University of Alberta

The role of landscape factors, predation, and demography in the ecology of anurans in boreal Alberta.

by

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Even glaciers get there…

…eventually

~ To Alana, for believing ~

Abstract

I examined basic anuran biology, and responses to habitat disturbance and predators, in Alberta, concentrating on the province's boreal mixedwood ecoregion. Using landscape data for a 504 km^2 area, I found that loss of small wetlands increased the distance between remaining water bodies, potentially exceeding the movement capabilities of most wood frogs (*Rana sylvatica*). Using movement cost maps derived from slope, habitat, and moisture data, I found that most upland portions of the study area were potentially appropriate for wood frog use and travel.

I used fish and anuran abundance estimates from 12 lakes over five years to examine relationships between these groups. Severe fish winterkills were often followed by large anuran recruitment events; young-of-the-year wood frog abundance was related most strongly to changes in abundance of small-bodied fish species, whereas toad (western, *Bufo boreas*, and Canadian, *B. hemiophrys*) abundance was related to changes in populations of large-bodied fish species. I ran whole-pond experiments over 2 years to examine interactions between anuran larvae and small-bodied fish species. Wood frog larval activity and survival to metamorphosis were dramatically reduced in the presence of fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*); western toad larvae were unaffected by fish presence.

Growth rates, longevity, and size at age of anurans often vary across latitude. Using skeletochronology, I examined these parameters for Canadian toads at four sites in three ecoregions across an 850 km latitudinal gradient from Brooks to Fort McMurray, Alberta. I also examined variation in age and size structure across three sites at a local scale. Growth rate, adjusted for length of active season, was higher at the two northern

sites. Growth rates were similar at three boreal sites that were within 10 km of each other, but size structure of toad populations at these sites varied. Longevity varied from seven to 12 years across sites.

Results of my research on the ecology of northern anuran populations can be used in conservation efforts focused on these species in western Canada.

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ANOVA	Analysis of variance
Chl*a*	Chlorophyll *a*
dd	Degree days
DEM	Digital elevation model
GIS	Geographic information system
ha	Hectare
km	Kilometre
LAG	Line of arrested growth
n	Sample size
SD	Standard deviation
SUL	Snout-to-urostyle length
TN	Total nitrogen
TP	Total phosphorus
TROLS	Terrestrial Riparian Organisms Lakes and Streams
YOY	Young-of-the-year
yr	Year

Chapter 1: General Introduction

Declines in amphibian populations at local, regional, and global scales (Blaustein et al. 1994*a*; Houlahan et al. 2000; Corser 2001; Carrier and Beebee 2003) have recently focused attention of the scientific community on this group of animals. Amphibians have long been used to examine the role of competition and predation on survival, community structure, and the evolution of life history strategies. Within the last decade or so, however, ecological investigations and conservation efforts centred on amphibians have increased; identification of agents causing declines has been a central goal of many of these studies. Multiple causes of amphibian declines have been proposed, including habitat destruction or alteration (deMaynadier and Hunter 1995; Kolozsvary and Swihart 1999), increased UV-B radiation (Blaustein et al. 1994*b*), pollution (Rowe et al. 1992; Rouse et al. 1999; Hayes et al. 2002), climate change (Carey and Alexander 2003), emerging infectious diseases (Dazak et al. 2003), invasion or introduction of alien species (Hecnar and M'Closkey 1997; Knapp and Matthews 2000; Moore et al. *in press*), and synergisms between these factors (Kiesecker et al. 2001; Blaustein and Kiesecker 2002). There does not appear to be one underlying reason for amphibian declines, but rather a suite of factors that may operate at different scales, affect species differently, and have different degrees of impact at any particular geographic location (Blaustein and Kiesecker 2002; Collins and Storfer 2003).

Amphibian declines, although part of a global biodiversity crisis, are especially alarming, as declines in this group have occurred simultaneously over great distances and in protected natural areas (Collins and Storfer 2003). Amphibians may be especially vulnerable to environmental change. In general, amphibians have permeable skin that easily absorbs chemicals. Most species produce shell-less eggs that develop without parental care, usually in aquatic habitats, where they are vulnerable to chemicals, UV radiation, and predators. A biphasic lifecycle is the general rule, with an aquatic larval stage followed by a terrestrial post-metamorphic phase; thus, individuals are exposed to both aquatic and terrestrial environments. Some workers have suggested that certain amphibian species may act as a "canary in a coal mine", with increased deformities or declines in these species indicating a decline in environmental quality (Wake 1991; Blaustein 1994). However, this assertion has not been well documented (Pechmann and Wilbur 1994).

There is little question that amphibians are important components of many ecosystems; for instance, in New Hampshire forests, adult salamander biomass is equal to that of small mammals, and twice that of birds during the breeding season (Burton and Likens 1975*a*). Salamanders, because they are ectotherms, are efficient at converting prey into biomass and represent a high-quality energy source, relative to birds and small mammals, for predators in this system (Burton and Likens 1975*b*). Amphibians are also important prey in other systems; in the Sierra Nevada of California, occurrence of mountain garter snakes (*Thamnophis elegans elegans*) is tightly linked to the presence of anurans at mountain lakes (Matthews et al. 2002). Amphibians are important predators of invertebrates, and may influence ecosystem functions such as decomposition rates, by consuming detritivores (Burton and Likens 1975*b*; Wyman 1998). Amphibian larvae are important members of many biological communities, linking primary productivity to higher trophic levels, and influencing the structure of aquatic communities (Seale 1980);

some species act not only as microphagus suspension feeders but opportunistically as macrophagus predators (Petranka and Kennedy 1999).

Efforts to conserve amphibian species as elements of ecosystems in many regions of the world have become increasingly active in the past few decades. These have included habitat protection (Banks et al. 1994; Denton et al. 1997), translocation programs (Dodd and Seigel 1991), and captive breeding programs (Bloxam and Tonge 1995). Habitat protection has usually centred on breeding ponds. In the United States, for instance, current legislation protects water bodies >4 ha in area; a number of researchers have argued that this is much too lenient, and that smaller wetlands need protection as well (Kaiser 1998; Semlitsch and Bodie 1998). Translocation of wild-collected eggs, larvae, or post-metamorphic individuals to refound locally extinct populations, or bolster existing ones, has been controversial and success has been highly variable (Dodd and Seigel 1991). A more costly option, which has been used in a few cases, is the captive breeding of individuals for release into areas where the species formerly occurred (Bloxam and Tonge 1995). One of the problems with this approach is that the agent causing the decline of the species in the first place is not always identified before reintroduction (Dodd and Seigel 1991).

One of the main challenges faced by those attempting to understand amphibian declines is the lack of long-term data on most species. Relatively few long-term datasets are available, and these are predominantly from Western Europe and North America (Houlahan et al. 2000). Within North America, most amphibian research is done in the United States and the southern parts of Canada, where most amphibian species are concentrated. Little work has been done in the northern portion of Canada, although this is a vast area, and some species range as far north as the Arctic circle (Stebbins 1985); in some regions data as fundamental as complete species lists are not yet available (Maunder 1997).

My work concentrated on amphibian ecology in the boreal mixedwood forest of Alberta, Canada. This is the largest ecoregion within the province, representing 43.2% of the total land area (Strong and Leggat 1981), and is a subregion of the boreal forest region, which comprises the majority of the forested area of Canada (Rowe 1972). In Alberta, the aspen-dominated (*Populus tremuloides*) boreal mixedwood is a semiarid area (Strong and Leggat 1981) that has been relatively undisturbed in the past; for instance, the majority of the forest has never been harvested. However, in 1992 forestry companies began removing aspen in the area for pulp and paper production (Hannon et al. 2002), and such companies now lease over 75% of the boreal mixedwood (Prepas et al. 2001; Hannon et al. 2002). The effects of anthropogenic stresses such as logging on amphibians are poorly understood and have not been well examined in the boreal forest (deMaynadier & Hunter 1995), though some research on this question has been done (Constible et al. 2001; Hannon et al. 2002).

The boreal mixedwood provides a relatively pristine area in which to conduct baseline research on amphibian ecology. Human population density in the region is low, as is the density of roads and cropland. Amphibian deformities in the area are at normal background levels (Eaton et al., *in press*), suggesting chemical contamination of breeding ponds is not occurring, at least not at high levels. Most lakes in the region contain natural fish assemblages, without introduced predatory fish species.

Amphibian diversity in the boreal mixedwood is low; only two frog species (wood frog, *Rana sylvatica*, and the boreal chorus frog, *Pseudacris triseriata*), and two toad species (western toad, *Bufo boreas*, and Canadian toad, *B. hemiophrys*) occur in the area (Russell and Bauer 2000). All four species breed in lentic waters ranging from small ephemeral ponds to large lakes (Hannon et al. 2002; personal observation).

Reduction in the number of small ponds across a landscape may impede the ability of amphibians to move between populations, or recolonize areas where local populations have gone extinct (Semlitsch and Bodie 1998; Gibbs 2000). In order to explore the role of small ponds and seasonally flooded wetlands in providing connectivity in the boreal mixedwood, I used Alberta Vegetation Inventory (AVI) datasets in a geographic information system (GIS) environment to model loss of small water bodies and the effect such loss has on distances between remaining water bodies (Chapter 2). I used data on the wood frog to examine how the loss of such small "stepping-stone" water bodies might change the ability of frogs to move between potential breeding sites. Disappearance of small water bodies in the semiarid boreal mixedwood periodically occurs during drought (personal observation); in other areas of North America such loss has been related to human activities such as agriculture (Gibbs 1993; Semlitsch 2002).

Although aquatic habitats are critical to the persistence of anuran populations in the boreal mixedwood, the terrestrial environment also plays an important role in the movement of anurans across the landscape (Dodd and Cade 1998; Guerry and Hunter 2002). I used AVI datasets and a digital elevation model (DEM) to examine the influence of habitat, moisture, and slope on potential movement patterns of wood frogs in a relatively undisturbed portion of the boreal mixedwood (Chapter 2). I also examined the impact that cutblocks in this area could have on patterns of potential frog movements.

For the purposes of the analyses above I did not make any attempt to classify water bodies according to quality as potential breeding sites. However, water bodies vary across gradients of predator communities and hydroperiods: ephemeral ponds contain no fish and few invertebrate predators, but often dry before young-of-the-year anurans emerge. Ponds which dry only once every few years often contain no fish but large invertebrate predator populations; more permanent ponds and lakes, which rarely or never dry, often contain populations of predatory fish (Wellborn et al. 1996). In surveys of lakes (n = 102; size range: 1.7 to 362 ha; B. Tonn, unpublished data) in the boreal mixedwood 52% were dominated by small-bodied non-piscivorous species, 27% contained large-bodied piscivorous fish, and the remaining 21% were fishless. Thus, potential breeding sites for anurans in the boreal mixedwood vary in quality both spatially and temporally: ponds dry then refill, or are destroyed by succession (Skelly et al. 1999), and fish populations are reduced or eliminated by winterkill, then recover (Danylchuk and Tonn 2003).

Much of the literature on interactions between fish and amphibian populations concerns the effects of introduced, usually large-bodied, fish species on native amphibians (Bradford 1989; Hecnar and M'Closkey 1997; Knapp and Matthews 2000). However, interactions between native fish and amphibian assemblages, and especially between small-bodied, nonpiscivorous fish and amphibians, have rarely been examined. I used data collected over five years to examine relationships between changes in fish and anuran populations at 12 boreal mixedwood lakes (Chapter 3). These data were collected by the Terrestrial Riparian Organisms, Lakes, and Streams (TROLS) project, which evaluated the impacts of buffer strips of varying width left around lakes during forest harvest (Prepas et al. 2001; Hannon et al. 2002). I used relative abundance estimates for fish and amphibians to ask whether changes in anuran abundance (wood frog and toads [western and Canadian toads]) were related to changes in fish abundance, and whether anuran populations responded to fish winterkill events with pulses of recruitment. I also asked if different anuran species (frogs and toads) responded differently to the type of fish community (large-bodied piscivores vs. small-bodied non-piscivores). Bufonid larvae, for instance, produce bufotoxins that render them distasteful to many predators (Kruse and Stone 1984; Kats et al. 1988). Species such as the wood frog, however, lack these defences and are palatable to predators (Kats et al. 1988).

Small-bodied, non-piscivorous fish are not usually considered as predators of anuran larvae (Brönmark and Edenhamn 1994; Hecnar and M'Closkey 1997). However, responses of anuran populations to small-bodied fish abundance in the field (Chapter 3) suggested that interactions between these two groups in boreal Alberta lakes are important. Although predation was the likely mechanism underlying these interactions, controlled experiments were necessary to demonstrate and better understand the impact of small-bodied fish on anuran species native to boreal Alberta. Therefore, I ran whole-pond experiments over 2 years at Meanook Biological Research Station (MBRS; Chapter 4). I released wood frog (year 1) and western toad larvae (year 2) into ponds stocked with fish (fathead minnow, *Pimephales promelas*, and brook stickleback, *Culaea inconstans* (Kirtland)) and monitored tadpole activity, survival, length of time to metamorphosis, and size at metamorphosis. I predicted that tadpole activity, growth rates, and survival would be reduced, whereas time to metamorphosis would be increased, in the presence of both fish species as a result of direct (e.g. predation) or indirect (e.g. reduced tadpole foraging rates in the presence of potential predators) interactions between fish and tadpoles. I also predicted that the effects of fish would be greater on wood frog than on western toad larvae because bufonid tadpoles are thought to be distasteful to many predators (Kruse and Stone 1984; Kats et al. 1988), and that fathead minnow would exert a greater effect on tadpoles of both species than brook stickleback because fathead minnow have larger bodies and mouths.

If anuran populations are impacted by factors such as pond drying or fish predation, how long can they persist in the face of repeated low recruitment? Anuran populations are often subject to large fluctuations in abundance (Pechmann and Wilbur 1994; Green 2003), with complete reproductive failure in many years (Griffiths 1997; DiMauro and Hunter 2002). If a site has not been isolated due to loss of other ponds from drought or human activities, then immigration of new individuals to the site may rescue the population. In addition, many anurans are highly philopatric to their breeding sites as adults, so a population has the potential to recover for as long as reproductive adults return to attempt to breed (Marsh and Trenham 2001). While demographic factors such as growth rates and longevity have been estimated for the wood frog in other areas of Canada based on skelotochronology (Bastien and Leclair 1992; Sagor et al. 1998; Leclair et al. 2000), little is known about these parameters for species such as the western and Canadian toads. These species are more likely to be sensitive to natural factors such as drought and human disturbances such as logging because they occur at lower densities and are more patchily distributed across the landscape than wood frogs and boreal chorus frogs (Hannon et al. 2002; Eaton, unpublished data). In addition, toads are not freeze tolerant, as are wood frogs (Storey and Storey 1984), and must find suitable areas in which to burrow down below the frost line (Kuyt 1991; Hamilton et al. 1998).

I used skeletochronology to estimate ages of Canadian toads collected in four areas of Alberta: two in the boreal mixedwood, one in the aspen parkland, and one in the grassland ecoregion (Chapter 5). My goal was to determine if age-at-size relationships varied across a latitudinal gradient within the province, and estimate the longevity of toads in different areas. I also examined the age structure, age at maturity, and differences in the size-at-age relationship for male and female toads from one area, as specimens from this location were collected from breeding aggregations and the sex of the animals was known. I chose to examine the Canadian toad, rather than work on wood frogs or western toads, because the Canadian toad seems to be experiencing declines in some regions of Alberta, and we lack much of the basic data necessary to formulate suitable conservation plans for this species.

Lack of basic biological and long-term datasets seems to be a common theme for many amphibian species. This is particularly true for more northern populations of these animals, such as those found in boreal Alberta. Here I provide insight into some factors affecting anurans in Alberta, particularly the boreal mixedwood region. These include the potential impact of drought on connectivity between water bodies (Chapter 2), a model of potential wood frog movement related to landscape factors (Chapter 2), an examination of the interaction between fish and anuran populations at boreal lakes (Chapter 3), elucidation of the relationship between small-bodied fish species and anuran larvae (Chapter 4), and comparison of Canadian toad size-at-age and longevity across a latitudinal gradient within Alberta (Chapter 5). This information will be useful in the formulation of appropriate management plans and conservation strategies, so that the anuran species studied here remain a part of the fauna of Alberta far into the future.

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Chapter 2: Modeling wood frog distribution in Alberta's boreal forest: loss of small wetlands and impact of environmental factors on frog distribution

Introduction

Studies of recent declines in amphibian populations in Canada (Bishop and Pettit 1992; Green 1997) and worldwide (Wake 1991; Blaustein et al. 1994; Pounds and Crump 1994; Alford and Richards 1999) have focused attention on interactions between amphibians and their environment, and the potential impact of human activity on this relationship (Collins and Storfer 2003). In many cases the obvious causes of population declines and the contraction of amphibian distributions at landscape scales are habitat change and destruction (Blaustein 1994; Alford and Richards 1999). Habitat destruction reduces availability of breeding sites (Gibbs 1993; Semlitsch 2002), and may cause loss of connectivity between these sites (Semlitsch 2000). Even in the absence of human destruction of breeding sites, availability of wetlands will fluctuate in response to precipitation patterns (Skelly 1996; DiMauro and Hunter 2002; personal observation) and hydroseral succession of wetlands to more terrestrial habitats (Williams 1997; Skelly et al. 1999).

Many North American amphibian species, especially anurans, must deposit their eggs in standing water such as ponds or lakes (Stebbins 1985; Duellman and Trueb 1986). Therefore, availability of wetlands is of substantial importance to the richness and persistence of anuran communities in a given area (Semlitsch and Bodie 1998; Russell et al. 2002). The distribution of wetlands is also important, because many amphibians have relatively poor dispersal abilities (Duellman and Trueb 1986; Marsh and Trenham 2001), limiting their ability to recolonize sites after local extinctions. The proximity of wetlands is thus an important factor in connecting breeding populations across the landscape, maintaining gene flow. Small wetlands seem to play an especially critical role in connectivity, as they form stepping stones across the landscape, allowing individuals to move between populations and to recolonize breeding sites following local extinctions (Semlitsch and Bodie 1998; Gibbs 2000). Although the successful use of any potential breeding site by amphibians is influenced by factors such as water chemistry (Gascon and Planas 1986; Rowe and Dunson 1993; Hecnar and M'Closkey 1996*a*), interspecific competition (Resetarits and Wilbur 1989; Petranka et al. 1994), and the presence of fish (Hopey and Petranka 1994; Knapp et al. 2001), modeling the distribution of wetlands is one approach which can be used to gain an understanding of amphibian distribution at landscape scales (Gibbs 1993).

Although simple measurement of distance between wetlands is a valid approach to modeling amphibian distribution, other factors, such as the composition of terrestrial habitat lying between breeding sites, likely play a role in how well amphibians move across the landscape (Dodd and Cade 1998; Guerry and Hunter 2002). Composition of the landscape around wetlands may influence amphibian distribution (Vos and Stumpel 1995; Kolozsvary and Swihart 1999; Guerry and Hunter 2002), abundance (Knutson et al. 1999; Scribner et al. 2001; Russell et al. 2002), and species richness (Findlay and Houlahan 1997; Findlay et al. 2001). Movement of animals in and out of ponds may be non-random, and related to surrounding habitat (Dodd and Cade 1998; deMaynadier and Hunter 1999; Rothermel and Semlitsch 2002). Habitat may have important implications for the isolation of some amphibian populations, with the occupancy of ponds being related, in part, to habitats surrounding a pond (Vos and Stumpel 1995; Findlay and Houlahan 1997; Guerry and Hunter 2002). For example, Roberts and Lewin (1979) found that the wood frog (*Rana sylvatica*) in boreal Alberta was most often found near water, and was never found in pine stands; moisture is an important determinant of wood frog activity and survival (Bellis 1962). Similarly, a number of studies have shown reduced amphibian numbers in cut blocks or managed tree plantations, compared to nearby mature forest (see deMaynadier and Hunter 1995 for a review). By combining information from a number of sources, a spatial model of probable distribution for species of interest can be constructed for a particular landscape. Such a model would be an important tool for land managers who want to minimize the effects of human activities, such as logging, road-building, and agriculture, on amphibian populations.

I used spatial data on a portion of the boreal mixedwood forest of Alberta to model the effect of loss of small wetlands on connectivity between potential amphibian breeding sites, and the influence of landscape factors (slope, moisture, habitat) on potential movements of the wood frog (*Rana sylvatica*) in the area. The boreal mixedwood forest ecoregion is a large and important forest region in Canada, situated between the aspen parkland to the south and the conifer-dominated forest to the north (Rowe 1972). In Alberta this semiarid region covers over 43% of the province and is dominated by aspen (*Populus tremuloides*) (Strong and Leggat 1981). Until 1992, when timber harvest for aspen began, this area was largely undisturbed by forestry; natural disturbances in the area are primarily fire, windthrow, and insect outbreaks (Hannon et al. 2002). Over 75% of the boreal mixedwood is now leased to forestry companies (Prepas et al. 2001; Hannon et al. 2002). Thus, the area represents relatively pristine, primeval forested habitat that is currently being impacted by industrial activities.

Few amphibian species exist in the boreal mixedwood forest. In the study area only three species were found (Hannon et al. 2002): the wood frog, boreal chorus frog (*Pseudacris triseriata maculata*), and western toad (*Bufo boreas boreas*). These species all make use of terrestrial habitats for feeding and overwintering (Russell and Bauer 2000). More information is available in the literature for the wood frog than for other amphibians occurring in the area, so this species was chosen to serve as a model for anuran response to wetland distribution and abundance in Alberta's boreal forest. No salamanders occur in the study area (Russell and Bauer 2000).

Here, using spatial data for a small part of boreal mixedwood Alberta in a geographic information system (GIS) environment, I develop spatial models to ask the following: (1) how is drought likely to affect the distribution and abundance of water bodies across an actual landscape, and (2) how do habitat, moisture, and slope influence the probable movement of wood frogs across the study area? This is a first step in using landscape-level data in a GIS environment to examine the large-scale distribution of an amphibian in an area of relatively pristine habitat, and provides a baseline against which to compare the effect of anthropogenic impacts in the region in the future.

Materials and Methods

Study species. Wood frogs have not been well studied in the boreal mixedwood forest, so little is known about their habitat requirements and dispersal abilities in this region (Roberts and Lewin 1979; Constible et al. 2001). This species is freeze tolerant (Storey and Storey 1984), overwintering in upland habitat and moving to breeding sites as soon as the ice melts in the spring. Wood frogs breed in open water such as ponds and lakes, usually ovipositing in shallow water on emergent or submergent vegetation (Russell and Bauer 2000). During the non-breeding season wood frogs are chiefly terrestrial, though most remain relatively close to water throughout the summer (Roberts and Lewin 1979). Young-of-the-year (YOY) frogs emerge from the water in mid to late summer and disperse into the upland to overwinter. Although adult wood frogs show high fidelity to the site at which they first breed, approximately 18% of juveniles disperse to wetlands other than their natal site to breed (Berven and Grudzien 1990). Wood frog movements, therefore, can be classified as (a) movement of adults from overwintering to breeding sites in spring, (b) from breeding sites to upland summer and/or overwintering habitat (adults) from spring to fall, (c) from natal wetlands to upland feeding and /or overwintering habitat (YOY) from mid-summer to fall, and (d) dispersal between populations (adults and YOY) from spring to fall. Of these movements, dispersal of YOY is probably the most important in linking populations (Sinsch 1997; deMaynadier and Hunter 1999; Semlitsch 2002).

Berven and Grudzien (1990), working in Virginia, found that wood frogs rarely disperse more than 1000 m from the ponds where they went through metamorphosis, though movements of up to 2.5 km did occur. Newman and Squire (2001) documented interpond movements by adult wood frogs of up to 422 m (mean = 118 m, n = 29), and of up to 1119 m (mean = 314, n = 7) by juveniles in North Dakota. Roberts and Lewin (1979), working in the boreal forest of Alberta, used visual surveys to sample amphibians on 10 x 100 m plots perpendicular to water bodies. The mean distance at which they found wood frogs during each month (May – August) that populations were sampled was less than 50 m for all age classes. Wood frog movements within a Minnesota peat bog were even smaller; Bellis (1965) found adults moved a mean of 11.2 m, while the longest distance moved was 99.7 m by a young-of-the-year individual. Based on these data, I use 1000 m as a reasonable upper limit of movement by most individual wood frogs.

I assumed that all wetlands in the study area were potentially suitable for use by wood frogs; however, this does not mean that reproduction occurred or that a self-perpetuating breeding population was established at each site. Rather, I merely assumed that all wetlands could be used as hydration and feeding sites by wood frogs, such that these sites could act as stepping stones for individuals moving between existing populations, or dispersing from a population and founding a new one at an unoccupied site. Fieldwork suggests that this assumption is correct: surveys of 33 small ponds (a subset of these wetlands were measured and ranged from 0.0046 to 0.18 ha [mean = 0.038 ha, n = 20] in area; Eaton, unpublished data) in the region (1 to 12 visits per pond) from 1996 to 1999 indicated that some life history stage of the wood frog occurred at least once at 72.7% of the wetlands, and at least one of the three amphibian species in the region was encountered at 90.9% of the wetlands surveyed. Wood frogs were also present and breeding at four large lakes (mean size = 63.5 ha, range = 18 – 109 ha) in the study area (Hannon et al. 2002).

During visual surveys of ponds in Elk Island National Park, a relatively undisturbed area located in the aspen parkland ecoregion to the southeast of the study area, wood frogs were encountered at least once at 223 of 232 ponds (Browne et al. 2003). Although wood frog egg and larval survival is influenced by pH of water at the breeding site (Pierce and Harvey 1987; Grant and Licht 1993), pH in lakes (mean = 9.0, range = 8.3 – 9.7, n = 4; Prepas et al. 2001) and ponds (mean = 7.2, range = 5.0 – 8.4, n = 33; Eaton, unpublished data) in the study area were above the critical pH (3.6 – 4.5) at which survivourship drops below that for neutral water (Gosner and Black 1957; Grant and Licht 1993).

Study area. I obtained Alberta Vegetation Inventory (AVI; Alberta Environmental Protection 1991) datasets, and a digital elevation model (DEM) for 6 townships (70-24, 70-25, 71-24, 71-25, 72-24, and 72-25) covering 504.2 km^2 of aspen-dominated boreal mixedwood forest near Athabasca, Alberta (Figure 2-1) from Alberta-Pacific Forest Industries Inc. (Al-Pac). Al-Pac was one of the cooperating forestry companies involved in a large collaborative research project (called Terrestrial Riparian Organisms Lakes and Streams, or TROLS) examining the impact of the width of buffer strips (left around lakes during timber harvest) on lake water chemistry, hydrology, and aquatic and terrestrial organisms (Devito et al. 2000; Prepas et al. 2001; Hannon et al. 2002). I limited the spatial datasets to one of the areas where Al-Pac was harvesting forest in conjunction with the TROLS project, as fieldwork in this area provided additional information about amphibian distribution and wetland dynamics.

AVI datasets are vector coverages constructed using interpretation of 1:20000 maps and air photos. Each dataset contains multiple parameters associated with each polygon in the coverage; these include ratings for moisture regime, the five dominant canopy species and their canopy closure, non-forest vegetated cover (e.g. shrubs), naturally non-vegetated areas (e.g. lakes), anthropogenic vegetation (e.g. crops), and anthropogenic non-vegetated sites (e.g. industrial sites). Resolution of AVI datasets is limited by the physical constraints of digitizing forest type boundaries, such that no constrictions less than 20 m in size can occur in any forest cover type (Alberta Environmental Protection 1991). The DEM (cell size = 50 m) was a raster coverage based on point elevation data taken at 100 m intervals. All coverages were manipulated and processed using ArcMap 8.0 and ArcView 3.2.

In the context of this study I defined 2 subsets of water bodies, based on their classifications in the AVI dataset. All polygons classified as permanent standing water were defined as "ponds", and are probably rarely dry. All polygons classified as periodically flooded lands, plus all ponds, were defined as "wetlands"; I took these former sites to represent ephemeral ponds, flooded meadows, fens, etc. Thus, "wetlands" is an inclusive term that includes all standing water, whether permanent or not, while "ponds" is more restrictive, referring only to those water bodies unlikely to dry in the course of the summer. Hereafter I also use the term "water body" to refer generically to ponds or wetlands.

Modeling water body distribution. I created 2 coverages from the AVI dataset: one with ponds only (Figure 2-2A), and one with all wetlands (Figure 2-2B). I compared these two coverages (ponds and wetlands) to examine the effects of wetlands that are periodically flooded on connectivity between more permanent water bodies. Note that all analyses used here assume that the land is flat, when in reality movement over relief on the actual land surface would add to the actual distance that would be traveled between ponds. Therefore, distances described here may be considered minimal.

The distribution of ponds and wetlands within the study area was examined using "Nearest Neighbour v.1.8" Avenue script for ArcView 3.2 (Brooks 1998); this script uses the test of Clark and Evans (1954) to determine if water bodies are randomly distributed or clumped across the landscape, and incorporates a boundary strip into the analysis to ensure the Clark and Evans test is unbiased. Because the coverages of the study area have an artificial edge, an artificially restricted set of nearby water bodies can be detected as water bodies that are close to the edge. If water bodies are significantly clumped across the landscape, then the effect of the edge is relatively low, as most ponds and wetlands would already lie close to other water bodies. If water bodies are randomly distributed, however, then it is necessary to add a boundary strip around the edge of the study area; water bodies in this strip would not be used as origin points for wood frogs in the distance analysis, but could serve as destinations for frogs from other water bodies within the study area.

Water bodies that intersected the edges of the AVI coverages were deleted before further analysis was done, as the size of these water bodies was unknown. The attribute tables of the pond and of the wetland coverages were then exported to Excel for characterization of water body size.

The distance from each water body to its nearest neighbour was measured separately for the pond and wetland coverages using the "Nearest Features v3.5" extension for ArcView 3.2; distance between water bodies within each coverage was calculated from closest edge to closest edge. To model changes in the distribution and abundance of ponds and wetlands during drought years I sequentially removed water bodies less than 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 10, and 15 ha in size. Removal of water bodies from smallest to largest in area mimicked the effects of dry periods on the landscape. I repeated the distance analysis with each reduced set of polygons. Data were exported to Excel for further analysis.

To produce a graphic image of the changes in water body abundance and distribution, and the impact of these changes on the connectivity of remaining water bodies, I selected subsets of the pond and wetland data sets for inclusion in further analysis based on arbitrary size classes. I used the buffer tool to produce 1000 m buffers around all ponds or wetlands in a coverage for the following sets of data: all water bodies, and water bodies > 0.5, 1.0, 1.5, 2.0, and 5 ha in area. I used a buffer size of 1000 m because wood frogs are rarely found more than 100 m from water during the summer (Roberts and Lewin 1979), and even YOY frogs dispersing from natal to new breeding ponds rarely move more than 1000 m (Berven and Grudzien 1990).

Modeling potential wood frog movement. To examine the impact of slope, habitat, and moisture regime on potential wood frog movement over the landscape, I ranked habitat and moisture ratings from the AVI datasets on a scale of 1 to 10, with 1 representing the least friction to movement, and 10 the most (see Tables 2-1 and 2-2 for summary of the rankings, and below for an explanation of how these rankings were assigned). Polygons with a ranking of 1 can be thought of as being easy for wood frogs to move through, while areas with higher rankings are more difficult to traverse. These two coverages (one for habitat and the second for soil moisture) were exported to the raster environment for further analysis. I also created a raster-based slope coverage from the DEM, and assigned slope intervals a ranking from 1 to 10, with each rank containing 2.1 degrees of slope (i.e. a ranking of 1 would include all slopes between 0 and 2.1).

