University of Alberta

The Role of Beaver in Amphibian Ecology and Conservation in the Boreal Foothills

by

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Abstract

The Rocky Mountain foothills of west-central Alberta are a multi-use industrial landscape of deciduous boreal and coniferous cordilleran forests. Dam-building beaver active on small streams may create most of the breeding habitat for amphibians. My goal was to provide new ecological information that aids in preventing amphibian declines in this landscape and to evaluate techniques used for measuring breeding densities and juvenile recruitment. A major focus of this research is the use of beaver as a surrogate species for amphibian conservation. Results from call surveys and pitfall-trapping on 9 pairs of beaver-obstructed and unobstructed streams during 2001-2 showed that beaver may be a good indicator of the presence of wood frog, boreal chorus frog and western toad populations. The high percentage of ponds constructed by beaver in the study area (96%) suggests they are important in maintaining local amphibian populations. The distribution of beaver ponds, however, was not random. Stream order and proximity to cutblocks were important correlates of their occurrence in 15 watersheds examined with GIS. I also assessed whether succession of ponds mediated by beaver foraging in riparian zones affected amphibian populations. Results from call surveys on 57 beaver ponds in 2001-2 showed that wood frog densities were negatively related to % riparian canopy cover and positively related to pond age; the best *a priori* models included % riparian canopy cover rather than pond age as a significant covariate. A mesocosm experiment in 2002-3 showed that higher growth and development rates of larval wood frogs in 5 old (>25 yrs) *vs.* 5 new ponds (<10 yrs) coincided with reduced canopy cover plus higher indices of submergent vegetation, thermal degree days, and dissolved oxygen concentrations in old ponds. Unlike the common wood frog, identification of key breeding ponds for western toad (IUCN red-listed) was difficult due in part to its low density population and patchy distribution. However, results from pitfall trapping suggested that anthropogenic ponds (borrow pits) may be ecological sinks for the western toad. Management practices that avoid constructing ponds but protect beaver colonies and their food supply in riparian zones may ensure healthy populations of amphibians in the Boreal Foothills.

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Chapter 1. General Introduction

High rates of global deforestation, polluted air and water, and climate change resulting from an increasing use of natural resources has prompted society and scientists to understand how the quality of their life may be affected and to set guidelines that maintain sources of drinkable water, biodiversity and the general health and integrity of ecosystems. The investigation of the biology of amphibians has played a key role in addressing conservation questions since the discovery in the 1980s that many populations and species were declining throughout the world (Alford and Richards 1999, Houlahan et al. 2000, Stuart et al. 2004). Declines have been linked to many factors (see recent reviews by Collins and Storfer 2003, Blaustein et al. 2003, Carey and Alexander 2003); however, most biologists agree that local destruction or alteration of habitat (e.g., draining of wetlands, poor water quality) is a major cause of declines (Blaustein et al. 1994, Wake 1998, Alford and Richards 1999, Semlitsch 2002). The complex life cycle of most amphibian species make populations particularly vulnerable to landscape changes at multiple scales (Vitt et al. 1990). Critical principles for management include the protection of ponds and wetlands where amphibians reproduce and recruit juveniles into the population (Semlitsch 2000). Maintaining adequate number of ponds on a landscape is also critical to metapopulation source-sink processes because greater pond densities increases the probability that populations will be rescued from extinction (Marsh and Trenham 2001).

In North America, the majority of amphibian research is heavily biased towards lower latitudes and the species that occur there (but see Herreid and Kinney 1966, 1967, Roberts and Lewin 1979, Leclair et al. 2000, Constible et al. 2001, Hannon et al. 2002) and may not be applicable to our understanding of the ecology of species in northern ecosystems which include the wood frog (*Rana sylvatica* Le Conte), boreal chorus frog (*Pseudacris maculata* Agassiz), and western toad (*Bufo boreas* Baird and Girard) in the Boreal Foothills of west-central Alberta (Russell and Bauer 2000). The Boreal Foothills is also known as the Boreal-Cordilleran ecoregion because it is an ecotone between boreal and cordilleran climatic conditions, as well as between deciduous boreal and coniferous cordilleran vegetation (Strong and Leggat 1992). The rolling topography created a landscape dominated by networks of low-to-moderate gradient streams (first to fourth order) with numerous beaver ponds, but relatively few basin wetlands or ponds (Chapter 4; Strong and Leggat 1992). The majority of work within this thesis took place near the town of Lodgepole (approximately 53° 06' N-115° 19' W) located within both the Weyerhaeuser Drayton Valley Forest Management Area and Pembina Oilfield. The forestry and energy sectors have built over 240 km of roads to drill 446 oil and gas wells and to harvest trees from approximately 10% of 15 watersheds totalling 14 548 ha in the Lodgepole region (Chapter 4). Thus, the first goal of this thesis is to provide new ecological information on landscape and local processes affecting the distribution and abundance of boreal amphibians that can be used as part of conservation strategies to maintain biodiversity in Alberta and boreal ecosystems of North America. My second goal is to ensure the quality and accurate interpretation of this information by evaluating field techniques used to collect data under my first research goal.

Two common field techniques used in monitoring amphibian populations and their habitat-use patterns are pitfall trapping and anuran call surveys. Chapter 2 explores pitfall trap designs and their effectiveness in estimating numbers of post-metamorphic individuals and rates of juvenile recruitment to metamorphosis on ponds (Bury and Corn 1987, Corn 1994). I compare, in a boreal landscape, the total number of anuran captures per species and age class (< 1 yr, ≥ 1 yr) between a pitfall trap similar to the conventional model (see Corn 1994) with one encompassing modifications to the previous design, which I used in collecting data for Chapters 4-6. In conjunction with pitfall trapping, call surveys were used in Chapters 4 and 5 to detect the presence of breeding (i.e. chorusing) males on ponds (Bishop et al. 1997, Shirose et al. 1997). This survey technique is relatively new in ecological research and monitoring programs in North America (Bishop et al. 1997, Lehtinen et al. 1999, Waldick et al. 1999, Kolozsvary and Swihart 1999, Knutson et al. 1999, Skelly et al. 1999, Bridges and Dorcas 2000, Zampela and Bunnell 2000, Palik et al. 2001, Weir 2001, Crouch and Patton 2002, Guerry and Hunter 2002, Stevens et al. 2002). In fact, the standardized protocol for anuran call surveys in the United States and Canada was only developed in 2001 (Wier 2001). Assessments of this protocol in various regions of North America represent measures to improve researchers' ability to detect and monitor anurans (Bridges and Dorcas 2000, Crouch and Paton 2002, MacKenzie et al. 2002); however there has been no published study that determined whether the abundance of breeding male amphibians engaged in advertisement and territorial behaviour serves as an indicator of reproductive activity or success. In Chapter 3, my primary objective is to determine whether perceived numbers of calling males (i.e., ranks of chorus size) recorded from multiple surveys of a pond predict female reproductive activity (i.e., number of egg masses) for the wood frog. My second objective is to develop a more quantitative measure of abundance than ranks based on aural estimates of calling intensity (see Wier 2001).

Because many amphibian species are cryptic and their populations are often difficult to estimate reliably in the field (e.g., Chapter 2, Paszkowski et al. 2002), a simple, ecologically-based shortcut for estimating population changes, such as the use of surrogate species, may be useful for managers and conservation biologists (Simberloff 1998, Caro and O'Doherty 1999, Roberge and Angelstam 2004). The beaver (*Castor canadensis*) is a potential surrogate species in amphibian conservation because of its profound influence on the physicochemical properties of streams through damming that may be beneficial for pond-breeding amphibians (Naiman et al. 1986, Naiman et al. 1988, Snodgrass and Meffe 1998, Schlosser and Kallemyn 2000). In addition, beaver populations can be easily monitored through delineation of beaver ponds with aerial photography (Slough and Sadleir 1977, Howard and Larson 1985, Johnston and Naiman 1990). In Chapter 4, I assess the relationship between beaver and amphibian populations on small streams by comparing breeding activity and the abundance of the wood frog, boreal chorus frog and western toad through call surveys and pitfall trapping on beaver ponds and unobstructed streams. To assess the potential role of beaver in maintaining amphibian populations in the Boreal Foothills of west-central Alberta, I also examine patterns of occurrence of beaver ponds relative to basin ponds (i.e., non-beaver ponds and wetlands) and characterize the distribution of beaver ponds in a managed landscape with roads and cutblocks using a combination of a digital elevation model and vegetation inventory layers (Franklin et al. 2002) in GIS.

Given the global scale of recorded extinctions and recent declines in numbers of amphibian species (Houlahan et al. 2000, Alford et al. 2001, Stuart et al. 2004), an understanding of natural variation in amphibian densities and underlying mechanisms represent an important component for ensuring their survival. Succession through habitat change is a fundamental ecological process influencing the population dynamics of animals and is often driven by fire in the boreal forest (e.g., Connell and Slatyer 1977, Johnson 1992, Skelly et al. 1999). On streams, beaver (*Castor canadensis*) disrupt flow with dams and mediate pond succession through continued foraging in riparian zones (Donkor and Fryxell 1999, Barnes and Mallik 2001). In Chapter 5, I examine use of beaver ponds by the wood frog in a network of boreal streams in west-central Alberta by quantifying relations between breeding densities estimated from call surveys with pond age and riparian canopy cover. I predict that older ponds would be characterized by lower levels of riparian canopy cover because of long-term impacts of beaver foraging (Donkor and Fryxell 1999, Barnes and Mallik 2001). I also predict that older ponds would support higher densities of breeding wood frogs because of both 'inertia mechanisms' (yearly colonization events, juvenile recruitment to metamorphosis and site fidelity; Gill 1978) and habitat selection by breeding adults for open canopy ponds and associated larval environments (e.g., warm water; Werner and Glennemeier 1999, Skelly et al. 2002). In a subset of newly formed (<10 yrs) and older (>25 yrs) beaver ponds, I: i) quantify variation in physiochemical characteristics; ii) describe the structure and relative abundance of wood frog populations and estimate rates of juvenile recruitment to metamorphosis using pitfall traps; and iii) complete a field experiment using in-pond enclosures to identify key breeding habitats for the wood frog by comparing larval performance between pond-age classes. I predict that larval performance measured as survival, development rate, and growth rate would be higher in older beaver ponds because they receive more light under reduced riparian canopies and are therefore characterized by higher temperatures and a more abundant algal food base. Higher light levels in older ponds may also result in higher dissolved oxygen concentrations owing to increased levels of photosynthesis by algae and submerged macrophytes. Thus, Chapter 5 also includes a short-term laboratory experiment to examine the extent that growth and development of larval wood frogs were influenced by varying concentrations of dissolved oxygen

One of the most threatened species of amphibian in western North America is the western toad (IUCN red-listed; Hammerson et al. 2004). Populations have either declined or disappeared throughout most of the species' southern range in the U.S., including the Southern Rocky Mountains (Carey 1993, Livo and Yeakely 1997, Corn 2000), and California's Sierra Nevada and Central Valley (Drost and Fellers 1996, Fisher and Shaffer 1996). In Chapter 6, I asses the status of the western toad in the Pembina and North Saskatchewan watersheds of the Alberta foothills using visual surveys and a comparison of encounter rates with that of wood frog, a species that generally has stable populations throughout Canada and northern United States. Also in Chapter 6, I estimate the age structure of a population of western toad in a landscape under high-use by forestry and energy sectors near Lodgepole, AB. Common practice during road construction in industrial landscapes is to dredge adjacent land for gravel and soils to raise roads above wet areas. The resulting borrow pit often fills with water, attracting breeding anuran amphibians (Bunnell and Zampella 1999, Graham 2002); however, few studies have examined whether anthropogenic ponds are population sinks or sources (habitats with low or high rates of juvenile recruitment; but see DiMauro and Hunter 2002). Thus, I compare juvenile recruitment of the western toad and wood frog on borrows pits versus beaver ponds (natural reference sites) using pitfall traps and drift fences.

The present thesis is in paper format such that Chapters 2-6 represent manuscripts submitted to peer-reviewed journals in the fields of ecology, wildlife management or amphibian biology. Chapter 7 summarizes important findings in Chapters 2-6 and highlights hypotheses and topics requiring further study.

