottages and other human accessed (and potentially disturbed) areas on the shoreline of each lake.

I was also interested in examining any link between amphibian species richness among sites of different hydroperiod in relation to precipitation between the two years of my study. I specifically wanted to know if amphibian species richness increased at semi-permanent and permanent wetlands during a drier year when temporary sites are not as plentiful. This would indicate that amphibian species may prefer to breed in temporary sites when available, but that they are capable of using other wetlands. To compare amphibian species richness between 2001 and 2002 in relation to precipitation, I used data from the Atmospheric Environment Service of Canada (2001 – 2002). I performed paired t-tests to determine if any significant difference existed between normal mean monthly precipitation values for Thunder Bay between 2001 and 2002. I also used paired t-tests to determine any differences between amphibian species richness in 2002 versus 2001, of the temporary, semi-permanent and permanent wetlands, respectively.

Results

Mean amphibian species richness of lakes was 4.3 ± 0.17 and each lake was unique in terms of its habitat, predatory fish and human use (Table 3.1).

Table 3.1. Some properties of 31 lakes examined in this study including species richness, presence of predatory fish and/or refuge habitat (P, R), the number of different habitats on the perimeter, the percentage of suitable amphibian habitat and the number of cottages and other human used areas.

Name	SR	Pred. Fish / Refuge	Habitats	% 'Good' Habitat	Human Use
Boulevard	4	R	9	6.7	3
Joeboy	5	P, R	5	4.8	1
Lizard	5	P	6	0	1
Pounsford	3	P, R	4	0.5	1
Rita	4	neither	2	0	0
Pass	3	P	5	0	1
Beaverkit	4	R	4	7.5	0
Cummins	6	P, R	6	4.5	32
Goodman	5	P, R	6	5.3	2
Greenpike	4	R	6	12	26
Howcum	3	P	3	0	5
Island	4	P	4	0	53
Lottit	6	R	6	2.7	16
Missing	4	P	4	0	3
Paul 1	3	P, R	4	19.4	8
Timmus	5	P, R	3	7.9	6
Unnamed 2	4	neither	1	0	0
Unnamed 3	5	P	5	0	0
Warnica	3	P	2	0	26
Whitelilly	5	R	6	47.4	2
Little Dog	3	R	8	0.9	3
Gravel	3	P	3	0	1
Jones	6	P, R	3	12.1	1
Mallard	6	P,R	3	37.2	1
Mudhole	4	R	4	16.5	1
Paul 2	4	R	2	44.5	2
Windy	4	P, R	4	2.7	1
East Divide	4	P, R	2	8.6	0
Mathe	5	P, R	5	31.5	0
Mud	5	P, R	5	9.4	0
Pistol	4	P, R	5	9.3	0

Amphibian species richness did not differ (F = 0.12, 1df, p = 0.728, R^2 = 0.004) between predatory fish lakes (4.3 ± 0.23, n = 21) and non predatory fish lakes (4.2 ± 0.25, n = 10) (Figure 3.1)

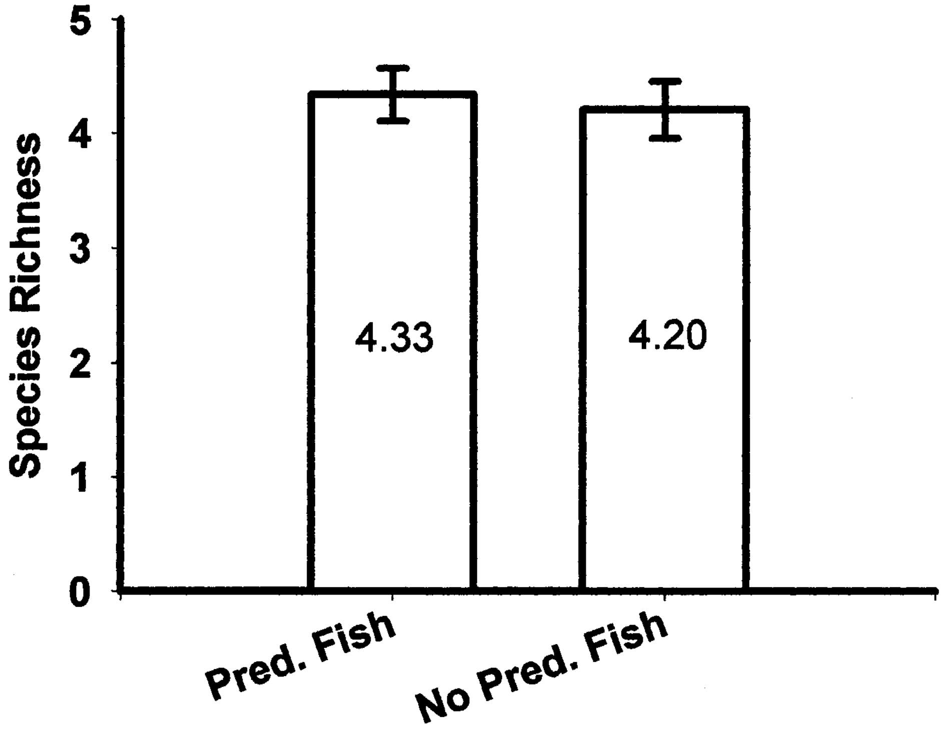

Figure 3.1. A comparison of mean amphibian species richness of lakes that contained predatory fish (n=21) and those that did not (n=10).

Species richness in lakes with refuge (4.5 ± 0.21, n = 21) was significantly (marginal) higher (F = 4.14, 1df, p = 0.051, R^2 = 0.13) than lakes without refuge habitat (3.8 ± 0.25, n = 10) (Figure 3.2).