I used the Cost-Weighted Distance function within ArcMap to perform cost-distance analysis for ponds and wetland coverages. Cost-distance analysis uses an input coverage with a set of focal points (in this case, ponds or wetlands), and a friction map (e.g. habitat), to compute the least-cost path that an animal would take from any point on the landscape to reach a focal point. Thus, each point on the cost-distance map is assigned the lowest possible cumulative cost to reach a pond or wetland, resulting in a map of probable distribution of animals in a study area, based on the input parameters. In this analysis both distance and the cost of moving through each cell are important in determining the accumulated cost of each cell.

I used cost-distance analysis to model potential wood frog movement in the study area separately with ponds and wetlands as starting points, for friction maps based on habitat, moisture, and slope. I then used the Reclassify function within the Spatial Analyst extension for ArcMap to classify the output maps from the cost-distance analysis into 10 classes of equal intervals; cells with a classification of 1 represented areas most likely, and those with 10 the least likely, to contain wood frogs. I compared the reclassified cost-distance maps based on the three friction maps (habitat, moisture, and slope) for the two input coverages (ponds and wetlands) to examine the impact of seasonally flooded areas (included in the wetland but not pond coverage) on movement of wood frogs across the landscape. Comparisons were made using the Raster Calculator function of Spatial Analyst to subtract cost-distance maps based on the same friction maps, but different input layers. For example, I subtracted the cost-distance map for slope based on ponds from that for wetlands.

I also used the Raster Calculator function to add all three friction maps together (habitat + moisture + slope) to obtain a map of cumulative friction based on these factors. Cost-distance analysis was run on this combined layer using ponds as the input layer; I only present results from the pond analysis, as patterns for the wetland analysis were similar. I then did pairwise comparisons between outputs from the cost-distance analysis for ponds (moisture-habitat, moisture-slope, and habitat-slope) using Raster Calculator to determine if data from these different friction maps produce similar patterns of potential wood frog movement.

To examine the effect of forestry on potential wood frog movement in the study area, I also used a coverage containing harvested cut blocks to recode polygons in the habitat layer using the Union tool of the Geoprocessing Wizard of ArcMap. Where the habitat ranking prior to cutting was 5 or greater, based on rankings assigned to the AVI data, the ranking remained the same. If the original ranking was less than 5, the area was recoded as 5. This coverage was exported as a raster, and cost-distance analysis was performed using ponds as the input layer. Because I wanted to examine the impact of cutblocks on movement costs, and the effect of cutblocks was expected to be greatest when using ponds as the input layer, I did not repeat this analysis with wetlands as the input layer. If there were little effect of cutblocks on movement costs when only ponds were considered, then when all wetlands were considered the effect would be even smaller. While salamander abundance is often much lower in control stands than in cut blocks (median of 4.3 times as many salamanders in control stands), anurans are not as strongly affected (median of 1.7 times as abundant in control stands; deMaynaduer and Hunter 1995).

Assigning rankings for habitat cost layer. A variety of criteria were used when assigning rankings for polygons based on habitat characteristics. Where the crown closure of the overstory within a polygon was greater than 30%, the dominant tree species (in terms of the percentage of the polygon that was covered by this species) was used to characterize the polygon. In the vast majority of cases, the dominant species represented more than 50% of the canopy closure of a polygon; where this was not true, the composition of the entire stand was examined to determine what groups of species (e.g. deciduous trees) were dominant, and a ranking was assigned based on these data. If deciduous and coniferous species were equally represented in terms of canopy closure, a ranking intermediate between those for the pure stands was used. Where crown closure of the overstory was equal to or less than 30%, and the understory had a crown closure of 30% or more, a rating was assigned based on characteristics of both the under and overstories. Where crown closure for both canopy layers was 30% or less, other information was used in assigning rankings; if none was available, the ranking was applied based on the canopy layers. Any polygon where crown closure was less than 6% was classified as non-forested, and other data were used to assign rankings for the habitat coverage.

Pine-dominated stands were assigned a rank of 10 (least hospitable to wood frogs) based on the work of Roberts and Lewin (1979), who never found amphibians in pine stands in the boreal forest near Fort McMurray. Other conifers (spruce [*Picea spp.*] and balsam fir [*Abies balsamea*]) were given a rank of 7, as anurans are often less abundant in conifers as compared to deciduous stands (Bennett et al. 1980; Degraaf and Rudis 1990). Tamarack (*Larix laricina*) stands were ranked as 4 because this species has softer needles than the other conifers, and may form a litter layer more amenable to wood frogs. Hardwoods (aspen, poplar [*Populus sp.*], and birch [*Betula papyrifera*]) were assigned a 2, as amphibians seem to be most abundant in forests dominated by these tree species (Degraaf and Rudis 1990; deMaynadier and Hunter 1995).

Polygons classified as wetlands (ponds, lakes, seasonally flooded areas) were assigned a ranking of 1, as these should provide good habitat for wood frogs. Areas dominated by bryophytes, herbaceous vascular plants (forbs and natural grassland), and closed shrubs (crowns of the shrubs overlapping) were ranked as 3 as they would provide some shelter for amphibians, and some of these factors (i.e., grass cover) have been associated with the presence of wood frogs (Constible et al. 2001). Areas with open shrubs, annual crops, areas seeded to perennial grass, perennial forage crops for livestock, and farmsteads were ranked as 5, due to the lack of cover and increased disturbance in these areas (Rothermel and Semlitsch 2002; Eaves 2003). The Athabasca River, which runs through the northern portion of the study area, was ranked as a 10 as it is wide (mean width = 220.9 m in the study area; range = 162 – 294 m) and fairly fast-flowing. Gravel pits, roads, and industrial sites were assigned a ranking of 10 as these areas contain little cover and are often disturbed; roads may represent physical and behavioural barriers to some amphibian species (deMaynadier and Hunter 1995; Ashley and Robinson 1996; Gibbs 1998; Findlay et al. 2001).

Assigning rankings for moisture cost layer. Ranks for moisture regime were assigned primarily based on the moisture regime parameter of the AVI dataset. For those polygons without an associated moisture regime code, other parameters were used in estimating the potential use of a polygon by an anuran. Bellis (1962) found that moisture was an important determinant of anuran activity and survival; polygons with a moisture regime of 'dry' were thus assigned a ranking of 10, mesic polygons were given a ranking of 5, while wet and aquatic sites (ponds, lakes, flooded areas, and the Athabasca River) were given rankings of 1. Roads, gravel pits, and areas with industrial activity were assigned a 10, as these areas are likely inimical to wood frogs due to lack of moisture. Although roads may contain puddles after rain, these are usually transient and, for the purposes of the model, I assumed that roads were dry. Polygons classified as annual crops were assigned a moisture ranking of 3, as these crops are usually planted in areas with soil moisture suitable for growth. Areas with perennial grass or pasture, and farmsteads were ranked as 5, as these areas can usually be characterized as mesic.

Note that the rankings used in the cost-distance analyses are, to some extent, subjective, and are based on relevant literature and personal experience and observations from working in the study area. The model I constructed with this information is a starting point that may lead to further efforts in the future.

Data analysis. For each cost-distance map, I calculated the frequency distribution of individual cell values after reclassification into 10 classes. I then compared frequency distributions between friction maps with ponds and wetlands as input layers using a two-sample Kolmogorov-Smirnov Goodness of Fit test. I used the same method to compare cost-distance maps based on slope, moisture, and habitat within input layer type (e.g. ponds), and between habitat friction maps with and without cutblocks, with ponds as the input layer. An α level of 0.05 was taken as significant for these tests.

Results

Distribution and abundance of wetlands. Both ponds and wetlands within the study area were randomly distributed (ponds: $R = 0.95$, $z = -1.01$, $p < 0.05$, $n = 106$; wetlands: $R = 0.97$, $z = -0.73$, $p < 0.05$, $n = 168$). Because water bodies were randomly distributed, those within the study area, but less than 1 km from its outside edge, were not used as potential origin sites for frogs during the distance analysis. These water bodies remained in the dataset during the distance analysis so that they could serve as the nearest neighbours for other ponds and wetlands.

A total of 106 ponds were identified using the AVI coverage of the study area, but 5 of these were deleted from the dataset because they were truncated by the edge of the study area and so their size was unknown. The remaining ponds ranged in size from 0.092 to 216.5 ha (mean = 10.9 ha, SD = 27.5, median = 1.6 ha, n=101), with the majority being < 2 ha (Figure 2-3). The total area represented by small ponds was substantially less than that covered by the few large bodies of water in the study area (Figure 2-4). Pond density was 0.20 / km^2.

A total of 62 additional wetlands, representing seasonally flooded areas, were identified in the study area; 4 were deleted from the dataset because they were truncated by the edge of the study area. The remaining seasonally flooded areas ranged in size from 0.14 to 19.5 ha (mean = 2.6, SD = 3.07, median = 1.9 ha, n = 58; Figure 2-3). Total area represented by seasonal wetlands was not large compared to that of ponds (Figure 2-4). Water body density, including all ponds and seasonally flooded areas, was 0.32 / km^2.

Removal of small water bodies, as would occur with drought or seasonal drying, caused an increase in the mean minimum distance between ponds and wetlands that remained on the landscape; this distance increased steadily as larger and larger water bodies were removed (Figure 2-5). For example, mean minimum distance between ponds increased from 621.6 m to 1328.0 m with the loss of ponds of 4 ha or less; a similar doubling of mean distance was found for wetlands, with distance between water bodies increasing from 490.9 to 1134.9 m when wetlands 4 ha or smaller disappeared. Distance between water bodies increased more quickly for ponds than wetlands; for instance, mean minimum distance between water bodies exceeded 1000 m when ponds less than 1.5 ha disappeared, but the 1000 m threshold was not passed for wetlands until those smaller than 3.5 ha disappeared (Figure 2-5). Note that the mean distance between wetlands actually decreases with loss of water bodies in the 4.5 and 5 size classes (Figure 2-5). This occurs because a small number of very isolated water bodies occurred in these size classes; because these water bodies were isolated, the minimum distance to their nearest neighbour was relatively large, inflating the mean distance between water bodies. When these isolated water bodies are removed, the mean distance between those water bodies that remain decreases.

Removal of small water bodies also decreased the amount of upland habitat close to a pond or wetland (Figure 2-6). For instance, the percentage of the study area within 1000 m of a water body dropped from 50.3% when all ponds were considered, to 35.7%

when ponds less than 2 ha were removed. The corresponding values for wetlands are 61.5% and 42.3%.

Nearly all the ponds and wetlands have at least one other water body within 1000 m, forming chains of connectivity through the study area (Figures 2-7 and 2-8). Although the distribution of water bodies across the study area was random, there was some clumping of ponds and wetlands in the southwest corner of the region (Figures 2-7 and 2-8). As smaller water bodies were lost, ponds in the centre and northern portions of the region became increasingly isolated, and eventually even the dense clump of water bodies in the southwest corner began to lose connectivity (Figure 2-7). Similar patterns were evident with the loss of wetlands, though connectivity between water bodies remained greater for the wetland coverage than the pond coverage until quite large water bodies (e.g. 5 ha) start to disappear (Figure 2-8).

The effect of slope, habitat, and moisture on potential wood frog movement. Construction of slope, habitat, and moisture / land use maps is useful for examining the potential effects of each of these factors on potential wood frog movement patterns. The study area is relatively flat; most high slopes are associated with the Athabasca River, with a number of other high slope areas scattered across the region (Figure 2-9A). The moisture regime map indicated that the majority of the study area is mesic, with a band of wet areas running from the northwest to the southeast across the centre of the region (Figure 2-9B). Very few areas of extreme avoidance (i.e. ranking of 10) by wood frogs exist within the region based on the moisture layer (Figure 2-9B). The habitat map was the most complex of the three friction maps, displaying a high degree of heterogeneity across the region (Figure 2-9C). High cost areas, those that are theoretically avoided by wood frogs, are scattered throughout the study area, with concentrations of these locations in the northeast and in the middle portion of the region (Figure 2-9C).

Cost-surface analysis suggests that there were probably relatively few areas that would be avoided by wood frogs based on the slope, moisture, and habitat coverages used in this study (Appendix A, Figures A1 – A3). High cost areas were mainly concentrated along the northern and southern ends of the Athabasca River, and resulted mainly from a lack of ponds in these areas. In some cases, however, bands of moderate to high cost separate water bodies from one another, suggesting that areas exist on this landscape that are unlikely to be crossed by wood frogs thus isolating some ponds and wetlands (Appendix A, Figures A1 – A3).

Patterns of potential wood frog movement were similar when either ponds or wetlands were used as source layers; the few differences that occurred reflect the influence of wetlands that occur in the absence of ponds (Appendix A, Figures A1 – A3). Frequency distributions of movement costs did not differ significantly when ponds or wetlands were used as source layers (Figure 2-10; Kolmogorov-Smirnov test, P>0.75 in all cases).

Within a source layer (e.g. ponds or wetlands), cost-distance rating did not differ significantly between different friction maps (Kolmogorov-Smirnov test, P>0.75 in all cases). Differences between cost-distance surfaces derived from different friction maps were not large for most cells, with most cells being the same, or only different by one ranking interval across cost-distance maps (Figure 2-11), indicating that the different friction maps contained similar information related to potential wood frog distribution.

Cost-distance analysis based on the combined friction map supports the suggestion made earlier, on the basis of individual friction maps: few regions of the study area were unlikely to contain wood frogs because of isolation (Appendix A, Figure A4), although animals might be absent at specific sites because of water quality, predators, and other factors. Most of the differences between cost surfaces based on different friction maps are associated with the Athabasca River and nearby areas, and some locations in the centre and northwest portion of the study area (Appendix A, Figure A4).

Cost-surfaces based on the habitat friction map with and without cutblocks, with ponds as the input layer, were very similar. Frequency distribution of cells among cost categories was not significantly different for cost-surfaces with and without cutblocks (ks = 0.1, P = 1.0).

Discussion

Distribution and abundance of water bodies. This study suggests that small ponds and wetlands in the boreal forest can promote connectivity between breeding sites of anuran amphibians due to their prevalence and distribution on the landscape. Small water bodies dominate in the study area: ponds and wetlands less than 1 ha in size represent approximately 35% of the water bodies in the study area, and more than 65% of all water bodies are less than 4 ha in size. A similar pattern was found on the southeastern coastal plain of the USA, where 87.3% of wetlands in a 780 km^2 area were 4.0 ha or less in size (Semlitsch and Bodie 1998). Within a 600 km^2 study area in Maine, USA, Gibbs (1993) found that 61.6% of wetlands were 4.05 ha or less in size. Also within Maine, Calhoun et al. (2003) surveyed 304 vernal pools and found that 67% were less than 0.0399 ha in size.

Predominance of small wetlands across landscapes seems to be a general rule in forested regions of North America.

When ponds less than 4.0 ha are removed from the system, the mean minimum distance between the remaining ponds increases by 2.1 times; distance between wetlands increases by 2.3 times with the loss of 4.0 ha and smaller water bodies. Other studies have found similar effects of the removal of small wetlands on distance between remaining water bodies. Gibbs (1993) found that the distance between neighbouring wetlands increased by 1.7 times with loss of wetlands <4.05 ha; Semlitsch and Bodie (1998) found that nearest neighbour distance increased by 4 times with similar losses of wetlands.

Gibbs (1993) reported that, with the loss of small wetlands, the portion of the landscape within 1 km of a wetland decreased from 90% to 54%. Similarly, I found that the portion of upland within 1000 m of water bodies decreased from 50.3 % to 31.5% with loss of ponds under 4 ha in size, and from 61.5% to 37.1% with loss of wetlands under 4 ha. Thus, loss of small wetlands increases the distance between those water bodies that remain, and reduces the proportion of upland habitats within relatively easy reach of aquatic habitats.

Inclusion of wetlands classified as seasonally flooded in the AVI dataset increased the connectivity between more permanent wetlands, and increased the amount of terrestrial habitat close to a water body by 11.2%. Seasonally flooded, or temporary, wetlands may be used as breeding sites by wood frogs and other anurans, even though they sometimes dry before metamorphs are produced (Griffiths 1997; Babbitt and Tanner 2000; DiMauro and Hunter 2002). Even if these temporary wetlands are not suitable as breeding sites in most years, they can be used as hydration sites for postmetamorphic anurans; I have observed wood frogs in the study area resting in tiny puddles of water along cutlines, trails, and in cutblocks. Different life history stages of amphibians are therefore probably faced with different landscapes, with greater connectivity in the spring when snowmelt has filled seasonally flooded wetlands and adults are moving to breeding sites, and reduced connectivity in the fall, when shallow wetlands may have dried and metamorphs are emmigrating from ponds. Thus, small, more permanent ponds may play a greater role in connectedness during the dispersal of juveniles than for adults.

There are limitations to the AVI data used here because they are based on interpretation of aerial photographs, a process that can severely underestimate the number of wetlands on the landscape. This is particularly true of small, forested wetlands, which are missed during photointerpretation much more often than larger, non-forested wetlands (Gibbs 2000). Calhoun et al. (2003) found that interpretation of aerial photography underestimated the density of vernal pools by 3.5 times in deciduous forest, and by 15 times in mixed wood or evergreen forest. Although 52.8% of the study area consists of stands dominated by deciduous tree species, where wetlands should be more readily detectable, I believe that a large proportion of wetlands were not included in the AVI dataset. During related fieldwork in the study area, I measured a number of small wetlands; mean size was 0.091 ha (range = 0.0046 – 0.72 ha, n = 26). The smallest wetland occurring in the AVI dataset was 0.09 ha, similar in size to some of the wetlands I measured in the field. The presence of undetected small wetlands means that the model I have developed here is conservative and that loss of small wetlands would actually accentuate, rather than reduce, differences between the existing distribution of water bodies and that remaining after the loss of wetlands and ponds as modelled in this study (Semlitsch and Bodie 1998; Gibbs 2000). However, many of the smaller wetlands I measured in the field were present during unusually wet years (1996 and 1997) in the study area (Prepas et al. 2001), but disappeared in 1998 and 1999, when conditions were drier (Eaton, unpublished data). This suggests that modeling the disappearance of small wetlands in response to dry conditions is a realistic reflection of wetland dynamics in the study area.

Increased isolation of water bodies with dry conditions or land-use change has important implications for the gene flow between amphibian populations, and their ability to recolonize ponds left vacant due to local extinctions (Sjögren-Gulve 1994; Russell et al. 2002), a process which appears to be common in some systems (Hecnar and M'Closkey 1996*b*; Skelly et al. 1999). Disappearance of small water bodies in the boreal landscape would, in many cases, result in distances between ponds which exceed the dispersal distances of most individual wood frogs, thereby restricting movement of individuals to new breeding sites.

Loss and protection of small wetlands is currently a controversial topic in the United States, where the federally mandated threshold size for protected wetlands is presently 4 ha. Proposed legislation in the United States would reduce this threshold size to 1.2 ha, a threshold which is still considered too high by some (Kaiser 1998; Semlitsch and Bodie 1998). Additional regulations limiting dredging and filling of vernal pools are in place in some states such as Massachusetts, New Hampshire, Connecticut, and Maine (Paton and Crouch 2002; Calhoun et al. 2003). Gibbs (2000) suggests that all wetlands > 0.4 ha in size must be protected in order to support wetland-dependent biota. In Alberta, wetlands greater than 4 ha with recreation, waterfowl, or sport fishing potential, or those greater than 16 ha without such potential, are protected by 100 m buffer strips during timber harvest (Alberta Environmental Protection 1994).

Although wetland size may be an important factor in determining which water bodies should be protected, Semlitsch and Bodie (1998) argue the local and regional distribution of wetlands may be more critical in maintaining ecological connectivity between physically separated wetlands. Others contend that hydroperiod should be considered when designating protected wetlands, and that wetlands covering the entire hydroperiod spectrum are required to protect amphibian species (Snodgrass et al. 2000; Paton and Crouch 2002). Marsh and Trenham (2001) argue that concentrating on "ponds-as-patches" may be an oversimplification of amphibian metapopulation dynamics, and suggest that the distribution of terrestrial habitats may play a larger role than the distribution of wetlands in influencing the connectivity between populations.

Effect of terrestrial environment on amphibian movement. My analysis, which is based on slope, moisture, and habitat attributes of the landscape, attempts to add realism to the modeling of potential frog movement in the boreal forest of Alberta. The effectiveness of such a model is related to the quality of the spatial data that is used in constructing it, and the actual relationship between the factors used and the response of amphibians to these factors (Ray et al. 2002). For instance, differential habitat use by amphibians has been demonstrated numerous times (Heatwole 1961; Roberts and Lewin 1979; Bennett et al. 1980; Haynes and Aird 1981; Degraaf and Rudis 1990), and wood frog activity is influenced by moisture (Bellis 1962). It is the application of this knowledge to discern large-scale patterns of potential amphibian movement that is challenging.

Cost-distance maps developed in this study based on slope, moisture, and habitat were similar; this concordance between individual friction maps suggests that the three different layers are closely related. For instance, areas of low slope likely have higher soil moisture, which in turn influences the type of vegetation that grows in those areas. Because the three cost maps produced such similar results, it should be possible to perform large scale modeling of potential amphibian distribution using only one of the layers. In this case, the slope map derived from the digital elevation model is probably the best candidate, as construction of this map did not involve interpretation of aerial photographs, or assignment of particular rankings to habitat polygons. However, if there are significant anthropogenic disturbances in an area, they may disassociate relationships between slope, moisture, and habitat by replacing natural vegetation adapted to specific environmental factors with other species (e.g. perennial grasses in cutlines), structures (e.g. roads, houses), or by affecting natural moisture regimes (e.g. draining wetlands). In this case, data on habitat or land use changes might be necessary.

Construction of a relatively simple model of potential amphibian movement, as done here, is the first step in developing a model, which could be used by forest or wildlife managers for reducing the effects of anthropogenic activities, such as logging, on amphibian populations. Because amphibians often respond negatively to clear cuts (deMaynadier and Hunter 1995, 1998), it may be important to assess the potential impact that logging may have on corridors between nearby amphibian breeding sites. In this study, inclusion of cutblocks in the habitat model had very little effect on the predicted movement of wood frogs, possibly because the friction value assigned to the cut areas was not very high. I made no attempt to model responses by different life history stages of wood frogs to the effect of timber harvest, but others have shown that YOY wood frogs (deMaynadier and M. L. Hunter 1999), and other anurans (*Bufo* americanus; Rothermel and Semlitsch 2002) avoid open areas in preference for forest habitat. Therefore, care should be taken in applying the results of my model to actual forest management practices without first conducting preliminary investigations in the field; this is even more important when considering species other than the wood frog, as the model created here may not transfer well to species with different habitat requirements.

In the study area the impact of timber harvesting on wood frogs is probably transitory: harvest stands of mature (70-100 years old) aspen are allowed to regenerate naturally (Constible et al. 2001; Hannon et al. 2002), with sucker growth from stumps and roots rapidly re-establishing cover within cutblocks (Eaton, personal observation). Hannon et al. (2002) found that wood frog abundance in riparian forest buffer strips (20, 100, 200, or 800 m wide) around 12 boreal mixedwood lakes (4 of which were in my study area) did not change after timber harvest, probably because the wood frog in this region is a resilient habitat generalist.

Although large-scale maps may be useful for constructing predictive models of factors influencing amphibian distribution (Knutson et al. 1999), it is not only the proximity of water bodies to one another, or the ability of amphibians to move through intervening habitat to reach them that may be important. Some workers have reported that individual ponds differ in their quality as breeding sites (Saber and Dunson 1978; Rowe and Dunson 1993; Richter and Azous 1995, Hecnar and M'Closkey 1996*a*; Paton and Crouch 2002). In the boreal mixedwood we have no evidence that specific physical or chemical characteristics of individual water bodies have any impact on breeding effort. However, in larger water bodies the presence of fish may influence abundance of YOY anurans (Chapter 3). Therefore, at a local scale, the characteristics of the wetland may be an important factor for making management decisions. Combination of assessment of local conditions (wetland suitability, surrounding habitat) with landscape-scale estimates of factors affecting amphibian distribution (distribution of wetlands, character of terrestrial habitat between wetlands) would forge a powerful management tool for use in conserving amphibians and their habitat.

Implications for amphibian distribution. My study suggests that removal of small wetlands, through drought or anthropogenic disturbance, may hinder the ability of wood frogs to disperse across the landscape to found new populations or provide gene flow between existing populations. Wood frogs are highly philopatric as adults (Berven and Grudzien 1990), returning to breed in the same water body year after year. Catastrophic reproductive failure may occur in some years due to pond drying (DiMauro and Hunter 2002; personal observation). Wood frogs live a maximum of four to five years in populations in southern Quebec (Bastien and LeClair 1992; Sagor et al. 1998), and five years in boreal Alberta (Stoyanowski 1999). Thus, populations of wood frogs might be able to persist for up to five years without successful reproduction in the total absence of immigration of individuals from other populations.

Little is known about movement of individual wood frogs in northern regions. Wood frogs in other regions are known to move long distances (Berven and Grudzien

1990; Newman and Squire 2001), but how commonly this occurs is unknown; long-distance movements probably occur more often than has been documented (Koenig et al. 1996; Marsh and Trenham 2001). Gibbs (1993), using a simple metapopulation model, suggested that amphibians were able to maintain populations in a simulated configuration of large and small wetlands because of the ability of one female to produce large numbers of eggs. Therefore, only a small number of animals would be needed to establish a viable population at a new breeding site, or to provide gene flow. Indeed, genetic work suggests that high gene flow occurs between wood frog populations at neighbouring ponds, with little genetic differentiation at distances < 1 km, and some differentiation emerging when populations are separated by 3 km (Newman and Squire 2001).

More basic life history data are urgently needed for many amphibians if we are to effectively conserve these species. For example, we know that wood frogs in the study area will breed in water bodies ranging from small, ephemeral wetlands to large, permanent lakes. However, some of the larger water bodies contain fish; of 102 water bodies sampled in boreal Alberta (ranging in size from 1.7 to 362 ha), 52% contained non-piscivorous fish, 27% contained piscivorous fish, and 21% were fishless (W. Tonn, unpublished data). At present the impact of fish, including small-bodied, non-piscivorous species, on anuran populations in boreal Alberta is not fully understood (Chapters 3 and 4). If fish presence influences survival of anuran larvae to metamorphosis, it may be an important consideration in management decisions related to amphibian conservation at specific water bodies in the region. However, until more detailed information is available, broad-scale approaches such as described here in this study can provide useful insight on the potential impact of environmental factors (e.g. drought) and human activities (e.g. logging) on amphibian distribution (Ray et al. 2002; Semlitsch 2002).

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Table 2-1. Habitat rankings for the AVI data used in the analysis. Rankings were generally based on the dominant tree species (in terms of canopy closure) within a polygon. In instances where canopy closure was < 6% for a polygon, other parameters were used to assign rankings; see text for details. A ranking of 1 is assigned to polygons considered the easiest for wood frogs to traverse, while a ranking of 10 is given to polygons most difficult for wood frogs to move across.

Parameter	Assigned ranking (see text)
Water (wetlands)	1
Trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), paper birch (*Betula papyrifera*)	2
Bryophytes, herbaceous vegetation (forbs and natural grassland), closed shrubs	3
Tamarack (*Larix laricina*)	4
Open shrubs	5
Annual crops; transmission lines, pipelines, well sites, etc., seeded to perennial grass, perennial forage crops for livestock	5
Farmsteads	5
White spruce (*Picea glauca*), black spruce (*P. mariana*), balsam fir (*Abies balsamea*)	7
Jack pine (*Pinus banksiana*)	10
River and associated sandbanks	10
Gravel pits, roads, industrial sites	10

Table 2-2. Moisture rankings for the AVI data used in the analysis. Rankings were based on the moisture regime parameter when it was applied to a polygon. In instances where no soil regime was available for a polygon, other parameters were used to assign rankings; see text for details. A ranking of 1 is assigned to polygons considered the easiest for wood frogs to traverse, while a ranking of 10 is given to polygons most difficult for wood frogs to move across.

Parameter	Assigned ranking (see text)
Moisture regime - wet or aquatic	1
Naturally non-vegetated - ponds / lakes, flooded areas, Athabasca River (includes sandbanks associated with the edges of the river)	1
Anthropogenic vegetated – annual crops	3
Moisture regime - mesic	5
Anthropogenic vegetated - perennial grass or crops (well sites, pipelines, pasture, etc.)	5
Anthropogenic non-vegetated – farmsteads	5
Moisture regime - dry	10
Anthropogenic non-vegetated - gravel pits, roads, industrial activity	10

Figure 2-1. Location of study site in Alberta.

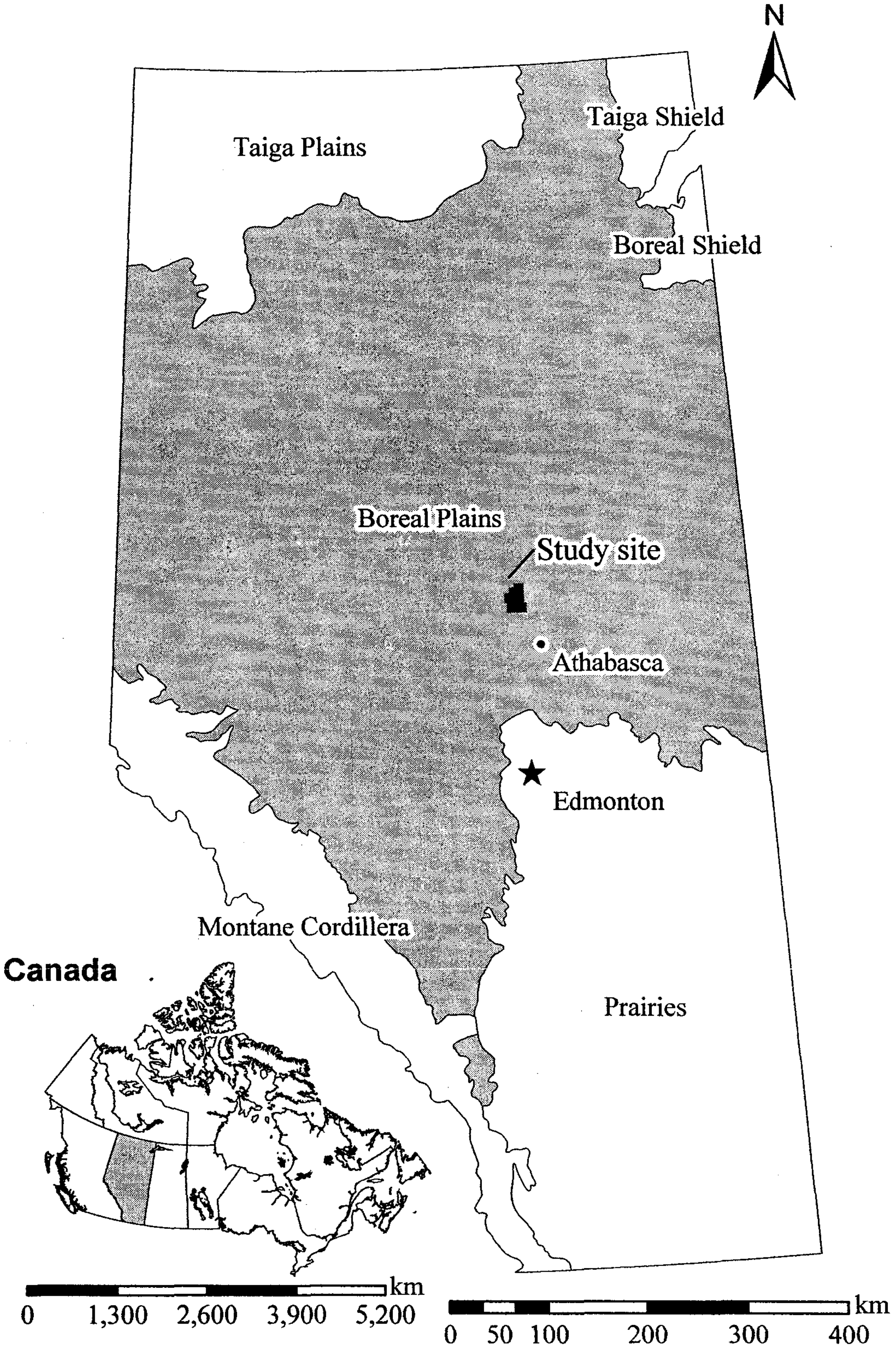


Figure 2-2. Study area with (A) ponds, and (B) all wetlands.