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Chapter 2. A Comparison of Two Pitfall Trap Designs in Sampling Boreal Anurans*

The ecology of amphibians in Canada's boreal forest is poorly documented (but see Constible et al. 2001; Hannon et al. 2002; Leclair et al. 2000; Roberts and Lewin 1979). Sound ecological techniques are needed to properly assess population sizes, distributions and habitat use patterns (Paszkowski et al. 2002). Use of pitfall traps with drift fences is a common and effective method to assess the presence and abundance of many species of amphibians (Bury and Corn 1987; Corn 1994). They are easy to construct (although installation can represent a significant time investment), generally less expensive and require less maintenance than use of funnel traps (Jenkins et al. 2003).

The conventional pitfall trap is constructed from two coffee cans (one with bottom removed) fastened together with duct tape and a plastic funnel made from a margarine container (with bottom removed) inserted at the top (Corn 1994). New research has since evaluated the effectiveness of pitfall traps to improve monitoring and increase our knowledge of sampling biases for various species and habitat types. In general, the best pitfall trap is a wider bucket or can (Mitchell et al. 1993) that is dark in color (Crawford and Kurta 2000) and has a rim or funnel to prevent individuals from escaping (Mazerolle 2003). The objective of my study was to compare in a boreal landscape the total number of anuran captures per species and age class (<1 yr, ≥1 yr) between a pitfall trap similar to the conventional model (see Corn 1994) with one encompassing modifications to the previous design.

Methods.—I conducted this study adjacent to beaver ponds in the boreal foothills eco-region on the eastern slopes of the Rocky Mountains near the town of Lodgepole, Alberta, Canada (53° 06' N - 115° 19' W) during summer 2003. Common species of amphibians in the region are the wood frog (*Rana sylvatica*), boreal chorus frog (*Pseudacris maculata*), western toad (*Bufo boreas*), and red-sided garter snake (*Thamnophis sirtalis*; Russell and Bauer 2000). All three species of anurans were heard calling on the study ponds in the spring prior to pitfall trapping.

My study compared two types of pitfall traps: an 'old' versus 'new' model. The 'old trap' was similar to, but smaller than the one described in Corn (1994): I used 1.5

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*Published as Stevens and Paszkowski (2005) in Herpetological Review 36:147-149.

coffee cans (1 kg size) rather than 2 coffee cans (1.36 kg size). The inserted funnel in the coffee can was a margarine container (907 g) with the bottom cut out (Figure 2:1). The ‘new trap’ was a 7.6 L plastic bucket; black in color with a soft-sloping funnel constructed from polyethylene plastic (i.e. vapor barrier) and duct tape (Figure 2:1). This trap type was wider than the old model (23 cm vs. 15 cm in diameter). However, trap depth, diameter of the funnel hole, and distance of the funnel hole to the bottom of the trap were similar between trap types (Figure 2:1). A small quantity of moss was added to the bottom of each trap to keep animals moist and shaded (I did not use cover boards above traps). A stick (1.0 cm diameter) was also inserted into each trap to allow small mammals to escape (Perkins and Hunter 2002). Traps were installed in pairs along drift fences; each fence consisted of one new trap placed at one end and one old trap at the opposite end. The drift fence was a polyethylene sheet 5 m long and 30 cm wide above ground with approximately 5 cm of plastic buried in the soil. All fences were 5-10 m from, and parallel to, the shoreline associated with four beaver ponds within a 200 km^2 study area. Approximately 20% of the shoreline of each pond was covered with drift fences resulting in 10, 9, 8, and 6 fences randomly located on the four ponds for a combined total of 33 trap pairs. Pitfall traps were opened from June 28 to July 30, 2003 and checked every 3-4 days.

Captured anurans were identified to species and age class (<1 yr or young-of-year and ≥1 yr or adult) and a sample of individuals were measured for snout-urostyle length (SUL) and mass. Individuals categorized as young-of-the-year (YOY) were < 21 mm SUL for boreal chorus frogs and < 27 mm SUL for wood frogs and western toads, or had remnants of a larval tail (in some cases anurans with a larval tail were counted but not measured for SUL). All anurans were released 5-10 m from their point of capture. Animals were not marked (e.g., toes clipped) because previous pitfall trapping in 2001 and 2002 resulted in very low recapture rates for anurans in the area (< 2%; C. E. Stevens and C. A. Paszkowski, unpublished data).

I determined if there were differences in the total number of individuals captured per species and age class between old and new traps from all 33 fences combined (N = 33) using a Wilcoxon paired-sample test. I chose this analysis because each data set consisted of a non-normal distribution even after square-root and logarithmic transformations, and because trap types were installed in pairs to account for possible microhabitat differences among fence locations that can affect capture rates (deMaynadier and Hunter 1999; Melbourne 1999). I accepted significance at the 5% level.

Results.—Sixty-six pitfall traps captured 1274 anurans: 1111 YOY wood frogs, 84 YOY boreal chorus frogs, 43 adult wood frogs, 32 adult western toads, 4 adult boreal chorus frogs, 0 YOY western toads (Table 2:1), and 0 snakes. Significantly more individuals were captured in new versus old pitfall traps for adult wood frogs ($z = -2.28$, $P = 0.022$) and YOY boreal chorus frogs ($z = -4.03$, $P < 0.001$; Table 2:1). However, there were no significant differences in numbers caught between trap types for YOY wood frogs ($z = -0.13$, $P = 0.893$) and adult western toads ($z = -1.28$, $P = 0.202$; Table 2:1).

Discussion.—The new pitfall trap design was as effective or more effective in trapping boreal anurans than the more commonly used coffee can design (e.g., Corn 1994). This difference may reflect anuran avoidance of the silver color inside the coffee cans or the white color associated with the margarine container used as the funnel (Crawford and Kurta 2000). In addition, adult ranids may avoid the narrower traps (i.e. coffee cans) by jumping over the hole. The structure and shape of funnels in pitfall traps could also influence their effectiveness in trapping anurans. For example, the margarine container in my study had a hard rim or lip that could provide a solid platform for individuals inside the trap to grasp with their forelimbs or to rest on, rather than falling into the deeper can, particularly for YOY boreal chorus frogs (C. E. Stevens, personal observation). In contrast, the funnel in the plastic bucket was a soft or flexible polyethylene sheet with a constant sloping surface that lacked distinct surfaces for support (Figure 2:1).

Very few adult boreal chorus frogs and no YOY western toads were captured in my study. Hylids, in general, are difficult to sample with pitfall traps because of their ability to climb vertical structures (Dodd 1991). The lack of captures of YOY western toads, however, may reflect the fact that partial fencing of ponds failed to intercept individuals that emerged in a non-uniform pattern rather than failings of the trap designs. For example, newly metamorphosed toads may have emerged from concentrated locations in the pond where the water was warm or highly oxygenated (Noland and Ultsch 1981). It is also possible that the beaver ponds in my study were poor larval environments for toads (e.g., too cold, inadequate food) leading to low juvenile recruitment to metamorphosis.

My field experience with both types of pitfall traps suggests that the plastic bucket-polyethylene funnel design is easier to construct than the one made from a coffee can and margarine container. The special cutting device and time needed to remove the bottom of coffee cans and cut tin to create the 1.5 coffee can was not required for the plastic bucket. In addition, large numbers of plastic buckets can be stacked because of their tapered design (Figure 2:1) and carried into field locations with greater ease than when using non-stackable coffee cans. Cans can also rust with extended use and eventually need to be replaced. Finally, although coffee cans and margarine containers can be obtained for free, the costs of plastic buckets and polyethylene plastic are relatively low when bought in large quantities: $ 2 per 7.6 L plastic bucket, and $ 13 per 46 m^2 roll of polyethylene plastic (Cdn dollars).

In summary, the new model (plastic bucket with flexible polyethylene funnel) was a better pitfall trap than the old model (coffee can with margarine container) both in terms of ease of use and trapping performance. Funnel designs may play a key role in reducing the number of hylids and large ranids that escape from traps. Understanding the biases of various methods and improving ecological techniques to monitor more accurately population trends is critical to the conservation of anurans in boreal habitats.

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Table 2:1. Total number of captures and number of drift fences that captured higher numbers of individuals in 'new pitfall traps' (i.e., plastic buckets with polyethylene funnels) versus 'old pitfall traps' (i.e., coffee cans with margarine funnels) adjacent to 33 drift fences per anuran species and age class on four beaver ponds in west-central Alberta during June 28 to July 30, 2003. *P* determined by a Wilcoxon paired-sample test and reflects differences in captures between trap types. Mean (± SE) snout-urostyle length (SUL) for each category is based on a sample of captured individuals.

	Anurans < 1 yr old				Anurans ≥ 1 yr old			
	Old Trap Captures	New Trap Captures	New Trap Fences†	*P*	Old Trap Captures	New Trap Captures	New Trap Fences†	*P*
Wood Frog	476	635*	15 (4)	0.89	13	30	13 (16)	0.03
SUL (mm)	21.6 ± 0.1	21 ± 0.1			39.5 ± 2.6	38.4 ± 1.4		
	N = 351	N = 344			N = 13	N = 30		
Boreal Chorus Frog	7	77	21 (10)	< 0.01	1	3	2 (30)	na
SUL (mm)	16.1 ± 0.9	17.3 ± 0.2			46.8 ± na	26.8 ± na		
	N = 6	N = 72			N = 1	N = 3		
Western Toad	0	0	0 (0)	na	12	20	11 (16)	0.2
SUL (mm)	na	na			50.8 ± 4.9	45.9 ± 2.9		
					N = 12	N = 20		

na=Value not available due to low number of captures

*Relatively large value because one new trap captured 168 individuals, whereas the paired old trap caught 60 YOY wood frogs only

†Number of fences or trap pairs with higher captures in the new trap (and number of fences with equal captures between trap types)

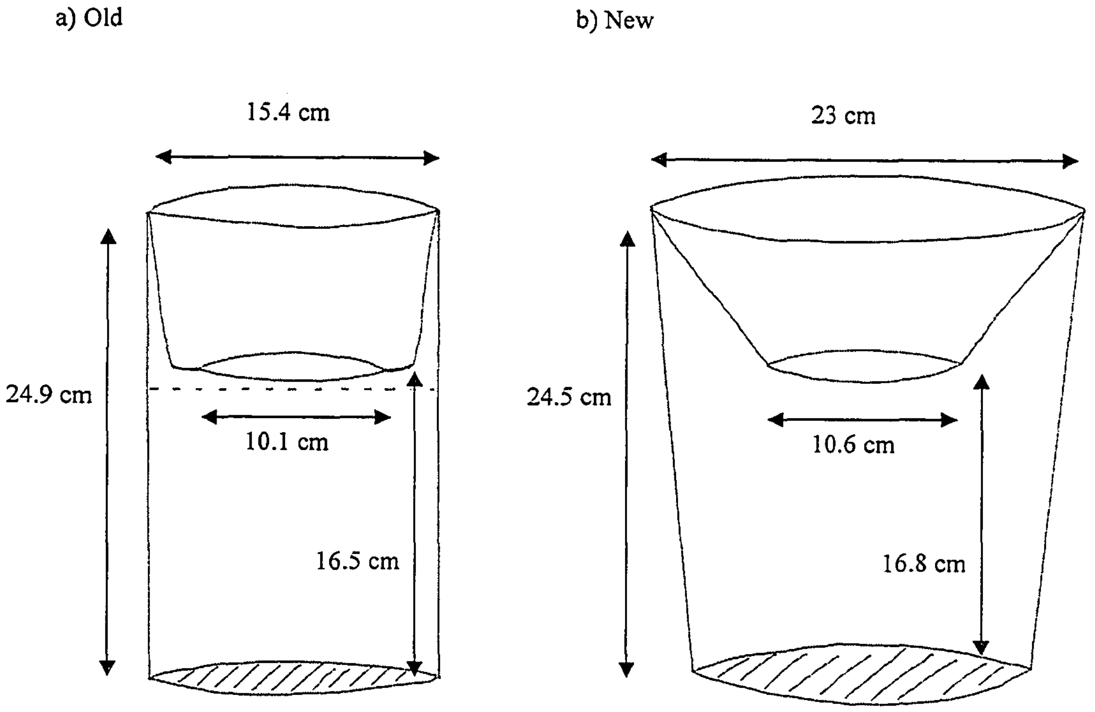

Figure 2:1. Pitfall trap dimensions and design for the 'old trap' (a) made from 1.5 coffee cans (1 kg size) with a margarine container (hard) funnel, and the 'new trap' (b) constructed from a 7.6 L black plastic bucket with a sloping, polyethylene (soft) funnel.