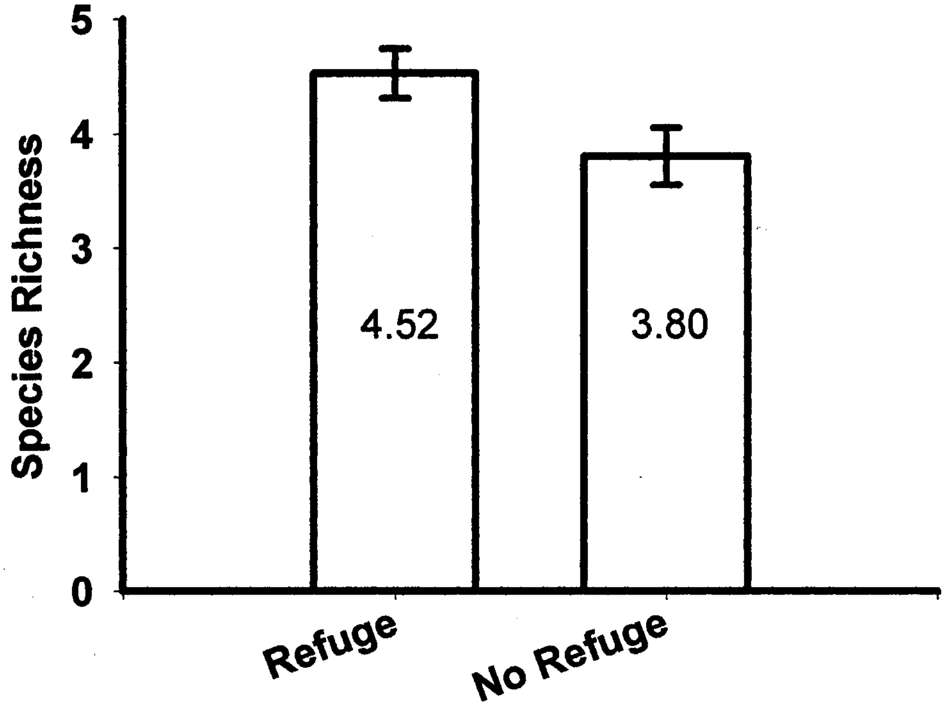

Figure 3.2. A comparison of mean amphibian species richness of lakes that had refuge habitats (n=21) and those that did not (n=10).

I found no significant difference ($F = 1.75$, 3 df, $p = 0.181$, $R^2 = 0.16$) between mean species richness of lakes that had refuge habitat and no predatory fish (n = 13), predatory fish and refuge habitat (n = 8), no predatory fish or refuge habitat (n = 8) and predatory fish and no refuge habitat (n = 2) (Figure 3.3).

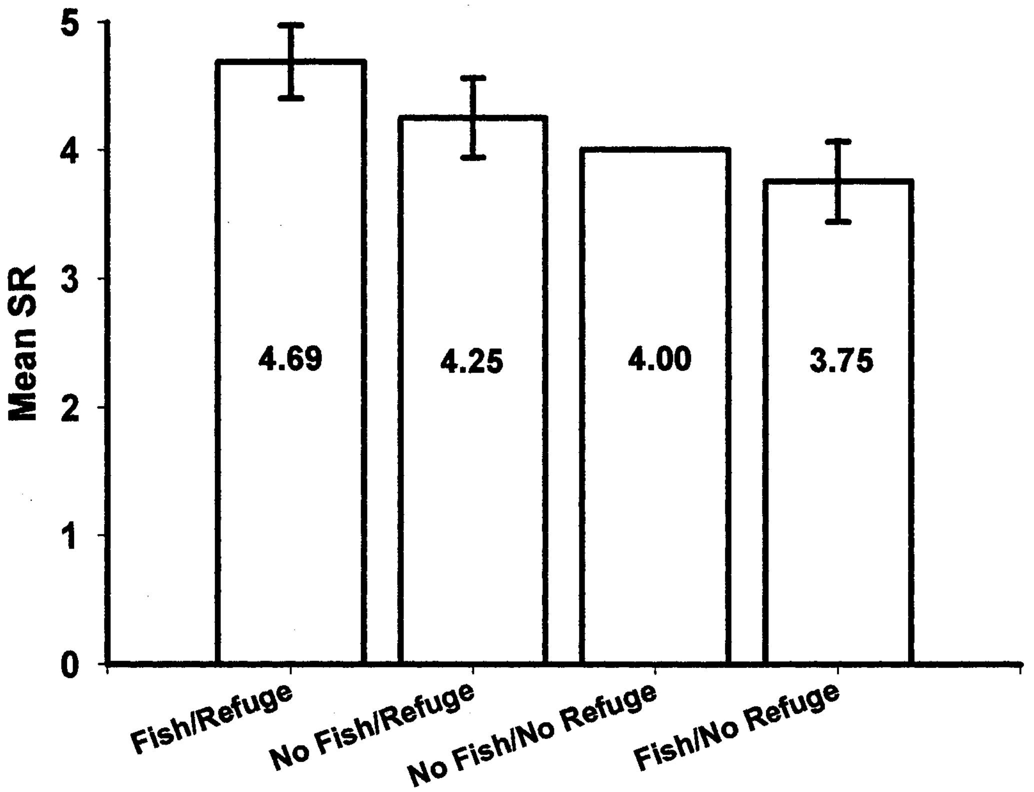

Figure 3.3. A comparison of mean amphibian species richness of lakes with predatory fish and refuge habitat (n = 13), no predatory fish and refuge habitat (n = 8), no predatory fish or refuge habitat (n = 8) and predatory fish and no refuge habitat (n = 2).

Stepwise multiple regression analyses between amphibian species richness and the local and landscape scale variables produced a significant model (F = 6.752, 5df, $p<0.001$, $R^2 = 0.49$). The model suggested positive associations between amphibian species richness and the number of habitats on the shoreline of a lake, the area of potentially suitable amphibian habitat, and elevation. Negative relationships between amphibian species richness and the total length of roads within two km of the perimeter of a lake, as well as the landscape heterogeneity in that same area were also suggested.

Table 3.2. Detailed results of the final stepwise multiple regression model, including the variables retained and their respective coefficient, tolerance, t- and p-values ($F = 6.75$, 5df, $p < 0.001$, $R^2 = 0.49$).

Variable	Coefficient	Tolerance	t-vaiue	p-value
Constant	0.826	n/a	7.53	<0.001
Number of habitats	0.022	0.661	2.45	0.022
Area of suitable habitat	0.017	0.854	2.33	0.028
Total Roads	-0.404	0.707	-2.16	0.041
Landscape heterogeneity	-0.081	0.788	-4.50	<0.001
Elevation	0.0001	0.644	2.78	0.010

The detailed results of a full regression model including all variables are in Table A5 (Appendix 2).