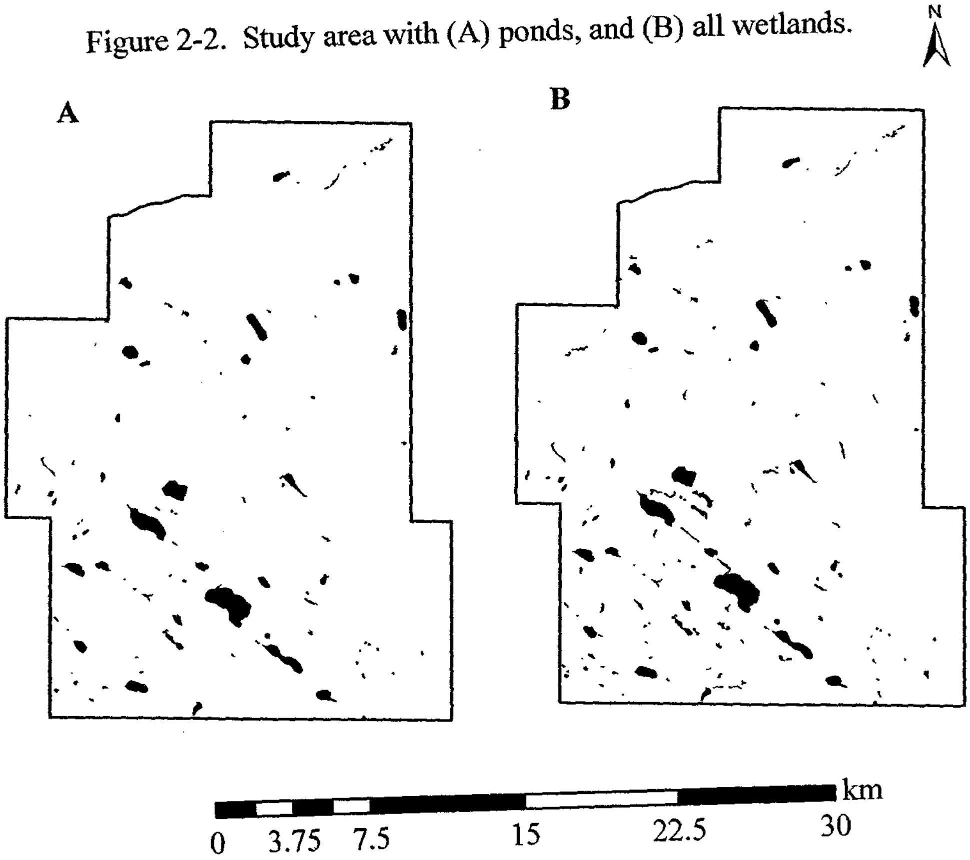


Figure 2-3. Frequency distribution of water bodies in study area by size. Class 1 includes those water bodies less than 1 ha in area, class 2 those greater than or equal to 1 ha and less than 2 ha, etc. Ponds are water bodies that rarely dry; temporary wetlands are those classified as seasonally flooded in the Alberta Vegetation Inventory dataset. Entire bar represents total number of all wetlands in that size class.

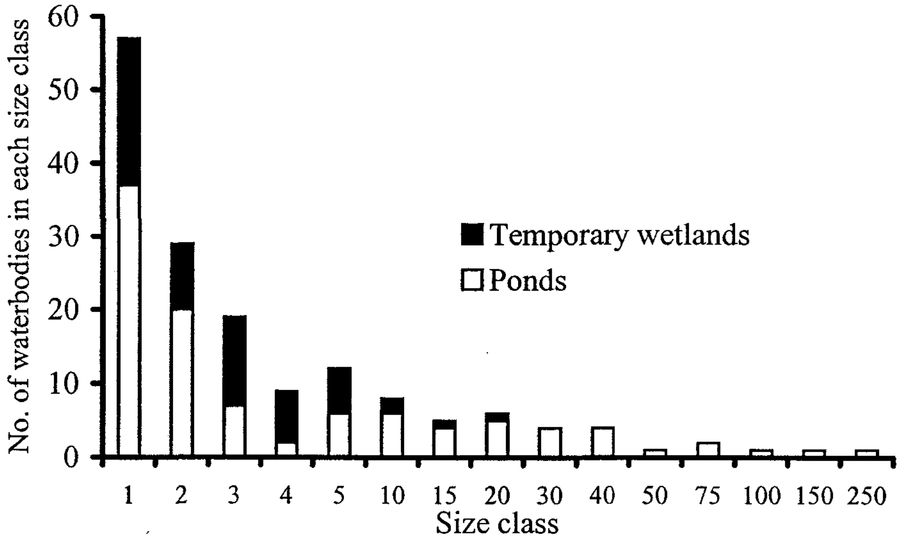


Figure 2-4. Area represented by water bodies of a given size class within the study area. Class 1 includes those water bodies less than 1 ha in area, class 2 includes those greater than or equal to 1 ha and less than 2 ha, etc. Ponds are water bodies that rarely dry; temporary wetlands are those classified as seasonally flooded in the Alberta Vegetation Inventory dataset. Entire bar represents total number of all wetlands in that size class.

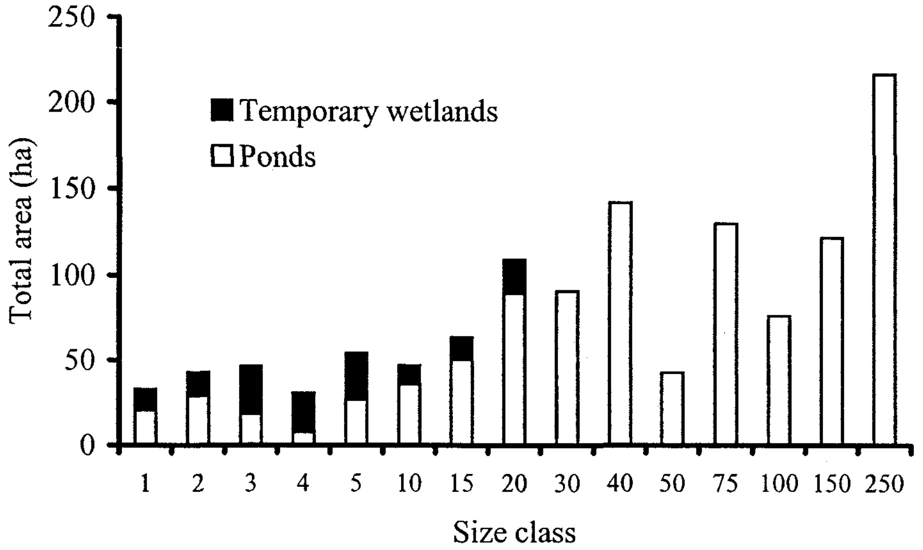


Figure 2-5. Mean minimum distance between water bodies for simulation of removal of small waterbodies. Class 0.5 includes those water bodies 0.5 ha in area or smaller, class 1 includes those to 1 ha, etc. See text for definitions of ponds and wetlands. The dashed line denotes the 1000 m mean distance between water bodies.

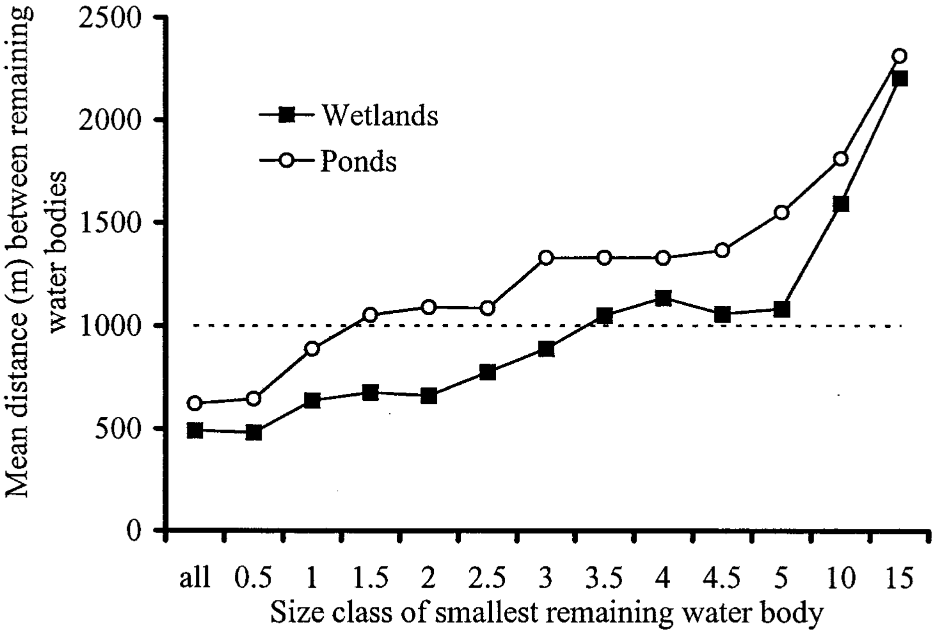


Figure 2-6. Percentage of total landscape within 1000 m of a water body as water bodies on the landscape disappear. Class 0.5 includes those water bodies 0.5 ha in area or smaller, class 1 includes those from 0.5 ha to 1 ha, etc. See text for definitions of ponds and wetlands.

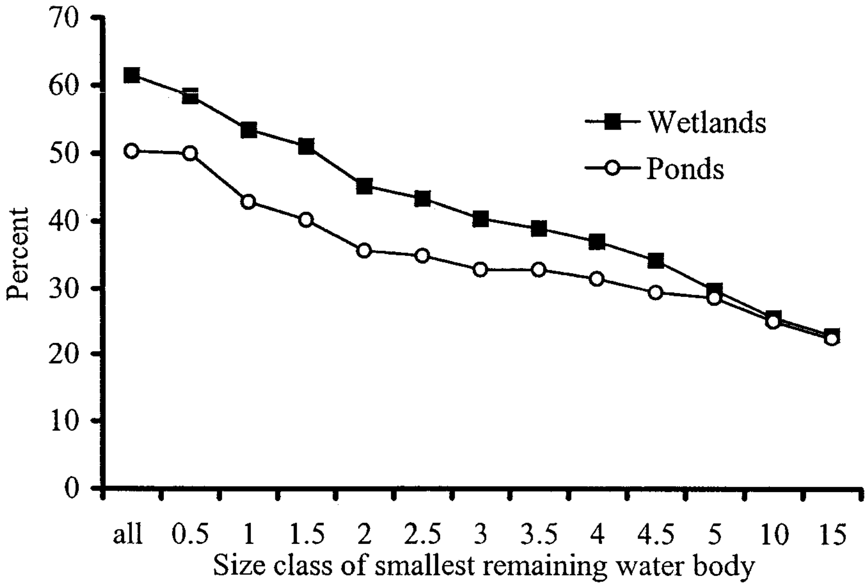
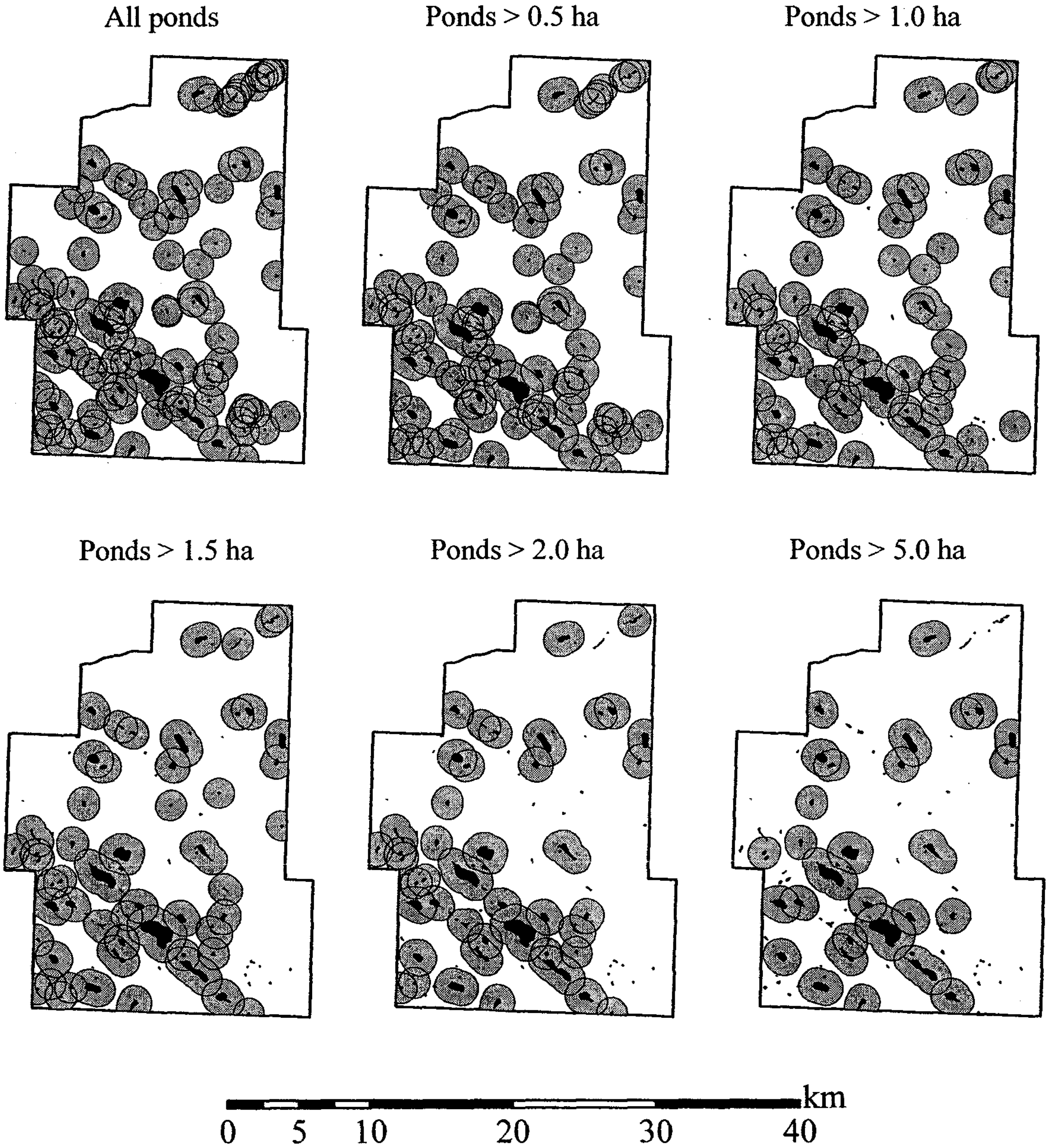


Figure 2-7. Results of placing 1000 m buffers around ponds. The minimum size of ponds that remain in the coverage is indicated on each panel. Ponds are shown in black, buffers in gray. All ponds are shown in each panel to indicate where connectivity has been lost.



All ponds

Ponds > 0.5 ha

Ponds > 1.0 ha

Ponds > 1.5 ha

Ponds > 2.0 ha

Ponds > 5.0 ha

Figure 2-8. Results of placing 1000 m buffers around wetlands. The minimum size of wetlands that remain in the coverage is indicated on each panel. Wetlands are shown in black, buffers in gray. All wetlands are shown in each panel to indicate where connectivity has been lost.

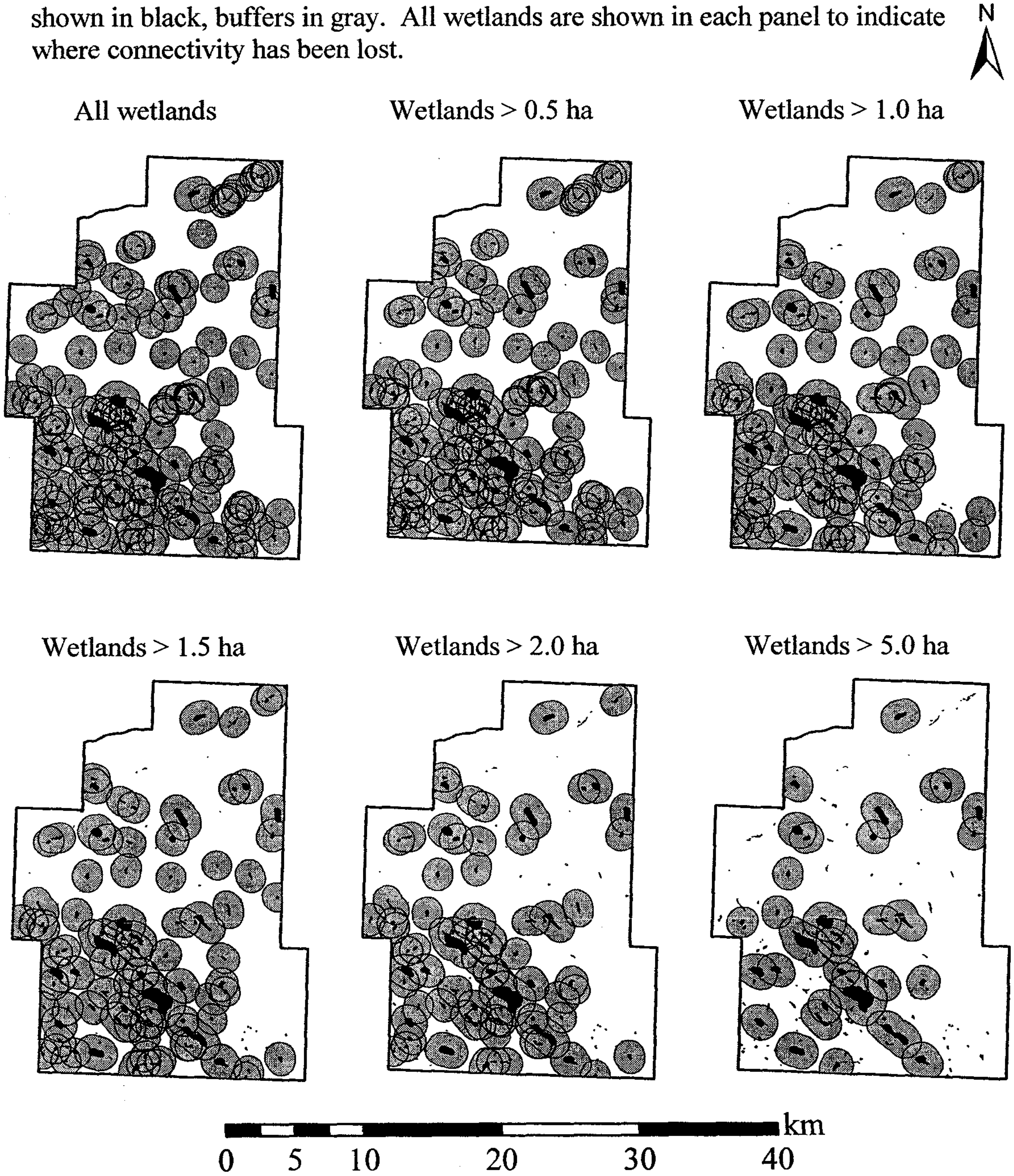


Figure 2-9. Input raster surfaces for slope, moisture, and habitat. All three surfaces have cell values from 1 to 10, with 1 being the most amenable to wood frogs.

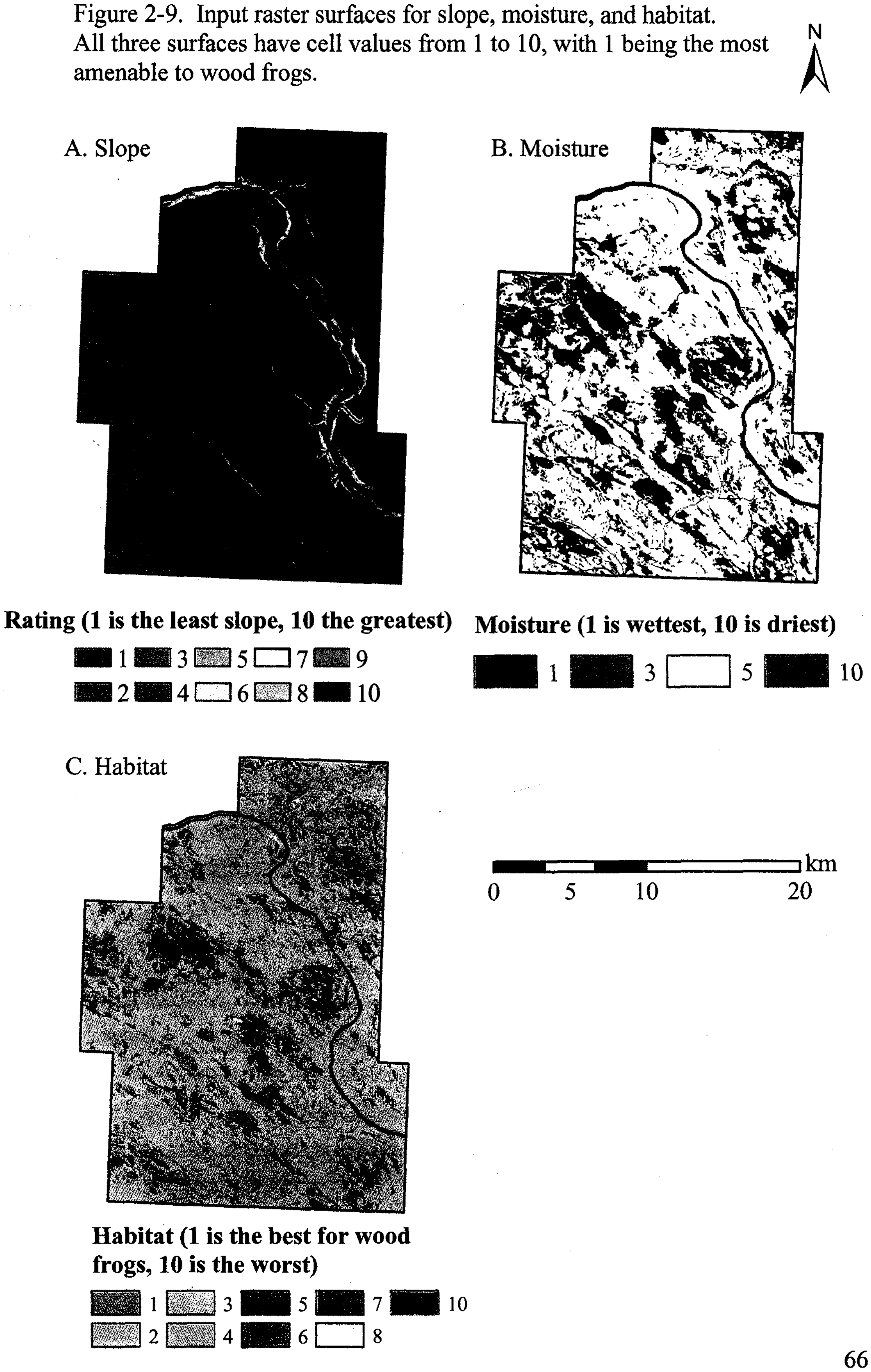


Figure 2-10. Distribution of friction ratings for cells based on different cost surfaces used in modelling potential wood frog movement. Cost surfaces were based on (A) moisture rankings, (B) slope, and (C) habitat rankings. Higher numbers indicate greater difficulty for wood frogs to cross a cell. See text for definitions of ponds and wetlands.

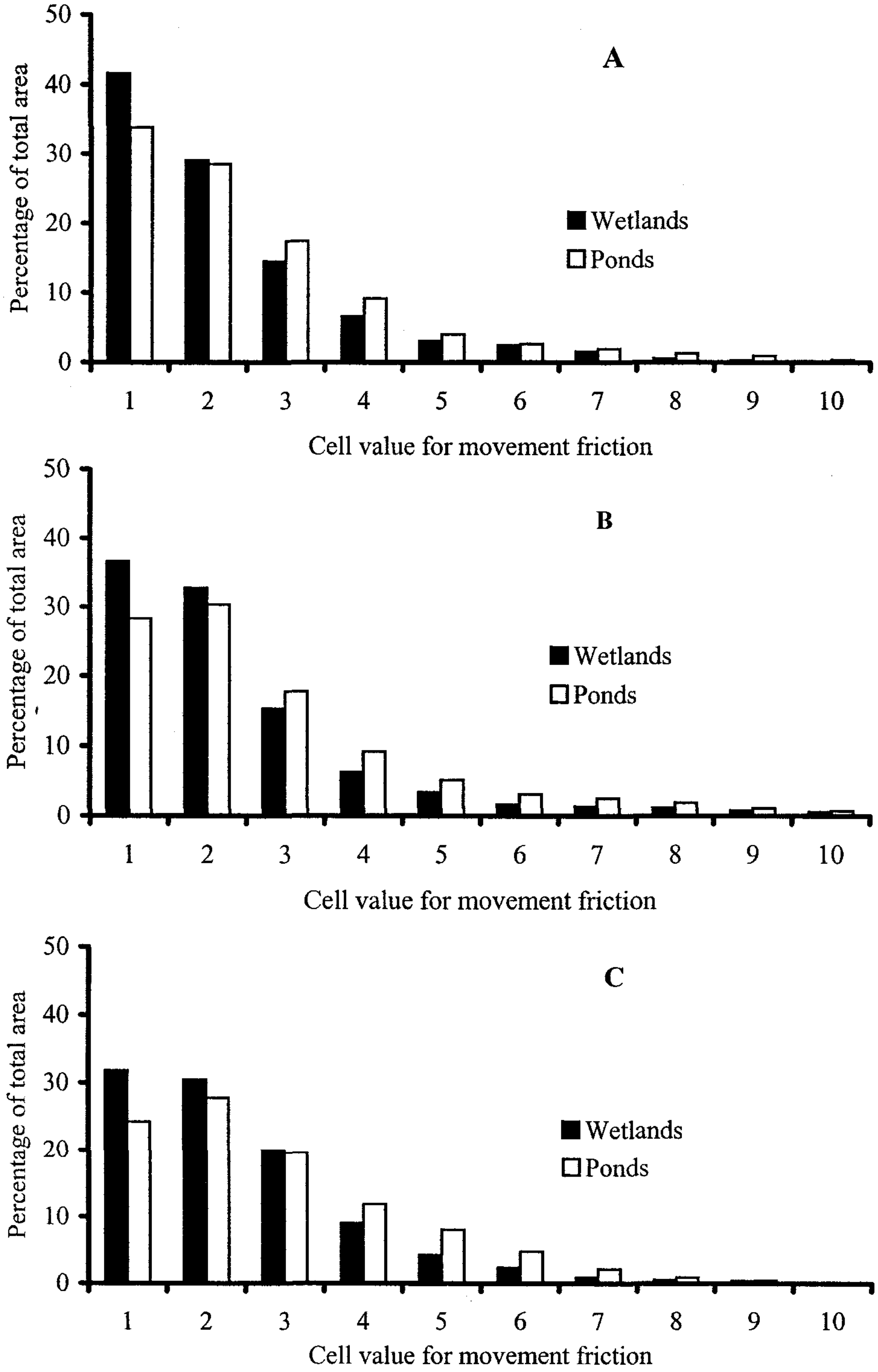
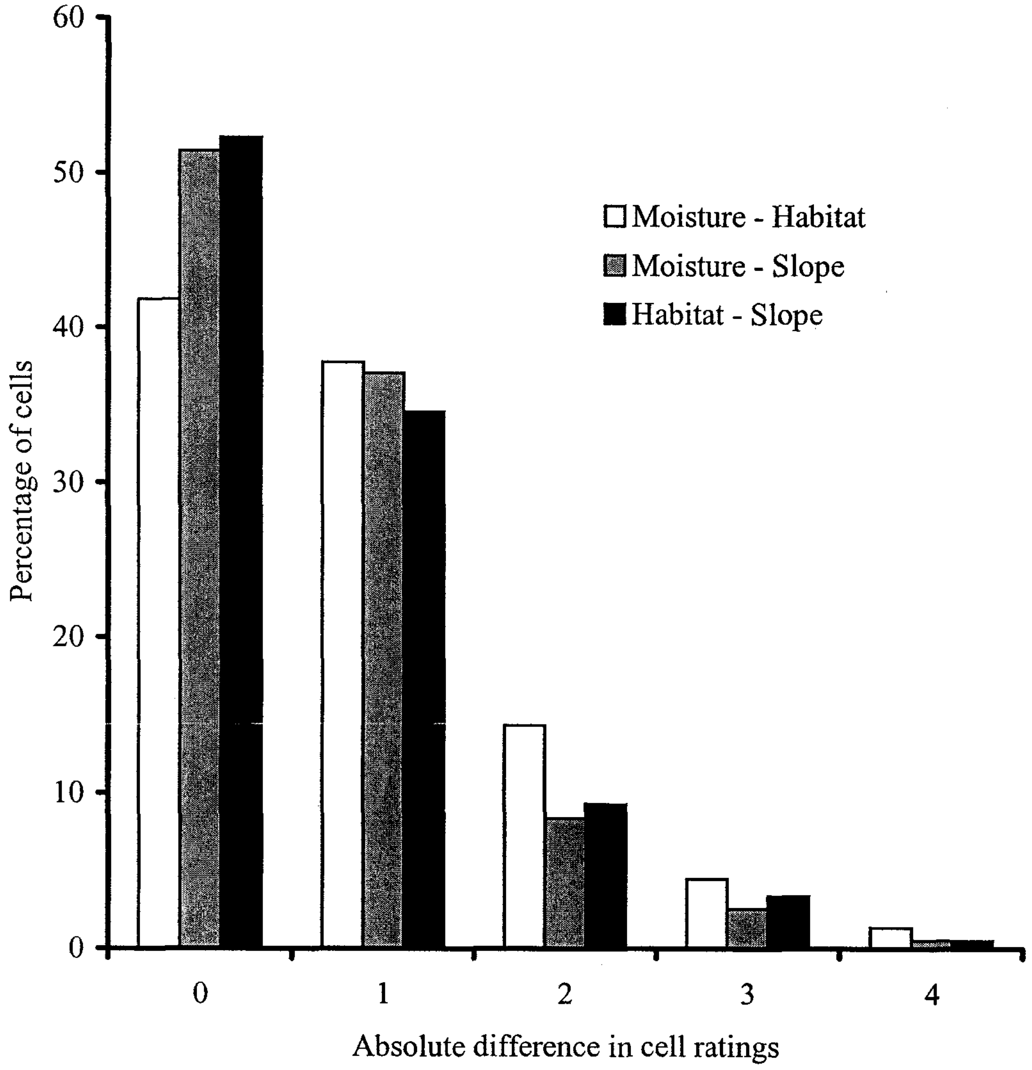


Figure 2-11. Pairwise differences between cost surfaces derived from simulations using different factors (moisture, habitat, slope) that potentially influence movement costs for wood frogs . Costs for each surface were ranked from 1 to 10, with 1 as the most amenable to wood frogs, before the cost surfaces were compared. Differences in cell ratings of 5 or 6 were less than 0.25% for each pairwise comparison, and are not shown on the figure.