Chapter 3. Using Chorus-Size Ranks from Call Surveys to Estimate Reproductive Activity of the Wood Frog (*Rana sylvatica*)*

Abstract.—Call surveys are a relatively new and efficient technique for detecting the presence of breeding male anurans. Using data from multiple surveys of breeding choruses of wood frogs (*Rana sylvatica*) combined with counts of egg masses on ponds in west-central Alberta I determined: i) if ranks of chorus size adequately predicted total number of egg masses in ponds, and ii) the number of breeding males in standard chorus-size ranks (1, 2 and 3). Estimates for Rank 3 choruses were based on a formula with number of egg masses present per pond and a fixed male to female ratio of 2:1 calculated from the literature. Calling males were recorded on all ponds that had evidence of female reproductive activity (i.e. egg masses). Generalized linear models suggested that ranks were positively and linearly correlated with the number of egg masses in a pond. In addition, call data from only the second of four sampling periods (each 3-6 days) significantly predicted number of egg masses in ponds, suggesting that timing is important when surveying calling wood frogs. The mean number of chorusing males per rank did not correspond to aural ranks of calling intensity: Rank 1 = 1.3 males, Rank 2 = 3.7 males, and Rank 3 = 118. I recommend similar assessments for other widely distributed species to improve our ability to detect and interpret habitat-use patterns and population trends of amphibians through monitoring programs.

3:1 INTRODUCTION

Call surveys are a relatively new technique in anuran conservation that detect the presence of breeding (i.e. chorusing) males in aquatic habitats and provide indices on the status of regional populations with relatively low effort and cost to researchers (Bishop et al., 1997; Shirose et al., 1997). These surveys originated under conservation initiatives in the Great Lakes region and have become an important technique in a growing number of monitoring programs (Bishop et al., 1997; Bridges and Dorcas, 2000; Weir, 2001;

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Crouch and Patton, 2002), and ecological studies that seek to understand habitat-use patterns of anuran amphibians in North America (Lehtinen et al., 1999; Waldick et al., 1999; Kolozsvary and Swihart, 1999; Knutson et al., 1999; Skelly et al., 1999; Zampela and Bunnell, 2000; Palik et al., 2001; Guerry and Hunter, 2002; Stevens et al., 2002). In 2001, the North American Amphibian Monitoring Program (NAAMP) developed a standardized protocol for anuran call surveys in the United States and Canada (Wier, 2001). Although recent assessments of NAAMP protocols in various regions in North America represent measures to improve researchers' ability to detect and monitor anurans (Bridges and Dorcas, 2000; Crouch and Paton, 2002), it is unclear if call surveys can effectively provide an index of abundance of calling anurans on ponds and wetlands (but see Shirose et al., 1997). No published study has determined if the abundance of breeding male amphibians is an indicator of female reproductive activity even though other fields of study, such as avian ecology, have clearly demonstrated that density of breeding males engaged in advertisement and territorial behavior alone serves as a poor indicator of a species' reproductive success and habitat quality (e.g., Van Horne, 1983; Vickerey et al., 1992).

The majority of habitat studies that use call surveys do so to detect the presence or absence of breeding species (Lehtinen et al., 1999; Waldick et al., 1999; Kolozsvary and Swihart, 1999; Skelly et al., 1999; Palik et al., 2001; Guerry and Hunter, 2002). Fewer researchers examine the size of breeding populations with call data (Knutson et al., 1999; Zampela and Bunnell, 2000; Stevens et al., 2002), possibly because of the inherent difficulties in counting calling males in ponds and wetlands and the interpretation of such data. The current method of estimating the size of calling anuran populations and choruses is based on indices of abundance: Rank 1 indicates no overlap in calls and the number of individuals can be reliably estimated, Rank 2 suggests some overlap in calls and the number of males can be estimated (but less accurately than those in Rank 1 choruses), and Rank 3 indicates a full chorus and the number of individuals can not be estimated (Bishop et al., 1997; Shirose et al., 1997; Wier, 2001). In addition, statistical analyses associated with ranks can be complicated (Zar, 1999), and whether ranks are appropriately scaled to sizes of breeding aggregations is unknown. A quantitative index that can be converted to a meaningful estimate of the size of male choruses is needed to analyze anuran population trends and habitat relationships.

My first objective is to compare perceived numbers of calling male anurans with female reproductive activity (i.e. egg masses) and determine if ranks of chorus size developed from multiple surveys predict the number of egg masses in a pond. My second objective is to develop a more quantitative measure of abundance, than ranks based on aural estimates of calling intensity, by estimating the number of calling males in a Rank 3 chorus and comparing this value with the number of individuals assigned to Rank 1 and 2 choruses.

3:2 MATERIALS AND METHODS

Study Species.—The wood frog (*Rana sylvatica*) is one of the most abundant and widely distributed amphibians in North America occurring throughout most of Canada, Alaska, and the northeastern United States (e.g., Conant and Collins, 1998). Wood frog egg-masses can be readily counted because of their large size and occurrence in clusters in early spring when ponds support low levels of algal growth (Crouch and Paton, 2000). In addition, pitfall trapping is an effective tool for estimating wood frog abundance (e.g., Crouch and Paton, 2000; Paszkowski et al., 2002), and call surveys can be used, if timed appropriately, to estimate the number of breeding males in a pond (Stevens et al., 2002). Finally, the mating behavior and ecology of the wood frog is relatively well studied (Howard, 1980; Berven, 1981, 1988; Berven and Grudzien, 1990; Seale, 1982; Howard and Kluge, 1985; Petranka and Thomas, 1995). Wood frogs are explosive, synchronized breeders that deposit egg masses into one or a few restricted areas in a pond during early spring (Howard, 1980; Seale, 1982). Males typically mature earlier than females, and outnumber them in populations. Larger males have a greater probability of mating because of competition for females, and males that do mate, typically do so only once during a year (Howard, 1980; Berven, 1981; Howard and Kluge, 1985). Thus, the wood frog is an ideal amphibian to use in conservation programs and environmental research, because, unlike many amphibians, this species has a wide distribution, is well studied, and populations can be reliably estimated with standard sampling techniques (Hily and Merenlender, 2000).

Study Area and Ponds.—I conducted this study in the boreal foothills eco-region on the eastern slopes of the Canadian Rocky Mountains, near the town of Lodgepole, Alberta (53° 06' N - 115° 19' W) during May 2002. The boreal foothills is a forested region dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and lodgepole pine (*Pinus contorta*) (Rowe, 1972). In addition, the rolling landscape contains numerous beaver ponds on small, high gradient streams. My study included 17 beaver ponds and 7 'borrow-pits' (basin ponds created during road construction) within a 200 km^2 area and was part of a larger investigation on anurans in beaver ponds. All ponds were separated by a distance > 200 m, relatively small (65 - 7900 m^2), and held water throughout the larval period (approximately June 1 to July 15). All ponds supported calling anurans in the previous year (2001). In late May, the study ponds contained very little living or dead emergent or floating vegetation (< 10%). Vegetative cover included horsetail (*Equisetum* spp.), bulrush (*Scirpus* spp.), calla (*Calla* spp.), rushes (*Juncus* spp.), and sedges (*Carex* spp.).

Call Surveys.—To determine if the abundance of calling male wood frogs was related to female reproductive activity, I conducted call surveys and egg searches in spring 2002. To estimate the number of calling males, multiple call surveys were completed on each pond over a period of 20 days beginning when ice cover receded from all ponds and ending when few or no calling males were recorded. One visit was made to each pond during four survey periods: Call Survey #1) May 11-15; #2) May 16-18; #3) May 19-23; and #4) May 24-30. All surveys were conducted within a 3 hr window starting 0.5 hr after sunset and under optimal weather conditions (i.e. light or no rain, Beaufort Wind Scale < 4, air temperature > 5° C; Shirose et al., 1997). Each survey consisted of a 180° point count for 5 min during which time observers assigned a rank to each group (or chorus) of calling males (Rank 1, 2, and 3). A group was a spatially distinct aggregation of calling males that quickly responded to each others' calls but were generally less responsive to and unsynchronized with other choruses in the pond.

Pond habitat encompassed by surveys extended no more than 50 m from a point count so that most ponds had one survey station; three ponds had two stations because of their large size (> 0.5 ha) and elongated shape. Surveys on large ponds were conducted simultaneously by two observers to minimize redundancies in data and increase accuracy in estimating all individual choruses. To minimize disturbance, surveys were conducted 7-10 m from the pond margin and from the south side of the pond. Most calling and reproductive activity was restricted to the north side of ponds (C. E. Stevens, unpublished data). Upon arriving at a pond, I also waited 1 min before recording to allow nearby anurans to recover from any disturbance that I created.

Egg Searches.—Reproductive activity was estimated using egg searches that were conducted simultaneously with call surveys in spring 2002. During May 11-13 I monitored ponds known to have egg deposits the previous year, and began to systematically search all ponds for eggs two days after the first signs of egg-deposition. Thirteen egg masses were noted in one pond on May 13, thus, I systematically surveyed all ponds for eggs on May 15-19 (Egg Search #1), and May 20-23 (Egg Search #2). I also initiated a third survey on May 28 but were unable to complete the survey on 6 (of 24) ponds due to logistical constraints and excluded data from this survey in analyses. On 18 study ponds that were searched in this last survey, however, only 6 new egg masses were observed, all of which were on ponds where high numbers (> 50) of egg masses had been recorded during previous searches.

During a survey, two observers thoroughly searched the entire littoral zone and pond edge for egg masses. The age of each egg mass was estimated during Egg Search #2 to determine the number of egg masses that were typically missed during a search. A new egg mass was characterized by clear jelly capsules approximately 3-5 cm in diameter and was deposited ≤ 5 days before it was encountered during a search. An old egg mass had a thin grey-brown film of sediment and algae, and jelly capsules that were relatively large in diameter (>5 cm) due to swelling from uptake of water (Duellman and Trueb, 1994). These egg masses were deposited > 5 days from the time they were recorded during a search. I also recorded the time spent searching and marked the position of each egg mass cluster (i.e., all deposits < 2 m from any egg mass at a particular location in the pond) with a flag to allow for later calculation of mean number of egg mass clusters and distance between clusters in each pond.

Statistical Analyses.—To determine the relationship between calling wood frogs and female reproductive activity I used generalized linear models (GLM) in S-PLUS with a logarithmic link function and robust Quasi-likelihood error (McCullagh and Nelder, 1989; Crawley, 2002) to predict total number of egg masses per pond based on ranks of chorus sizes. I chose this error structure because preliminary assessments of my egg mass (count) data suggested that they did not conform to a Poisson distribution and had a residual deviance that was greater than the residual degrees of freedom (i.e. overdispersion; Crawley, 2002). Two types of chorus-size ranks were therefore calculated and analyzed for each pond. I assigned the maximum rank recorded during any of the four surveys to each pond (Call Rank M). I also calculated the average-maximum rank (Call Rank A-M) over the four call surveys for each pond. This rank was used in a simple GLM regression with an F-test to assess the fit of the model in explaining variation in egg mass data (i.e., deviance) and a t-test on the slope coefficient. I also constructed a multiple regression model using a backward stepwise procedure to predict total number of egg masses per pond based on Call Rank M data from all surveys combined. I addressed multicollinearity among the four surveys with a Spearman Correlation analysis and removed one of any two explanatory variables that were highly correlated prior to the stepwise procedure ($r > 0.5$) and re-ran the GLM analysis with all surveys but with the other highly correlated survey excluded. At each step, the survey that contributed the least explained variation to the model was dropped and assessed by the magnitude of the Cp statistic associated with each term until removal of terms did not further improve the model (Crawley, 2002). The statistical significance of the change in deviance after excluding an explanatory variable in the model was determined by an F-ratio. I accepted statistical significance at $\leq 5\%$ level for all F- and t-tests.

Quantification of Call Ranks.— To determine the number of calling individuals in each chorus-size rank, I summarized call survey data collected during spring 2002 on 59 ponds in the study region, including the 24 ponds mentioned previously. First, I calculated the mean number of calling males in a Rank 1 and 2 using absolute numbers for each chorus recorded during the four survey periods. Next, I estimated the number of calling individuals in a full chorus (Rank 3) on ponds surveyed for egg masses and calling wood frogs with the following formula:

$$\textbf{Males in Rank 3} = \frac{\textbf{(male:female ratio * number of egg masses) -- counted males in Rank 1 \& 2}}{\textbf{No. of Rank 3's}}$$

Data on ranks used in the formula were obtained from the survey that recorded the highest number of calling males. I used a fixed sex ratio of 2 males: 1 female based on a mean value calculated from 48 breeding populations on ponds in Howard and Kluge (1985), Berven and Grudzien (1990), and Crouch and Patton (2000; Table 3:1).