Mean monthly precipitation in 2001 (60.2 ± 12.30 mm) did not differ significantly ($t = 0.116$, 11df, $p = 0.91$) from normal mean monthly values (58.6 ± 6.49 mm) (Figure 3.4) but in 2002 the mean monthly precipitation (37.5 ± 6.73 mm) was significantly lower ($t = -4.56$, 11df, $p < 0.001$) than normal values (58.6 ± 6.49 mm) (Figure 3.5). Amphibian species richness of temporary wetlands in 2001 (2.9 ± 0.21) was significantly higher ($t = 4.69$, 30df, $p = < 0.001$) than in 2002 (1.8 ± 0.28). Mean species richness of the semi-permanent sites was significantly lower ($t = -2.34$, 30df, $p = 0.026$) in 2001 (4.4 ± 0.23) than it was in 2002 (4.8 ± 0.21). Mean species richness of permanent sites did not differ significantly ($t = 0.17$, 30df, $p = 0.865$) between 2001 (3.7 ± 0.16) and 2002 (3.74 ± 0.19).

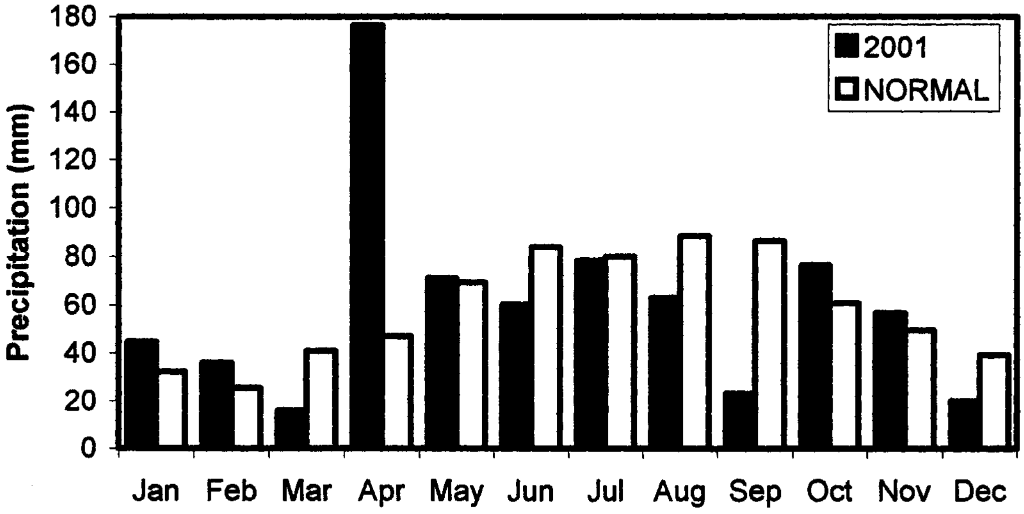

Figure 3.4. Total precipitation (mm) for the city of Thunder Bay in 2001, compared to normal values.

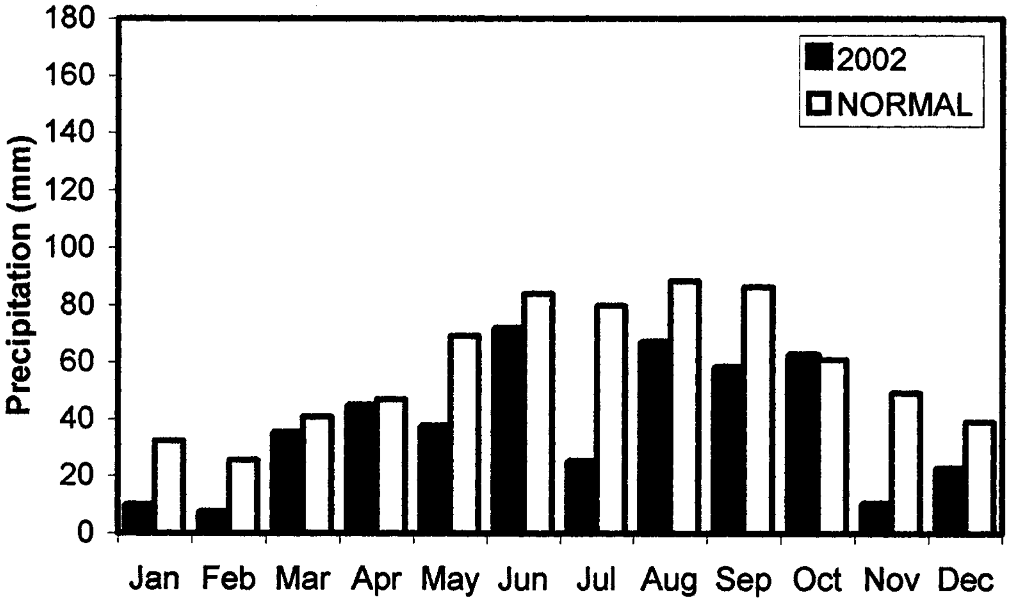

Figure 3.5. Total precipitation (mm) for the city of Thunder Bay in 2002, compared to normal values.

Discussion

A diverse fauna of nine amphibian species occurs in Northwestern Ontario lakes. Although many of these lakes contain predatory fish species, their spatial heterogeneity apparently allows amphibians to persist. Although permanent water bodies (lakes) did not have the greatest mean species richness, it was still higher than that of the temporary wetlands and nearly equal to the overall average (Chapter 1; Figure 1.4). This result alone suggests that lakes do provide suitable amphibian habitat.

However, species richness of permanent wetlands was still lower than in semi-permanent ones in my study area. The theorized reason for lower amphibian species richness in permanent wetlands is due to the presence of predatory fish. This may not be the case in my study sites as, surprisingly, there was no significant difference in mean amphibian species richness between lakes with or without predatory fish (Figure 3.1). The lack of a difference in species richness between these two groups suggests that predatory fish are not significantly affecting the amphibian species richness in these wetlands. It seems likely, that amphibian species in lakes are able to use habitats that allow them to escape predation from fish but still perform regular life functions such as foraging and breeding. Support for this idea is seen in Figure 3.2: amphibian species richness was higher (although only marginally significant) in lakes that have refuge habitats than in those that do not. The ten lakes without refuge habitat had on average, nearly one less species than the 21 that did not have refuge habitats. This is consistent with observations made in other studies; adult amphibians of some species may choose to oviposit in fish-free areas (Resetarits & Wilbur, 1989; Hopey & Petranka, 1994; Holomuzki, 1995) or that larval amphibians will quickly disappear from an area in which predatory fish are present (Sih, Kats & Moore, 1992). Although predatory fish may be present in some of these lakes, adult amphibians may perceive the risk to be smaller if refuge habitat is present. The availability of refuge habitat must come into play in the decision of a female's oviposition site, because most species of the regional pool are found in at least some lakes, even those containing predatory fish. Breeding adults may discriminate between sites where predation risk is high for their young and those where it is lower and the energy invested into laying eggs is well spent (Resetarits & Wilbur, 1989; Spieler & Linsenmair, 1997). However, the adults also need to consider the threat of desiccation (from breeding in temporary pools) and may choose shallow, inaccessible areas of permanent water bodies to oviposit (Holomuzki, 1995). In addition, larvae tend to change behaviour, increasing refuge use and decreasing mobility in the presence of predatory fish, which ensures their survival (Petranka, Kats & Sih, 1987). Contrary to what might be expected, amphibian species richness was actually highest in permanent wetlands that have both predatory fish and refuge habitats (Figure 3.3). Amphibian species richness in lakes that lack predatory fish is approximately equal (but lower than the first category), regardless of the availability of refuge habitat and it is lowest, as expected, in lakes that contain predatory fish and no refuge habitat. The results of an ANOVA between mean amphibian species richness of these four groups indicates no significant difference, however. I suspect that significant differences may be detected if the sample size was higher and a little more evenly distributed. There are only two lakes that contained predatory fish and lacked refuge habitat. Further research is needed to examine these possibilities.