CHAPTER 3: Fish winterkills shape amphibian recruitment in boreal lakes

Introduction

In temperate North America, amphibian distribution, metapopulation dynamics, and life history strategies have been largely shaped by two interacting factors: permanence of aquatic habitats and the presence of aquatic predators (Wellborn et al. 1996). In permanent aquatic habitats, the most important predators are fish (Wellborn et al. 1996); not surprisingly, the introduction of fish into previously fishless waters has been identified as one factor behind recent declines in amphibian populations (Hecnar and M'Closkey 1997, Alford and Richards 1999). Such introductions into breeding lakes can extirpate local amphibian populations (Bradford 1989, Knapp and Matthews 2000), and the presence of fish in rivers can prevent amphibians from dispersing between lakes (Bradford et al. 1993).

Interactions between amphibians and fish have been examined both in short-term, small-scale experiments and as landscape-level patterns of co-occurrence. Experimental work suggests that adult amphibians may avoid ovipositing in water bodies containing predatory fish (Resetarits and Wilbur 1989, Hopey and Petranka 1994), and that amphibian larvae often decrease their foraging when exposed to predatory fish (Holomuzki 1995, Eklöv and Werner 2000), resulting in slower growth and smaller size (Lawler 1989, Figiel and Semlitsch 1990). Large-scale surveys of fish and amphibian distribution indicate that some amphibians are rarely found in the presence of predatory fish, especially non-native fish species (Alford and Richards 1999), although the same amphibians may co-occur with non-predatory fish species (Hecnar and M'Closkey 1997).

Over a 5-year period, I quantified the dynamics of native fish and amphibian populations from 12 small lakes in the boreal forest of Alberta, Canada to examine relationships between these two groups in a natural, large-scale setting. Fish communities in the study lakes were characterized by either large-bodied, predominantly piscivorous species, or small-bodied species (Paszkowski and Tonn 2000; see below). Lakes in this region are naturally productive and relatively shallow and, when combined with the long boreal winters, are subject to under-ice oxygen depletion that can cause substantial fish kills (Cooper and Washburn 1949, Casselman and Harvey 1975). I asked the following questions: (1) Is abundance of amphibian metamorphs emerging from boreal lakes related to fish abundance, and more specifically, can amphibian populations respond to fish winterkills with pulses of recruitment? (2) Does the type of fish community influence the response of different amphibian species to changes in fish abundance?

Materials and methods

Of the twelve study lakes, four were located in each of three roadless regions within the aspen-dominated mixedwood forest of northern Alberta [Lac La Biche (LLB), South Calling Lake (SCL), and South Pelican Hills (SPH)]. The approximate locations of the three regions are: LLB - 55.2° N, 111.7° W; SCL – 55.1° N, 113.7° W; SPH – 55.3° N, 113.7° W. Within a region, inter-lake distances averaged 5.64 km (range: 1.8 – 12.2). Access to all lakes was limited to all-terrain vehicles. Mean area of study lakes was 66.9 ha (range: 13.8 – 156.5), mean maximum depth was 5.3 m (range: 2.0 – 11.2), and mean total phosphorus was 56.2 µg/L (range: 24.0 – 132.0) (see Prepas et al. 2001).

Five lakes were characterized by fish assemblages containing large-bodied piscivores, northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*), along with the benthivorous white sucker (*Catostomus commersoni*). Six lakes contained assemblages of small-bodied species, comprising combinations of fathead minnow (*Pimephales promelas*), brook stickleback (*Culaea inconstans*), and finescale dace (*Phoxinus neogaeus*). One lake was naturally fishless. Amphibian species consisted of the wood frog (*Rana sylvatica*), western toad (*Bufo boreas boreas*), and Canadian toad (*B. hemiophrys*). The striped chorus frog (*Pseudacris maculata*) was also present, but was not included in analyses because it could not be monitored reliably.

Fish and amphibian abundance were monitored from 1995 to 1999 using standard trapping methods, and abundance estimates were standardized by sampling effort. After initial surveys to determine community type, fish abundance was estimated in lakes dominated by piscivorous and small-bodied fish using gillnets and minnow traps, respectively. Gillnets were benthic survey nets of 14 panels, 3 m x 1.5 m, with mesh sizes ranging from 6 to 75 mm (Lundgrens Fiskeredskup, Stockholm, Sweden); minnow traps were standard Gee traps with 6-mm wire mesh (Nylon Net Company, Memphis, Tennessee). Gear was set overnight (ca. 18-20 hrs) at random locations stratified by depth. Fish captured in gill nets were weighed and measured (total length); fish captured in minnow traps were simply counted. Population estimates for fish in piscivorous lakes were standardized as biomass per unit effort (BPUE: kg fish captured / hr), as individuals of these species vary greatly in body size and predatory impact. The small-bodied fish species captured in minnow traps vary little in body size, therefore, catch per unit effort (CPUE: number of fish captured / hr) is a direct index of abundance. Fish were sampled from May 11 to October 1, with most gillnetting effort in July-August and most minnow trapping in May – June. Gillnetting effort averaged 184 net hrs/lake/yr (range: 68.7 – 346.1) and minnow trapping averaged 2013 trap hrs/lake/yr (range: 145.5 – 5165.3); effort was adjusted by lake size.

Amphibians were sampled around each lake with two grids of pitfall traps and drift-fences. Each grid contained three lines of traps that paralleled the lakeshore. One line was located at the edge of the untreed riparian zone, while the second and third were located 50 and 100 m upslope from the first. Each line contained five sets of three pitfall traps joined by two 5-m lengths of plastic drift fence to form a “V”. A pitfall trap consisted of a metal can (25.5 cm deep, 15.5 cm diameter) buried to its rim with a plastic margarine container (with a 10 cm diameter opening cut in the bottom) inside, acting as a funnel. Upright sticks placed in traps provided escape routes for small mammals. Pitfall traps were checked approximately every two days; captured amphibians were identified, assigned to an age class (young-of-the-year (YOY) or adult), weighed, measured (snout-to-urostyle length), marked, and released. Captures were standardized as the number of new individuals captured / 100 trap nights. Amphibians were trapped July 14 - September 2, with most trapping occurring in August so as to sample YOY emerging from study lakes. Trapping effort averaged 553.6 trap nights/lake/yr (range: 299 to 1533).

Statistical analyses

Abundance estimates for each fish species were combined to determine total fish abundance within each study lake. Abundance estimates of newly metamorphosed YOY amphibians were determined for all species combined, and separately for YOY wood frogs and toads; YOY were used because we expected amphibians in the aquatic larval stage, rather than as adults, to be strongly affected by fish, and emergence of metamorphs represents an important ecological milestone for recruiting juveniles (Berven 1990). Data from both *Bufo* species were combined because they are ecologically similar and study sites included both sympatric and allopatric populations (Eaton et al. 1999, Russell and Bauer 2000). In years where no fish or amphibians were captured at a lake, but were previously or subsequently captured at the same site, a value of 0.001 was assigned to indicate low abundance and avoid division by zero in analyses (see below).

To standardize changes in fish (BPUE or CPUE) and amphibian (CPUE) abundance over time, I calculated an Index of Population Change (IPC) for fish and amphibian populations using the formula $IPC = \ln(N_{t+1}/ N_t)$, where N_t and N_{t+1} are estimated abundance in years t and t+1, respectively (Cooper et al. 1990, Osenberg et al. 1997). IPCs were usually calculated using data from consecutive years for both fish and amphibians; when a group was not sampled for a given lake-year (e.g., fish in six lakes in 1997), IPCs were calculated for the closest two years for which data were available for both fish and amphibians (e.g., 1996 and 1998). A positive IPC indicates an increase in abundance between estimates, a negative IPC reflects decreased abundance.

Concordance of changes in fish and amphibian abundance was quantified by totaling the number of cases in which corresponding IPCs had the same or opposite signs, reflecting population changes of fish and amphibians in the same or opposite directions over a given time period for a given lake. These totals were compared to a binomial distribution that assumed equal likelihood for coincident or opposite changes.

Comparisons were done separately for five lakes containing piscivorous fish, and six lakes with small-bodied fish; the single fishless lake (LLB_2) was not included in these analyses. Within each lake type, comparisons were done for all YOY amphibians combined, and for toads and frogs separately. Because relatively small increases and decreases in fish abundance, unlikely to affect amphibian populations, will still produce IPCs with positive and negative signs, respectively, a second, more restrictive analysis was done to examine amphibian response to large changes in fish abundance. This analysis included only lake-year pairs where fish $|IPC| > 1$.

Results

Fish populations were relatively variable in most lakes, but winterkill, caused by under-ice hypoxia, produced several dramatic decreases in fish abundance during the course of this study. Fish kills resulting in fish abundance approaching zero were recorded for LLB_3, LLB_4, and SCL_4 in winter 1995-96, for SPH_4 likely in 1996-97 (W. Tonn et al., unpublished data), and for SCL_3 and SCL_4 in 1998-99. Total abundance of metamorphic amphibians increased dramatically in the summer following winterkills in both LLB lakes and moderately in the two SCL lakes, but not at all for SPH_4 (Figure 3-1). Fish recoveries in these winterkill lakes were typically modest, at best, in the short term, and were not accompanied by large changes in amphibian abundance. In SCL_4, however, strong fish recovery in the second post-winterkill year corresponded with decreased amphibian abundance in 1998 (Figure 3-1). A large change in amphibian recruitment (increase in total abundance > 10 YOY / 100 trap nights) independent of a fish winterkill occurred in only one case (SCL_2 in 1997; Figure 3-1). Substantial fish kills occurred in

SCL_1 in winter 1995-96, and LLB_1 in winter 1997-98; no marked response in amphibian recruitment accompanied either of these partial winterkills, possibly because fish abundance remained high relative to the more severe winterkills listed above (Figure 3-1).

A total of 26 lake-year pairs were used in IPC analyses for all YOY amphibians combined, and 15 and 26 lake-year pairs for the separate toad and frog analyses, respectively. Overall, frog, toad, and total amphibian abundance did not respond consistently to changes in abundance of piscivorous or small-bodied fish ($P > 0.15$ in all cases). Nevertheless, opposite changes in abundance, including amphibian responses to both decreased and increased fish abundance, occurred in five of seven cases for toads in piscivorous-fish lakes, and in 11 of 17 cases for frogs in lakes with small-bodied fish (Figure 3-2).

The more restrictive analyses, involving only those lake-year pairs where fish $|IPC| > 1$, included 12 lake-year pairs for all YOY amphibians combined, 10 for toads only, and 12 for frogs only. Total amphibian abundance did not respond significantly to large changes in either piscivorous or small-bodied fish abundance ($P > 0.10$ for both lake types). However, toad abundance responded inversely to large changes in piscivorous fish abundance in four of four cases ($P = 0.06$), but showed no response to small-bodied fish ($P = 0.98$; Figure 3-2). In constrast, wood frog abundance responded oppositely to large changes in small-bodied fish abundance in seven of eight cases ($P = 0.04$), but did not respond to piscivorous fish abundance ($P = 0.69$; Figure 3-2).

Discussion

Under-ice consumption of dissolved oxygen varies among lakes as functions of lake productivity and depth (Barica and Mathias 1979), and differences among lakes in the frequency of winterkills likely contribute to the occurrence of different fish communities in boreal Alberta (Robinson and Tonn 1989) and elsewhere (Tonn and Magnuson 1982). Although the probability of a fishkill in a particular lake in a particular winter is related to factors such as water level, length of the ice-covered period, and thickness and quality of the ice and snow (Greenbank 1945, Cooper and Washburn 1949), fish winterkills are not easily predicted by limnologists, nor likely by amphibians. The anuran species in my study are disconnected from lakes in winter, since all three complete their larval development in a single summer and hibernate in the surrounding terrestrial landscape (Russell and Bauer 2000). Therefore, the recruitment responses we documented following fish winterkills may reflect one of two scenarios: 1) each spring, adult amphibians assess sites for the presence of fish and breed preferentially in water bodies that have low or no fish populations (Resetarits and Wilbur 1989, Kats and Sih 1992, Hopey and Petranka 1994), or 2) amphibians breed in lakes indiscriminately (Laurila and Aho 1997), but mortality of larvae is high in lakes supporting fish, except in years following winterkills.

Many amphibians show high philopatry, with adults returning to breed at the same site every year, and most metamorphs return to their natal sites to breed as adults (Marsh and Trenham 2001). Wood frogs breed synchronously over short time periods in early spring, shortly after ice out, a behavior thought to reduce cannibalism (Petranka and

Thomas 1995). Thus, female wood frogs may not have sufficient time to sample multiple potential breeding sites before ovipositing. These factors, combined with the presence of at least some YOY amphibians at all lakes in every year, tend to support the second scenario, that amphibians breed in the study lakes regardless of the presence of fish. Qualitative spring surveys in LLB lakes also document the occurrence of adult anurans in the presence of abundant fish (S. Boss, University of Alberta, personal communication).

In the semi-arid western Canadian boreal forest, lakes offer physically dependable breeding habitats, but typically contain fish, albeit at variable densities, so are associated with significant predation risk. A promising alternative on the landscape might be the more numerous small waterbodies (e.g., of 109 waterbodies > 0.1 ha in the 500 km^2 South Calling Lake region, 36.7% are < 1 ha, and 76.2% are < 10 ha). The smallest of these ponds (< 1 ha, < 1 m deep) are generally fish-free, but may also dry prior to larval metamorphosis or may even hold no water at all during drought years (B. Eaton, personal observation). Larger waterbodies that are fishless, such as LLB_2 (14 ha, 6 m deep), would seem to offer a good compromise, but these sites are rare and may have higher concentrations of large invertebrate predators than lakes with fish (Wellborn et al. 1996). Thus, because fish winterkills are relatively frequent in this landscape, the resulting reduction in predation by fish and subsequent boom in recruitment of YOY may keep it profitable for amphibians to breed in fish-bearing yet winterkill-prone lakes. An increase in invertebrate predators, themselves released from fish predation in years following severe winterkills (Bradford et al. 1998, Smith et al. 1999, Zimmer et al. 2000), may however, explain why booms in amphibian recruitment are transient.

Large changes in fish abundance in my study lakes caused by winterkill affected recruitment of both bufonids and ranids, but effects depended on fish community composition. Strong responses by toads occurred in lakes with piscivorous fishes, whereas wood frogs responded to changes in the abundance of small-bodied fishes. This pattern could reflect the fact that the two fish community types typically occur in lakes with different habitat features, i.e., lakes with piscivorous fish tend to be larger and deeper than lakes with only small-bodied species (Robinson and Tonn 1989, Paszkowski and Tonn 2000). Thus, it could be that the positive response of toads to winterkill on lakes with piscivorous fish, but not with small-bodied species, reflects an underlying preference for and, therefore, greater baseline abundance of toads on larger, deeper lakes, regardless of fish community. In turn, wood frogs may prefer smaller, shallower lakes. Preliminary analyses did not, however, indicate any clear differences between the two lake types in the number of adult toads or wood frogs during the breeding season (B. Eaton and C. Paszkowski, unpublished data).

An alternative explanation for the observed dichotomy is that it directly reflects differences in predatory capabilities between large- and small-bodied fishes, and the relative palatability of adult anurans. Breeding wood frogs appear vulnerable to piscivorous fish, whereas toads may be protected by repellent bufotoxins (Flier et al. 1980). Predation, or the threat of predation, on adult frogs might hold breeding populations at low levels or limit the number of "safe" breeding sites within piscivorous lakes during non-winterkill years, limiting the ability of frog populations to respond significantly to declines in the abundance of large-bodied fish. Longer-lived, more fecund, and noxious toads may be better adapted to exploit winterkills in lakes with piscivorous fish. On the other hand, although adult wood frogs are not likely vulnerable to predation by small-bodied fishes, pond experiments demonstrate that fathead minnows can have significant impacts on wood frog tadpoles (see Chapter 4), explaining the increases in frog recruitment following winterkills in the small-fish lakes.

Observed responses in the recruitment of wood frogs, but not of toads, to small-bodied fish abundance in part reflected differences in the regional distribution of the two species. Toads were never as common as wood frogs, especially in the SCL and SPH regions, where five of the six lakes with small fish occurred. During the breeding season, mean captures of adult wood frogs averaged 14 and 36 times higher than toad captures at SCL and SPH lakes, respectively, but only 4 times higher than toads at LLB lakes (B. Eaton and C. Paszkowski, unpublished data). Because adults appear safe from predation by small minnows and sticklebacks, breeding wood frogs can persist in all regions at sufficient densities to capitalize on occasional winterkills. Wood frog larvae may, in turn, eat toad eggs and larvae (Petranka et al. 1994), thereby suppressing toad populations in years with high wood frog recruitment.

In years when fish abundance is low, winterkill lakes may serve as sources of recruiting juveniles that disperse to found or augment populations in smaller water bodies; when fish abundance is high, the same lakes may be temporary population sinks if breeding adults are philopatric without regard to fish densities. Thus, although stocked populations of fish can produce catastrophic effects on naïve amphibian populations, we propose that native fish populations and unpredictable, but frequent, winterkills influence the structure and dynamics of amphibian metapopulations on the boreal landscape. As periodic winterkills may be important in some areas for the recruitment of large numbers of juveniles to local anuran populations, the management of native, as well as introduced, fish stocks should be integrated into conservation strategies for amphibians (Semlitsch 2000).

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Figure 3-1 (see figure on next page). Fish and amphibian abundance estimates in lakes from three regions in boreal Alberta with piscivorous fish, small-bodied fish, or no fish. Abundance estimates for fish are in biomass per unit effort (BPUE, kg of fish / hr of netting) for lakes with piscivorous fish, and in catch per unit effort (CPUE, number of individuals captured / hr of trapping) for lakes with small-bodied fish, and as number of captures per 100 trap nights for YOY amphibians. Line and points, total fish abundance; open bars, YOY wood frog abundance; grey bars, YOY toad abundance; † fish present at low abundance; ‡ YOY amphibians present at low abundance; * no amphibians captured. Note that amphibians were not sampled at any of the SPH lakes in 1995, or at SCL_1 and SCL_2 in 1999. Fish were not sampled at LLB_2, LLB_3, or any of the SPH lakes in 1997.

Figure 3-1. See previous page for legend.

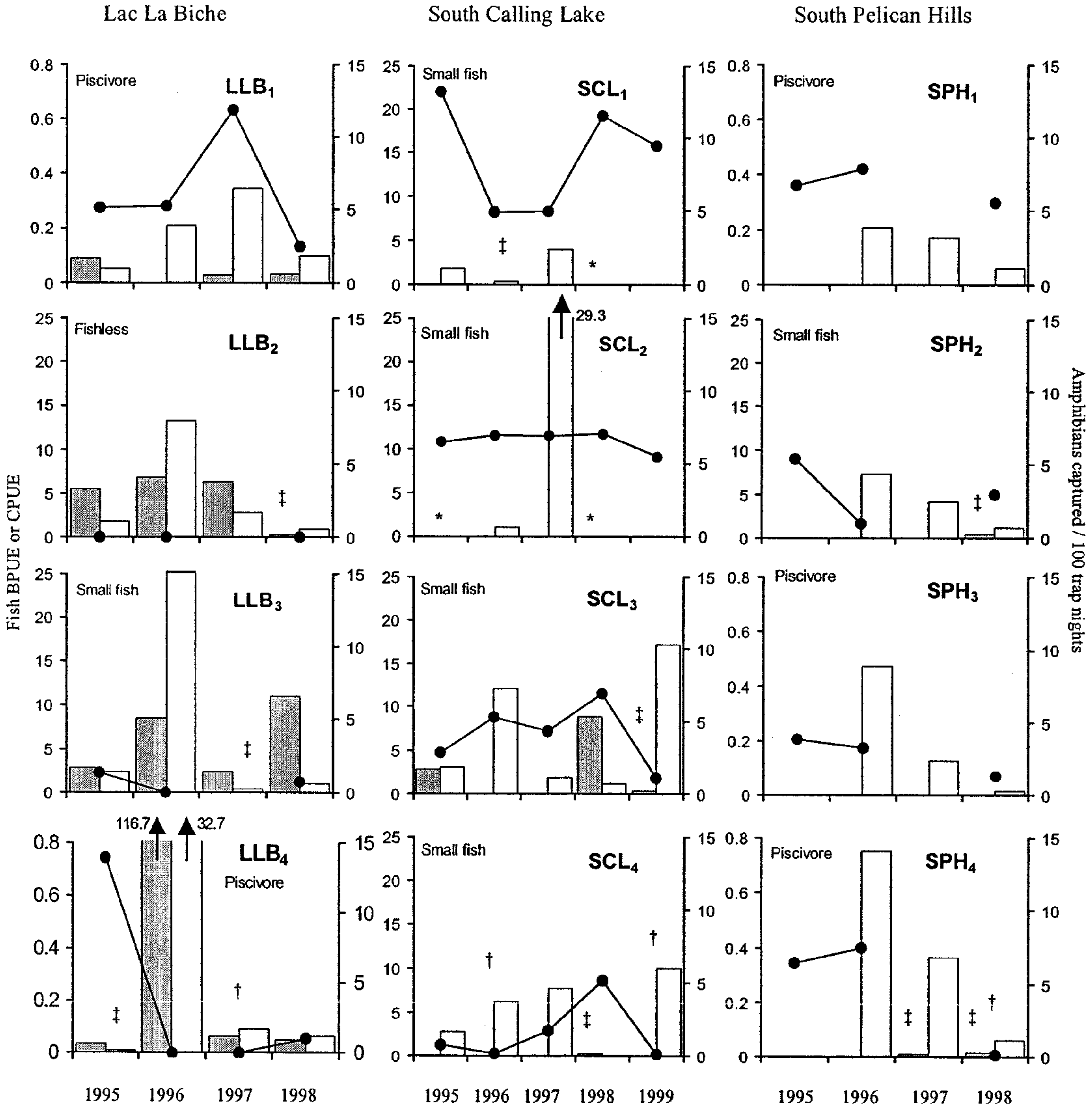
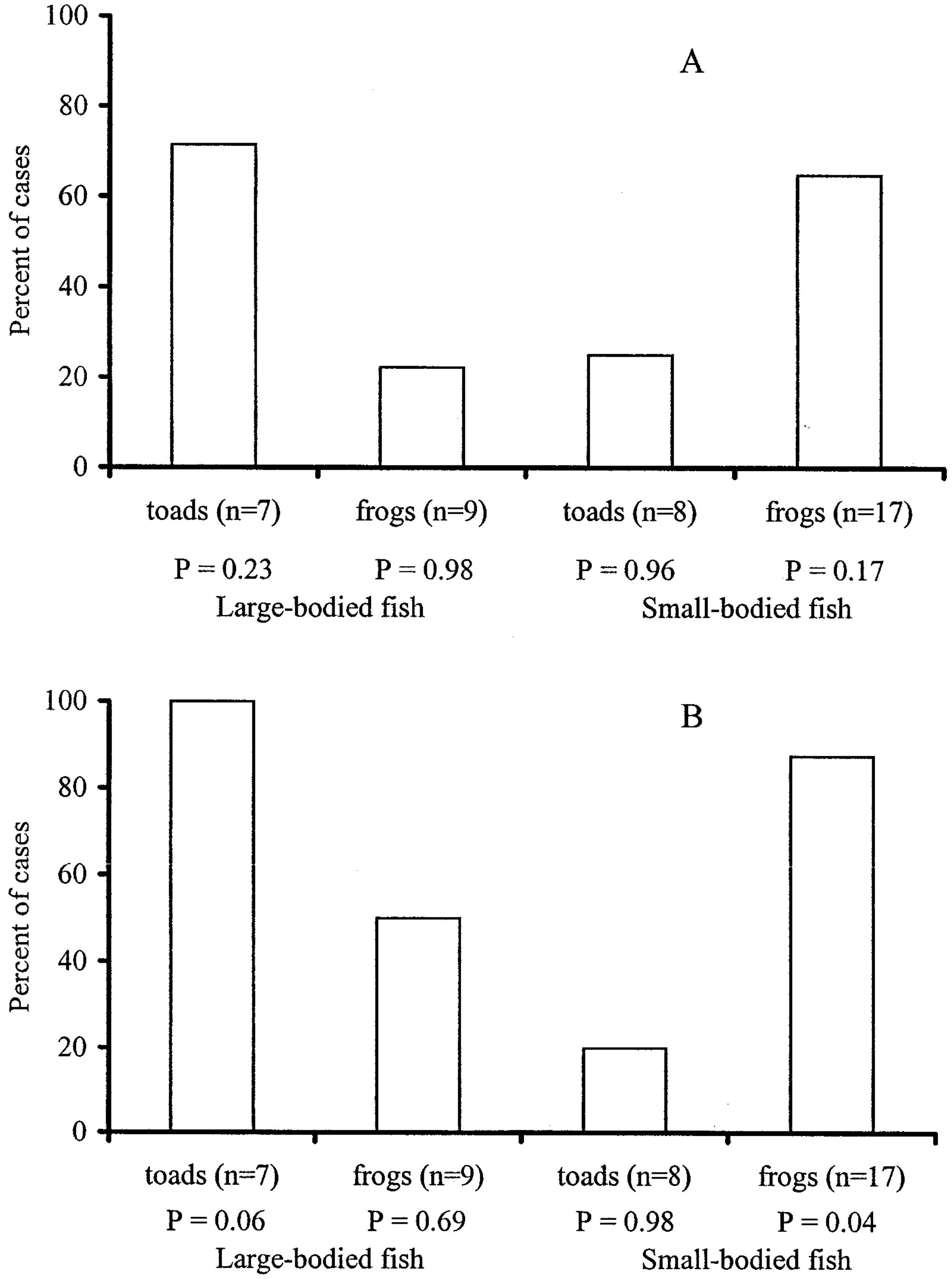


Figure 3-2. The percentage of cases in which the Index of Population Change (IPC) for fish and amphibians changed in opposite directions for (A) all cases, and (B) cases in which large changes in fish abundance (|IPC| > 1) occurred. The number of cases in which fish and amphibian abundance changed in opposite directions were compared to a binomial distribution (see P-values on figure).



CHAPTER 4: Effects of small-bodied fish species on survival and growth of wood frog (*Rana sylvatica*) and western toad (*Bufo boreas*) larvae.

Introduction

Predators have strong impacts on populations and communities of prey species, either directly through consumption or injury (Morin 1985), or indirectly by influencing prey behaviour (Lima and Dill 1990; Kats and Dill 1998) or inducing changes in prey morphology (McCollum and Leimberger 1997). The effects of predation seem to be especially strong in aquatic systems, where predators may control food web structure through top-down effects (Sih et al. 1985; Chase 2000).

Predators have been important in influencing the life history strategies and geographic distributions of anurans in temperate regions of North America and elsewhere (Wellborn et al. 1996). In permanent aquatic habitats, fish are usually the principal predators of anuran larvae (Heyer et al. 1975) and a variety of anuran species exhibit adaptations for co-existence with fish. Adult anurans may avoid fish when choosing oviposition sites (Resetarits and Wilbur 1989; Hopey and Petranka 1994). Larval adaptations include behavioural shifts (Holomuzki 1995; Eklöv and Werner 2000), morphological plasticity (Relyea 2001*a*), and synthesis of noxious skin compounds (Kruse and Stone 1984; Kats et al. 1988).

Fish species are sometimes classified as "predatory" or "non-predatory" with respect to amphibian larvae (e.g. Hecnar and M'Closkey 1997); fish species with larger adult body size (body size > 15 cm) are considered more important amphibian predators. Among the fish species that have been examined as predators on anurans, centrarchids, salmonids, percids, and esocids appear to be the most effective predators. Of these "predatory" groups, centrarchids are the most often used in laboratory and field investigations of anuran responses to fish (Table 4-1), whereas salmonids are the most common focus of field surveys (Table 4-1; e.g. Pilliod and Peterson 2001; Knapp et al 2001). A number of fish families containing typically smaller-bodied species have also been examined as potential amphibian predators (Table 4-1). Although many of these "nonpredatory" fish are small, species such as the central mudminnow (Umbridae: *Umbra limi*) and mosquitofish (Poeciliidae: *Gambusia affinis*) are aggressive. Most of the "nonpredatory" species will eat anuran larvae during laboratory feeding trials, although consumption of larvae is usually reduced when alternative prey is offered (Laurila and Aho 1997; Lawler et al 1999).

Few studies have examined impact of small-bodied fish species on anurans in the field (Table 4-1). The limited work that has been done suggests small-bodied fish can reduce larval amphibian abundance in structurally simple habitats, such as small rock pools, through predation (Laurila and Aho 1997). Adult male Trinidadian stream frogs (*Mannophryne trinitatis*), which carry tadpoles from their terrestrial hatching sites to aquatic habitats to complete their development, avoid depositing tadpoles in natural pools containing small-bodied fish (Rivulidae: *Rivulus hartii*; Downie et al. 2001). In more complex habitats (ponds), tree frogs (*Hyla arborea*) were able to breed successfully in ponds that contained only ten-spined stickleback (*Pungitius pungitius*), but not in ponds containing large-bodied fish (Brönmark and Edenhamn 1994).

My field work in the boreal mixedwood forest of Alberta, Canada, suggests that wood frogs (*Rana sylvatica*) and toads (western toads, *Bufo boreas*, and Canadian toads, *B. hemiophrys*) will breed in water bodies ranging from temporary ponds (mean surface area=0.032 ha, SD=0.030; mean depth=0.42 m, SD=0.25; n=12 ponds) to large permanent lakes (mean surface area=66.9 ha, SD=41.9; mean depth=2.6 m, SD=1.3; n=12 lakes) containing fish (Hannon et al. 2002). Fish assemblages in the region are relatively simple and are usually dominated by either large-bodied, piscivorous species, e.g. northern pike (*Esox lucius*), or by combinations of small-bodied species such as fathead minnow (*Pimephales promelas*), and brook stickleback (*Culaea inconstans*) (Robinson and Tonn 1989). In a survey of 103 lakes (median surface area=56 ha, minimum = 2 ha, maximum = 362 ha; median depth=2.5 m, minimum = 0.5 m, maximum = 38 m) in boreal Alberta, approximately half were dominated by small-bodied fish species (48%), 31% were dominated by large-bodied species, and 21% were fishless (W. Tonn, unpublished data). Field data collected over five years indicate that production of metamorphic amphibians from lakes is negatively correlated with fluctuations in abundance of both large and small-bodied fish species (see Chapter 3). This suggests that both large and small-bodied fish species may impact amphibian production in boreal lakes, although precise mechanisms are unknown.

Although the majority of lakes in Alberta containing fish are dominated by small-bodied species, few studies have examined the impact of small-bodied fish, which typically feed on non-vertebrate prey, on anuran larvae. The fathead minnow is omnivorous, but relies primarily on small invertebrates and detritus (Price et al. 1991). The brook stickleback feeds primarily on small aquatic insects and crustaceans (Nelson and Paetz 1992; W. Tonn, unpublished data). I conducted experiments exposing wood frog and western toad larvae to fathead minnow and brook stickleback in large (mean surface area = 94.4 m^2, mean volume = 87200 L) man-made ponds. Most field experiments on amphibian larvae are done in artificial enclosures including wading pools (85 L volume; Semlitsch 1988), cattle tanks (2100 L volume; Semlitsch and Gibbons 1988), and enclosures in ponds (1200 L; Relyea 2000). Use of whole-pond experiments allowed us to simulate conditions in small boreal lakes while controlling a range of environmental factors. Because my experiments were run in relatively large ponds in a semi-natural setting, over a relatively long time, the results will significantly increase understanding of the impact of small-bodied fish species on anuran populations in boreal lakes.