3:3 RESULTS

Descriptive Summary.—My call surveys and egg searches of 24 ponds recorded breeding males on 21 ponds and egg masses on 20 ponds. The total number of groups (or choruses) of calling males recorded during call surveys on these ponds were as follows: Call Survey #1 = 23, #2 = 41, #3 = 40, and #4 = 56. The mean number of egg masses per pond was 91.13 (± 33.96, $N = 24$). Total number of egg masses was 2187. Egg Search #1 counted 1034 egg masses and Egg Search #2 noted 1153 egg masses (0.78% old and missed during Egg Search #1). Egg masses were distributed among 51 egg mass clusters. Each egg mass cluster covered an area < 4 m^2. On seven ponds all egg masses were aggregated in one location; the remaining 13 ponds had egg masses clustered at 2 to 7 locations. The mean distance between nearest clusters was 26.39 m (± 5.01, $N = 44$).

The mean value for Call Rank A-M (i.e. the average maximum rank across 4 surveys) was 1.52 (± 0.2, $N = 24$). No egg masses were found at Rank 0 ponds. Of all ponds with calling activity, only one pond (assigned an average maximum rank of 0.25), or 4.8% of ponds surveyed contained no egg masses. The number of ponds assigned Rank 0 peaked on Call Survey #1 (Figure 3:1). Call Survey #3 recorded the most Rank 1's and Rank 3's, and the number of Rank 2 ponds was highest on Call Survey #4. Values for Spearman correlation coefficients comparing the ranks of individual ponds between pairs of survey periods ranged from 0.28-0.66. The only pair with a correlation higher than 0.50 was Call Survey #3 and #4 (0.66 correlation, $P < 0.01$; Figure 3:1).

Relationships between Chorus-Size Ranks and Abundance of Egg Masses.—GLM's predicting numbers of egg masses based on call data are presented in Table 3:2 with their coefficients. The Call Rank A-M model was a good predictor of egg masses in ponds as indicated by the deviance (i.e., fit) associated with model ($F_{1,22} = 10.06$, $P =$

0.004), and includes a slope coefficient indicating a positive and linear relationship between Call Rank A-M and the number of egg masses ($t_{22} = 2.73$, $P = 0.012$; Table 3:2).

I conducted two stepwise regressions because of the high correlation of Call Rank M values between Survey #3 and #4 (Table 3:3) to determine which survey(s) significantly predicted the abundance of egg masses in ponds. One analysis excluded Survey # 3 and the other excluded Survey # 4. In both analyses, stepwise deletion of surveys revealed that ranks from Survey #2 (May 16-18) contributed the most to explained variation in number of egg masses; no other survey improved the predictive power of this model (Table 3:2 and 3:3). The Survey #2 model based on Call Rank M was a good predictor of number of egg masses in ponds ($F_{1,22} = 18.81$, $P < 0.001$) and included a slope coefficient indicating a positive and linear association between call data from this survey with the number of egg masses ($t_{22} = 2.95$, $P = 0.007$; Table 3:2).

Quantification of Call Ranks.—During spring 2003, I recorded 250 choruses on 59 ponds during four visits. Ranks were distributed among these choruses as follows: Rank 1 = 116, Rank 2 = 55, and Rank 3 = 79. The mean (± SE) number of calling males equaled 1.34 (± 0.06) in a Rank 1, and 3.73 (± 0.13) in a Rank 2. Of the 15 ponds assigned a Rank 3 that were examined for egg masses, the average number of calling males was calculated as 118.07 males (± 19.29; range = 16-313.8 males). Thus, the number of calling males in a Rank 2 is 2.8 times greater than the number of calling males in a Rank 1, and the number of calling males in a Rank 3 is 31.7 times greater than the number of calling males in a Rank 2.

3:4 DISCUSSION

Previous research on call surveys or studies that have evaluated this technique have emphasized that these surveys are an effective method to detect the presence of breeding anurans. Few studies have assessed the value of call data in estimating sizes of breeding populations and female reproductive activity in ponds. Validation tests of call surveys in southern Ontario found linear relationships between call counts and chorus sizes for the Fowler's toad (*Bufo fowleri*) and bullfrog (*R. catesbeiana*; Shirose et al., 1997). My study indicates that chorus-size ranks associated with call surveys are an easily collected indicator of the relative number of egg masses in a pond. Future amphibian research and monitoring initiatives should take this under consideration by collecting and analyzing chorus-size rank data as part of population and habitat-use studies. These ranks could also be transformed to a metric similar to proportion of area occupied (PAO; MacKenzie et al., 2002) so that the detection probabilities associated with the chorus-size ranks can be accounted for, allowing researchers to make useful inferences on the dynamics of anuran populations on the landscape.

Since other research indicates that the number of wood frog egg masses in a pond is highly correlated with the number of females breeding there (Crouch and Patton, 2000), my study also suggests that calling intensity of male wood frogs reflects the number of breeding females present at a pond. The excess number of male wood frogs characteristic of breeding aggregations results in the high probability of females finding mates and their eggs being successfully fertilized (Howard, 1980; Berven, 1981). The nature of the relationship between the number of breeding males and calling intensity in a pond or chorus requires further study. Male wood frogs can be highly mobile and actively seek out females in a pond (Howard, 1980; Berven, 1981). Thus, calling activity in a pond may be a group acoustic display that attracts females to a pond rather than to the location of a particular calling male (e.g., Brooke et al., 2000). As a result, a proportion of male anurans may stop vocalizing at a certain decibel of calling intensity or abundance of calling males in a chorus to conserve energy and search for females. For males of some anuran species, however, researchers have observed calling intensity to increase in the presence of breeding females (e.g., Murphy, 1999).

Although average maximum rank (Call Rank A-M) incorporated data from all surveys and represented a good picture of female reproductive patterns, the best predictive model for the number of egg masses in a pond was based on ranks from a single survey alone, Survey #2. I initially expected Survey # 3 to have more predictive power because the number of ponds receiving Rank 3 peaked during this survey period. This suggests a pattern of increased calling activity but decreased egg mass deposition later in the breeding season. The presence of post-laying females and communal egg-mass deposits could have acted as a cue for males to call and congregate in ponds where few females were actually receptive (Howard, 1980). It is also possible later choruses included males that had emerged slowly from winter refugia and joined calling males that had mated earlier with females that had since finished breeding.

It is noteworthy that data from only one survey successfully predicted the number of egg masses in a pond suggesting that timing may be crucial in surveying calling wood frogs. Others have suggested that surveys for wood frogs can be challenging due to the variability in calendar date associated with the onset of calling activity and the explosive breeding (Stevens et al., 2002; Crouch and Patton, 2002). Critical environmental factors that influence the start of calling activity for the wood frog, include nightly temperature (Howard, 1980), absence of ice cover (> 95% in my study), and possibly April and May (spring) degree days (> 0°C). The short and synchronized (i.e. explosive) breeding season for wood frogs results in the deposition of large aggregates of egg masses that increases internal egg temperatures relative to ambient water temperatures (Howard, 1980; Seale, 1982; Waldman and Ryan, 1983) and the reduction of cannibalism during larval development (Petranka and Thomas, 1995).

My study also estimated the number of males in choruses receiving different ranks in my surveys and found that calling intensity did not accurately translate into numbers of breeding males in a chorus. Thus, I propose that prior to analyses, researchers should correct the ranks based on empirical data for the species and habitat of interest. Specifically, based on abundance of egg masses, I estimated 1.3 males in a Rank 1 chorus, and a modest increase to 3.7 males in a Rank 2 chorus. Rank 3 choruses appeared to be significantly larger (118 males) and encompass a large range of breeding males. However, this number is dependent on a ratio of males to females in the breeding population that can vary among ponds and years (e.g., Berven and Grudzien, 1990; Crouch and Paton, 2000). I did not quantify this ratio and based my Rank 3 estimate on a 2:1 ratio on data in the published literature which may not be representative of breeding populations in my study. Even with a conservative 1:1 sex ratio, the number of males in a Rank 3 is much greater than the number of males in a Rank 2 chorus. This large difference suggests the need for an intermediate rank that distinguishes between a low and high intensity Rank 3 chorus during surveys. This could be achieved using a sound-level meter and by calibrating decibels with the estimated distance to the chorus.

Summary.—Ranks of chorus sizes in call surveys can be a good indicator of reproductive activity and may be used to draw conclusions concerning local populations if quantitatively assessed. Timing of call surveys for wood frogs is crucial and the best method to capture 'good' data may be to conduct multiple surveys over a relatively short period. I recommend similar studies for other widely distributed species, such as the northern leopard frog (*R. pipiens*) to improve our ability to detect and understand habitat-use patterns and population trends for amphibians through the NAAMP.

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Table 3:1. Mean sex ratios of breeding wood frog populations in ponds from three published studies in various regions of the northeastern United States.

	Study Area	*N*	Sex ratio
Berven and Grudzien (1990)	Virginia	34	1.82 (± 0.19)
Howard and Kluge (1985)	Michigan	4	2.67 (± 0.47)
Crouch and Paton (2000)	Rhode Island	10	2.64 (± 0.57)
All Populations		48	2.05 (± 0.19)

Table 3:2. Coefficients and fit (deviance) for generalized linear models predicting total number of wood frog egg masses in a pond based on chorus-size ranks. The models employ a robust quasi-likelihood error with a logarithmic link function. Model #1 uses Call Rank A-M (average-maximum rank per pond) based on all four call surveys and Model #2 uses Call Rank M (maximum rank per pond) based on Call Survey #2 that had the most explanatory power (Table 3:3). *P* values are presented for *t*-tests on the rank coefficient and *F*-tests on explained deviance for both models.

Model	Variable	df	Coefficient	*P* for *t* test	Deviance	*P* for *F* test
Both	Null	23			4187.5	
1)	Intercept		2.4 ± 0.94	0.018		
	Call Rank A-M	1	1.1 ± 0.40	0.012	1631.9	0.004
	Residual	22			2655.7	
2)	Intercept		1.4 ± 1.26	0.298		
	Survey #2 (Call Rank M)	1	1.3 ± 0.45	0.007	2243.8	<0.001
	Residual	22			1943.8	

Table 3:3. Summary of backward stepwise procedures to build generalized linear regression models for number of wood frog egg masses in ponds based on chorus-size ranks and four call survey periods. These models employ a robust quasi-likelihood error with a logarithmic link function and are built using Call Rank M (maximum rank per pond) for each survey. At each step, the survey that contributed the least explained variation in the model was dropped and assessed by the magnitude of the Cp statistic associated with each term until removal of terms did not further improve the model. Two stepwise procedures were conducted because of the high correlation of Call Rank M data between Call Survey #3 and #4. Procedure I examines Call Survey #1 (May 11-15), Call Survey #2 (May 16-18), and Call Survey #3 (May 19-23). Procedure II examines Call Survey #1, Call Survey #2, and Call Survey #4 (May 24-30). Both stepwise procedures resulted in a similar conclusion: Call Survey #2 alone successfully predicted variation in numbers of egg masses in ponds (Table 3:2).