It is also surprising that the lakes containing predatory fish and refuge habitat seem to have (although not significant) higher amphibian species richness than any of the other groups (Figure 3.3). Richter and Azous (1995), concur; they stated that predators do not exclude amphibian species from permanent wetlands and in fact may increase species richness in these sites through selective predation on amphibian species that are superior competitors. Species richness was also higher in lakes that have refuge habitat (Figure 3.2) regardless of the presence or absence of predatory fish. Perhaps this type of habitat benefits amphibians not only as a refuge from predatory fish but also in other ways, such as a greater food supply. There may be a "bottom up" effect being observed here, where shallow shoreline areas with abundant emergent vegetation offer ideal habitat not only for amphibians but aquatic insects, small fish, etc. as well. Predatory fish would benefit from this type of habitat due to an increased abundance and variety of food. A lake with this type of habitat is likely to be the most productive and have the ability to support a greater number of all species.

Species richness is lower in permanent wetlands than in semi-permanent ones (Figure 1.4). Theory suggests that predatory fish either prevent adult amphibians from using these water bodies or quickly remove those that are susceptible to predation. However, amphibian species richness was actually higher in lakes with predatory fish, providing that refuge habitat was available (Figure 3.2). What other features of these wetlands then, might be driving the pattern of lower species richness that we are observing? Multiple regression between amphibian species richness of these lakes and landscape-level and local-scale properties of these lakes helps to answer the question (Table 3.2). As I observed in Chapter 2 when comparing the species richness of all 93 wetlands to local and landscape variables, amphibian species richness in permanent wetlands was negatively affected by the total length of roads within two km of the lake's edge and the landscape heterogeneity in that same area. The negative impact of roads on amphibian species richness is clear and well-documented. When amphibians move in the landscape either to forage or to colonize another wetland, they are at an increasing risk to be killed on the road with increasing road and traffic density. It is also logical to assume that, as with species richness of all wetlands, amphibian species richness of lakes is negatively associated with landscape heterogeneity due to the way that I have measured it. Other authors have discovered that with increasing landscape heterogeneity comes increased habitat heterogeneity, which in turn benefits species richness (Atauri & de Lucio, 2001; Kretzer & Cully, 2001). However, my method for measuring the landscape heterogeneity (see Habitat Variable Determination in Methods; Chapter 2) may reflect features on the landscape such as mountains or large hills, which act as barriers to amphibian movements or as unsuitable habitat.

There was a positive association indicated between amphibian species richness and elevation. I suggest that permanent wetlands at higher elevations are likely to have more amphibian species present at them because of a lower availability of semi-permanent or temporary wetlands. It makes sense that at higher elevations or hilly regions, all water will collect at the lowest point, forming a lake. There is not likely to be as many ponds or ephemeral wetlands on this type of a landscape, as there might be on the flat forest floor in an area of lower elevation. The lack of other wetlands represents a kind of target effect, where amphibians in the region are forced to use permanent wetlands, thus increasing species richness at wetlands of higher elevation. It is also possible that this observation is being confounded by an urban gradient. Thunder Bay is at a relatively low elevation in comparison with the less disturbed areas surrounding it. However, no relationship was indicated between species richness and the distance from Thunder Bay (my measure of an urban gradient).

The multiple regression model also indicated that amphibian species richness was positively associated with two variables unique to lakes: the number of shoreline habitats and the area of suitable amphibian habitat. I suggest that this relationship is due to the species area effect, where species richness increases with area (Brown, 1995). A lake that has a greater area of suitable amphibian habitat should be able to support a greater number of amphibian species.

Lakes differ from smaller and less permanent water bodies in that they are large enough to have a number of different microhabitats, and theoretically offer habitat to a greater number of amphibian species. Positive relationships have been reported between amphibian species richness and habitat heterogeneity (Burbrink, Phillips & Heske, 1998). It is logical to infer that, since amphibian species differ in their life-history requirements, a greater number of habitats can support a greater number of species. Lakes are also more stable chemically and thermally than less permanent water bodies. However, their larger size makes them slower to warm in the spring, potentially delaying amphibian egg and larval development. Despite the tradeoff, one advantage to breeding in lakes is the lack of desiccation stress.

It is interesting to note that amphibian species richness in lakes did not appear to be affected (negatively or positively) by human use and/or disturbance of the lake. Multiple regression indicated no relationship between species richness and the number of human areas on a lake. Human disturbance and the habitat changes that come with it (in moderation) may actually sustain a greater number of amphibian species on lakes in Northwestern Ontario by providing a greater variety of habitat types (I did observe a positive association between amphibian species richness and the number of shoreline habitats). However, Woodford and Meyer (2003) noted that *Rana clamitans* abundance was lower in lakes with greater amounts of human-caused shoreline disturbance. Further research is needed to examine the relationship between shoreline disturbance, amphibian species richness and abundance in lakes.

From an applied perspective, lakes may serve a dual role. The conservation value for amphibians is clear, however people also use these areas for recreational activities such as canoeing, swimming, fishing and hiking. A great example of this sort of area is the Hazelwood Lake Conservation Area (48' 35"N, 89' 19W) near Thunder Bay, Ontario. This area is used extensively for all sorts of recreational activities and still appears to have a healthy amphibian population. I surveyed this lake over a week's time in July of 2000, while working as a field assistant for Dr. S. J. Hecnar. I observed a total of five amphibian species (*Bufo americanus*, *Pseudacris crucifer*, *Rana clamitans*, *Rana septentrionalis* and *Rana sylvatica*), despite the presence of predatory fish (Hartviksen and Momot, 1989) and numerous human activities in and around the lake. I observed adults, larvae and metamorphs of all five species, indicating a healthy amphibian population and demonstrating the potential for lakes as excellent amphibian habitat. If lakes provide suitable amphibian breeding habitat, it may appeal to decision-makers to conserve this type of 'multi-purpose' land, which can be used for anthropogenic reasons as well.