My overall goal in these experiments was to demonstrate and better understand the impact of small-bodied fish populations on populations of anuran larvae; predation by fathead minnow and brook stickleback on wood frog and western toad larvae, although suggested by my fieldwork, has not been demonstrated directly. Wood frog larvae are considered palatable to fish (Kats et al. 1988), whereas toad larvae are not (Kruse and Stone 1984; Kats et al. 1988), so individuals of these species should respond differently to fish. I predicted the following: (1) activity of anuran larvae would be reduced in the presence of fish; (2) tadpole survival to metamorphosis would be reduced in ponds with fish; (3) larval growth rates would be reduced, and time to metamorphosis would be increased, in ponds with fish; (4) the effects of fish will be greater on wood frog than western toad tadpoles; (5) the negative effects of fish on wood frog and western toad larvae would be greater in ponds with fathead minnow than brook stickleback, because the former species has a greater body and mouth size.

Materials and methods

Study site. Experiments were carried out at the University of Alberta's Meanook Biological Research Station (MBRS; 54° 62' N, 113° 35' W) within the boreal mixed wood region of Alberta. Both fish and both anuran species used in this study occur naturally in the area.

Experimental design. Experiments were conducted with wood frog tadpoles in 1999, and western toad tadpoles in 2000. Procedures were similar between years; relevant differences are noted.

Three naturalized man-made ponds (dug in 1991) were used for experiments. Ponds had moderately sloping sides, and had been colonized by a variety of plant and invertebrate species. To increase replication, each pond was divided by a 3 m high impermeable polyethylene curtain to create 2 pond halves (hereafter called "sections"), each approximately 12 m by 15 m. During the experiments, maximum depth was maintained at approximately 1 m by adding or removing water. Total volume of each section averaged 87200 L (range = 76000 - 102000 L; Table 4-2).

Three treatments were used in the experiments: (1) tadpoles alone (hereafter called "Reference"); (2) tadpoles and fathead minnow ("Fathead"); (3) tadpoles and brook stickleback ("Stickleback"). Treatments were assigned randomly to ponds; both sections of each pond were assigned the same treatment to avoid transmission of water-borne chemicals (Kats et al. 1988; Kats and Bill 1998) and accidental movement of fish between sections if the curtain ruptured.

Pond preparation. In 1999, each of the ponds had a resident population of fathead minnows remaining from a previous study. From 28 April - 8 May 1999 most of the water was pumped out of the ponds, each was seined 13 times and all captured fish removed. After seining was complete, the ponds were refilled to 1 m maximum depth. After trials were finished in fall 1999, water levels were not regulated and ponds froze nearly to the bottom. Ponds were pumped out and seined 3 times from May 2-4, 2000; only 1 fathead minnow was captured. Ponds were again refilled to 1 m maximum depth.

To capture metamorphic amphibians emerging from the experimental ponds, and to control access by adults, each pond was completely surrounded by a 40 cm high drift fence constructed of silt fencing material (Heyer et al. 1994; Enge 1997) with the bottom edge buried 10 cm.

Fish collection and stocking. Fish were collected from nearby lakes using Gee traps on May 7, 1999 and May 8/9, 2000. Fish were maintained in two large holding tanks (1170 L) until released into experimental ponds; during this period, fathead minnow were fed TetraMin flakes and brook stickleback tubifex worms.

Fish were randomly assigned to experimental ponds at a density of 1 fish/m^3, resulting in populations ranging from 76 – 95 fish per section (Table 4-2). This density is well within the natural range of densities for fathead minnow populations in the area, which range from less than 0.1 to more than 5.0 fish/m^3 (Danylchuk and Tonn 2003); I used the same density of brook stickleback to keep experimental conditions similar between the two treatments and because the two species are similar in size. I tried to stock only male fish in the experiment, to hold the population relatively constant by preventing reproduction. Fathead minnow could be reliably sexed based on secondary sexual characteristics, but brook stickleback could not. I used the largest brook sticklebacks (mean total length ± SD, 1999: 57.3 ± 5.3 mm; 2000: 60.4 ± 4.3 mm) available to match, as closely as possible, the size of the fathead minnows (mean total length ± SD, 1999: 70.9 ± 4.0 mm; 2000: 72.6 ± 2.4 mm).

Fish were released into experimental ponds on May 11-12, 1999 and May 9, 2000. Prior to release fish were marked with section-specific fin clips, so that leaks between sections within the same pond could be detected.

Although every effort was made to remove resident populations of fish from each pond section before experiments commenced, a few fathead minnows were missed in one of the reference sections (Reference1) in 1999, as indicated by the capture of minnow fry starting July 18, 1999 (see below). This event simulated an occurrence common in some Alberta lakes: the recovery of a fathead minnow population following a winterkill (Danylchuk and Tonn 2003). During such a recovery few adult fish would be present in spring, so the lake would be functionally fishless. High egg and fry survival would result in a population dominated by small fry; the largest fry captured in the experimental ponds by early August was 40 mm total length, which would be effectively harmless to amphibian larvae. I therefore considered Reference1 as a fishless treatment. In 2000, no fish or fry were captured in the reference sections.

Tadpole collection and stocking. From April 26 – May 8, 1999, 142 wood frog egg masses were collected from nine sites in the Meanook area, including 48 egg masses from the six experimental pond sections prior to fence construction. Egg masses were held under ambient conditions in screened cages or buckets set in additional ponds, or in large outdoor tanks (1170 L) filled with pond water until eggs hatched and most larvae had reached Gosner stage 25 (subsample of larvae: mean = 24.9, range = 24-25, n = 255) (Gosner 1960), when operculum development was complete and tadpoles were free swimming. Larvae were then counted and stocked into the divided ponds at experimental densities (see below).

Nine western toad egg strings were collected from three ponds at MBRS from May 29 – June 6, 2000, and held in 2 large tanks (1170 L). Western toad tadpoles were released into experimental ponds when they had reached at least Gosner stage 20 (mean = 22.4, range = 20-25, n = 608; Gosner 1960).

In both years, tadpoles from each egg mass were distributed equitably across the 6 sections. A subsample of larvae was preserved in 70% ethanol to determine developmental stage and size at release.

Initial densities for wood frog tadpoles was set at 74 tadpoles/m^3, resulting in 5657 to 7564 wood frog tadpoles per section (Table 4-2). Wood frog egg masses collected in the area contain an average of 633 eggs/mass (range: 328 – 1009, n = 21; Eaton, unpublished data). Therefore, each section contained tadpole numbers equivalent to approximately 9 to 12 egg masses, well within the range of natural egg mass densities observed in the area, and in fact 20 egg masses were deposited in one of the pond sections in 1999 before the drift fence was in place. Wood frog tadpoles (mean total length 10.3 mm; SD = 1.24; n = 254) were released May 18-23, 1999.

Western toads are not as common in boreal Alberta as wood frogs, and I was unable to find as many egg masses. Initial densities for western toad tadpoles was set at 39 tadpoles/m^3, resulting in 3000 to 4000 tadpoles per section (Table 4-2). Single western toad egg strings may contain up to 16,500 eggs (Russell and Bauer 2000), so the density of tadpoles in each section was relatively low. Western toad tadpoles (mean total length 6.7 mm; SD = 0.091; n = 607) were released June 6-7, 2000.

Sampling

Pond environment. To characterize environmental factors in the six pond sections, water samples were collected periodically from each section and analyzed using standard laboratory techniques. Variables sampled included pH, conductivity, total nitrogen (TN), and total phosphorus (TP). In 1999, water samples were collected weekly for pH and conductivity, and biweekly for TN, and TP, from May 25 to August 17. In 2000, samples were collected biweekly for all water chemistry variables, from June 10 to August 24.

To estimate food availability for tadpoles, water column chlorophyll *a* (a measure of phytoplankton biomass) was sampled biweekly from May 25 to August 17 in 1999, and from June 10 to August 24 in 2000. In 2000, periphyton availability was also estimated. Periphyton is an important food source for tadpoles, and tadpoles can influence periphyton biomass (Nyström et al. 2001; Peacor 2002). Periphyton abundance in the experimental pond sections was estimated using artificial substrates (acrylic rods) placed vertically in each pond section (Goldsborough et al. 1986). Rods were removed every 2 weeks for processing; removed rods were immediately replaced with new substrates. Processing followed standard procedures for chlorophyll *a*. Periphyton samples were collected from June 9 to September 14, 2000.

Macroinvertebrates can be important predators of tadpoles in some systems, especially those without fish (Wellborn et al. 1996), and even small-bodied fish species such as fathead minnow suppress macroinvertebrate abundance (Zimmer et al. 2000). In 2000, I used activity traps to estimate abundance of macroinvertebrates that were potential tadpole predators in each of the pond sections; these included larval anisopterans, adult and larval dytiscids, nymphal and adult notonectids, and leeches.

Activity traps were constructed by cutting the top off a clean 2 L pop bottle, inverting the top into the rest of the bottle. Two traps were placed on their sides on pond bottom during each sampling period. Traps were open for 43 days (July 8 – August 30), and checked every 1 to 4 days.

Fish sampling. Fish populations were sampled periodically (12 times between May 27 and August 19, 1999; 14 times between May 21 and August 24, 2000) with five Gee minnow traps (1 placed in the centre of the section, and 4 placed around the edges) set overnight. When captured, fish were sexed and examined for fin clips; females or injured fish were replaced with new male fish of similar size. Adult fish abundance in both fathead minnow and brook stickleback sections declined as individuals died after mating. Although both species are short-lived, a greater percentage of the fathead minnow populations survived to the end of the experiments (>50%) than did brook stickleback (<25%).

Tadpole surveys. Tadpole abundance and activity were estimated by visual surveys. An observer stood for 1 minute at the midpoint along each of the three accessible sides of each section and counted all the tadpoles visible (total of 3 minutes of observation per section). Visual surveys were done in the morning (AM counts; 0800 – 1200 hrs) and afternoon (PM counts; 1300 – 1800 hrs) to account for possible diel differences in tadpole movement. Visual surveys for wood frog tadpoles were conducted 67 times for AM counts, and 59 times for PM counts, from May 26 to August 19, 1999. Surveys for western toad tadpoles were done 70 times for both AM and PM counts, from June 8 to August 18, 2000.

Tadpole trapping. In order to estimate population size, tadpoles were sampled using minnow traps set for 24 hours. In 1999, Gee traps and collapsible mesh minnow traps (mesh size: 2 x 4 mm, Nylon Net Company, Memphis, Tennessee) were used; capture rate by the two trap types was similar. Four traps were placed in the shallow water at the edge of each section for 24-hour periods 23 times from July 18 to August 19, 1999. In 2000, only collapsible mesh traps were used; five traps (4 around the edge and 1 in the deeper water in the middle of the section) were set for 24-hour periods 9 times between July 5 and July 25, 2000.

My intention was to track tadpole growth and development to determine if the presence of fish affected these parameters. I measured (total length and body length) captured tadpoles and placed them in developmental categories, but so few tadpoles were captured in most sections that no meaningful analysis could be conducted.

Metamorph sampling. Metamorphs were collected using pitfall traps, by actively searching the area around each pond section, and by hand-capturing metamorphs observed on land during other activities around the ponds. Regular area searches were instituted when metamorphs were first observed in the shallow water of any pond section. In 1999, searches were done daily from July 18 to August 19, then sporadically until October 18. In 2000, area searches were done daily from July 18 to August 15, then sporadically until September 28. Searches were conducted for 10 minutes per section between the edge of the water and the drift fence. Any metamorphs found were captured and retained for measurement. Metamorphs that were still in the water were not collected.

A total of seven pitfall traps (one every 7 m) were placed around the inside of the drift fence surrounding each pond section. Pitfall traps were metal cans 25 cm deep and 15 cm in circumference. A plastic funnel (15 cm in circumference, and 12 cm deep) was placed in each pitfall trap to prevent captured amphibians from escaping. A small stick was placed in each trap to allow small mammals to escape. Moss and water were added to the traps to keep conditions cool and moist. Pitfall traps were opened on the same date that area searches began. In 1999, pitfall traps were checked daily from July 18 to August 20, then sporadically until November 7. In 2000, pitfall traps were checked 33 times at 1 to 8 day intervals from July 28 to October 31. Traps were checked less frequently in the fall, when ambient temperature was lower and fewer individuals were being captured.

Of the methods described, hand captures during area searches and incidental activities gave the best indication of when metamorphs actually emerged from the water, as individuals captured in this way had probably just left the ponds whereas metamorphs had to travel at least 5 m uphill before encountering a pitfall trap. The presence of the pitfall traps ensured that most of the metamorphs were eventually captured, providing a good estimate of total metamorph production from each pond section.

Captured metamorphs were measured (snout-to-urostyle length (SUL)), weighed, and examined for injuries or deformities; a single toe was removed to identify the type of section (reference, fathead, or stickleback) from which each metamorph originated. Any individual with a tail was kept indoors in aquaria until the tail was completely resorbed (approximately 1 to 2 days), at which time it was weighed, measured, and marked. All metamorphs were eventually released outside the drift fence adjacent to the pond from which they originated.

Analysis

Pond environment.

Data for water chemistry variables were graphed and visually examined for patterns across pond section and time.

For each sampling session, counts of macroinvertebrates were combined by taxonomic groups (anisopterans, dytiscids, notonectids, and leeches) and standardized as catch per unit effort (number of animals captured per trap night). The means of these values for each section were square-root transformed ($\sqrt{x}+0.5$) to normalize data. I performed 1-way ANOVAs on these means, with treatment as a fixed factor, followed by multiple comparisons using the Tukey method when there was a significant effect.

Tadpoles. Visual surveys were used to estimate tadpole activity levels in each section. Counts of tadpoles from visual surveys at each section were divided by the original number of tadpoles released in that section and multiplied by 100 to obtain the percentage of the original population that was seen during a survey. Data was graphed and visually inspected for patterns.

Tadpoles were trapped to estimate tadpole abundance in each pond section; I expected to capture fewer tadpoles in sections containing fish because tadpoles would be consumed by fish, tadpole activity would be inhibited by the presence of fish (and the tadpoles would therefore encounter traps less frequently), or a combination of these two effects. I used a Chi-square goodness of fit test to determine if the total number of tadpoles captured was proportional to the number of tadpoles originally released in each section.

Metamorphs. To determine if survival of tadpoles to metamorphosis differed across sections, the proportion of individuals stocked as tadpoles was compared to the proportion captured as metamorphs using a G-test on the contingency data (Sokal and Rohlf 1981).

To examine the influence of fish on length of time to metamorphosis, the number of Julian days between release of tadpoles into the experimental ponds and capture as a metamorph was calculated for each individual. Because I expected that metamorphs collected by hand had emerged more recently from ponds than those caught in pitfall traps, time to emergence was compared separately for hand-captured and pitfall-captured individuals. Mean time to metamorphosis was compared across treatments using a one-way ANOVA with treatment as a fixed factor, followed by multiple comparisons using Tukey's test.

Data on size (SUL) at metamorphosis was graphed and visually inspected for patterns. Data on size of metamorphs collected by hand and in traps were handled separately as preliminary analysis indicated that metamorphs collected in pitfall traps were significantly larger than those caught by hand. Data on metamorph weight were collected and analyzed, but are not reported here as mass always showed the same patterns as SUL (Eaton, unpublished data).

Results

Pond environment. Water chemistry variables were relatively similar for all experimental sections at the time of tadpole release in both 1999 and 2000. Over the summer, water chemistry did not show any consistent pattern related to treatment in either year. In 1999, ranges of water chemistry variables measured across all sections and dates were TN: 804.4 – 1038 µg/L, TP: 32.6 – 82.1 µg/L, conductivity: 462 – 490 µS/cm, and pH: 7.6 – 8.2. In 2000, ranges were TN: 395.3 – 716.0 µg/L, TP: 22.7 – 44.4 µg/L, conductivity: 294 – 471 µS/cm, and pH: 7.7 – 8.3.

In 1999, mean water column chlorophyll *a* concentrations ranged from 4.45 to 23.5 µg/L, with those in the reference sections only 25 to 50% of those from sections containing fish (Table 4-3).

In 2000, mean water column chlorophyll *a* concentrations ranged from 3.97 to 7.57 µg/L with no discernible patterns across treatments (Table 4-3). Periphyton chlorophyll *a* was generally similar across all pond sections, and ranged from 0.042 to 0.094 µg/L across 5 of the 6 sections. In the remaining section (one of the stickleback sections) periphyton chlorophyll *a* was 0.24 µg/L; the reason for this unusually high periphyton growth relative to the other sections (Table 4-3) is unknown.

In 2000, abundances of both dytiscids ($F_{2,3}$=39.6, P=0.0070) and notonectids ($F_{2,3}$=25.6, P=0.013) were significantly higher in the reference treatments than in the remaining treatments (Figure 4-2). Abundances of anisopterans and leeches did not differ across treatments (P>0.05; Figure 4-2).

Wood frog

Tadpoles. The number of wood frog tadpoles observed was much greater in the reference treatments than in the fish treatments (Table 4-4). The only tadpole ever seen in fathead minnow sections was observed on the first day of the surveys. Tadpoles were seen in relatively high numbers in the stickleback sections over the first four sampling days, but virtually disappeared within 3 weeks of release (Figure 4-2a). In contrast, large numbers of tadpoles were regularly observed in reference sections, and tadpoles were seen throughout the survey period (Figure 4-2a).

The total number of wood frog tadpoles trapped over the summer varied across the pond sections, with many more tadpoles captured in the reference sections, especially in Reference2, than in any of the fish sections (Table 4-5). The distribution of total tadpole captures differed significantly from catches expected based on initial population sizes (χ^2_5=36928.53, $P<0.001$). The mean number of tadpoles captured per sampling session was much higher in Reference2 than in any of the other sections (Table 4-5).

Metamorphs. The proportion of the stocked wood frog tadpoles that survived to metamorphosis differed significantly across the pond sections (G_5=1102.6, $P<0.001$), with a significantly higher proportion emerging from the reference sections than from the other sections. The two reference sections differed significantly from each other, with more metamorphs emerging from section Reference 2N (G-test with test of independence within the contingency table; Table 4-6). The next highest number of metamorphs occurred in the Stickleback1 section, which had significantly higher emergence than the other sections stocked with fish; number of metamorphs in these latter three sections did not differ significantly from each other (G_5=3.02, $P>0.05$; Table 4-6).

Most metamorphs were captured by hand during patrols or other activities around each pond; relatively few were caught in pitfall traps (Table 4-6). Emergence of metamorphs began in late July and continued until mid-October.

The mean number of days from the release of tadpoles to capture of metamorphic wood frogs did not vary significantly across treatments for animals captured by hand or in pitfall traps ($P>0.25$ in both cases). Metamorphs were captured earliest from Stickleback1 and Reference1 sections (Table 4-6), with the shortest mean time to emergence for the Reference1 and Fathead1 sections for hand captures, and Stickleback1 for pitfall captures (Table 4-6). For each section mean number of days from release to capture was greater for pitfall-captured individuals than for those captured by hand (Table 4-6).

Wood frog metamorphs emerging from stickleback and fathead sections were much larger than those from the reference sections (Table 4-7). Metamorphs emerging from the stickleback and fathead sections were very similar in SUL, and metamorphs emerging from the two reference sections were almost identical in mean SUL (Table 4-7).

Western toad

Tadpoles. The number of tadpoles seen during surveys were fairly similar across treatments for AM and for PM surveys; more tadpoles were observed at stickleback sections than in the other treatments (Table 4-4). The distribution of tadpole observations over time was similar in all section types, but tadpoles were seen on later dates in the stickleback and reference sections than in the fathead minnow sections (Figure 4-2b). Overall, toad tadpoles disappeared sooner after stocking than did wood frogs in the previous year, suggesting that toad tadpole survival was low over all the experimental ponds, which is consistent with the low number of toads metamorphs that emerged from the ponds (see below).

Despite trapping for nine nights in each pond section, only one western toad tadpole was ever caught (from Reference2). Because the mesh traps did not seem useful in catching western toad tadpoles, each pond was sampled haphazardly with a dipnet to collect some tadpoles to determine growth and developmental rates. This method was also unsuccessful; only 8 tadpoles were collected by dipnet.

Metamorphs. Total captures of western toad metamorphs were relatively low in all pond sections. Captures of metamorphs began in late July and continued until mid-October; around each pond more metamorphs were captured in pitfall traps than by hand (Table 4-6). Proportions of the original tadpole populations that were captured as metamorphs were not consistent with treatment ($G=15.32$, $P<0.01$); the highest survival to metamorphosis was in the Stickleback1 section (Table 4-6).

The mean number of days from the release of toad tadpoles to capture of metamorphs was greater for stickleback sections than other sections for hand captures, and slightly greater for pitfall captures (Table 4-7).

Western toad metamorphs were similar in SUL across treatments, based on both hand captures and pitfall traps (Table 4-7).

Discussion

Do small-bodied fish pose a predation threat to anuran larvae? My experiments strongly suggest that small-bodied fish can dramatically reduce survival of wood frog larvae to metamorphosis, and have indirect effects on the size of metamorphs. Unfortunately, so few western toad metamorphs emerged during my experiment that little can be said about the effect of small-bodied fish on this species. Small-bodied fish are not usually considered predators of amphibian larvae (Brönmark and Edenhamn 1994; Hecnar and M'Closkey 1997), although they are able to reduce larval abundance through predation in some structurally simple habitats (Laurila and Aho 1997).

The presence of fish was the main difference between my experimental pond sections. Other factors were similar across ponds, or more favourable for tadpole survival in the fish ponds. For example, water chemistry variables were similar across ponds, while chlorophyll *a* concentrations were higher in fish ponds, possibly because fish suppressed zooplankton populations (Zimmer et al. 2002) or improved nutrient cycling in the ponds (Schindler et al. 2001); elevated chloropyll *a* concentrations suggests there was more food available for tadpoles in fish ponds. *Rana sylvatica* and *Bufo* tadpoles are capable of feeding on phytoplankton (Seale and Beckvar 1980), though their willingness to feed in the water column may be influenced by the presence of predators (Eklöv and Halvarsson 2000).

Although many factors were more favourable for tadpoles in fish-containing ponds, survival to metamorphosis in my experiments was dramatically lower for wood frog tadpoles in the fish sections than in the reference sections (Table 4-6). Wood frog survival in all ponds fell within the range observed in nature, which is generally between 0 and 10% (Herreid and Kinney 1966; Berven 1990). Capture rates from a natural population of wood frogs at a nearby pond (the RANA pond), sampled using pitfall traps, ranged from 0.32 to 44.6 juveniles/100 trap nights from 1997 to 2001, with the lowest captures in 1999, the same year as the wood frog experiment. Pitfall captures of wood frog juveniles at the experimental ponds in 1999 ranged from 0 to 13.0 juveniles/100 trap nights for the same dates the RANA pond was sampled. No data on larval survival in natural populations of *Bufo boreas*, and little for *Bufo* in general, exist. Miller (1909) estimated survival from egg to metamorph at 15% for a population of American toad (*B. americanus*). Survival of natterjack toad (*B. calamtia*) from egg to metamorph was only 0.3% (Kadel 1975), a value similar to that obtained for the experimental populations in the present study. Low production of western toads in the experimental ponds (pitfall capture rates ranged from 0 to 1.1 juveniles/100 trap nights) was probably not unusual; captures of toad juveniles at the RANA pond were low (3.7 juveniles/100 trap nights) in 2000, the same year as the western toad experiment. Captures over five years (1997 – 2001) of juvenile western toads at the RANA pond fluctuated widely, ranging from 0 to 44.6 juveniles/100 trap nights. Capture rates of both wood frog and western toad juveniles at the experimental ponds therefore fell within the range documented at the RANA pond, indicating the experimental ponds were suitable environments for the production of these anurans.

Enhanced survival of wood frog larvae in non-fish pond sections in my experiments suggests that larvae were preyed upon by fathead minnow and brook stickleback. The rarity of wood frog tadpole sightings and captures after the first few days following release, combined with low emergence of metamorphs from fish ponds, support the explanation that fish predation played a direct role in reduced wood frog tadpole survival. This pattern is consistent with Macan's (1966) observation, where tadpoles (*Rana sp.* and *Bufo sp.*) in a pond stocked with brown trout (*Salmo trutta*) disappeared within a few days of starting to swim. Tadpoles are more vulnerable to predation at early developmental stages (Semlitsch and Gibbons 1988; Anholt et al. 2000; Eklöv and Werner 2000), when their ability to escape predators is low (Richards and Bull 1990). In aquarium trials, both fathead minnow and brook stickleback were able to consume small wood frog tadpoles ranging from 7 - 13 mm in total length (Gartner, unpublished data).

Similar activity of western toad tadpoles across all pond sections suggests that fish presence was not central in determining tadpole behaviour. Bufonid tadpoles are unpalatable to most fish species (Kats et al. 1988; Nyström and Åbjörnsson 2000; Relyea 2001*b*), so I would expect that fish predation on western toad tadpoles would be relatively low. In aquarium feeding trials with western toad larvae, however, both fathead minnow and brook stickleback were able to consume small tadpoles (12 – 20 mm total length) (Waldron-Lacelle, unpublished data). Kruse and Stone (1984) found that although largemouth bass (*Micropterus salmoides*) initially avoided feeding on toad (*B. americanus* and *B. woodhousei*) tadpoles, as the bass grew hungrier they eventually consumed toad tadpoles.

In addition to fish, macroinvertebrates are potential predators of amphibian larvae. Sampling of predatory invertebrates in 2000 suggested that both fatheads and sticklebacks reduced the overall abundance of these organisms. This is consistent with the patterns seen in other investigations, where addition of small fish to small ponds or wetlands reduced abundance of aquatic insects (Lawler et al. 1999; Smith et al. 1999; Zimmer et al. 2000). For wood frog, potential benefits of reduced predatory invertebrates in the fish ponds (Lawler et al. 1999) must have been offset by the presence of efficient fish predators (Wellborn et al. 1996), as survival was low compared to reference ponds. Based on similarities in the number of tadpoles seen in the ponds during the tadpole surveys, it seems unlikely that invertebrate predation appreciably reduced western toad tadpole abundance in the reference ponds.

The length of time to, and size at, metamorphosis of anurans are influenced by numerous factors, including predation risk (Babbitt 2001), larval density (Smith 1983; Morin 1986), and resource availability (Skelly and Werner 1990), with increased competition for resources at high larval and/or low resource density, and reduced feeding activity in the presence of predators (Anholt et al. 2000; Babbitt 2001). These factors generally result in prolonged larval periods and smaller body size at metamorphosis (Semlitsch and Caldwell 1982), which have important implications for the fitness of individuals. Increased time to metamorphosis increases the length of time larvae are exposed to aquatic predators and, in more northerly and alpine areas, decreases the likelihood that an individual will successfully complete metamorphosis before winter. Smaller size at metamorphosis translates into reduced survival postmetamorphosis (Berven 1990; Morey and Reznick 2001) and smaller size as an adult (Smith 1987; Berven 1990). For males, smaller body size means fewer matings, whereas smaller females produce fewer eggs (Howard 1980; Berven 1981; Howard and Kluge 1985).

In my experiments, time to emergence of metamorphs showed no clear pattern related to treatment for wood frog; this was opposite to my original prediction that wood frog metamorphosis would be delayed by reduced tadpole activity, feeding, and growth rates in the presence of fish. Lack of a clear response to fish presence in terms of time to metamorphosis probably reflects the small sample size of metamorphs emerging from fish ponds (Table 4-6). Time to emergence for western toad, again based on hand captures, was longest for the reference sections, and shortest for the fathead sections. These results fail to support my original prediction that western toad time to emergence would not vary in relation to fish presence. Chivers et al. (1999) showed that western toad tadpoles metamorphosed earlier in the presence of conspecific alarm cues, even in the absence of predator cues. If fish attempted to prey on tadpoles, release of alarm cues from injured individuals might result in decreased time to metamorphosis; this is consistent with my results. However, the small number of toad metamorphs emerging from any of the ponds (Table 4-6) makes inferences weak.

I did not make any predictions about the size of metamorphs emerging from sections with vs. without fish. However, wood frog metamorphs emerging from the reference sections were dramatically smaller than those from fish-containing sections (Table 4-7), probably because of unfavourable conditions in the reference sections resulting from high intraspecific competition. Metamorphs from the reference sections were similar in size to metamorphs captured at the nearby RANA pond in 1999 (SUL = 17.5 mm, SE = 0.50); however, only two metamorphs were captured at the RANA pond in this year. In other years, when more individuals were captured, metamorphs were larger (SUL: 20.9 – 21.9 mm). Initial tadpole densities in the experimental ponds were not unusually high for small ponds in boreal Alberta; ponds contained the equivalent of tadpoles from approximately 9 to 12 egg masses. In the fish ponds, predation presumably removed enough tadpoles that those surviving experienced a release from competition (Nyström and Åbjörsson 2000), resulting in increased growth rates and production of larger tadpoles than the reference ponds or the fishless RANA pond (Wilbur 1987). The presence of predators may reduce grazing by tadpoles (Nyström and Åbjörnsson 2000), allowing increased periphyton growth, which can produce increased growth among surviving tadpoles (Peacor 2002). Although there were many more metamorphs produced from the reference sections, they probably had a low chance of survival in the terrestrial environment because of their small size (Morey and Reznick 2001). Size of western toad metamorphs did not vary significantly across ponds (Table 4-7) and was similar to sizes of metamorphs from the RANA pond in 2000 (SUL = 22.6 mm, SE = 0.40, n=77).

My prediction that fathead minnow would have a greater effect on anuran larvae than brook stickleback was not strongly supported by the data, although the responses of tadpoles to the two fish species were generally in the predicted direction. Thus, the last sighting of tadpoles occurred earliest, the total number of tadpoles seen was lowest, and total emergence of metamorphs from the fathead sections was lower than from the stickleback sections for both wood frog and western toad. There were no consistent patterns in mean time to emergence of metamorphs related to fish species for either anuran species.

The selection of experimental venue for investigations of species interactions has a critical impact on the validity of conclusions drawn from experiments (Skelly and Kiesecker 2001; Skelly 2002). I feel use of whole-pond experiments to examine tadpole response to the presence of small-bodied fish probably represents the best compromise between the realism of large-scale field studies, and the replication and control inherent in mesocosm studies using wading pools, cattle tanks, and enclosures (Carpenter 1996). My experiments demonstrate that small-bodied fish can influence wood frog tadpole survival and growth, but I found no clear evidence for effects on western toad tadpoles. This suggests that populations of small-bodied fish in the relatively small, shallow, productive lakes of boreal Alberta may influence the abundance of juvenile wood frogs produced in these lakes, either through direct predation on tadpoles, by inducing changes in the behaviour of tadpoles, or a combination of these factors. The largest impact of predation is likely on the early developmental stages, when tadpoles are not able to escape predators easily (Semlitsch and Gibbons 1988; Richards and Bull 1990). Even though tadpoles are small enough to enter shallow water to escape predators, small-bodied fish are also small enough to pursue them into these habitats (Holomuzki 1995).

My fieldwork suggests that anurans in boreal Alberta breed year after year in habitats ranging from ephemeral ponds to permanent lakes. A large proportion of these lakes contain fish, including the small-bodied species used in this study; both fathead minnows and brook sticklebacks had similar effects on the anuran larvae tested in my experiments. In years of low precipitation permanent lakes, which are more likely to harbour fish, probably become increasingly important in maintaining local amphibian populations. Stocking of predatory fish has been identified as a major concern related to the management of aquatic-breeding amphibians (Hecnar and M'Closkey 1997; Semlitsch 2000). My work indicates that even small-bodied fish species may also impact the reproductive success of boreal anurans.

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Table 4-1. Summary of previously published studies of fish interactions with anurans. Note that a single study may involve more than one venue (e.g. lab experiment and field survey) or family of fishes. A total of 36 published studies, spanning the years 1966 to 2002 and taken from 19 journals*, were examined.