	Residual df	Residual Deviance	Deviance Change	F-value	*P* for F-test
Procedure I					
Survey 1 + Survey 2 + Survey 3	20	1748.8			
Step 1					
minus Survey 1	21	1754.9	6.1	0.06	0.82
Step 2					
minus Survey 3	22	1943.8	188.9	1.89	0.19
Procedure II					
Survey 1 + Survey 2 + Survey 4	20	1808.2			
Step 1					
minus Survey 1	21	1855.9	47.7	0.42	0.52
Step 2					
minus Survey 4	22	1954.8	87.8	0.82	0.38

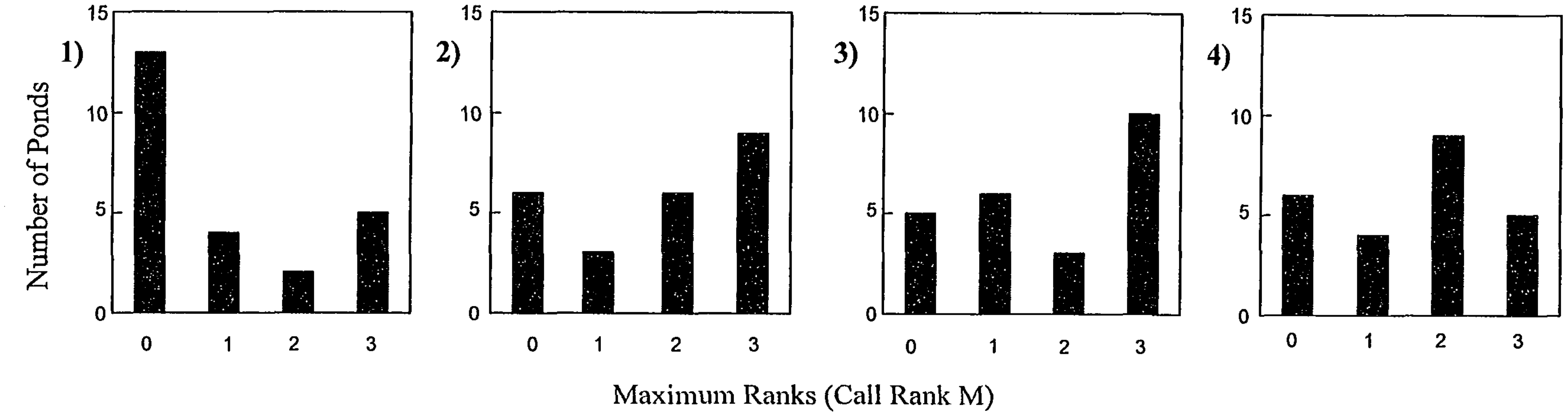

Figure 3:1. Distribution of maximum ranks (Call Rank M) for chorus size on 24 ponds from four survey periods: 1) May 11-15; 2) May 16-18; 3) May 19-23; and 4) May 24-30. Rank 1 indicates no overlap in calls, Rank 2 indicates some overlap in calls, and Rank 3 indicates a full chorus and the number of individuals can not be estimated. Call surveys 3) and 4) were highly correlated (r > 0.50, $P <$ 0.01).

Chapter 4. Beaver (*Castor canadensis*) as a Surrogate Species for Conserving Anuran Amphibians on Boreal Streams*

Abstract.—I explored the use of beaver (*Castor canadensis*) as a surrogate species for amphibian conservation on small (1st-4th order) streams in the Boreal Foothills of west-central Alberta. First, I examined if the presence of beaver affected the abundance of anuran amphibians using call surveys and pitfall trapping on unobstructed streams and beaver ponds. I also characterized the distribution of beaver ponds and the potential effects of landscape features, road construction and forest harvesting on beaver pond occupancy of streams using a novel combination of a digital elevation model and vegetation inventory data in GIS. Call surveys clearly suggested that beaver create breeding habitat for the boreal chorus frog (*Pseudacris maculata*), wood frog (*Rana sylvatica*) and western toad (*Bufo boreas*). No calling males of any species were recorded on unobstructed streams. Pitfall trapping showed that the wood frog exhibit high rates of juvenile recruitment on beaver ponds given that more individuals were captured on beaver ponds versus unobstructed streams and that young-of year represented the majority of wood frog captures (84%). A strong correlation between percent landscape occupied by beaver ponds and abundance of young-of-year wood frogs on unobstructed stream suggests that anurans captured along streams originated from beaver ponds. Using a generalized linear mixed-effect model, I found that the probability of beaver pond occurrence on streams was positively associated with elevation and stream order but unrelated to riparian forest height and distance to nearest road. In addition, proximity of streams to cutblocks reduced the probability of beaver pond occupancy even if *Populus* spp. was regenerating in the logged area. The high number and area of beaver ponds relative to basin (i.e., non-beaver) ponds in the Boreal Foothills suggests that beaver can play a key role in maintaining regional populations of amphibians. Beaver food requirements and dam-building patterns should be incorporated in management strategies as part of a surrogate species approach to amphibian conservation.

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4:1 INTRODUCTION

The concept of surrogate species in conservation biology has received growing attention largely because it is intuitively appealing and offers simple, ecologically based shortcuts for the management of communities and ecosystems (Simberloff 1998, Caro and O'Doherty 1999, Roberge and Angelstam 2004). Surrogate species can be indicators of anthropogenic impacts, population changes in other species, or act as "umbrellas" protecting a large number of naturally co-occurring species. For example, Noss et al. (1996) found the umbrella value of proposed grizzly bear (*Ursus arctos*) recovery zones to include >10% of the state-wide distributions of most bird, small mammal, and amphibian species in Idaho, USA. Generally, large vertebrates are good umbrella or indicator species for wildlife that require large tracts of habitat, various types of habitat (e.g., both terrestrial and aquatic), or are sensitive to habitat fragmentation (Simberloff 1998). A surrogate species can also be a keystone species, which is a species with disproportionately large effects on ecosystem structure and function relative to its density or abundance (Power et al. 1996). Thus, loss of a keystone species or reduction in its numbers will have ramifications for other co-occurring species.

Beaver (*Castor canadensis*) is a well-known keystone species in boreal ecosystems in North American that profoundly influences the physicochemical properties of streams through dam construction (Naiman et al. 1986, Naiman et al. 1988, Snodgrass and Meffe 1998, Schlosser and Kallemyn 2000). Densities of dams can exceed 16 per km on small streams in boreal landscapes (Naiman et al. 1988, Hillman 1998). Beaver activity on small streams may influence the distribution and abundance of aquatic vertebrates, such as fishes (Snodgrass and Meffe 1998, Schlosser and Kallemyn 2000), birds (Brown et al. 1996, McCall et al. 1996), and possibly amphibians. Abiotic and biotic changes to streams such as reductions in flow, higher water temperatures and increased rates of primary production may favour pond-breeding amphibians (Naiman et al. 1986, Naiman et al. 1988, Snodgrass and Meffe 1998). Russell et al. (1998) noted a higher abundance of anuran amphibians on beaver ponds versus unobstructed streams in South Carolina, USA. The generality of this trend in other eco-regions and the nature of underlying mechanisms remain unclear. Beaver dams could produce either an attractive habitat for non-breeding, post-metamorphic amphibians or an environment that increases juvenile recruitment to metamorphosis.

As a potential contributor to landscape heterogeneity and biodiversity in the boreal forest, the beaver has been the subject of surprisingly few studies that examine where colonies are most abundant and where dams are most likely to be built on streams (but see Slough and Sadleir 1977, Howard and Larson 1985, Barnes and Mallik 1997). Some patterns are evident, however. Studies in both a northern hardwood forest of New England, USA (Howard and Larson 1985) and a boreal-shield forest in Ontario, Canada (Barnes and Mallik 1997) suggest that beaver pond establishment is strongly influenced by stream hydrology (e.g., stream size, gradient) and is dependent on a reliable water source that can be effectively dammed. The structure and composition of vegetation in riparian zones may also influence beaver distributions on streams (Slough and Sadleir 1977, Howard and Larson 1985, Barnes and Mallik 1997) because the beaver employs a central-place foraging strategy harvesting trees and shrubs near open water (Schoener 1979, Jenkins 1980, McGinley and Whitam 1985). In addition, beaver are very selective in choosing woody food stems and often show strong preference for *Populus* spp. (e.g., Johnston and Naiman 1990, Fryxell and Doucet 1993, Basey and Jenkins 1995, Gallant et al. 2004). Despite the apparent link between riparian zones and beaver, no studies have examined impacts of logging on beaver or the distributions of beaver and beaver ponds in landscapes dominated by forestry.

Conservation has become the underlying rationale for investigating many aspects of the biology of amphibians since the discovery in the late 1980s that many populations and species throughout the world were declining (Alford and Richards 1999, Houlahan et al. 2000, Stuart et al. 2004). Declines have been linked to many factors and the large number of studies concerning threats to amphibians is a good indicator of the complexity of causes behind declines (see recent reviews by Collins and Storfer 2003, Blaustein et al. 2003, Carey and Alexander 2003). Most biologists agree, however, that local habitat loss, degradation or alteration (e.g., draining of wetlands, forest fragmentation) are major causes of declines (Blaustein et al. 1994, Wake 1998, Alford and Richards 1999, Semlitsch 2002). The strategy of protecting and restoring ponds and wetlands is arguably a critical step for conserving pond-breeding amphibians because low juvenile recruitment associated with either a paucity of ponds or sub-optimal conditions in remaining ponds on a landscape (i.e. reproductive sinks) can lead to the extirpation of amphibian metapopulations (Gill 1978, Marsh and Trenham 2001).

Currently, conservation strategies for amphibians are often part of larger programs that aim to maintain natural biodiversity or restore the integrity or functions of ecosystems, and generally promote protection, mitigation or enhancement of wetland habitat (Pechmann et al. 2001, Stevens et al. 2002, Calhoun et al. 2003). For example, Ducks Unlimited, through its waterfowl habitat programs has been instrumental in the conservation of amphibians in many parts of North America (Stevens et al. 2002, Tori et al. 2002). Components of programs specifically designed for conserving amphibians also include monitoring of population trends and examination of habitat-use patterns. Unfortunately, many amphibian species are cryptic, fluctuate widely in abundance, and their populations are often difficult to estimate reliably in the field (e.g., Paszkowski et al. 2002, Stevens and Paszkowski 2005). A valuable short-cut for identifying amphibian habitat and assessing the status of populations on landscapes may be through use of a surrogate species. The beaver, whose presence and influence can be easily monitored through delineation of ponds with aerial photography (Slough and Sadleir 1977, Howard and Larson 1985, Johnston and Naiman 1990), could serve as such a surrogate over large areas of North America.

The first objective of my study was to determine the relationship between beaver and amphibian populations on small streams in the Boreal Foothills of west-central Alberta. I compared breeding activity and the abundance of three species of amphibians [wood frog (*Rana sylvatica* Le Conte), boreal chorus frog (*Pseudacris maculata* Agassiz), and western toad (*Bufo boreas* Baird and Girard)] on beaver ponds versus unobstructed streams using data collected from call surveys and pitfall trapping. I predicted that if beaver created breeding habitat for an amphibian species, then estimates of population size based on numbers of breeding males and post-metamorphic individuals would be higher on beaver ponds than on unobstructed streams. My second objective was to measure patterns of occurrence of beaver ponds relative to 'basin ponds' (i.e., non-beaver ponds and wetlands) and to characterize their distribution in a managed landscape with roads and forestry cutblocks using a novel combination of a digital elevation model and vegetation inventory data (Franklin et al. 2002) in GIS. I also discuss the potential effects of beaver and the distribution and abundance of beaver ponds on the ecology and conservation of anuran amphibians.

4:2 METHODS

Study area

My study was conducted in the Boreal Foothills in west-central Alberta (approximately 53° 06' N-115° 19' W). The area supports a forest dominated by trembling aspen (*Populus tremuloides* Michx..), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh), white spruce (*Picea glauca* Voss), black spruce (*Picea mariana* Mill.) and lodgepole pine (*Pinus contorta* Dougl.) (Strong and Leggat 1992). The climate in the region is relatively dry (mean total annual precipitation = 464 mm), cold (mean annual temperatures near 0°C) with a short growing season (growing degree days average 1008) and mean temperature May through August = 12.8°C (Strong and Leggat 1992). Soils in the study area are predominately orthic gray luvisols on lacustrine clays or gray luvisols on morainal clay loams. Both types are considered moderately well-drained soil units in the region (Agriculture Canada 1981). The amphibian fauna consists of the wood frog, boreal chorus frog and western toad.

Amphibian sampling

To assess the role of beaver in providing habitat for breeding amphibians, first I randomly selected 15 beaver-obstructed stream reaches (mean ± SE length = 190 ± 11.9 m; stream order = 2.2 ± 0.24) from the watersheds of the North Saskatchewan and Pembina Rivers in the Boreal Foothills. Most beaver-obstructed stream reaches (10 of 15) were located >1 km from each other to minimize potential non-independence of ponds; five reaches were separated by 0.5–1.0 km. These distances probably prevent the large number of migrants needed for immigration to play a meaningful role in local recruitment and population dynamics on ponds (Newman and Squire 2001, Petranka et al. 2004). Each beaver-obstructed reach consisted of one to six consecutive beaver ponds that flooded areas ranging from 0.17 to 1.84 ha. On 15 beaver-obstructed reaches, I examined a total of 54 ponds in 2001 and 52 ponds in 2002. The lower number of ponds in 2002 reflected changing water levels in two reaches during heavy rain in July 2001 that resulted in the consolidation of two ponds on each reach. The same storm also resulted in the collapse of a dam on one pond (3rd order beaver-obstructed reach) that remained partially damaged in spring 2002, creating a flooded area substantially smaller than the previous year (i.e., 0.05 ha in 2002 versus 0.35 ha in 2001).