It appears then, that lakes in the Boreal/Great Lakes-St. Lawrence forest regions in Northwestern Ontario do offer suitable habitat for most amphibian species. Of the 11 species that I observed in the study region, all but the two ambystomatid species and *Pseudacris maculata* (boreal chorus frog) were observed breeding in the lakes with some frequency (Figure 1.3). My data suggested that only the chorus frog appears to prefer semi-permanent and temporary wetlands to permanent ones. I did, however, hear *Pseudacris maculata* calling at one lake (Missing Lake, June 06, 2001), indicating that it isn't impossible for them to breed in permanent wetland habitats. I also heard an intense chorus of these frogs in Dog Lake recently (July 2003) giving further support to the idea that they will breed in lakes, given the proper conditions. The two salamanders (blue spotted salamander and spotted salamander) occurred in such low numbers (Figure 1.2) that it is difficult to determine if they show preference on the hydrological gradient. Ambystomatid salamanders do breed in small lakes in the Algoma District (S. Hecnar, pers. comm.)

It is very important, from a conservation perspective, to understand that amphibian species can and will breed in permanent wetlands, and not just semi-permanent and ephemeral sites. Recent concerns over drought caused by climate change in the boreal forest (Schindler 1998) may also be evident in the Thunder Bay area. The amount and timing of precipitation can have important effects on water-dependent organisms such as amphibians. Amphibians in this region begin breeding in late April and therefore the amount of precipitation received before this time will go a long way to determining whether or not there are ephemeral water bodies available in which to breed. Because of this, the amount of precipitation received during the winter months is important to amphibians in my study area. First, it contributes a great deal to the filling of temporary and even semi-permanent wetlands in which many early breeding amphibians may prefer to breed. Second, some amphibian species hibernate on land under vegetation and rely on a blanket of snow for insulation purposes. Even species such as *Pseudacris crucifer* (spring peeper), *Pseudacris maculata* (boreal chorus frog), *Hyla versicolor* (gray treefrog) and *Rana sylvatica* (wood frog) that can tolerate temperatures below the freezing mark (Layne & Lee, 1995;

MacCulloch, 2002), will suffer mortality if temperatures drop too far below freezing for too long. The mean amount of precipitation per month for 2001 was slightly higher, but not significantly different from the normal (Figure 3.4). However, this may be due to much higher than normal precipitation in April, which was caused by two abnormally high precipitation events that month (Atmospheric Environment Service of Canada, 2001). However, this precipitation came at a good time, and there was a lot of water in temporary wetlands when the amphibians began breeding that year.

Conversely, the mean monthly precipitation for 2002 was significantly lower than the normal mean monthly precipitation (Figure 3.5). Precipitation was lower than normal in nearly every month (except October) including the crucial winter and early spring months. This observation was reflected in the fact that many temporary wetlands were either dry at the beginning of the 2002 field season or dried very quickly afterwards, preventing amphibian species from breeding or larvae from developing at those locations. Casual observations suggest that fewer amphibians breed in ephemeral habitats such as roadside ditches in drier years (S. Hecnar, pers. comm.)

As the lack of precipitation in 2002 resulted in less ephemeral wetlands for amphibians to breed in, I expected to see a decrease in the mean species richness of those sites and a corresponding increase in species richness values in the more permanent wetlands. There was in fact a significant decrease in amphibian species richness of temporary wetlands from 2001 to 2002. There was also a significant increase in the species richness of semi-permanent wetlands in the same time period. The mean species richness of the permanent sites was slightly higher at 3.74 ± 0.19, in 2002 than it was in 2001 (3.71 ± 0.16) but this difference is not significant. These observations are similar to a scenario that I proposed in Chapter 1. Recall that I proposed that wetlands closer to the permanent end of the hydrological gradient may act as sources, supplying species to other less permanent wetlands when conditions are right. This might in fact be what is being observed between the years 2001 and 2002. In 2001, when precipitation was greater and there were more ephemeral water bodies available, the species richness of semi-permanent wetlands was lower than in 2002 when a lack of precipitation forced amphibian species to shift into wetlands closer to the permanent end of the hydrological gradient. This shift is not dramatic, it is actually quite subtle, in fact the species richness of the lakes in my study region increased only slightly and not significantly. However, this is not a long-term study and I am only looking at the differences between two years. I suspect that if drought-like conditions continue or worsen that this pattern will become more pronounced. In Southwestern Ontario spring peepers have decreased use of temporary sites and increased use of semi-permanent sites over the past decade (S. Hecnar, unpublished data).

In summary, although amphibian species richness isn't as high in the permanent wetlands of Northwestern Ontario as it is in the semi-permanent ones, it appears that lakes provide suitable habitat for amphibians. Any negative effects of predatory fish on amphibian species richness at these sites appears to be offset by the presence of refuge habitat. Amphibian species richness values are actually highest in lakes containing both predatory fish and refuge habitat, suggesting that coexistence with predatory fish is possible and perhaps even beneficial to amphibians, providing that refuge habitat is present. Most species, even those considered ‘temporary’ are found in at least some lakes, indicating that given the proper conditions, lakes offer suitable habitat for all amphibian species in the regional pool. This is important, as lakes are likely more desirable as conservation areas given that the public can use lakes for recreational purposes while suitable amphibian breeding habitat is also available. In addition to the anthropogenic reasons for endorsing lakes as areas of amphibian conservation, there are environmental ones as well. Permanent water bodies are much more stable environments. They are also persistent, even during periods of drought when ephemeral wetlands are not. I believe that permanent water bodies are suitable amphibian habitat and, given the right conditions, can be effective as conservation areas.