Fish Family	Venue			
	Lab experiment	Field experiment	Field survey	**Total**
Large-bodied (total length of adults > 100 mm)				
Centrarchidae	8	6	0	**14**
Salmonidae	3	2	4	**9**
Percidae	2	0	1	**3**
Cyprinidae†	1	0	1	**2**
Esocidae	0	0	1	**1**
Total	**14**	**8**	**7**	**29**
Small-bodied (total length of adults < 100 mm)				
Umbridae‡	4	2	0	**6**
Gasterosteidae‡	3	1	0	**4**
Lebiansinidae‡	2	0	1	**3**
Cottidae‡	1	1	0	**2**
Poeciliidae‡	1	1	0	**2**
Rivulidae‡	1	0	1	**2**
Fundulidae‡	1	0	0	**1**
Total	**13**	**5**	**2**	**20**
"Fish" (species not specified)	0	0	2	2
Grand Total	**27**	**13**	**11**	**51**

* studies were from the following journals: Freshwater Biology, Ecosystems, Oikos, Journal of the North American Benthological Society, Archiv für Hydrobiologie, Conservation Biology, Zoologischer Anzeiger, Herpetologica, Biological Journal of the Linnean Society, Copeia, Ecology, Animal Behaviour, Journal of Herpetology, Oecologia, Journal of Chemical Ecology, Biotropica, Ecological Monographs, Biological Conservation, Herpetological Journal.

† the species of cyprinid in both studies was the roach (*Rutilus rutilus*), a large-bodied member of this family.

‡ although small-bodied, members of these taxa are aggressive and/or possess well-developed teeth.

Table 4-2. Pond volume and number of experimental animals released in each section.

Section	Volume (m^3)	Fish species	No. fish per pond	No. wood frog tadpoles - 1999	No. western toad tadpoles - 2000
Reference1	102	None	0	7564	4000
Reference2	76	None	0	5657	3000
Stickleback1	86	Stickleback	86	6364	3360
Stickleback2	76	Stickleback	76	5657	3000
Fathead1	95	Fathead	95	7039	3720
Fathead2	88	Fathead	88	6514	3440

Table 4-3. Water column and periphyton chlorophyll *a* measured in experimental ponds. Water column chlorophyll *a* was sampled biweekly from May 25 to August 17, 1999, and from June 10 to August 24, 2000. Periphyton chlorophyll *a* was sampled periodically from June 9 to September 14, 2000.

	Water column chlorophyll *a* (µg/L): mean (SE)		Periphyton chlorophyll *a* (µg/cm^2): mean (SE); 2000 only
Pond	1999	2000	
Reference1	4.45 (1.3)	5.83 (1.9)	0.057 (0.017)
Reference2	4.88 (2.0)	3.97 (1.4)	0.048 (0.013)
Stickleback1	9.81 (2.4)	6.57 (1.4)	0.24 (0.10)
Stickleback2	14.0 (4.3)	7.40 (3.0)	0.042 (0.010)
Fathead1	12.1 (6.0)	7.57 (2.4)	0.084 (0.024)
Fathead2	23.5 (9.6)	5.38 (1.3)	0.094 (0.010)

Table 4-4. Number of tadpoles seen during 3-minute surveys.

Section	AM surveys		PM surveys	
	Mean # tadpoles seen (SE)	Total # tadpoles seen	Mean # tadpoles seen (SE)	Total # tadpoles seen
Wood frog	n = 67		n = 59	
Reference1	3.58 (0.62)	240	7.85 (1.8)	463
Reference2	12.99 (2.9)	870	16.86 (3.7)	995
Stickleback1	2.13 (1.2)	143	0.51 (0.39)	30
Stickleback2	0.64 (0.37)	43	0	0
Fathead1	0	0	0	0
Fathead2	0.015 (0.015)	1	0	0
Western toad	n = 70		n = 70	
Reference1	26.17 (9.1)	1832	32.10 (11.4)	2247
Reference2	31.17 (8.0)	2182	37.67 (9.3)	2637
Stickleback1	51.51 (10.5)	3606	60.39 (14.6)	4227
Stickleback2	35.69 (11.5)	2498	48.33 (16.1)	3383
Fathead1	26.56 (8.3)	1859	30.86 (10.8)	2160
Fathead2	14.09 (5.2)	986	18.29 (6.5)	1280

Table 4-5. Total number of wood frog tadpoles captured and mean number of tadpoles trapped per sampling session.

Section	Total number of tadpoles captured	Mean number of tadpoles captured / sampling session (SE; n=23)
Reference1	153	6.65 (1.54)
Reference2	839	36.48 (7.51)
Stickleback1	3	0.13 (0.072)
Stickleback2	1	0.043 (0.043)
Fathead1	0	0 (0)
Fathead2	1	0.043 (0.043)

Table 4-6. Patterns of emergence and capture of metamorphic anurans from experimental ponds. Values for the number of wood frog metamorphs followed by different letters are significantly different.

Section	Number of metamorphs			% survival	Date of:	
	Hand captures	Pitfall captures	Total		First capture	Last capture
Wood frog						
Reference1	320	88	408 **A**	5.39	July 19	Oct. 18
Reference2	169	30	199 **B**	3.52	July 26	Oct. 18
Stickleback1	25	2	27 **C**	0.42	July 21	Sept. 19
Stickleback2	1	0	1 **D**	0.02	Aug. 14	Aug. 14
Fathead1	3	3	6 **D**	0.09	July 28	Oct. 3
Fathead2	3	0	3 **D**	0.05	Aug. 18	Sept. 19
Western toad						
Reference1	3	10	13	0.33	Aug. 25	Oct. 17
Reference2	1	3	4	0.13	Sept. 4	Sept. 23
Stickleback1	7	13	20	0.60	Aug. 5	Sept. 18
Stickleback2	4	3	7	0.23	Aug. 15	Sept. 4
Fathead1	4	5	9	0.24	July 18	Sept. 30
Fathead2	1	4	5	0.15	Aug. 17	Sept. 6

Table 4-7. Characteristics of metamorphic anurans emerging from experimental ponds.

	Parameter: mean (range)		Parameter: mean (SE)	
	SUL (mm)		Number of days to metamorphosis	
Section	Hand	Pitfall	Hand	Pitfall
Wood frog				
Reference1	14.8 (9-28)	18.2 (13-26)	72.2 (0.74)	104.3 (2.4)
Reference2	14.7 (11-20)	16.9 (14-20)	83.6 (0.76)	110.9 (3.9)
Stickleback1	21.2 (17-29)	22.5 (22-23)	85.5 (3.3)	88.5 (11.5)
Stickleback2	23.0*	NC†	83.0*	NC†
Fathead1	23.3 (20-26)	24.3 (19-31)	72.3 (5.8)	102.3 (17.1)
Fathead2	25.3 (18-37)	NC†	98.0 (10.5)	NC†
Western toad				
Reference1	18.5 (17-20.5)	20.0 (17.5-26.5)	92.3 (6.7)	104.9 (4.9)
Reference2	18.5*	22.8 (19-26.5)	89*	95.3 (6.3)
Stickleback1	15.3 (12-18)	19.9 (17-25)	67.0 (2.2)	92.8 (2.3)
Stickleback2	18.2 (16-22)	21.8 (20.5-23)	72.0 (2.4)	81.3 (5.0)
Fathead1	15.9 (13-19)	18.2 (16-19)	64.0 (8.4)	89.8 (9.0)
Fathead2	14.5*	19.2 (17.5-20.5)	71.0*	84.5 (3.8)

* only one metamorph was caught by hand at this pond section, so data from this section is not included in analyses.

† NC = no animals caught.

Figure 4-1. Captures of macroinvertebrates which are potential egg or tadpole predators at experimental pond sections with and without fish in 2000. Captures of Anisoptera and leeches were not significantly different across treatments, while captures of both Dytiscidae (P = 0.007, df = 2) and Notonectidae (P = 0.005, df = 2) were higher in the reference ponds. Bars in the figure with different letters are significantly different.

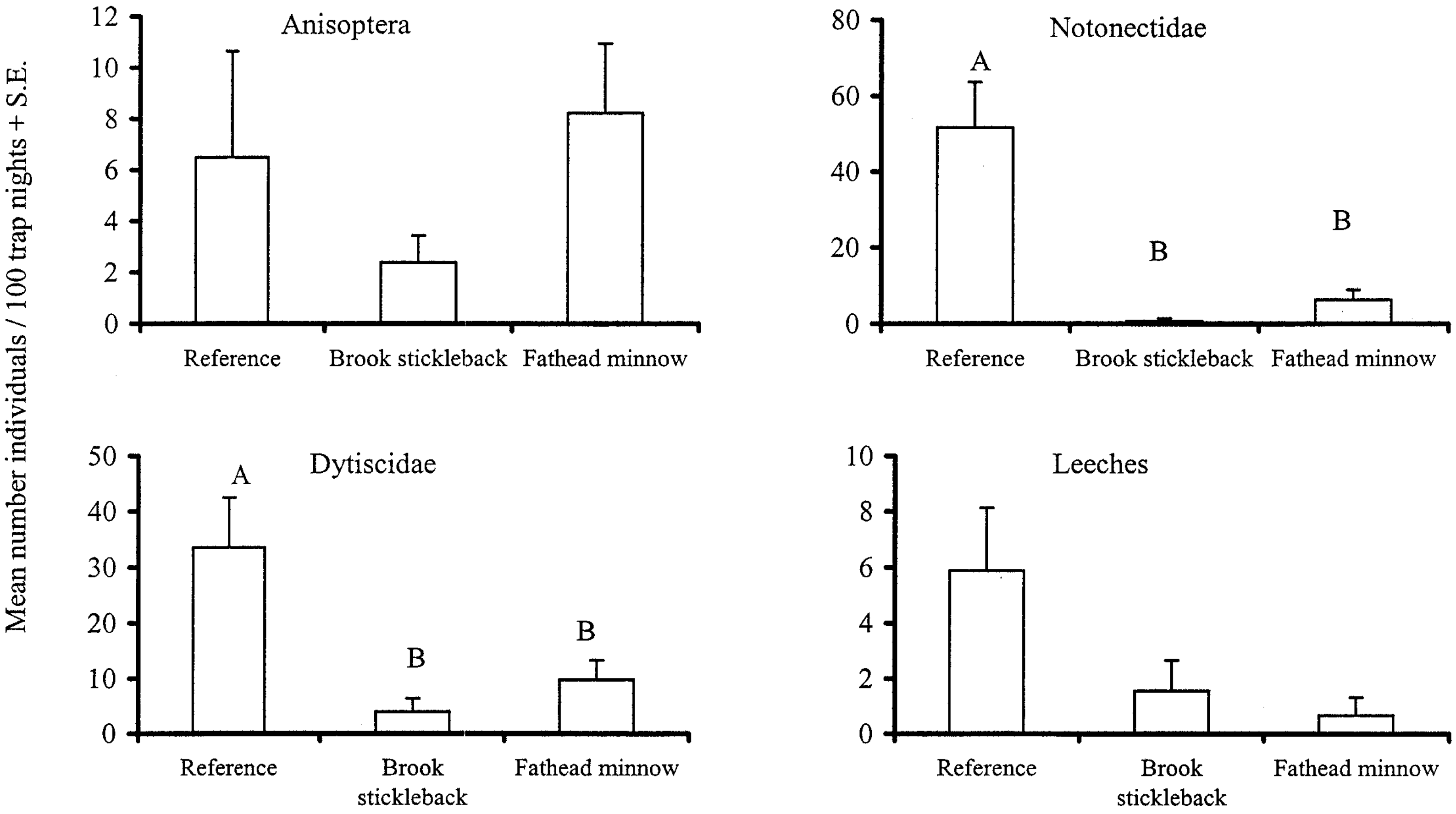
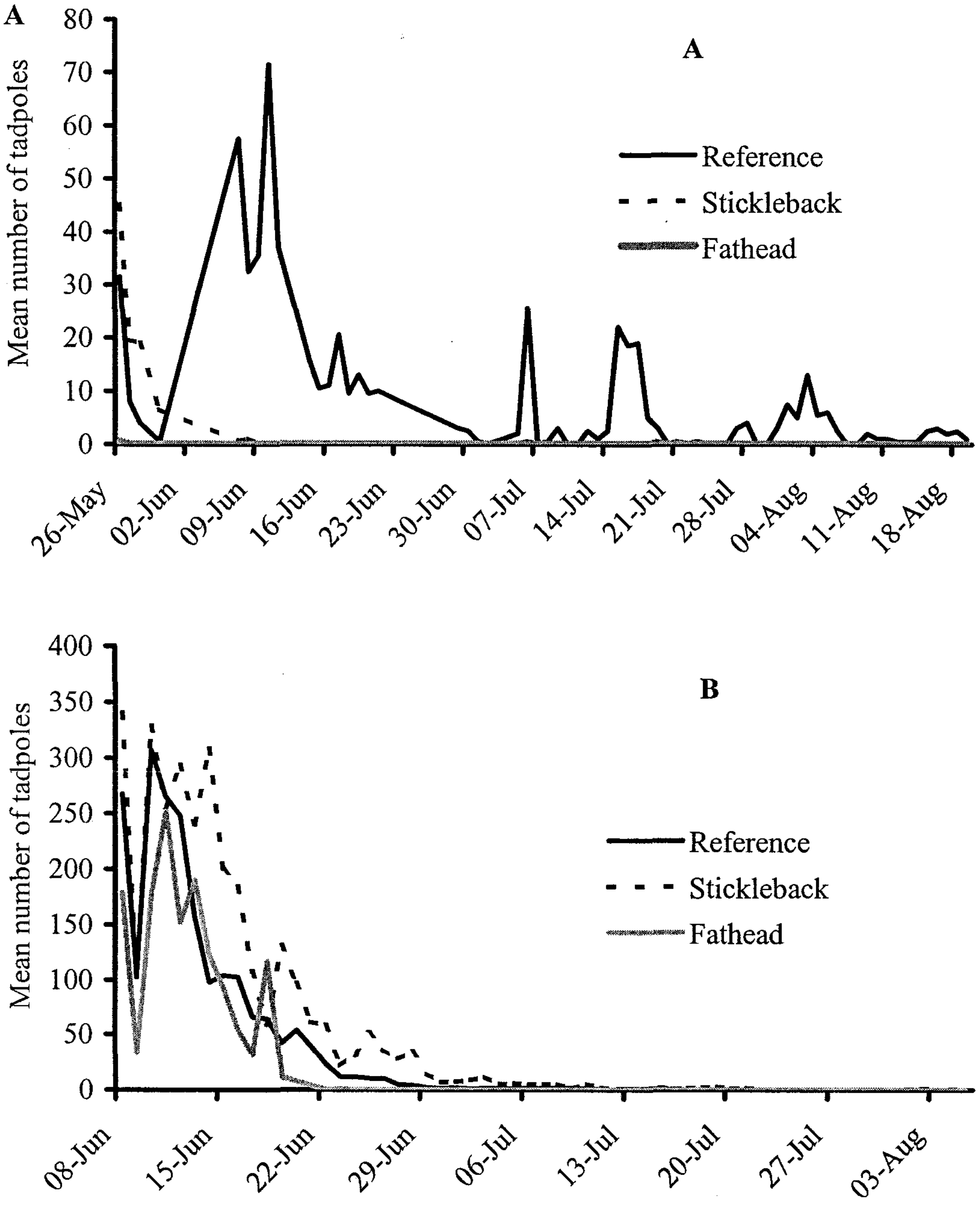


Figure 4-2. (A) Mean number of wood frog tadpoles seen during visual surveys, AM (0800 - 1200 hrs) counts; patterns were similar for PM (1300 - 1800 hrs) counts. Surveys started 3 days after tadpole stocking. Only 1 tadpole was ever seen in the fathead minnow ponds. (B) Mean number of western toad tadpoles seen during visual surveys, AM counts (0800 - 1200 hrs); patterns were similar for PM (1300 - 1800 hrs) counts. No tadpoles were seen after August 5th in any ponds. Surveys started one day after tadpole stocking. Values represent means for ponds of the same type.



CHAPTER 5: Skeletochronological analysis of Canadian toad (*Bufo hemiophrys*) populations in Alberta

Introduction

Growth rates, size at age, and age at sexual maturity of amphibians exhibit latitudinal and altitudinal gradients related to differences in seasonal activity. Individuals in populations at higher latitudes or altitudes experience shorter growing seasons and slower annual growth, but achieve older ages and larger maximum size than individuals at lower latitudes or altitudes (Berven 1982; Hemelaar 1988; Smirina 1994; Miaud et al. 1999; Leclair et al. 2000; Ashton 2002; Yamahira and Conover 2002). Amphibians in populations at high latitudes or altitudes may respond to reduced active seasons with higher growth rates (when adjusted by the length of the active season they experience) than seen in populations from lower latitudes or altitudes (Hemelaar 1988; Merilae et al. 2000; Laurila et al. 2001). In addition to these large-scale regional patterns, local habitat factors, such as quality of the pond environment, may influence growth rates and age and size at maturity (Augert and Joly 1993).

Comparison of age-related parameters between populations relies on collecting accurate age estimates; these can be obtained for amphibians in several ways. The most accurate method of obtaining age-related data for amphibians is to uniquely mark individuals in the year in which they metamorphose, and use capture-mark-recapture techniques to document growth rates, age at maturity, and longevity. This method has two disadvantages: (1) because recapture rates of amphibians are typically low from one year to the next (Berven and Grudzien 1990), a large investment in effort is necessary to capture and mark enough individuals to ensure a sample size sufficient for analysis, and (2) any study using this approach must be long term, which could exceed a decade for some species if longevity is to be documented (Halliday and Verrell 1988). Advantages of the capture-mark-recapture method are that the age of individual animals is known without error, and changes in growth over time can be tracked for animals that are recaptured in more than one year (Halliday and Verrell 1988).

A second method of collecting age-related data is skeletochronology. This method relies on counting layers formed in calcified tissue, with broad bands of bone produced during periods of rapid growth interspersed with denser zones of bone laid down during an individual's inactive period (e.g. winter in northern areas). The number of resting lines, known as Lines of Arrested Growth (LAG), can be counted to estimate the number of winters an animal has experienced, and therefore, the number of years it has been alive. Skeletochronology, while requiring technical expertise and appropriate laboratory facilities, requires as little as a single phalanx from each individual and provides a fairly accurate estimate of age. Collection of phalanges can be coupled with capture-mark-recapture programs that rely on removal of digits for marking animals.

Conservation requires basic data about amphibian populations and life history patterns (Beiswenger 1986); however, this information is lacking for most species, including the Canadian Toad (*Bufo hemiophrys*). Declines in the abundance of this species have been observed in central and southern parts of Alberta, Canada; permanent alteration of wetlands by agricultural practices may have contributed to declines in Canadian toad abundance in the southern half of Alberta (Hamilton et al. 1998). Declines within the province have occurred over 10 – 40 years, and include declines at sites monitored regularly for over a decade (Roberts 1992; Hamilton et al. 1998).

The Canadian toad occurs from Manitoba west to Alberta and north to the southern Northwest Territories in Canada, and from Minnesota west to Montana in the USA. In Canada, as a whole, *B. hemiophrys* is listed as "not at risk" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002). Provincially, *B. hemiophrys* is listed as "secure" in Manitoba and Saskatchewan, but "may be at risk" in Alberta and the Northwest Territories. Outside of Canada, the species has been assigned an "S1" (critically imperiled) status in Montana, while it is listed as "S5" (secure) in Minnesota; neither North or South Dakota currently have legal designations for the Canadian toad (Hamilton et al. 1998).

A disjunct population, originally assigned to *B. hemiophrys*, but now considered by some to be a distinct species (Wyoming toad; *B. baxteri*; Smith et al. 1998) was located in southeastern Wyoming (Baxter et al. 1982). Rapid declines in the abundance of Wyoming toads occurred from the mid-1970s to the mid-1980s (Beiswenger 1986); this population is now considered extinct in nature except for captive-bred individuals released into the wild (Smith et al. 1998). Beiswenger (1986) used the Wyoming toad to evaluate protection systems designed for early detection of extinction-prone species, and found that most approaches were insufficient as early-warning systems of potential extinction for the Wyoming toad, partly because of lack of basic biological data for this species.

Similarly, lack of data on Canadian Toad basic biology impedes the formation of management plans to help conserve this species in Alberta and elsewhere. Here I provide data on longevity, age at maturity, population structure, and size-at-age relationships across a latitudinal gradient of approximately 850 km. My study provides an important reference for future data collected on Canadian toad populations.

The objectives of my study were to (1) compare Canadian toad size-at-age relationships across (a) four sites over a 850 km latitudinal gradient within Alberta, Canada, and (b) across three sites occurring within a relatively small geographic area, and (2) examine the age structure, age at maturity, and size-at-age of male and female Canadian toads at a single site using museum specimens from a historic, intensively sampled, population.

Materials and methods

Specimen collection. Digits were collected from a total of 272 specimens, from five locations (Figure 5-1; Table 5-1). Elevations at the sampling sites were similar, with the highest elevations at the southern sites (Table 5-1). Many samples were taken from museum specimens; those of the largest sample (Brooks) were from sexed specimens collected from breeding choruses. Samples from other sites contained individuals collected or captured in the field, often outside the breeding season (e.g. Lac La Biche sites were part of the Terrestrial Riparian Organisms, Lakes, and Stream [TROLS] Project; see Hannon et al. 2000). These individuals could not be reliably sexed, so data from all individuals were pooled.

Where possible, the longest digit of a rear foot was removed; in some cases this was not possible (e.g. toe-clipping was being used to mark animals by sampling site) and a different digit was removed. In all cases digits were cut at the joint between the 2nd and

3rd distal phalanges using scissors. Snout-to-urostyle length (SUL) was measured for each specimen using a ruler. Russell et al. (1996) reported, for the long-toed salamander (*Ambystoma macrodactylum krausei*), that different digits from the same individual have the same number of LAGs. Conversely, Hemelaar (1985) found that resorption of LAGs in phalanges from the hind feet of male *B. bufo* occurred at a higher rate than for phalanges from the fore feet; females from the same population did not exhibit different resorption rates between fore and hind phalanges. I am assuming that resorption rates were similar for all phalanges used in this study.

Cut toes were stored in 70% ethanol. Prior to processing, toes were decalcified (RDO Rapid Decalcifier, Ingram & Bell Scientifique, Don Mills, Ontario) for 3 hours, and then stored in 70% ethanol. Phalanges were embedded in paraffin prior to sectioning, using standard histological techniques (Appendix B). Samples were cross-sectioned (8 μm thickness) using a rotary microtome, and series of sections from each individual were mounted on microscope slides using Mayer's Fixative (Merck, Darmstadt, Germany). Samples fixed to slides were stained using Harris' Haematoxylin (Appendix C). Cover slips were applied to stained slides using DPX (BDH Laboratory Supplies, Poole, England) mounting medium.

At least 20 mid-diaphyseal sections were examined for LAGs at 400x using a compound microscope. Sections were independently examined by two observers; where the number of LAGs counted by the observers did not agree, sections were examined again, and a consensus reached. For individual toads that were captured before May 31st, the outside perimeter of the digit was taken as a LAG, as insufficient time had passed since the animal emerged from hibernation for new bone to form peripherally to the previous year's LAG. In northern areas, Canadian Toads do not emerge from hibernacula until May (Kuyt 1991).

The annual periodicity of LAGs has been demonstrated for a number of temperate (Hemelaar and van Gelder 1980; Smirina 1994; Tejedo et al. 1997) and tropical (Kumbar and Pancharatna 2002) anurans, and I assumed that the same relationship was true for the Canadian Toad. Therefore, I took each LAG to represent one year of life. Minimum daily temperatures (climate normals for 1971-2000) were < 0°C for most days in the study areas from mid-October to mid-April, so strong LAGs should form in bones of Canadian Toads from the study populations during the long winter period.

Although the histological steps taken to prepare specimens for skeletochronology are fairly straightforward, challenges may arise when interpreting phalangeal cross-sections. False, double, or even triple lines may be present in some samples, resulting in overestimation of an individual's age (Smirina 1994); individuals in some species may also produce a "metamorphosis line" when they transform from larval to adult forms, again resulting in age inflation (Hemelaar 1985). Alternatively, resorption of periosteal bone may occur from the endosteal side of the bone during bone growth and marrow cavity enlargement, destroying early LAGs and resulting in underestimation of an individual's age (Smirina 1994). Careful examination of staining intensity and distribution of LAGs within a phalangeal cross-section may obviate the inclusion of false, double, triple, and metamorphosis lines (Tejedo et al. 1997). Hemelaar (1985) presented a method for estimating loss of early LAGs to resorption involving measurements of LAG diameters from a large number of individuals within a population, and comparison of LAG diameters from individuals with diameters derived from the entire population.

Extent of resorption (the number of LAGs destroyed by bone remodeling) varies across species and populations within a species, but seems to stop when anurans reach maturity (Hemelaar 1985).

I feel that careful examination of the intensity and distribution of haematoxyphilic lines within and across multiple cross sections per individual phalanx avoided inclusion of false lines as LAGs (Hemelaar and van Gelder 1980). Metamorphosis lines were not found in my samples; young-of-the-year (YOY) captured before their first winter and small individuals captured shortly after emerging from hibernation often lacked any lines whatsoever. Examination of a subsample of toads (n=20) from Brooks indicated that loss of LAGs to resorption rarely occurred in this population (Eaton, unpublished data). Based on this fact, combined with the relatively small sample size of individuals from some areas (i.e. Fort McMurray), and the lack of samples from individuals of known sex from others (i.e. Lac La Biche), I assumed that remodeling of periosteal bone occurred at low, and approximately equal rates, in all populations. Most workers have found that resorption only affects one LAG (Sagor et al. 1998; Marunouchi et al. 2002; Tsiora and Kyriakopoulou-Sklavounou 2002), and that relatively few individuals remodel bone (Kellner and Green 1995; Sagor et al. 1998; Reaser 2000).

Analysis. The relationship between estimated age and SUL was described using linear regression for the samples from each of the four regions, and for male and female toads within the Brooks sample. Other regression models were tried, but none provided superior line fits to the linear regression (Kristensen 2000). To examine differences in size-at-age relationships among geographic regions, among populations within a single region (samples from three lakes in the Lac La Biche area; lakes were 1.8 to 10.1 km apart), and between sexes within a single population (Brooks), slopes and elevations of the regression lines were compared following the methods of Zar (1999). Data for individuals for which no LAGs could be discerned were not included in size-at-age analyses. The sample for Wood Buffalo National Park was too small for analysis (n=5), but the data are included here for comparison with other samples.

Slopes of the regression lines were used to estimate mean yearly growth rates of individuals within each region. To adjust for potential differences in length of the active season experienced by toads at different latitudes I divided estimated growth rates by number of degree-days for each area. As amphibians are ectotherms, their development and activity levels are strongly influenced by ambient temperature (Brattstrom 1963; Herreid and Kinney 1967; Camp and Marshall 2000). Although some bufonids are active at temperatures as low as 3 °C, the temperature at which bufonids are active is usually over 20°C (Brattstrom 1963). However, as the maximum daily temperature at my study sites rarely exceeds 20°C during May, when toads emerge from hibernation, I have chosen 10°C (based on 30 year climate normals obtained from the Environment Canada website at http://www.climate.weatheroffice.ec.gc.ca/ climate_normals/index_e.html) as the base temperature for comparing degree-days among the study sites.

To determine if individuals within the 1 and 2 year classes (the only classes with sufficient sample size) at the three Lac La Biche sites differed in size, I compared SULs across sites within each year class with a one-way analysis of variance (ANOVA), followed by multiple comparisons using the Tukey method when there was a significant effect.

I used data from all Canadian toads that were captured during ecological studies at the three Lac La Biche lakes to determine if the distribution of body sizes was similar for all three sites, and if this pattern was reflected in the subsample of specimens I aged from these sites. Pairwise comparisons of the size-structure of samples were made using Kolmogorov-Smirnov Goodness of Fit tests, with the significant P-value adjusted using the Dunn-Sidak method for multiple comparisons.

I compared size of adult male and female toads at Brooks using a T-test to determine if there was sexual size dimorphism in the population. A significance level of $P<0.05$ was used in all statistical tests.

Results

A total of 255 toes were sectioned and examined; I was unable to score slides from 10 individuals, so these were excluded, resulting in a dataset representing 245 individuals.

The size of individual toads within an age class was variable for all regional samples, with much overlap in size between animals of different ages (Figure 5-2). The linear relationship between age and size of individual toads was significant for all four regional samples, for each of the three lakes within the Lac La Biche area, and for males from the Brooks sample, with r^2 values ranging from 0.24 to 0.63 (Table 5-2). The linear regression for females from Brooks was not significant, and had a low r^2 value (0.16), possibly because of a small sample size ($n = 10$; Table 5-2). Although I did not derive a regression equation for the sample from Wood Buffalo National Park, because I had data from few individuals (n=5), data points for these animals lie close to the regression line for the Lac La Biche area (Figure 5-3a).

Latitudinal gradient. Overall, the slope of the relationship between size and age for Canadian toads was significantly different across the four study regions (slope: F=9.88, P<0.0005, df=232; Figure 5-3a). Multiple comparisons between regions suggested that growth rates (represented by slope) were significantly different between Lac La Biche and Beaverhill (q=5.16, P<0.005, df=232), Lac La Biche and Brooks (q=3.84, P<0.05, df=232), and Fort McMurray and Beaverhill (q=4.26, P<0.01, df=234); the other three comparisons were not significant. Note that differences in the intercept of regression lines cannot be tested if the slopes of the lines are significantly different.

Adjusted growth rates were similar for the Brooks and Beaverhill samples, and for the Lac La Biche and Fort McMurray samples (Table 5-3); adjusted growth rates for the two more northerly samples were approximately two to three times higher than southern samples.

The oldest toads were found in the Lac La Biche sample (12 years of age), while the oldest individuals in the other populations were 7 (Fort McMurray), 8 (Beaverhill, Wood Buffalo National Park), and 9 years (Brooks).

Comparison of three populations in one region. The relationship between SUL and estimated age was similar for Canadian toads sampled at three lakes near Lac La Biche (Table 5-2; Figure 5-3b); there were no significant differences between either the slope (F=0.98, P>0.25, df=82) or elevation (F=1.60, P>0.05, df=84) of the regression lines for these populations. The size of one year olds did not differ across lakes (F=0.45, P=0.64, df=22). There were significant differences in the size of two year olds across the three lakes (F=3.6, P=0.04, df=28), but multiple comparisons (Tukey method) did not reveal any significant pairwise differences. However, for both one and two year olds, mean size was largest at Lake 1, and smallest at Lake 3.

Examination of the size structure of the populations at all three lakes, based on all Canadian toad capture data, reflects the pattern seen in the sample of aged animals, with the largest animals found at Lake 1, and the smallest at Lake 3. No individuals with an SUL smaller than 22 mm were captured at Lake 1, while animals in this size range were abundant at the other 2 lakes (Figure 5-4). The size structure of individuals captured at Lake 2 was significantly different from that at Lake 3 (ks=0.46, P=0.0071), with a preponderance of small animals captured at Lake 3 (Figure 5-4); all other comparisons were non-significant. The corrected critical p-value for these comparisons was 0.017.

Structure of a breeding population. The linear regression between SUL and estimated age for male and female adults captured near Brooks (CMNAR sample only) did not differ significantly for slope (t=-0.44, P>0.5, df=73), but did for elevation (t=6.17, P<0.001, df=74) with the regression line for females being higher than that for males (Figure 5-3c). Females were significantly larger than the males in the sample (t=3.34, P=0.0013, df=75; Figure 5-5a), but were not significantly older than the males (t=0.13, P=0.90, df=75; Figure 5-5b). The youngest males in breeding choruses were 1 year old, while the youngest breeding females were 2 years old (Figure 5-5b). The smallest male in a breeding chorus was 53.64 mm long (SUL), while the smallest female was 60.45 mm long. The largest individual in this population was a female (Figure 5-5a), but the oldest was a male (Figure 5-5b).