Of the 15 beaver-obstructed stream reaches mentioned above, I paired nine with a nearby stream reach (reach length = 200 m) that was unobstructed, had an intact canopy cover, and showed no evidence of beaver activity. Unobstructed stream reaches were within a distance of 90-640 m from a beaver-obstructed reach under study. The nine stream pairs (unobstructed and obstructed reaches) were located >1 km from other pairs. For unobstructed streams, the mean ± SE width (i.e. distance between lowest points of embankments) was 1.3 ± 0.4 m, and stream order was 2.3 ± 0.4. All unobstructed streams had flowing water with an average depth >10 cm in late May; however two 1st-order unobstructed streams were dry by mid-July of both study years.

To estimate the number of breeding wood frogs, boreal chorus frogs and western toads on beaver ponds and streams, I conducted five call surveys (Weir 2001) from May 3 to June 9 in 2001 and six call surveys from May 11 to June 11 in 2002. Surveys began when ice cover receded from all ponds and were completed when relatively few or no calling males were recorded. All surveys were conducted under optimal weather conditions (i.e., light or no rain, Beaufort Wind Scale <4, air temperature >5°C) at night within a 3 hr window starting 0.5 hr after sunset. Each survey comprised a 180° point count for 5 min that covered pond and stream habitat extending <100 m from a survey station. Most ponds in my study were relatively small and had one survey station. I established two stations on three ponds because of their large area (>0.5 ha) and elongated shape. All unobstructed streams had two survey stations to provide complete coverage of the 200 m reach. To minimize disruption of reproductive activity, all surveys were conducted 7-10 m from the shoreline. Recording consisted of observers first identifying spatially distinct choruses of calling males for each species present and assigning ranks of aural intensity to choruses: Rank 1 = no overlap in calls and the number of males can be reliably estimated, Rank 2 = some overlap in calls and the number of males can be estimated (but less accurately than for Rank 1), and Rank 3 = overlap in calls and the number of individuals can not be estimated (Weir 2001).

Next, I assigned a species-specific value for each Rank 3 chorus so that I could describe population sizes of the wood frog and boreal chorus frog (no Rank 3 groups of western toads were recorded during my study). Rank 3 choruses of wood frogs were estimated as 59 males (see Stevens and Paszkowski 2004) using counts of egg masses, multiple call surveys, and a conservative 1:1 male to female sex-ratio. To my knowledge, no study has quantitatively assessed the mean group size for Rank 3 choruses for the boreal chorus frog. I might expect, however, that their aggregations are smaller than that of wood frog choruses because 1) boreal chorus frogs may be less abundant than the wood frog in the western boreal forest (Roberts and Lewin 1979, Paszkowski et al. 2002); 2) calls emitted by the male boreal chorus frog are about twice as long in duration as calls of the wood frog (C. E. Stevens, personal observation) which may mean that a lower minimum number of individuals is needed to create a Rank 3 chorus; and 3) the boreal chorus frog is less likely than the wood frog to display temporally-compressed explosive breeding (C. E. Stevens, personal observation). Thus, I assigned 30 males to each Rank 3 group of boreal chorus frogs so that I could roughly estimate total number of calling males on dammed stream reaches.

In summer 2001 I employed pitfall traps and drift fences on the nine paired stream reaches (unobstructed reach paired with one pond on a nearby beaver-obstructed reach) to measure abundance of post-metamorphic individuals and juvenile recruitment to metamorphosis. Pitfall traps were installed in pairs along drift fences; each fence had one trap placed at each end. The drift fence was a polyethylene sheet 5 or 10 m long, 30 cm high and partly buried in the soil. All fences were installed 3-7 m from water. Drift fences running parallel to the pond edge or unobstructed stream covered 20% of that shoreline. In addition, one 5-meter drift fence running perpendicular to each shoreline was installed to capture moving post-metamorphic anurans associated with that stream reach. The pitfall trap was a 7.6 L plastic bucket with a plastic funnel (Stevens and Paszkowski 2005). Beaver ponds had 8-20 pitfall traps per site whereas each unobstructed streams had 16 pitfall traps. Traps were opened from July 10–August 15, 2001 and checked every 3-5 days. Captured anurans were marked (i.e., one toe clipped), weighed, measured for snout-vent length (SVL), and identified to age class. Individuals were identified as young-of-year (YOY) if they had remnants of a larval tail or SVL <27 mm for the wood frog, SVL <21 mm for the boreal chorus frog, and SVL <23 mm for the western toad. Classifications of YOY were based on maximum SVL lengths of captured newly metamorphosed juveniles with tail buds. Sub-adults (i.e., sexually immature individuals) and adults were lumped into one category (age-1+ or adult). All anurans were released 5-10 m from their point of capture. Trapping data were converted to catch per unit-effort [CPUE = (total captures x 100 days)/ (trap nights x number of pitfall traps)] for presentation of results. For each species, I examined statistical effects of stream type (unobstructed streams versus beaver ponds), anuran age (YOY versus adult) and the interaction of stream type × anuran age on CPUE using a split-plot ANOVA with error terms = stream location/stream type/anuran age.

To investigate habitat-use patterns of juvenile anurans and influences of key landscape features on their abundance along unobstructed streams, I correlated both (Euclidean) distance to nearest beaver pond and density of nearby beaver ponds with CPUE of juvenile wood frog using univariate linear regressions. Density of nearby ponds was measured as % area of landscape within 500 m and 1000 m of an unobstructed reach that was occupied with beaver ponds. I did not choose smaller distances (e.g., 250 m) because this resulted in most of the study sites being assigned a zero value for having no ponds in the surrounding landscape. Goodness of fit of linear regression models were evaluated with R^2 statistics. All analyses were on log10 transformed CPUE values to satisfy assumption of parametric analyses and executed in SPLUS (Insightful Corporation; Crawley 2002). Significance levels were set at a 0.05 probability.

GIS analysis

I focused my analyses using GIS on 15 contiguous, low-order (2-4) watersheds (total area = 14 548 ha); six drained in a northerly direction into the Pembina River (a tributary of the Athabasca River) and nine adjacent watersheds flowed south-easterly into the North Saskatchewan River (Figure 4:1). To examine the distribution of beaver ponds in the study watersheds, I used a combination of a digital elevation model (DEM), ArcGIS spatial analyst tools and digitized landscape metrics based on vegetation inventory data (Franklin et al. 2002) from geo-referenced, spatially-corrected aerial photographs taken in 1997 (at a scale of 1:15,000). Beaver ponds (i.e., pond with dam) and basin ponds (i.e., ponds and wetlands not associated with a dam) were delineated on-screen by C. E. Stevens. The DEM (10 m cell size) was created from a Triangulated Irregular Network (TIN) model of the terrain based on topographic information from points plotted at 100 m intervals, peaks, valleys, random locations and break-lines (e.g., shorelines) on 1:60 000 aerial photography. The DEM was employed to create a network of streams within the study watersheds using ArcGIS (i.e., raster sets of linear features). Using the flow accumulation function, cells with more than 800 cells flowing into them were categorized as a stream. I chose this threshold because it connected beaver ponds to low-order streams that were often difficult to identify on photographs and because it maintained a linear network similar to that delineated through interpretation of aerial photography. All streams were classified based on the number and size of their tributaries: order increased when streams of the same order intersected (Strahler 1964). I also created a slope raster by calculating the maximum rate of change between each cell and its neighbours such that the lower the slope value, the flatter the terrain.

Weyerhaeuser Canada Company, Ltd provided digitized GIS layers of anthropogenic disturbance (i.e., roads, cutblocks) and of vegetation inventory data (Franklin et al. 2002) describing forest height, *Populus* stands and deciduous stands (i.e., *P. tremuloides*, *P. balsamifera*, and *B. papyrifera*). Next, GIS layers of stream hydrology, disturbance, and forest structure and composition were converted to a raster output in spatial analyst. The focal statistic function (with neighbourhoods of 100 m radii) calculated the mean slope, mean forest height, percent deciduous trees, and percent *Populus* spp. for each raster cell in the respective output. Calculations for each cell in the forest output rasters were then adjusted to account for non-pond area only. Non-forested areas (e.g., roads) were excluded when calculating the forest height output raster. For each digitized layer of cutblocks and roads, I created Euclidean distance output rasters as correlates of industrial land-use. Finally, I randomly selected points every 400 m on streams in the 15 study watersheds to both maximize stream coverage and minimize autocorrelation (i.e., field observations indicated that beaver lodges were approximately 300-400 m apart on streams). These points were intersected with the focal and distance raster outputs, and a stream order (vector) layer using Hawth's Analyst Tools for ArcGIS (see www.spatialecology.com).

To examine the influence of stream hydrology, forest structure and composition, and industrial activity on beaver occupancy of streams I used 1) univariate nested ANOVAs (with watershed as an error term) comparing the mean value of each habitat correlate between occupied and vacant stream locations; and 2) the binomial family of generalized linear mixed models (GLME) with a random effect to predict beaver pond occurrence with a suite of habitat variables in SPLUS (Chao 2003, Gillies et al. 2005). Random effects were added to analyses because of potential correlation in the measured response among stream locations within a watershed. For example, dispersal routes used by beaver generally follow stream channels for distances up to 5 km (Van Deelen and Pletscher 1996, Sun et al. 2000). Prior to the GLME, potential multicollinearity among the habitat variables was assessed with Spearman correlation tests and one of the two highly correlated variables was eliminated ($r > |0.55|$) (Table 4:1). I excluded percent deciduous forest because it was highly correlated with percent *Populus* ($r = 0.91$), a well-documented preferred food plant of beaver.

My model consisted of correlates of beaver food plants (mean forest height and percent *Populus*; see Fryxell and Doucet 1993, Gallant et al. 2004), hydrological parameters (stream order and slope; see Howard and Larson 1985, Barnes and Mallik 1997), and distance to nearest cutblock and road because of their influence on forest composition and structure, and stream hydrology (Jones 2000, Swank et al. 2001). I also added elevation to the model as a correlate of watershed position because preliminary observations suggested that beaver ponds were clustered at higher stream elevations or locations within a watershed (Figure 4:1). Two 2-way interactions were added as correlates of complex hydrological scenarios: 1) stream order × stream slope; and 2) stream order × distance to nearest road. The first interaction was based on the prediction that a reliable but manageable source or volume of water was essential to the establishment and maintenance of beaver ponds (e.g., fast-moving, narrow streams or slow-moving, wide streams). The second interaction reflected the possibility that road crossings serve as useful 'pinch-points' for intercepting stream flow for beaver damming, particularly on high-order streams that move large volumes of water. Two 'forage' interactions of 1) percent nearby *Populus* × mean forest height, and 2) percent nearby *Populus* × distance to nearest cutblock, were also included to determine whether beaver modified their surroundings or selected stream locations for a particular height class of *Populus*. My final GLME model excluded non-significant interactions ($P > 0.10$) but retained all individual correlates. This procedure helped control 'confounding' as a source of biased estimation of effects for cases where effects of multiple correlates on a response were inseparable (Greenland et al. 1999).

The fit of the final GLME model was first assessed through a visual examination of the standardized residuals plotted against the fitted values. I also used receiver operator characteristics (ROC) on withheld subsets of my model data (20%) to assess fit and predictive performance as model verification. ROC-area under the curve estimates ≥0.7 was considered a model with good accuracy (Swets 1998). As an additional assessment of the predictive capacity of my GLME model, I used coefficients to estimate the probability of occurrence of beaver ponds for each study site, and obtained a probability cut-off point that maximized both specificity and sensitivity curves simultaneously with the model-training data (80% of data) only (Swets 1998). That cut-off point was used to determine whether or not a beaver pond was predicted for each site in withheld testing data (20%). Using observed and predicted occurrences of beaver ponds and unobstructed streams in this dataset I then estimated the percent correctly classified (PCC) sites. Models with a PCC score ≥70% are considered to be reasonably predictive (Nielson et al. 2004).

4:3 RESULTS

Amphibian populations

No calling anurans were recorded on unobstructed streams during repeated call surveys. In contrast, call surveys in 2001 and 2002 on beaver ponds produced pooled estimates of 1184 boreal chorus frogs, 3809 wood frogs, and 69 western toads. Note that values for boreal chorus frog and wood frog reflect, in part, estimated numbers of calling males in Rank 3 choruses based on methods described earlier. The number of breeding anurans per km of dammed stream for the boreal chorus frog was 107 males/km in 2001 and 282 males/km in 2002, comparable estimates for the wood frog were 573 males/km in 2001 and 831 males/km in 2002, and estimates for the western toad were 14 males/km in 2001 and 10 males/km in 2002 (Figure 4:2).