GENERAL CONCLUSIONS

Through my research, I have demonstrated the relationship between wetland hydroperiod and the richness and incidence of amphibians in the Boreal/Great Lakes-St. Lawrence forest regions of Northwestern Ontario. Amphibian species richness does vary with hydroperiod, peaking in semi-permanent wetlands. However, contrary to theories of other authors, the species richness of permanent wetlands in my set of wetlands is higher than that of temporary ones. In addition, even those species that are considered 'temporary' are found in wetlands across the entire hydrological gradient. Some species do seem to prefer wetlands in specific hydroperiod categories. Despite this, nearly all species were observed at least once in permanent wetlands. This indicates the potential for lakes to be very suitable as amphibian habitat. The presence of predatory fish does not have the anticipated negative effects on amphibian species richness, either. I attribute this to the availability of refuge habitat in many lakes. Although amphibians can detect the presence of predators in a wetland and may choose to oviposit elsewhere, I propose that the presence of refuge habitat allows them to "have the best of both worlds". The main threats to amphibian larvae are thought to be desiccation and predation. In a permanent wetland, there is not a desiccation threat and if the effect of fish predation can be neutralized through refuge habitat, amphibian species would find this to be optimal breeding habitat. The fact that all amphibian species appear to be able to use permanent water bodies to breed is good news when considering conservation of these organisms. During a time of rising global temperatures, changing weather patterns and drought, it is reassuring to know that amphibian species are capable of using permanent water bodies in the absence of more ephemeral ones.

I also discovered that the hydrological gradient is only one environmental variable contributing to the richness and incidence of amphibian species in my study region. A multiple regression between amphibian species richness and 15 local and landscape-scale wetland properties doesn't even include wetland hydroperiod, although maximum depth is related to wetland permanence and was a significant contributor. Other major contributors to this model include the presence or absence of fish, landscape heterogeneity, and the amount of roads surrounding the wetland. In fact, the length of roads (paved, unpaved or total) has a negative impact on many of the species that occur in the study region. This indicates that the amount of roads in the landscape should be considered in any amphibian conservation efforts. It is also interesting to note that although many amphibian species are classified as either 'temporary' or 'permanent', I found the presence of no amphibian species to be positively associated with only temporary wetlands. This suggests that although some amphibians may prefer temporary wetlands, they are capable of using other more permanent ones as well.

In conclusion, wetland hydroperiod is an important factor in understanding amphibian species richness and distributions in Northwestern Ontario. Amphibian species are found in all hydroperiod categories and their species compositions do not differ as much in the study region as originally thought.

Other factors are also important, and must be considered when discussing amphibian conservation. Further study is necessary to determine precisely how important some of these variables, such as roads, really are. I propose that permanent wetlands such as small lakes should not be overlooked as potential amphibian conservation areas, given that the negative effects of predatory fish appear to be negated by the presence of refuge habitat and the anthropogenic benefits that these areas will also have.

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Appendix 1: Additional Wetland Information

Table A1. Characteristics of the 93 wetlands studied. Maximum depth measured in m, perimeter in km, area in ha and volume in m^3. Amphibian species richness values for each year (01 and 02) and both years combined (C) are also included.

Site	Hydroperiod	Latitude*	Longitude	Max.Depth	Perimeter	Area	Volume	SR01	SR02	SR C
Boulevard	P	4827.7	8912.0	3.70	5.800	54.4000	939978.00	3	2	4
Joeboy	P	4828.5	8843.5	2.00	3.670	74.0000	691160.00	4	4	5
Lizard	P	4829.0	8845.2	2.40	3.920	88.0000	986304.00	5	3	5
Pounsford	P	4829.8	8846.5	11.50	6.100	127.0000	6820535.00	3	3	3
Rita	P	4827.5	8844.2	2.40	1.130	16.2000	181570.00	4	3	4
Pass	P	4833.5	8844.0	22.90	2.300	22.9000	2448995.00	2	3	3
Beaverkit	P	4839.2	8921.4	4.10	1.540	4.2800	81949.00	4	4	4
Cummins	P	4840.2	8915.6	11.10	3.280	15.1500	785331.00	5	5	6
Goodman	P	4836.5	8918.1	7.80	1.310	6.2800	228755.00	4	5	5
Greenpike	P	4837.7	8917.1	4.00	2.600	16.1180	39975.00	4	4	4
Howcum	P	4840.0	8918.1	13.00	1.580	6.5800	399471.00	3	1	3
Island	P	4840.9	8922.8	26.90	7.400	113.3000	14233086.00	4	4	4
Lottit	P	4838.5	8916.5	8.50	5.700	28.0000	1111460.00	5	5	6
Missing	P	4843.1	8921.5	3.80	1.700	5.0600	89795.00	4	3	4
Paul1	P	4843.0	8922.3	11.40	2.190	11.4900	611705.00	3	3	3
Timmus	P	4840.4	8905.4	24.50	1.600	17.6000	2013704.00	3	5	5
U2	P	4843.7	8922.2	4.70	0.900	3.4000	74627.00	4	4	4
U3	P	4844.5	8922.6	3.60	0.900	3.4600	58170.00	5	3	5
Warnica	P	4839.4	8917.8	4.60	1.450	16.2000	348008.00	3	3	3
Whitelilly	P	4840.0	8905.3	4.30	4.400	42.1000	845410.00	5	5	5
Little Dog	P	4839.0	8936.0	8.00	7.000	91.8000	3429648.00	3	3	3
Gravel	P	4813.3	9008.2	6.50	0.750	2.4400	74066.00	3	3	3
Jones	P	4812.5	9026.6	5.50	2.000	21.1000	541953.00	4	6	6
Mallard2	P	4811.3	9007.7	20.40	1.000	4.9000	466813.00	5	4	6
Mudhole	P	4811.4	9025.8	0.90	1.240	8.1200	34128.00	3	4	4
Paul2	P	4809.6	9004.4	10.40	1.500	7.7000	373974.00	3	3	4
Windy	P	4812.4	9026.0	10.00	2.540	13.8900	648663.00	3	4	4
East Divide	P	4839.6	9019.8	6.00	0.960	2.5300	70891.00	2	4	4
Mathe	P	4838.6	9014.0	1.90	2.470	9.1900	81543.00	4	4	5
Mud	P	4839.0	9023.2	1.50	1.520	10.9300	76565.00	4	5	5
Pistol	P	4838.9	9013.0	3.50	2.210	11.1800	182737.00	4	4	4
A1	S	4841.0	8903.5	0.94	0.260	0.3060	1343.00	4	4	6
A4	S	4842.4	8908.3	1.77	0.220	0.2340	1934.00	4	4	5
A5	S	4836.7	8904.2	0.65	0.080	0.0250	76.00	4	7	7
AL5	S	4823.1	8958.2	1.90	0.165	0.1062	941.00	5	7	7
G2	S	4833.6	8917.3	1.52	0.220	0.2800	1961.00	3	4	4
N1	S	4814.6	8928.4	0.78	0.097	0.0656	238.83	3	3	3
N2	S	4816.8	8926.5	1.78	0.399	0.8284	6886.00	3	4	4
O3	S	4826.0	8934.0	0.75	0.175	0.1624	568.94	5	5	5
O4	S	4825.8	8933.0	3.56	0.180	0.1460	2427.00	6	6	6
O7	S	4828.4	8933.8	2.76	0.300	0.4700	6058.00	4	5	5
O8	S	4824.8	8934.2	1.40	0.520	1.6840	10984.00	5	4	6
O9	S	4827.7	8932.5	0.89	0.090	0.0450	187.00	3	5	5
O12	S	4827.4	8931.0	1.50	0.060	0.0210	147.00	3	5	5
P2	S	4818.2	8924.0	1.46	0.240	0.2586	1763.00	4	4	4
P5	S	4819.7	8925.1	2.53	0.110	0.0684	808.00	7	6	7
P6	S	4819.9	8924.9	4.56	0.170	0.1800	3833.00	6	7	7
P7	S	4818.5	8928.6	2.60	0.390	0.5122	6219.00	6	5	5
P8	S	4818.5	8928.7	3.00	0.157	0.1109	1553.68	5	3	5
P10	S	4818.7	8927.0	6.60	0.570	0.9700	29897.00	5	6	7
P18	S	4822.8	8934.7	1.37	0.950	3.6770	23525.00	5	7	8
P19	S	4823.5	8937.7	1.20	0.200	0.2010	1126.00	6	5	6
P21	S	4818.7	8931.0	2.44	0.147	0.1331	1516.61	4	5	5
S1	S	4831.5	8907.7	2.60	0.640	0.4840	5876.00	5	5	5
S2	S	4830.2	8909.7	1.90	0.390	0.7210	6397.00	4	4	4
S4	S	4832.5	8910.9	1.67	0.170	0.1540	1201.00	5	5	5