Discussion

Linear relationships between size and estimated age for Canadian toads in Alberta were strong in almost all areas sampled, but there was much overlap in size between different year classes. A number of other studies have found similar patterns, in which variation in size within a year class precludes precise estimation of age based on body size alone, despite the often-strong relationship between size and age (Acker et al. 1986; Halliday and Verrell 1988). High variation in size amongst individuals of the same age may result from variation in size at metamorphosis (Berven 1990; Goater and Vandenbos 1997), differences in growth rates before maturity (Halliday and Verrell 1988; Ryser 1988), and decreased growth rates following sexual maturity (Ryser 1989; Smirina 1994; Kellner and Green 1995).

The relationship between size and age for Canadian toads varied across the four regions sampled. Relatively large individuals, especially in the younger age classes, and low growth rates were found in the two most southern regions (Brooks and Beaverhill) compared with the northern sites (Lac La Biche and Fort McMurray). The growth rate for the Beaverhill sample was especially low, so that toads in the two northern samples exceeded those of Beaverhill in size as they aged. It is surprising that growth rates did not differ significantly between Brooks and Fort McMurray, as these are the samples most widely separated latitudinally (Figure 5-1). This may have resulted from the small size of the Fort McMurray sample (n=13). The few samples I had for Wood Buffalo National Park were close to the Lac La Biche regression line, suggesting that growth rates of northern populations (Lac La Biche, Fort McMurray, and Wood Buffalo National Park) may be relatively similar.

When growth rates were adjusted for the potential active season at each site, estimated by degree-days, growth rates at high latitude sites remained substantially higher than those in more southern areas, but were very similar between the two northern and two southern sites (Table 5-3). Similarly, Hemelaar (1988) found higher daily growth rates in northern, compared to southern, populations of common toads (*Bufo bufo*), but due to shorter growing seasons at higher latitudes, toads in the northern populations grew less each year, were larger when they reached maturity, and ultimately reached larger sizes than those in southern populations. A similar pattern has been described for mink frogs (*Rana septentrionalis*), with individuals from northern localities reaching larger size due to higher daily growth rates, delayed maturity, and larger size at metamorphosis (Leclair and Laurin 1996).

Despite higher growth rates in the two northern populations, the largest toads in each year class came from the most southerly population (Brooks). This may reflect harsher conditions at more northern sites (e.g. shorter growing season) that toads cannot fully compensate for with higher growth rates. Ryser (1996) found that common frogs (*Rana temporaria*) from a high-elevation population grow more slowly than individuals from lower elevations, resulting in greater age, but similar size, at first reproduction at high elevations; however, within each year class, the lowland frogs were larger. Alcobendas and Castanet (2000) found that bone growth in *Salmandra salmandra* varied with environmental conditions that influenced the length of the active period; of 14 populations sampled, the smallest individuals were found in a high altitude site with extreme environmental conditions.

Growth rates, size at age, and longevity may also vary among populations at smaller geographic scales (Augert and Joly 1993). In my study, the linear relationship between size and age were very similar across Canadian toad populations sampled at three lakes in the Lac La Biche area. However, examination of the size structure of toads captured at these three lakes suggested that environmental conditions at these lakes for larvae and postmetamorphic toads differed. Lake 1 lacked very small individuals such as those found at the other 2 lakes, suggesting that Lake 1 was a particularly good environment for larval growth, with metamorphs emerging at a large size (Figure 5-4). This lake had slightly higher mean water temperatures (0.4 to 0.9°C higher than the other lakes) and more accumulated degree-days above 5°C (896.1 for Lake 1 vs. 871.5 for Lake 2 and 842.3 for Lake 3) during June and July than the remaining two lakes (P. Venturelli, personal communication). Lake 1 was not extreme for any relevant physical (i.e. depth, volume) or chemical (i.e. phosphorus, nitrogen) parameters measured (Prepas et al. 2001). Canadian toad larvae at Lake 1 may have experienced less competition than those at the other two lakes, if the number of postmetamorphic individuals captured is a reasonable index of tadpole populations in the lakes. Beebee et al. (1996), for example, found that production of metamorphs was positively correlated with egg deposition rates in natterjack toads (*Bufo calamita*), and that adult toad density was positively correlated with metamorph production. The number of animals captured at Lake 1 was substantially fewer than at Lakes 2 and 3 (Figure 5-4); lakes with lower larval densities may produce larger metamorphs than lakes with higher larval densities (Wilbur 1977; Berven 1990; Goater and Vandenbos 1997).

The sample from Brooks allowed me to examine the age structure of a breeding aggregation of Canadian toads collected over a short time frame. As in many anurans, males dominated at the breeding site (67 males vs. 10 females), and were generally smaller than females (Acker et al. 1986; Leclair and Laurin 1996). The youngest sexually mature females at Brooks were two years old, while the youngest males were one year old. This pattern is common in anurans, with females maturing one year later than males in many species (Gibbons and McCarthy 1984; Hemelaar 1988). Consistent with my findings, work on Canadian toads in Minnesota suggests that individuals mature after two winters, as the growth rate of individuals recaptured over several years was substantially reduced after two hibernation periods (Breckenridge and Tester 1961). Reduction in growth rate with maturation is a common phenomenon in anurans (Ryser 1989; Hota 1994).

Canadian toads in the populations sampled lived up to 7 – 12 years. Considering that males started breeding as early as age 1, and females at age 2, some individuals may be able to breed for up to 10 years. In reality, the number of years males successfully fertilize eggs may be considerably fewer (Berven 1981), if large male Canadian toads have a mating advantage over smaller individuals, as has been demonstrated for some populations of the closely related *B. boreas* (Olson et al. 1986). Females also may not breed every year, especially in high altitude or latitude populations, where the short active season means it may take two summers for a female to amass enough energy reserves to reproduce (Hemelaar 1988). However, given the potential longevity of Canadian toads, populations should be able to survive short-term environmental perturbations such as drying of breeding ponds, as long as suitable summer habitat is available for adult toads. Richter et al. (2003) suggested that populations of a rare frog, *Rana sevosa*, could experience complete reproductive failure in multiple consecutive years, as long as the maximum longevity of adults was not exceeded; in the case of *R. sevosa* this would mean that successful recruitment would be necessary every 4 or 5 years. For the Canadian toad, this period could potentially be as long as 7-12 years in some populations, though mortality of adults over time would result in an increasingly smaller breeding population, with concomitant loss of genetic diversity and increased susceptibility to local extinction.

Amphibian populations are currently experiencing declines at local to global scales (Houlahan et al. 2000); although many causes have been postulated, it seems likely that multiple factors are operating simultaneously to produce observed, but often unexplained, declines (Carrier and Beebee 2003; Collins and Storfer 2003). Declines in Canadian toads within Alberta may be related to loss of breeding sites; 60% of wetlands in the aspen parkland region of the province have been drained in the last 50 years and over 90% of wetlands in the prairie and parkland regions have been modified (Hamilton et al. 1998). Additonally, the low dispersal ability of Canadian toads (Beiswenger 1986), and the need for suitable overwintering sites (Kuyt 1991), may make them vulnerable to changes in terrestrial habitats (Hamilton et al. 1998). Although there is cause for concern, some populations of the Canadian toad are known to persist. A recent call survey of wetlands in Alberta found Canadian toads at 9 of 497 listening stations, including stations in the Brooks area (Takats and Priestley 2002).

Data on Canadian toad populations are scarce, particularly for northern populations. Here I have provided some of the first basic biological data for these populations, and for northern populations of *Bufo* in North America. My data indicate that Canadian toads mature relatively quickly in southern Alberta, and that adults can live for up to 7 years or more in the province. Canadian toad populations should therefore be able to survive in an area, if adult mortality is not too high, if they experience a year with high recruitment once every few years. These factors, combined with their high fecundity, suggest that re-introduction of Canadian toads (preferably as eggs or tadpoles) into areas where they formerly occurred might be a useful conservation strategy. This approach would only be successful, however, if critical habitat elements, such as overwintering sites, were available in the area.

A large part of my work was based on museum collections. Utilization of museum specimens to provide data on species or populations which are difficult to sample, or to provide historical information (Fisher and Shaffer 1996; Reaser 2000) is an important tool for understanding changes in amphibian populations over time. It would be instructive to resample some of these populations in the future, particularly the Brooks area, and compare the present age structure and growth rates to those provided in my study, which represent conditions > 40 years ago. Such information could be important in detecting changes in growth rates and longevity useful in directing conservation efforts in the future.

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Table 5-1. Sources of Canadian toad samples.

Location	Ecoregion	Latitude	Elevation	Dates collected	n	Source*
Brooks	Mixed Grassland	50.58°N	758 m	19-20 May 1962	80	CMNAR
				3 July 1950 – 22 June 1979	7	UAMZ
Beaverhill Lake / Buffalo Lake[†]	Aspen Parkland	53.45°N (Beaverhill Lake)	668 m	8 July 1950 – 20 May 1964	18	UAMZ
		52.45°N (Buffalo Lake)	780 m	27 May 1953 – 14 July 1977	21	UAMZ
Lac La Biche	Boreal Mixedwood	54.77°N	543 m	18 August 1954 – 7 July 1970	13	UAMZ
				9 June 1996 – 24 August 2000	106	field
Fort McMurray	Boreal Mixedwood	56.73°N	369 m	14 June 1976 – 18 September 1976	13	UAMZ
Wood Buffalo National Park	Boreal Mixedwood	60.0°N	205 m	2 June 1999 – 18 July 1999	5	field

* CMNAR = Canadian Museum of Nature; UAMZ = University of Alberta Museum of Zoology; field = collected during field studies.

[†] samples from Beaverhill and Buffalo Lakes were pooled, and will be hereafter known as the "Beaverhill" sample.

Table 5-2. Linear regressions between age and snout-to-urostyle length (SUL) for Canadian toad samples, Alberta; see Figure 5-1 for sample sites, and Figure 5-3 for graph of linear regressions.

Site	Regression equation	r^2	F	P-value	df
Regional samples (all specimens used at each site; no YOY used in analysis)					
Brooks	$y = 55.4 + 2.92x$	0.31	39.0	<0.0001	85
Beaverhill	$y = 49.4 + 1.51x$	0.24	11.5	0.0016	37
Lac La Biche	$y = 25.8 + 4.84x$	0.52	106.3	<0.0001	99
Fort McMurray	$y = 39.9 + 4.58x$	0.63	18.4	0.0013	11
Samples from specific lakes in the Lac La Biche area (no YOY used in analysis)					
Lake 1	$y = 29.5 + 3.63x$	0.30	12.7	0.0013	29
Lake 2	$y = 25.4 + 3.79x$	0.50	37.0	<0.0001	37
Lake 3	$y = 20.9 + 5.88x$	0.52	17.3	0.00075	16
Samples for Brooks from CMNAR, female and male adults only					
Brooks, Females	$y = 65.2 + 1.74x$	0.16	1.58	0.24	8
Brooks, Males	$y = 57.7 + 2.19x$	0.44	50.2	<0.0001	65

Table 5-3. Number of degree days above 10° C (1971-2000) for Canadian toad collection locations, growth rates (estimated as the slope of the linear relationship between age and snout-to-urostyle length [SUL]), and adjusted growth rates (calculated by dividing the growth rate by the number of degree days accumulated at a location).

Location*	No. degree days above 10° C	Growth rate (mm SUL/yr)	Adjusted growth rate (mm SUL/yr/dd)
Brooks, Alberta	867.0	2.92	0.0034
Beaverhill, Alberta	659.9	1.51	0.0023
Lac La Biche, Alberta	683.5	4.84	0.0071
Fort MacMurray, Alberta	645.8	4.58	0.0071

*weather data were obtained from the Environment Canada weather station closest to the collection sites. These stations were: Brooks AHRC (50.33° N, 111.85° W) for Brooks, Camrose for Beaverhill (53.03° N, 112.82° W), Cold Lake A (54.42° N, 110.28° W) for Lac La Biche, and Fort McMurray A (56.65° N, 111.22° W) for Fort McMurray.

Figure 5-1. Source of Canadian toad samples

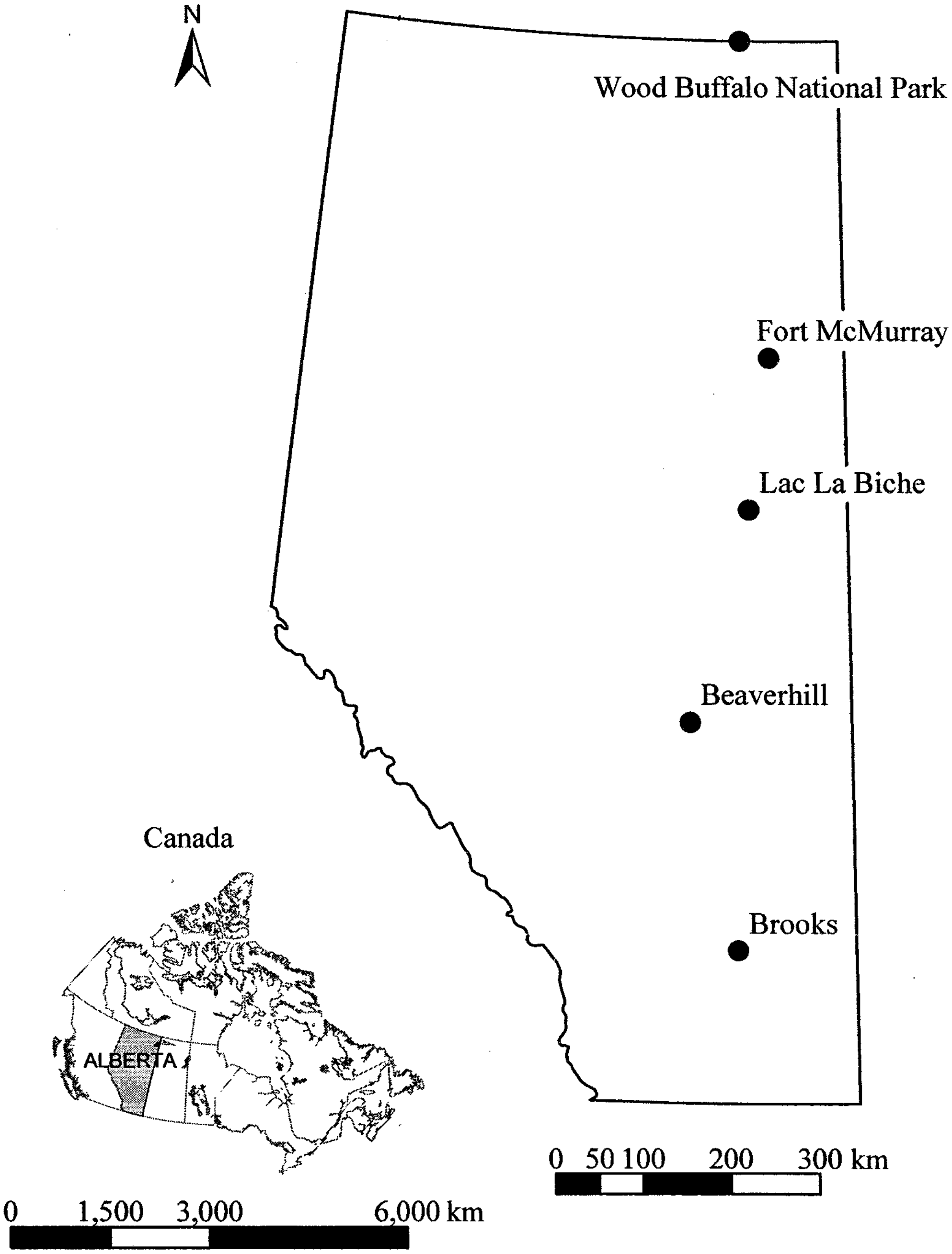


Figure 5-2. Mean snout-to-urostyle length (SUL) of Canadian toads at four sites within Alberta, Canada. Sample size is located over each data point. Bars indicate range of sizes within each year class.

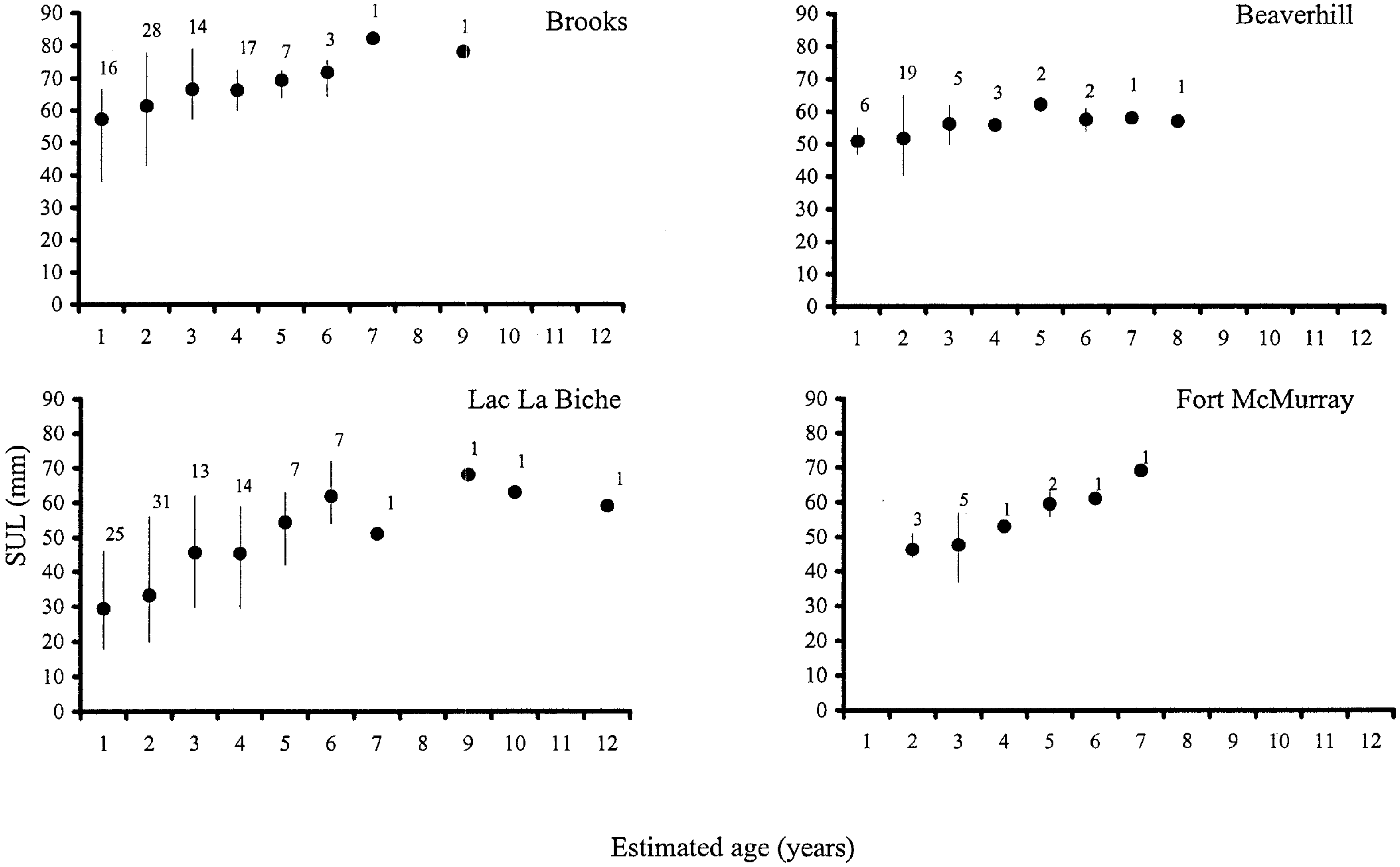


Figure 5-3. Linear regressions for (A) four regional Canadian toad samples (the five samples from Wood Buffalo National Park are included to show trend in age-size relationship at this northern site); (B) three lakes in the Lac La Biche region; (C) female and male toads from Brooks. See Table 5.2 for regression equations.

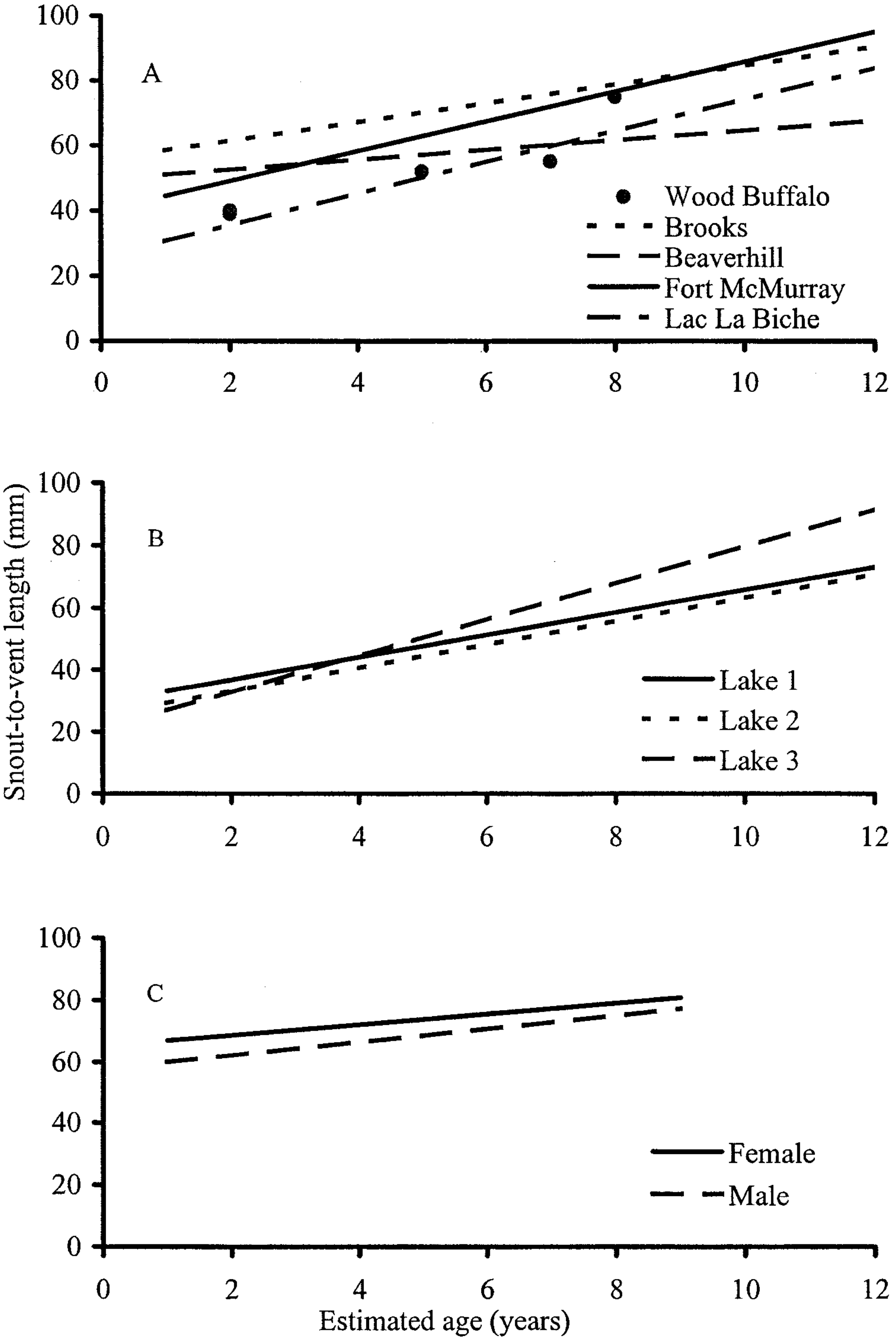


Figure 5-4. Snout-to-urostyle length (SUL) distributions for Canadian toads collected at three lakes in the Lac La Biche area.

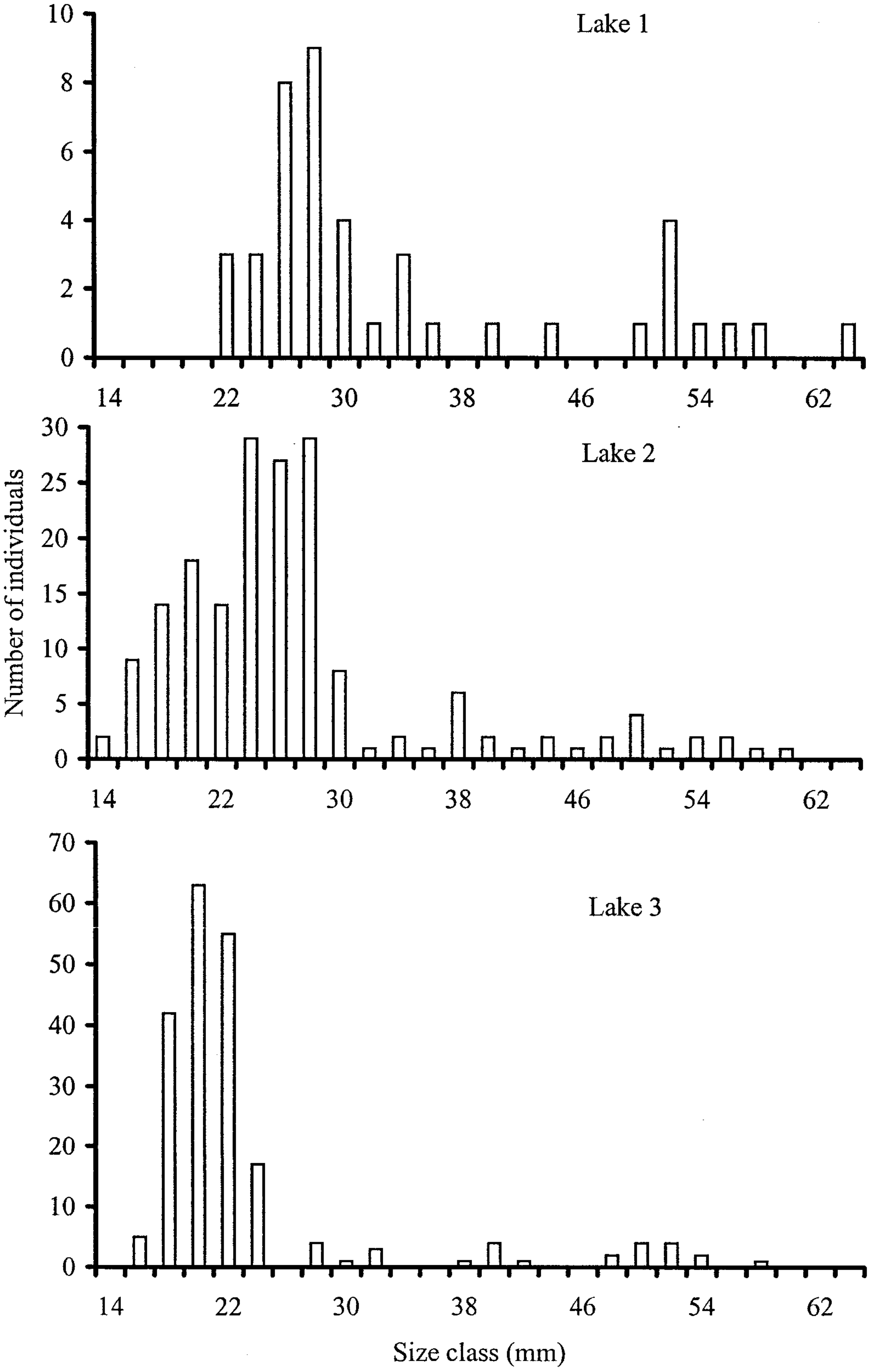
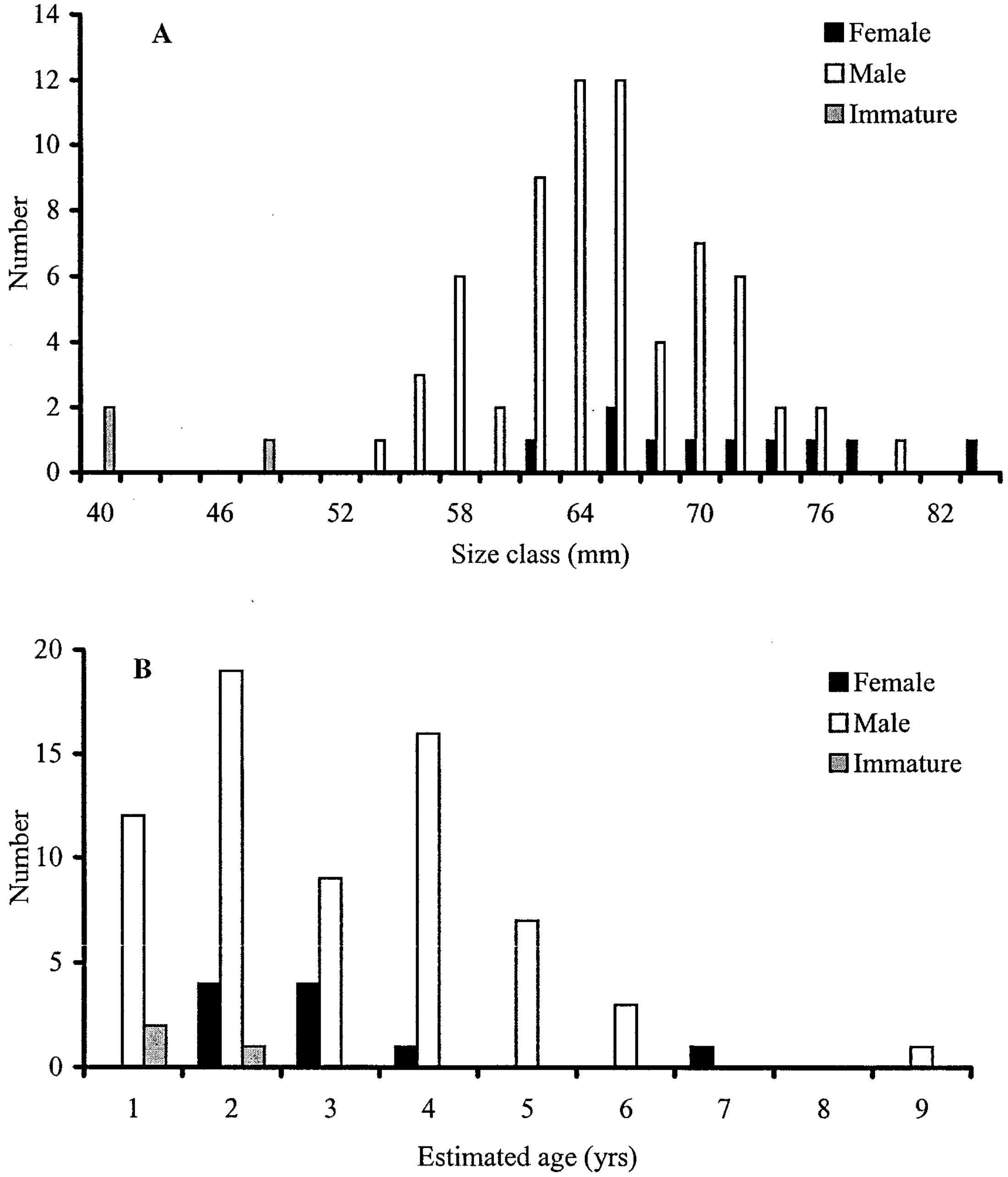


Figure 5-5. Snout-to-urostyle length (A, SUL) and (B) age distributions for Canadian toads from Brooks, Alberta (CMNAR sample only).



CHAPTER 6: General summary

Introduction

Human impacts on wildlife, either through direct (e.g. hunting) or indirect (e.g. habitat destruction) effects occurred in North America even before colonization by Europeans and subsequent industrialization (Laliberte and Ripple 2003). Present human exploitation of the natural environment has resulted in a biodiversity crisis on a global scale (Novacek and Cleland 2001). Although a multitude of reasons for loss of biodiversity have been proposed, the two most important drivers of change in biodiversity are land use changes leading to habitat loss, and climate change (Sala et al. 2000; Thomas et al. 2004).