The total number of anurans captured using pitfall traps and drift fences was 3264 individuals on both beaver ponds and unobstructed streams, the majority of which were wood frog (3064 individuals) followed by western toad (120 individuals) and boreal chorus frog (80 individuals) (Figure 4:3). Most wood frog captures were of YOY (i.e., 2648 individuals) representing 81% of total anuran captures. Less than 1% of YOY wood frogs were recaptured within a sampling year. Split-plot ANOVAs indicated that CPUE of the wood frog was significantly higher on beaver ponds than on unobstructed streams ($F_{1,8} = 10.44$, $P = 0.012$) and that significantly more YOY wood frogs were captured than adult wood frogs ($F_{1,16} = 8.04$, $P = 0.012$). CPUE of western toad was significantly higher on beaver ponds than on unobstructed streams ($F_{1,8} = 14.02$, $P = 0.006$) but similar between age classes ($F_{1,16} = 2.86$, $P = 0.11$). In contrast to the wood frog and western toad, CPUE of boreal chorus frogs was unaffected by both stream type ($F_{1,8} = 2.58$, $P = 0.147$) and anuran age class ($F_{1,16} = 0.125$, $P = 0.125$). However, CPUE of boreal chorus frogs was significantly affected by the interaction of stream type and anuran age class ($F_{1,16} = 5.88$, $P = 0.028$). Figure 4:3 clearly shows that more YOY boreal chorus frogs were captured on beaver ponds than on unobstructed streams whereas similar numbers of adult boreal chorus frogs were captured on both stream types.

On unobstructed stream reaches (n = 9) I observed a total of 412 YOY wood frogs. Capture rates were highly variable among sites: 0.2 to 24.4 CPUE. Varying CPUE among stream reaches may be due to the fact that some sites were far (e.g., 636 m) from a potential source of anurans whereas others were close (e.g., 90 m) to a beaver pond (overall mean ± SE = 253 ± 57.8 m). Unobstructed streams also varied in percent area of landscape occupied with beaver ponds: 0% to 5% at 500-m scale (mean ± SE = 2.0 ± 0.67%) and 0.04% to 5.76% at a 1000-m scale (mean ± SE = 2.1 ± 0.64%). Based on univariate linear regression, Euclidean distance to nearest beaver pond ($t_7 = -1.4$, $P = 0.21$) was negatively related to CPUE of juvenile wood frog; however, this relationship was not significant. In contrast, % landscape occupied with beaver pond at both the 500-m scale ($t_7 = 4.3$, $P = 0.004$; Figure 4:4) and 1000-m scale ($t_7 = 2.73$, $P = 0.029$) significantly predicted CPUE of juvenile wood frogs on unobstructed streams. More juveniles were captured in landscapes with higher densities of beaver ponds (Figure 4:4). The slope coefficient in the 500-m scale model ($b = 0.203$) was slightly (14%) higher than that in the 1000-m scale model ($b = 0.178$), and the goodness of fit was also considerably better for the smaller scale model: $R^2 = 0.72$ versus 0.52.

Beaver pond distributions

The total length of study-stream habitat (estimated with a digital elevation model) that was available for occupation by beaver in my study landscape was 325 596 m (1st order = 167 148 m, 2nd order = 87 552 m, 3rd order = 45 383 m, and 4th order = 25 513 m). Aerial photographs (1:15 000) from 1997 indicated that of the total length of stream habitat estimated with a digital elevation model, approximately 10% was flooded by beaver dams creating 590 beaver ponds (total area = 1 233 792 m^2). Only 24 basin (non-beaver) ponds or wetlands (total area = 78 934 m^2) were detected in the study watersheds. Fifty-eight percent of beaver ponds were on 1st and 2nd order streams, whereas the remaining 42% were on 3rd and 4th order streams. On average (mean ± SE), the area of beaver ponds was 2091 ± 148 m^2 (range 50 to 46 269 m^2). Based on Weyerhaeuser Canada Company, Ltd vegetation inventory data, forestry and petroleum sectors were active in the region and had built over 240 000 m of roads to drill 446 oil and gas wells, and to harvest trees from approximately 10% of the study area. Cutblocks were of varying age since logging (1-100 yrs); however most had been cut within 20 yrs (75% of total area harvested) and were comprised of trees under 5 m in height (72% of total area harvested). Some of the logging in my study area was immediately adjacent to stream reaches where there were no buffers: 12 648 m along 1st order streams, 3 580 m along 2nd order streams, 443 m along 3rd order streams, and 156 m along 4th order streams.

Of the 573 stream locations randomly chosen in the 15 study watersheds, 114 points were on beaver-obstructed stream reaches (Table 4:1). Of the eight habitat features examined with univariate ANOVAs, only stream order and distance to nearest cutblock differed significantly between unobstructed streams and beaver-obstructed streams when stream location was nested within watershed ($P < 0.05$; Table 4:1). Beaver ponds occurred on streams that were higher in order (36% higher) and greater distances from cutblocks (38% further) than unobstructed sites. My GLME model, which had adequate predictive power and accuracy (ROC = 0.78 and PCC= 70% for model testing data), also suggested that beaver pond occurrence was positively related to stream order (Table 4:2). However, the relation between distance to cutblock and beaver pond occurrence in the GLME was significantly dependent on available levels of *Populus* within 100 m of the stream location (Table 4:2; Figure 4:5). When *Populus* was scarce at a site, there was a low probability that beaver occupied the stream. When a site was surrounded by *Populus* stands, the probability of a beaver pond occurring at that location increased as distances to cutblock increased (Figure 4:5). I also noted significant interaction between stream slope and stream order (Table 4:2; Figure 4:5). Beaver ponds were more likely to occur either on high gradient streams of low order (1-2) or on low gradient streams of high order (3-4) (Figure 4:5). Finally, the presence of beaver ponds was significantly correlated with elevation in my GLME (Table 4:2). Beaver ponds were more likely to occur at high elevations.

4:4 DISCUSSION

The present study supports the use of beaver as a surrogate species aiding amphibian conservation. In my study area, calling wood frog, boreal chorus frog and western toad were recorded only in association with beaver dams. Thus, I infer that beaver create breeding habitat for anuran amphibians as suggested in a similar study by Russell et al. (1998) that found more post-metamorphic anurans in riparian zones on beaver ponds versus unobstructed streams in North Carolina, USA. Beaver may also have a particularly large role in maintaining amphibian populations in the Boreal Foothills of Alberta since the majority of standing water on the landscape was created by beaver impoundment of small streams. The distribution of beaver ponds, however, was not random: stream order and proximity to cutblocks were important environmental factors influencing their occurrence. These relationships are discussed in detail below and may have implications for industry in the region if the conservation of amphibians is a goal of resource managers.

Amphibians on beaver ponds

Critical to understanding the value of beaver ponds as amphibian habitat is an assessment of whether beaver ponds are potential population sources (e.g., Gill 1978) characterized by relatively high rates of juvenile recruitment to metamorphosis. Based on pitfall trapping, my results suggest that the wood frog and possibly the boreal chorus frog were the only species with high rates of juvenile recruitment in beaver ponds. For the wood frog, both the numbers (CPUE) of juveniles and adults were higher on beaver ponds than on unobstructed streams, and the number of juvenile wood frogs was higher than the number of adult wood frogs captured on unobstructed streams and beaver ponds combined. Although significant interaction of anuran age class with habitat type for CPUE of boreal chorus frogs was noted, considerably more juvenile boreal chorus frogs were captured on beaver ponds than on unobstructed streams. Unfortunately, the potential failure of pitfall traps to effectively sample adult boreal chorus frogs limits a conclusion on rates of juvenile recruitment to metamorphosis for this species (Stevens and Paszkowski 2005). However, given the relatively high number of beaver ponds on the landscape, I suspect that few of the captured juvenile wood frogs and boreal chorus frogs had emigrated from nearby basin ponds. In addition, the strong correlation between percent landscape occupied with beaver ponds and abundance of juvenile wood frogs on unobstructed streams suggests that the anurans recorded on these sites originated from beaver ponds.

In contrast to the wood frog, it is unclear if the western toad experience high rates of juvenile recruitment from beaver ponds. Although more western toads were captured adjacent to beaver ponds than unobstructed streams, the number of juveniles and adults recorded in pitfall traps were similar. This pattern may reflect the fact that beaver ponds are poor larval environments for toads (e.g., too cold, inadequate food) leading to low juvenile recruitment, or be an artefact of sampling biases (Stevens and Paszkowski 2005). For example, partial fencing of riparian zones around ponds could have missed either in-stream movements of juvenile toads (Adams et al. 2005) or emerging aggregations of juvenile toads from particular locations along the shoreline where the water was warm or the overhead canopy was open (Black and Black 1969, Noland and Ultsch 1981). However, during three years of pitfall trapping in my study area, no visual observations of western toads in ponds or streams were made outside of the breeding season, and only one observation of a large group of newly metamorphosed toads was made adjacent to a pond (by C. E. Stevens).

Despite the lack of strong evidence provided by my pitfall trapping for high recruitment of juvenile boreal chorus frogs and western toads from beaver ponds, the fact that these species occur in an eco-region where beaver ponds are the primary source of breeding habitat suggests that at the very least, some ponds in the regions are sources within a larger metapopulation. For example, older beaver ponds provide suitable breeding habitats because these sites can offer anuran larvae warm and well oxygenated environments that can enhance development and growth rates (Stevens et al. 2005). The seasonal hydroperiod of beaver ponds is also relatively stable (Gill 1978, Schlosser and Kallemyn 2000). Only one pond (of 54) surveyed for calling anurans disappeared due to dam collapse during the 2 years of my study. In addition, beaver ponds in boreal regions may support lower abundance and diversity of predatory fishes because of winterkill triggered by anoxic conditions (Tonn and Magnuson 1982) and of restriction of fish movements by dams (Schlosser and Kallemyn 2000). Beaver ponds on 1st-3rd order streams in the Boreal Foothills infrequently contained fish (i.e., 15 of 54 ponds surveyed), and the only fish present was the small-bodied brook stickleback (*Culaea inconstans*; Stevens et al. 2005) even though minnows (e.g., *Pimephales promelas*) and larger fishes such as salmonids (e.g., *Salvelinus confluentus*) and northern pike (*Esox lucious*) occur in local watersheds (Nelson and Paetz 1992).

Beaver pond distributions: implications for amphibians

Although there has been extensive research on beaver food habits (e.g., Schoener 1979, Jenkins 1980, McGinley and Whitam 1985, Johnston and Naiman 1990, Fryxell and Doucet 1993, Basey and Jenkins 1995, Gallant et al. 2004), relatively few studies have examined factors associated with colony distributions at a landscape scale (but see Slough and Sadleir 1977, Howard and Larson 1985, Barnes and Mallik 1997). My model identified important variables correlated with the occurrence of beaver ponds and associated amphibian populations in the Boreal Foothills. The clustering of beaver ponds at higher elevations in a watershed may reflect both selection for particular streams and a tendency of beaver to disperse to nearby stream locations (Sun et al. 2000). This spatial arrangement of beaver ponds has the potential to influence the presence or abundance of amphibians if clusters of breeding sites are isolated and the distance between clusters prevents emigrating anurans from colonizing new beaver ponds or rescuing existing populations (Marsh and Trenham 2001). Distances between clusters would have to exceed the capabilities of long-distance dispersers that can dominate habitat colonization and patterns of spatial dynamics (Marsh and Trenham 2001). For anurans in my study, 2-3 km may be the maximum dispersal distance made by one or few individuals in a population (Reimchen 1990, Berven and Grudzien 1990, Muths 2003, Adams et al. 2005). However, most individuals probably remain within a few 100 m of their natal pond resulting in minimal effects of immigration on local recruitment and population dynamics of ponds outside of this range (Newman and Squire 2001, Petranka et al. 2004). I did note that CPUE of juvenile wood frogs on unobstructed streams was highly correlated with percent landscape occupied with beaver ponds at a 500-m scale, and that correlations were weaker at a larger scale (1000 m).