Site	Hydroperiod	Latitude*	Longitude	Max.Depth	Perimeter	Area	Volume	SR01	SR02	SR C
TB1	S	4826.0	8923.7	1.86	0.150	0.0980	851.00	4	4	4
TB 3	S	4830.2	8914.7	1.57	0.091	0.0603	441.81	5	5	5
TB6	S	4824.6	8918.7	0.69	0.140	0.0880	284.00	2	4	4
TB10	S	4824.8	8916.6	1.60	0.070	0.0270	202.00	1	3	3
TB12	S	4826.1	8919.7	1.45	0.696	2.2369	15147.00	4	4	4
TB14	S	4827.8	8922.5	1.41	0.140	0.1000	658.00	5	5	5
1	T	4812.2	8926.9	0.40	0.490	0.0710	133.00	4	3	4
2	T	4812.2	8927.4	0.62	0.090	0.0050	145.00	2	1	2
3	T	4812.4	8928.0	0.56	0.110	0.0050	131.00	2	0	2
4	T	4812.7	8928.1	1.00	0.220	0.0200	93.00	3	2	3
5	T	4813.7	8928.6	0.35	0.470	0.0710	116.00	3	2	3
6	T	4816.4	8928.8	0.20	0.020	0.0003	0.28	2	0	2
8	T	4818.4	8928.6	0.30	0.050	0.0040	5.60	0	0	0
9	T	4818.5	8929.7	0.25	0.090	0.0220	26.00	1	0	1
11	T	4818.9	8929.8	0.45	0.210	0.0170	36.00	2	3	3
12	T	4819.4	8929.8	0.80	0.108	0.0633	236.00	3	5	5
13	T	4819.6	8931.0	0.30	0.025	0.0022	3.00	2	0	2
14	T	4820.5	8934.7	1.20	0.112	0.0706	396.00	6	5	6
15	T	4820.7	8934.5	0.36	0.044	0.0094	16.00	2	3	3
16	T	4820.7	8934.0	0.60	0.103	0.0400	112.00	3	2	3
18	T	4820.3	8926.3	0.70	0.464	0.0649	212.00	5	4	6
19	T	4820.2	8922.7	0.25	0.146	0.0611	71.00	4	0	4
21	T	4823.6	8933.4	0.75	0.052	0.0132	46.00	4	3	4
22	T	4823.9	8932.2	0.45	0.098	0.0580	122.00	3	2	3
23	T	4825.0	8922.7	0.40	0.078	0.0321	60.00	4	2	4
25	T	4825.3	8925.9	0.40	0.060	0.1300	243.00	3	1	3
26	T	4826.0	8925.8	0.50	0.260	3.1300	7308.00	4	3	4
27	T	4826.3	8927.0	0.60	0.190	0.3100	869.00	3	3	3
28	T	4825.3	8927.1	0.40	0.094	0.0365	68.00	3	1	3
29	T	4824.8	8928.1	0.60	0.089	0.0452	127.00	3	3	3
31	T	4825.6	8929.6	0.45	0.072	0.0171	36.00	3	3	3
34	T	4826.3	8924.0	0.50	0.130	0.0650	152.00	3	3	3
35	T	4825.2	8923.9	0.65	0.082	0.0395	120.00	2	0	2
37	T	4826.5	8922.7	0.30	0.034	0.0629	88.00	3	0	3
39	T	4825.7	8917.7	0.55	0.091	0.0514	132.00	1	1	1
40	T	4826.3	8917.6	0.45	0.072	0.0295	62.00	3	1	3
41	T	4826.6	8917.8	0.70	0.053	0.0138	45.00	3	0	3

* Latitude and longitude format: 4827.7 = 48' 27.7"N; 8912.0 = 89' 12.0"W

Table A2. Presence of predatory fish groups in 31 lakes surveyed in 2001 and 2002.