Habitat loss has large negative effects on biodiversity (Fahrig 2003). Forestry harvesting is now increasing in the boreal mixedwood ecoregion of Alberta (Prepas et al. 2001; Hannon et al. 2002) and conversion of forest to other land uses is occurring in some parts of the boreal region of western Canada (Hobson et al. 2002). Forest harvesting has a variety of negative impacts on vertebrates, including amphibians (deMaynadier and Hunter 1995; Waldick 1997), and may reduce connectivity between potential breeding sites (Semlitsch 2000) and influence amphibian movement over the landscape (Dodd and Cade 1998; Guerry and Hunter 2002; Rothermel and Semlitsch 2002). As well, habitat composition around wetlands may impact amphibian species richness (Findlay and Houlahan 1997; Findlay et al. 2001) and abundance (Knutson et al. 1999; Scribner et al. 2001; Russell et al. 2002).

Potentially exacerbating the effects of habitat fragmentation, climate change is predicted to adversely impact freshwaters in Canada, with disappearance of wetlands as evaporation rates increase with increasing temperature (Schindler 2001). Such changes may impact biotic interactions within boreal lakes; if, for example, incidence of winterkill events (e.g. Danylchuck and Tonn 2003) in boreal lakes increases in response to climate change, recruitment of anurans in these lakes may be affected. Changes in species interactions related to climate have already been documented for amphibians in some areas (Walther et al. 2002).

Here I have used amphibian species in the boreal mixedwood region of Alberta to examine questions related to habitat disturbance (e.g. logging), the potential effects of climate change (e.g. loss of wetlands to drought), trophic interactions (e.g. effects of fish on anuran survival), and demographic characteristics of populations related to climate (e.g. growth rates and longevity of Canadian toads related to latitude).

The ecology of amphibians in the northern regions of Canada, including the boreal mixedwood forest of Alberta, is poorly understood (Roberts and Lewin 1979). Few amphibian species occur in the region; these include the wood frog (*Rana sylvatica*), boreal chorus frog (*Pseudacris triseriata*), western toad (*Bufo boreas*), and Canadian toad (*B. hemiophrys*); no salamanders exist in the region (Russell and Bauer 2000). Species living in this area face many challenges: the boreal mixedwood is semi-arid (Strong and Leggat 1981), with little standing water relative to many other deciduous forests, the growing season is short, and winters are long and harsh. However, until recently there has been limited human impact on the region, which has low human population density, and relatively few roads and little agriculture. Non-native fish have not been introduced into lakes in the boreal mixedwood of Alberta; introduction of predatory fish often has severe impacts on native amphibian populations (Wellborn et al. 1996; Semlitsch 2000).

Industrial activity in the boreal mixedwood is now increasing, with over 75% of the ecoregion now leased to forestry companies, largely for pulp and paper production, and sawlogs (Prepas et al. 2001; Hannon et al. 2002). Timber harvesting usually has short-term negative effects on local amphibian populations, but these effects may be mitigated by appropriate harvest and post-harvest practices (deMaynadier and Hunter 1995). However, it is important to gather data now on the ecology of anurans in the region, before human impacts have altered too much of the landscape. If we have information on ecological relationships before the area is impacted, then we have a basis for comparison in the future to evaluate the consequences of development of the boreal mixedwood, and how anuran populations respond to such development.

Summary of findings. I tried to answer a number of research questions during my graduate studies, either as part of my thesis, or associated with that work. They covered aspects of the distribution and abundance of wetlands and how the intervening terrestrial habitat might influence wood frog movement patterns; the impact of fish on the suitability of breeding habitats; the longevity and size-at-age relationships of the Canadian toad in Alberta; the effects of buffer strips left around lakes during forest harvest on amphibian abundance; and the levels of deformities exhibited by wood frogs in Alberta and Saskatchewan (see Table 6-1 for a summary of research questions and outcomes). Although these questions might seem disparate, they are all related to the basic and applied ecology of anurans in the boreal mixedwood ecoregion.

Limitations of study / Future research. There are many questions that need to be answered about anurans in boreal regions. My work suggests, for instance, that small wetlands are important in maintaining connectivity across the landscape. However, we have little data on the actual ability of anurans to move through terrestrial habitats in this region, nor where they overwinter, spend the summer, how likely they are to move between populations, or how forest harvesting might alter movement patterns. Such questions can best be answered using radio-tracking techniques; unfortunately, only two species (the western and Canadian toads) are large enough to carry tracking radios available at this time.

Interactions between fish and anurans in boreal lakes is another area of research that has not been previously addressed. Lakes are stable environments for anurans, with water persisting throughout the summer. My work suggests that anurans may respond to fish winterkills in these lakes with unusually large pulses of recruitment. What happens to the young-of-the-year (YOY) produced in these lakes? Do they provide an important source of dispersers that maintain local populations around the lake? Do most of them return to the natal lake? Do YOY from winterkill lakes differ in quality from those produced in other areas because they often occur at high densities and may therefore be smaller? Monitoring of fish and anurans at lakes, preferably including larval populations, would provide important data on relationships between these two groups in the boreal mixedwood region.

My research suggests that small-bodied fish that occur naturally with anuran species are able to reduce the survival of some of these species. More research is needed to elucidate this relationship. For instance, what density of fish affects survival of anuran larvae? Can anuran larvae use microhabitats to escape fish predation, or are small-bodied fish able to enter most potential refuges available to anuran larvae? At what point in their development are anuran larvae most heavily impacted by small-bodied fish? Answering these questions would best be achieved by a combination of whole-pond and aquarium experiments.

In order to estimate the ability of anuran populations to persist, it is useful to obtain data on the longevity of individuals within these populations. I have provided some data for Canadian toad longevity and size-at-age relationships across Alberta. Similar data for other species in the boreal mixedwood would be useful. For instance, how long does it take for anurans to mature in this region? This could be answered by collecting toes from breeding individuals for age estimation using skeletochronology. Examinations of age structure of populations are also useful for estimating survival rates between year classes. If individuals are being marked by removal of toes during any monitoring activities, these toes should be archived, along with data about the individual animal they were obtained from and where it was captured.

Canadian and western toads co-occur in some regions of the boreal mixedwood (Hannon et al. 2002). The Canadian toad presently appears to be declining in some regions of southern Alberta (Hamilton et al. 1998), and may have been replaced by western toads in some areas, such as Elk Island National Park (Browne et al. 2003). The two species have been observed in mixed-species amplexus (Eaton et al. 1999), and at least one viable hybrid has been found in Alberta (Cook 1983). Although the extent of such interactions is presently unknown, surveys of breeding ponds in the boreal mixedwood to determine the percent occurrence of each toad species in breeding aggregations, and whether any mixed-species pairs occur, would be useful in documenting interactions between these two species.

Management recommendations. Based on my own work, and information gleaned from the literature, I make the following recommendations for the management of anuran populations in the boreal mixedwood ecoregion of Alberta.

(1) Stocking of natural ponds and lakes with native fish should be done with caution, as periodic winterkills may be important in some areas for the recruitment of large numbers of juveniles to local anuran populations.

(2) Destruction of small ponds and temporary wetlands should be avoided. Areas slated for industrial activity should be surveyed for the presence of such water bodies in the spring, as their presence might not be obvious later in the summer or during the winter.

(3) Construction of borrow pits during road construction, and other activities, may provide additional breeding, hydration, or feeding sites for anurans, and may ameliorate destruction of natural wetlands during these activities. However, caution must be taken to ensure that they do not dry too quickly, acting as ecological traps for local anurans (DiMauro and Hunter 2002).

(4) Yearly sampling of anuran populations at ponds and lakes in areas where forest harvesting is occurring would provide useful information on anuran distribution and relative abundance in relation to human impacts in the boreal mixedwood. Sampling could consist of call and egg surveys during the breeding season, larval surveys (dip net or visual) during the summer, visual encounter surveys or pitfall

trapping during any portion of the active season, or a combination of these methods depending on what life history stage was of interest. Call or egg surveys would be useful in sampling adult breeding effort, while visual surveys or pitfall trapping in the late summer / early fall would provide data on emergence of YOY from breeding sites. Larval surveys would be most useful in providing presence / absence data, and some indication of breeding effort.

(5) Species such as the western and Canadian toads have more specific overwintering habitat needs than wood frogs or boreal chorus frogs. As the Canadian toad in Alberta seems to be declining in the southern part of the province, and this species is listed as "may be at risk" in the province, care must be taken during industrial activities in the boreal region, where healthy populations of this species are still found. Identification and avoidance of potential overwintering sites (e.g. sandy areas; Kuyt 1991) may be especially important.

(6) If personnel are monitoring anurans in the area, they should examine each captured animal for deformities and record such abnormalities. Incidence of deformities in the area is presently low, but increases in deformities may indicate anthropogenic impacts are occurring (Stocum 2000; Kiesecker 2002; Blaustein and Johnson 2003).

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Table 6-1. Outcomes of thesis, and related, research.

Question	Answer	Reference
(1) Do amphibians respond to buffers of different widths left around boreal mixedwood lakes during timber harvest?	No. Wood frogs and toads (western and Canadian) showed no change in abundance relative to buffer width. However, there was great variability in capture rates across treatments and years, potentially masking treatment effects.	Hannon et al. 2002
(2) Are small ponds and temporary wetlands important in maintaining connectivity across landscape?	Yes. Distances between remaining water bodies increases markedly with loss of small (<4 ha) water bodies; this may result from drought or human activity.	Chapter 2
(3) Is terrestrial habitat in the boreal mixedwood important in influencing potential wood frog movement?	No. At present, there are probably few sites within the study area that would be strongly avoided by wood frogs moving overland. Slope, moisture, and habitat layers gave similar results when constructing movement cost maps, suggesting these data provide similar information regarding potential wood frog movement patterns.	Chapter 2

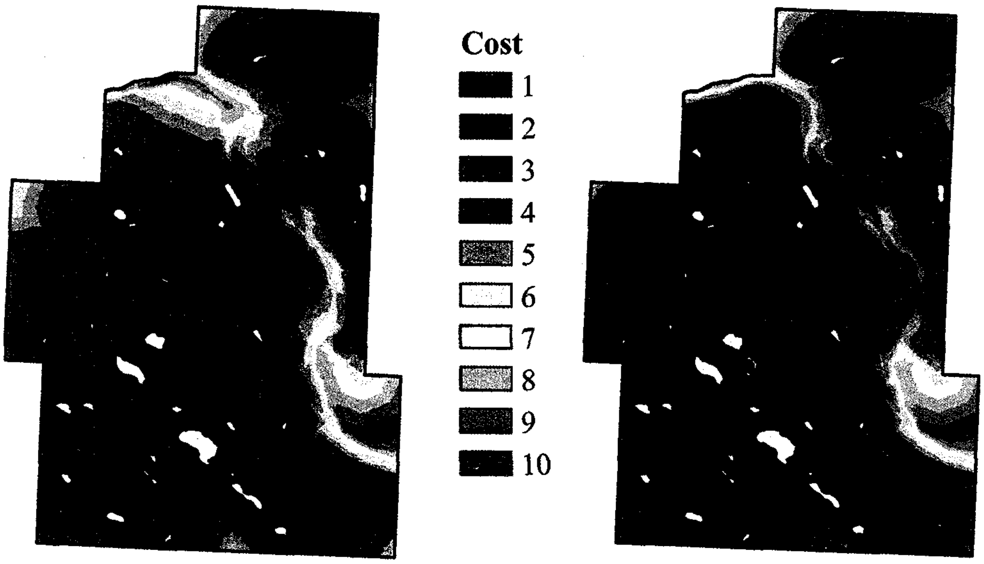
Table 6-1 (continued).

Question	Answer	Reference
(4) Do anuran populations in boreal mixedwood lakes respond to changes in fish abundance, especially related to winterkills?	Yes. Both wood frog and toad (western and Canadian) abundance responded to changes in fish abundance. Wood frogs responded to changes in small-bodied fish abundance, whereas toad abundance was more strongly influenced by large-bodied fish abundance.	Chapter 3
(5) Do small-bodied fish species (fathead minnows and brook stickleback) affect activity and survival of wood frog and western toad larvae under controlled experimental conditions?	Yes and no. Wood frog larval activity and survival were reduced in the presence of both fish species, whereas western toad larvae were unaffected.	Chapter 4
(6) Do longevity and size-at-age of Canadian toads vary across a latitudinal gradient in Alberta?	Yes. Toads at northern sites exhibit higher growth rates when adjusted for length of the active season than those at southern sites. Longevity ranged from 7 to 12 years in the regions sampled.	Chapter 5

Table 6-1 (continued).

Question	Answer	Reference
(7) What is the rate of deformities in wood frogs from the boreal mixedwood of Alberta, and how does it compare to deformity rates in other ecoregions of Alberta and Saskatchewan?	Deformity rates were low in all regions of Alberta and Saskatchewan that were studied, and are consistent with background levels of deformities found by other researchers. Deformity rates were similar across all areas sampled.	Eaton et al. *in press*

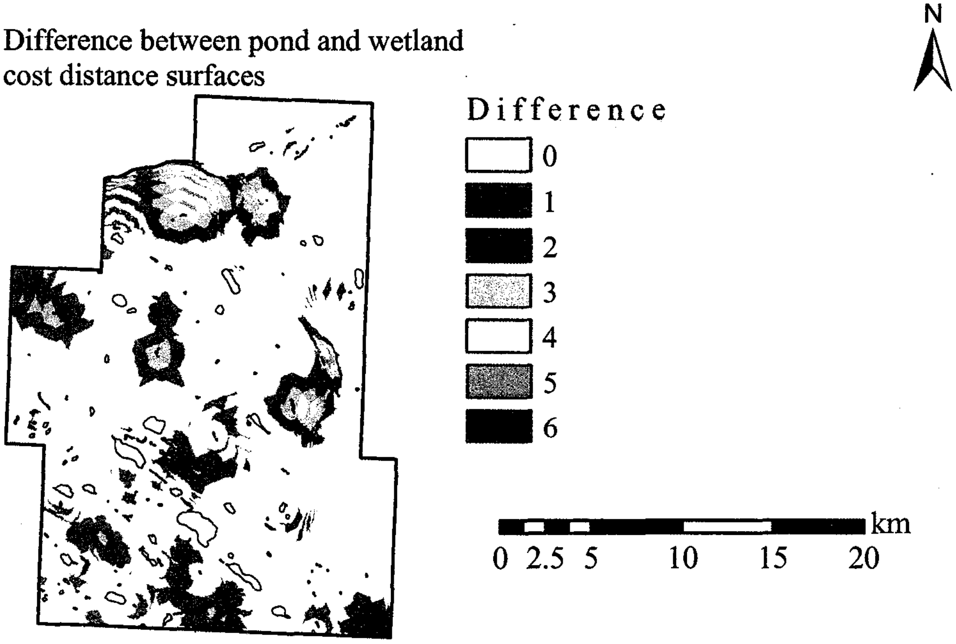
Appendix A, Figure A1. Cost distance surfaces based on slope for ponds, wetlands, and the difference between these cost surfaces. Costs range from 1 (least cost to cross a cell) to 10 (highest cost to cross a cell). The difference between the two cost surfaces was calculated by subtracting the cost surface for wetlands from that for ponds. Difference values range from 0 (the cells from the pond and weland cost surfaces had the same cost), up to 6 (the cells from the two cost surfaces had quite different costs). The cost surface for ponds was always higher, so the result was always positive. Differences between the cost surfaces reflect the increased cost of moving over the landscape in the absence of ephemeral wetlands.



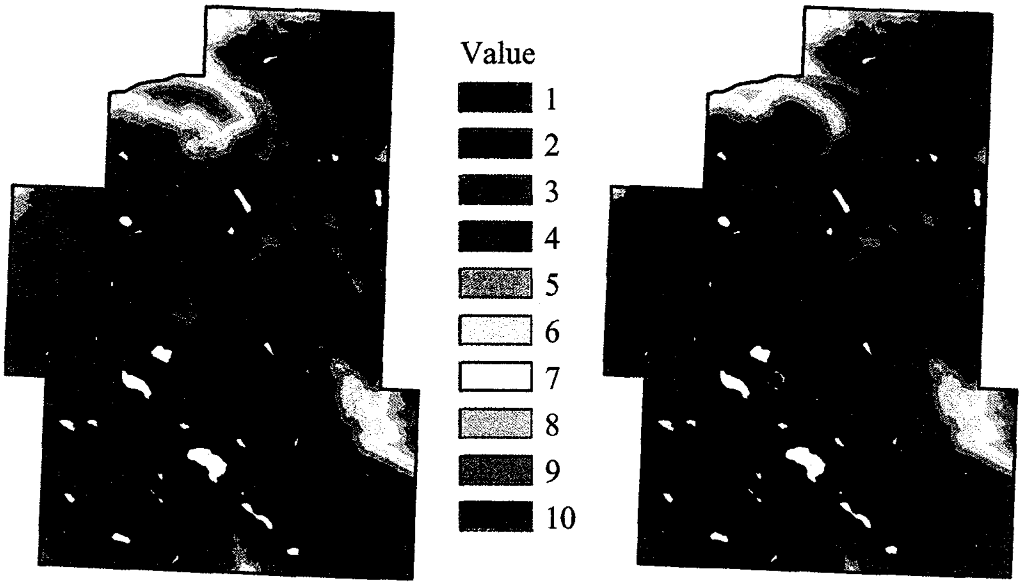
Cost distance surface for ponds

Cost distance surface for wetlands

Difference between pond and wetland cost distance surfaces



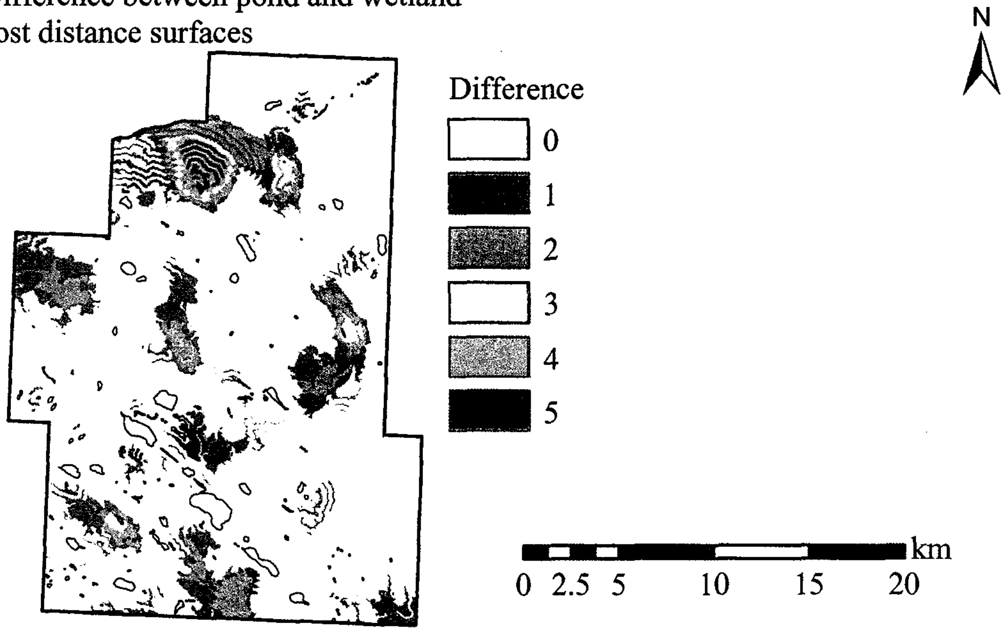
Appendix A, Figure A2. Cost distance surfaces based on moisture for ponds, wetlands, and the difference between these cost surfaces. Costs range from 1 (least cost to cross a cell) to 10 (highest cost to cross a cell). The difference between the two cost surfaces was calculated by subtracting the cost surface for wetlands from that for ponds. Difference values range from 0 (the cells from the pond and weland cost surfaces had the same cost), up to 5 (the cells from the two cost surfaces had quite different costs). The cost surface for ponds was always higher, so the result was always positive. Differences between the cost surfaces reflect the increased cost of moving over the landscape in the absence of ephemeral wetlands.



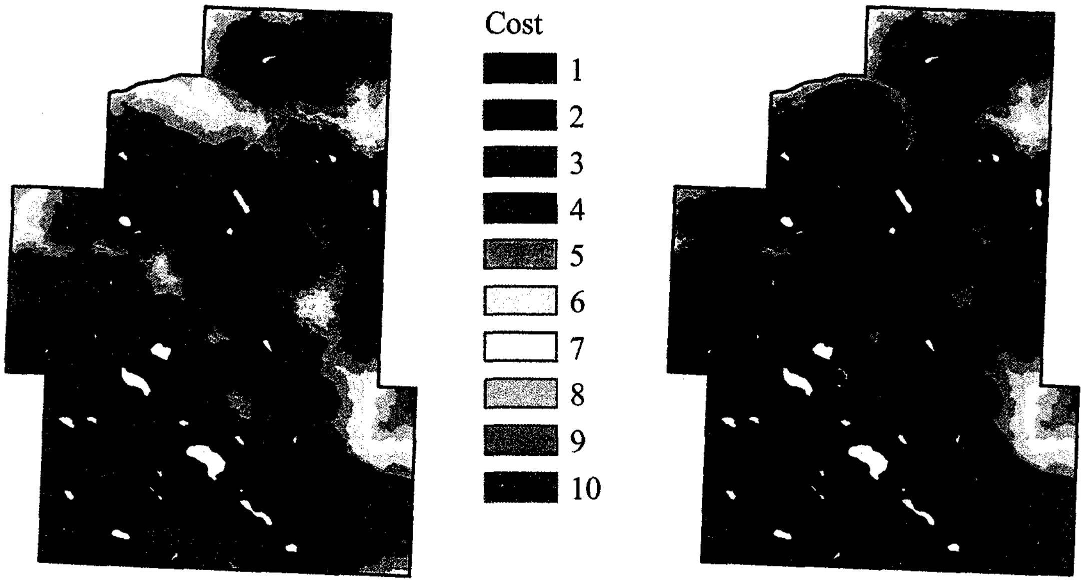
Cost distance surface for ponds

Cost distance surface for wetlands

Difference between pond and wetland cost distance surfaces

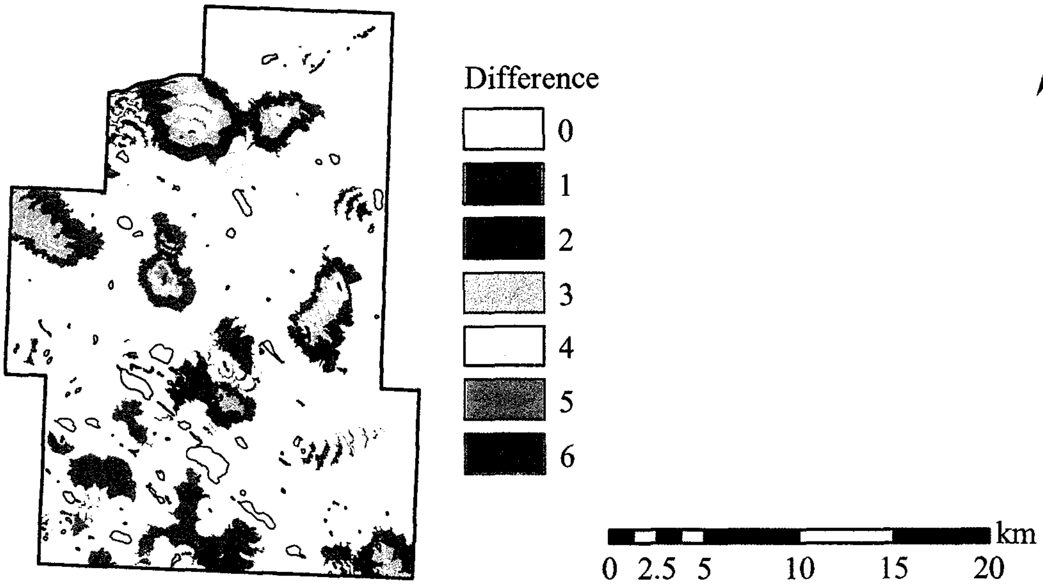


Appendix A, Figure A3. Cost distance surfaces based on habitats for ponds, wetlands, and the difference between these cost surfaces. Costs range from 1 (least cost to cross a cell) to 10 (highest cost to cross a cell). The difference between the two cost surfaces was calculated by subtracting the cost surface for wetlands from that for ponds. Difference values range from 0 (the cells from the pond and weland cost surfaces had the same cost), up to 6 (the cells from the two cost surfaces had quite different costs). The cost surface for ponds was always higher, so the result was always positive. Differences between the cost surfaces reflect the increased cost of moving over the landscape in the absence of ephemeral wetlands.



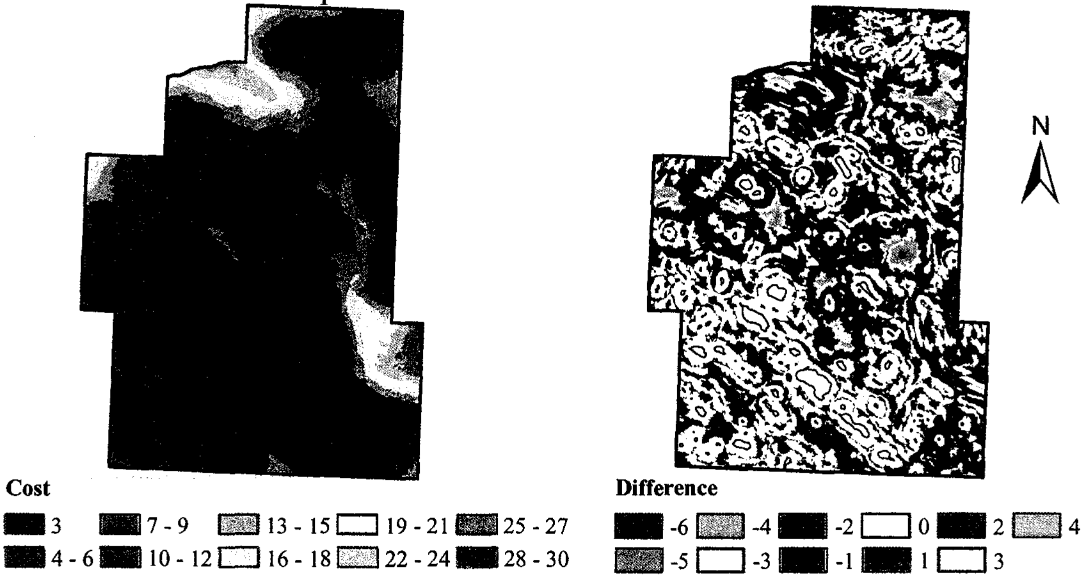
Cost distance surface for ponds

Cost distance surface for wetlands



Difference between pond and wetland cost distance surfaces

Appendix A, Figure A4. Cost distance surface produced by using cost distance analysis on a combined friction map. The friction map was produced by the addition of individual friction maps based on slope, moisture, and habitat. Costs range from 3 (least cost to cross a cell) to 30 (highest cost to cross a cell). Pairwise subtraction of cost surfaces based on different input layers (slope, moisture, and habitat) was used to compare how these different datasets influenced the cost distance models for wood frogs moving over the landscape. This analysis is only shown using ponds; ponds are outlined in black for reference.

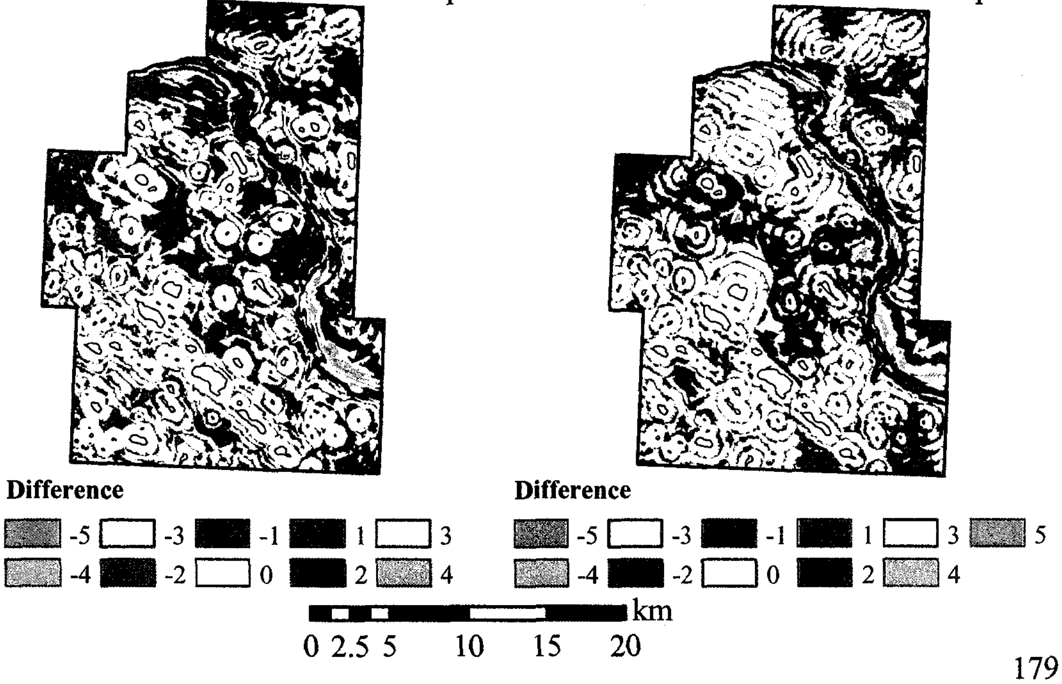


Cost surface map based on combined friction maps

Map of differences between cost surfaces based on moisture and habitat

Map of differences between cost surfaces based on moisture and slope

Map of differences between cost surfaces based on habitat and slope



Appendix C. Detailed methods for toe tissue sample staining.

Samples fixed to slides were stained using the following steps: (1) toluene (5 minutes), (2) toluene (5 minutes), (3) absolute ethanol (2 minutes), (4) absolute ethanol, 2nd rinse (2 minutes), (5) 90% ethanol (2 minutes), (6) 70% ethanol (2 minutes), (7) 50% ethanol (2 minutes), (8) distilled water (rinse), (9) Harris' Haematoxylin (3-10 minutes), (10) distilled water (rinse), (11) wash under running tap water (15 minutes), (12) 70% ethanol (2 minutes), (13) absolute ethanol (2 minutes), (14) absolute ethanol, 2nd rinse (2 minutes), (15) toluene (2 minutes), and (16) toluene (2 minutes). Cover slips were applied to stained slides using DPX (BDH Laboratory Supplies, Poole, England) mounting medium.

Appendix B. Detailed methods for toe tissue sample processing.

Cut toes were stored in 70% ethanol. Prior to processing, toes were decalcified (RDO Rapid Decalcifier; Ingram & Bell Scientifique, Don Mills, Ontario) for 3 hours, and then stored in 70% ethanol. Phalanges were prepared for sectioning using a Fisher Scientific Model 166 Histomatic Tissue Processor. Tissue was taken through a number of steps: (i) 1 hour in 90% ethanol, (ii) 1 hour in absolute ethanol, (iii) 1 hour in a 2nd bath of absolute ethanol, (iv) 1 hour in a 50:50 absolute ethanol:xylene mixture, (v) 30 minutes in xylene, (vi) 30 minutes in a 2nd bath of xylene, (vii) 1 hour in melted paraffin, (viii) 1 hour in a 2nd bath of melted paraffin. When processing was complete, tissue was embedded in paraffin for sectioning.