Lake	Esox sp.	Micropterus sp.	Perca sp.	Stizostedion sp.	Salvelinus sp.	Coregonus sp.	Non-Pred.
Boulevard	2		2				2
Joeboy	1		1				2
Lizard	1,2,3		2				2
Pounsford		1,2,3,4	1,2,3	2,3,4			2
Rita							1,2
Pass	1,2,3,4	1,2,3	2,3	3	3		2,3,4
Beaverkit							
Cummins	1,2		2				2
Goodman	1						
Greenpike	2,3		2,3				2,3
Howcum	2		1,2				2
Island	1,2,3	1,2,3	2,3				2,3
Lottit	2		2				2
Missing	1,2					2	2
Paul1	1,2						2
Timmus			1,2,3		2		2,3
U2							1
U3	1						
Warnica	1,3		1				3
Whitelilly	2		2,3	2			2,3
Little Dog	3,4	2,3	2	1,2,3,4		2,4	2,3,4
Gravel	1						
Jones	1,2,3						2,3
Mallard2	2,3,4	1	1,2,3		2,4	2,4	2,3,4
Mudhole							1
Paul2					2,3,4		2,3,4
Windy	1						
East Divide	1,2	1,2					
Mathe	1,2		2				2
Mud	1		1				
Pistol	1,2		2				2

1 – personal observations

2 - Hartviksen, C. & W. T. Momot, 1989. Fishes of the Thunder Bay area of Ontario: A guide for identifying and locating the local fish fauna. Wildwood Press, Thunder Bay, Ontario.

3 – Ontario Ministy of Natural Resources (Steve Shulton)

4 – Centre for Northern Forest Ecosystem Research (Rob Mackereth)

APPENDIX 2: COMPLETE REGRESSION MODELS

Table A3. Detailed results of a multiple regression (full model) measuring amphibian species richness against 13 wetland variables.

Variable	Coefficient	Tolerance	t-value	p-value
Constant	5.36	n/a	3.50	<0.01
Hydroperiod	0.41	0.11	0.82	0.42
Elevation	<0.01	0.34	0.27	0.79
Fish	0.45	0.42	1.05	0.30
Wetlands	1.25	0.60	0.70	0.49
Rivers/streams	1.24	0.79	0.63	0.53
Paved roads	-0.34	0.13	-0.33	0.74
Unpaved roads	0.70	0.23	0.60	0.55
Total roads	-3.63	0.13	-0.88	0.38
% Forest cover	<-0.01	0.43	-1.33	0.19
Perimeter	-0.01	0.23	-0.03	0.98
Maximum Depth	0.54	0.22	0.96	0.34
Distance from city	-0.03	0.31	-0.20	0.84
Landscape heterogeneity	-0.36	0.51	-2.02	0.05
Overall Model		**R^2 = 0.16**	**F = 2.42**	**0.008**

Table A4. Results of logistic regression analyses (full models) (estimate/p-value) measuring amphibian species incidence against 13 wetland variables for species with relatively even presence/absence ratios.

Variable	*P. maculata*	*H. versicolor*	*R. clamitans*	*R. septentrionalis*	*R. sylvatica*	*B. americanus*
Constant	6.39 / 0.13	-18.63 / 0.44	-829.63 / 0.70	-0.53 / 0.86	16.55 / <0.01	12.87 / 0.04
Hydroperiod (P)	-3.41 / 0.28	-67.63 / 0.09	227.08 / 0.75	1.91 / 0.43	-1.28 / 0.68	-0.24 / 0.95
Hydroperiod (S)	2.31 / 0.16	1.23 / 0.72	107.60 / 0.78	3.34 / 0.03	1.63 / 0.38	4.67 / 0.07
Elevation	<0.01 / 0.43	0.01 / 0.46	0.41 / 0.67	<-0.01 / 0.35	<-0.01/ 0.16	<-0.01 / 0.26
Fish	1.91 / 0.11	4.71 / 0.07	-289.44 / 0.70	-1.12 / 0.24	0.57 / 0.67	0.24 / 0.85
Wetlands	-5.85 / 0.29	-7.47 / 0.60	92.90 / 0.93	7.86 / 0.06	-1.66 / 0.73	-2.88 / 0.56
Rivers/streams	3.96 / 0.45	-14.51 / 0.37	300.05 / 0.79	11.58 / 0.03	-11.40 / 0.11	-4.67 / 0.49
Paved roads	-0.90 / 0.81	-116.39 / 0.15	-255.34 / 0.86	-0.90 / 0.73	10.50 / 0.29	-5.23 / 0.15
Unpaved roads	0.94 / 0.81	-123.82 / 0.16	-400.49 / 0.82	1.30 / 0.64	13.56 / 0.22	-3.24 / 0.35
Total roads	0.98 / 0.95	405.07 / 0.18	1936.73/ 0.84	-5.36 / 0.57	-65.17 / 0.16	5.44 / 0.67
% forest cover	<0.01 / 0.92	<-0.01 / 0.08	0.01 / 0.87	<-0.01 / 0.55	<-0.01 / 0.36	<-0.01 / 0.80
Perimeter	0.25 / 0.86	17.74 / 0.09	-20.70 / 0.95	1.08 / 0.36	1.15 / 0.40	4.48 / 0.01
Maximum depth	1.71 / 0.38	15.44 / 0.07	-128.63 / 0.86	0.43 / 0.70	0.15 / 0.91	0.94 / 0.58
Distance from city	0.10 / 0.81	11.09 / 0.05	11.09 / 0.94	-0.18 / 0.55	-0.22 / 0.55	-0.50 / 0.27
Landscape heterogeneity	-2.22 /<0.01	-6.06 / 0.15	-3.96 / 0.97	-0.28 / 0.49	0.14 / 0.80	0.28 / 0.62
Rho^2	**0.61**	**0.84**	**1.00**	**0.38**	**0.28**	**0.49**
p-value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.09**	**<0.001**

Table A5. Detailed results of a multiple regression (full model) measuring amphibian species richness against 16 lake variables.

Variable	Coefficient	Tolerance	t-value	p-value
Constant	0.62	n/a	0.82	0.43
# of habitats	0.03	0.22	1.62	0.13
Good habitat	0.01	0.39	0.81	0.43
Distance from city	0.16	0.05	0.57	0.58
Wetlands	-0.17	0.17	-0.48	0.64
Rivers/streams	0.20	0.13	0.77	0.45
Paved roads	0.09	<0.01	0.17	0.86
Unpaved roads	0.06	0.02	0.13	0.90
Total roads	-0.86	0.01	-0.43	0.67
% forest cover	<-0.01	0.07	-0.43	0.67
Landscape heterogeneity	-0.09	0.35	-2.59	0.02
Human used areas	0.03	0.20	0.42	0.68
Maximum depth	0.02	0.55	0.25	0.80
Perimeter	<0.01	0.11	<0.01	0.99
Elevation	<0.01	0.10	1.15	0.27
Predatory fish	-0.01	0.47	-0.26	0.80
Refuge habitat	0.01	0.35	0.19	0.85
Overall model		**R^2 = 0.20**	**F = 1.48**	**0.24**