Preferred locations for dam-building beaver in my study included higher-order streams. These streams may provide a reliable volume of water necessary for creating and maintaining deep ponds throughout the year and through periods of drought (Howard and Larson 1985, Barnes and Mallik 1997). Deep ponds provide escape from terrestrial predators, safe under-ice travel during winter, and a medium for transporting construction materials and food stores (Hill 1982). However, too much flow on a stream might result in the blow-out of dams, particularly during spring run-off (Stock and Schlosser 1991, Hillman 1998). Potentially consistent with my findings that beaver select streams with an intermediate level of flow, a New England study identified wide, slow-moving streams as beaver habitat (Howard and Larson 1985), whereas a study on the boreal shield characterized beaver habitat as small, fast-moving streams (Barnes and Mallik 1997). The implications of beaver site selection for amphibian populations are dependent on whether higher abundance and diversity of predatory fishes occur on beaver ponds associated with higher-order streams (Snodgrass and Meffe 1998). For example, fish can have a significant impact on larval survival, and even slow growth and development of larvae through behavioural changes and reduction in feeding (e.g., Werner and McPeek 1994, Baber and Babbitt 2003).

Forest management, beaver ponds and amphibians

Much to the annoyance of road maintenance personnel, beaver often build dams in culverts and occupy streams near roads (Payne and Peterson 1986, McKinstry and Andersen 1999). Thus, I was surprised that beaver pond occurrence was unrelated to distance to nearest road in my study and propose that trapping of road-side ponds (Loker et al. 1999) or the lack of woody vegetation adjacent to roads offset any hydrological benefits to pond creation (Curtis and Jensen 2004). Beaver pond occupancy on streams was also unrelated to levels of preferred food species (i.e., *Populus*) even though beaver spend a great deal of time and energy harvesting trees and shrubs near open-water (e.g., Schoener 1979, Jenkins 1980, McGinley and Whitham 1985), and can have substantial effects on the overstory and overall structure of riparian zones (Johnston and Naiman 1990, Donkor and Fryxell 1999, Barnes and Mallik 2001). Perhaps levels of *Populus* were similar on beaver ponds and unobstructed reaches because beaver had only partially depleted stands of *Populus* adjacent to ponds at the time (1997) of aerial photography interpretation (Donkor and Fryxell 1999, Barnes and Mallik 2001). I did find that stream reaches nearer to cutblocks were less likely to be occupied by a beaver pond regardless of the level of nearby *Populus*. Cutblocks, which were typically new (<20 yrs) and regenerating with *Populus* in my study landscape, may be avoided because of the paucity of large, standing trees that are generally preferred by foraging beaver (McGinley and Whitham 1985, Fryxell and Doucet 1993, Gallant et al. 2004).

As an amphibian conservation strategy, forestry planning and energy development in boreal ecosystems could incorporate landscape-use patterns of dam-building beaver generated by my study or from a model specific to the eco-region being developed. I noted that beaver pond occurrence was negatively related to nearby cutblocks, and propose that forestry activities that alter stand composition and age have the potential to impact beaver foraging, the persistence of colonies and associated amphibian populations, particularly on low-order streams. In Canada's boreal forest, both beaver ponds and intermittent streams typically receive no riparian buffers from logging (i.e., prescribed zones of uncut trees adjacent to a water body that are the remnant of older-aged stands), whereas permanent streams have buffer widths near 25-30 m (Lee et al. 2004). Developing efficient management plans based on sound ecological information of beaver as a surrogate species will aid in the conservation of boreal amphibians. Useful shortcuts may include the monitoring of beaver pond densities and the maintenance of riparian buffers around both established beaver ponds and unoccupied intermittent streams with high slopes. To enhance colony longevity on established sites, I recommend buffer widths of 20 m; beyond this distance the proportion of stems cut by beaver dramatically drops (Johnston and Naiman 1990, Donkor and Fryxell 1999, Barnes and Mallik 2001). Wider buffers may be required on potential pond sites to account for flooding after dam establishment. I also suggest that forest managers use maps that identify existing beaver ponds, as well as future potential pond sites from predictive spatial models, to reduce impacts on beaver and ensure breeding ponds for amphibian populations. Maintaining summer foraging habitat and the connectivity of ponds for amphibian along stream networks should also be a part of management plans, particularly on unobstructed streams in regions of high densities of beaver ponds (e.g., 5% of landscape occupied by ponds). Given that industrial activity continues to expand, conservation biologists and wildlife managers should act now to prevent declines in amphibian populations in the boreal forest as have occurred in other regions of the world.

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Table 4:1. Mean (±SE) values of habitat parameters on unoccupied versus beaver-occupied sites randomly chosen on a network of streams in 15 watersheds in west-central Alberta. Elevation, stream order and slope were based on a digital elevation model created in ArcGIS.

	Unoccupied stream sites ($N = 459$)	Beaver sites on streams ($N = 114$)	% Difference in means	$F_{1,13}$	$P^{\dagger}$
Mean elevation (m)	919 ±2.4	933 ±3.5	+2	1.73	0.211
Stream order (1-4)	1.65 ±0.04	2.25 ±0.09	+36	6.26	0.026
Stream slope	3.51 ±0.17	2.87 ±0.21	-18	0.07	0.791
Forest structure and composition within 100m:					
Mean height (m) [a]	16.9 ±0.29	15.9 ±0.62	-6	0.16	0.695
Percent deciduous [ab]	55.4 ±1.5	49.1 ±2.6	-11	0.01	0.919
Percent *Populus* [b]	48.7 ±1.5	43.4 ±2.7	-11	0.28	0.605
Nearest anthropogenic disturbance:					
Cutblock (m)	627 ±30.8	866 ±63.2	+38	6.61	0.023
Road (m)	241 ±9.9	224 ±21.3	-7	0.76	0.399

a,b = each letter corresponds to high correlation (>0.55) between a pair of parameters

$^{\dagger}P$ reflects differences between stream types and was assessed using univariate ANOVAs with sites nested within watershed.

Table 4:2. Coefficients (±SE) associated with habitat correlates in a generalized linear mixed model (GLME) predicting beaver pond occupancy on low order (1-4) streams grouped on 15 adjoining watershed in west-central Alberta.

	Coefficient ±SE	t_{549}	*P*
Intercept	-15.46 ±3.339	-4.63	<0.0001
Mean elevation (m)	1.3 ±0.348*	3.73	0.0002
Stream order (1-4)	1.482 ±0.2089	7.09	<0.0001
Stream slope	0.2276 ±0.1285	1.77	0.0770
Percent *Populus* (within 100 m)	-0.093 ±0.00632*	-1.47	0.1421
Mean forest height (m; within 100 m)	-0.0152 ±0.02421	-0.63	0.5303
Distance to nearest cutblock (m)	-0.005 ±0.0035*	-1.29	0.1965
Distance to nearest road (m)	-0.01 ±0.006*	-1.52	0.1292
Stream order x mean slope	-0.1425 ±0.0468	-3.05	0.0024
Percent *Populus* x nearest cutblock	0.002 ±0.0006*	2.7	0.0072

*change per 10 units

Note: ROC = 0.78 and PCC = 70% for GLME model testing data.

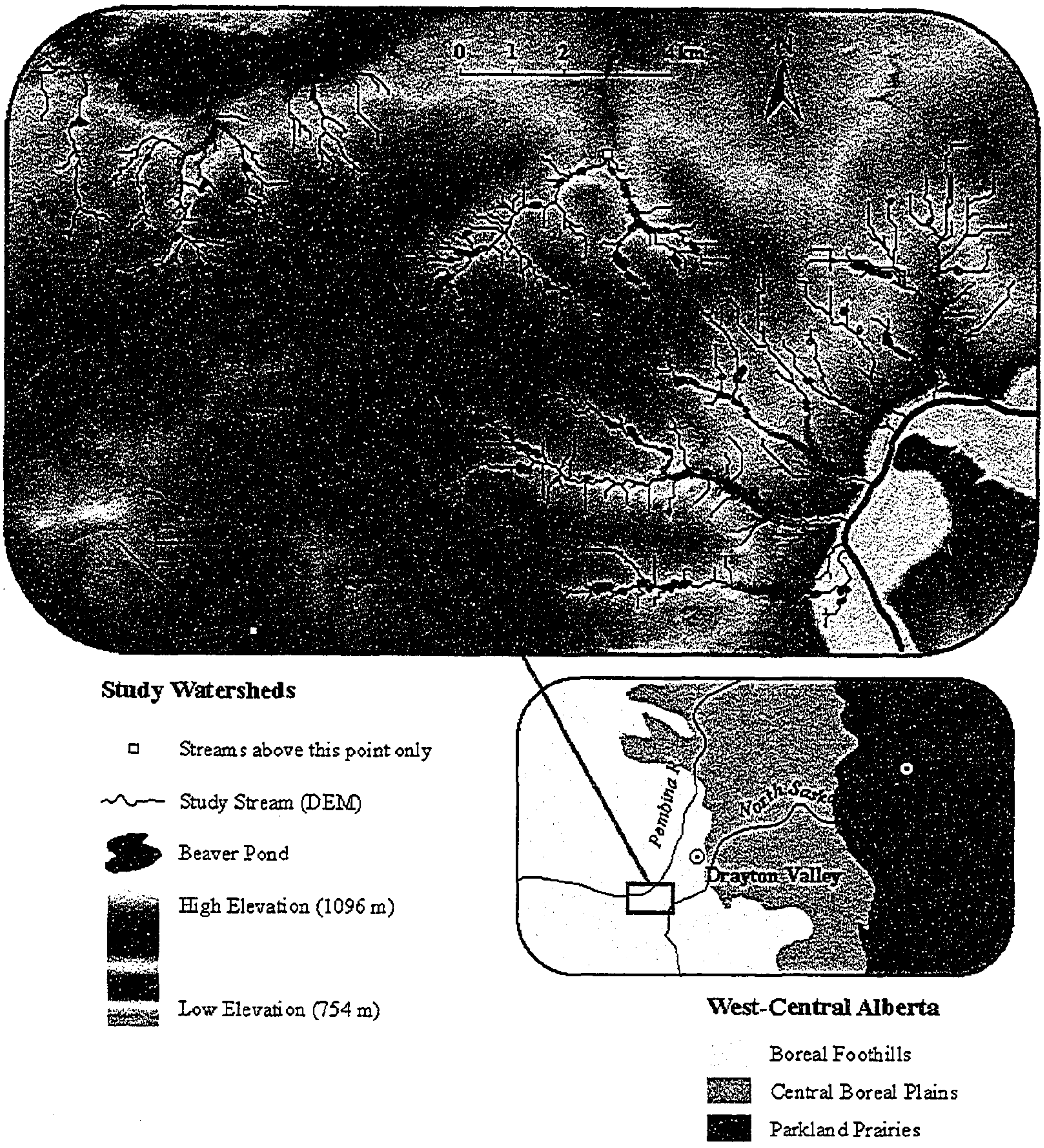

Figure 4:1. Study streams and watersheds examined for the presence of beaver ponds in west-central Alberta. Streams were delineated with a digital elevation model (DEM) in ArcGIS whereas beaver ponds were identified from aerial photography taken in 1997.

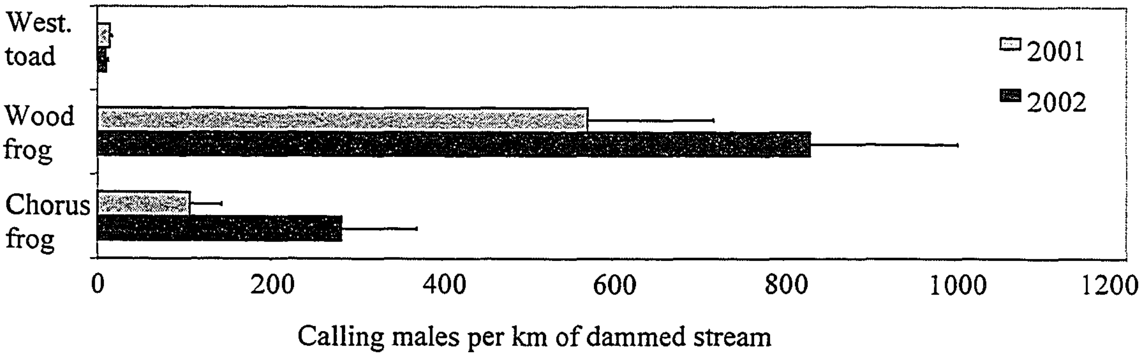

Figure 4:2. Mean (±SE) number of calling male western toad, wood frog, and boreal chorus frog per km of 15 beaver-obstructed stream reaches in west-central Alberta surveyed during spring 2001 and 2002. Abundance estimates were derived by counting males in each Rank 1 and 2 chorus, and assigning 59 and 30 males to each recorded Rank 3 chorus for the wood frog and boreal chorus frog, respectively (see Stevens and Paszkowski 2005). No Rank 3 choruses were encountered for western toad.

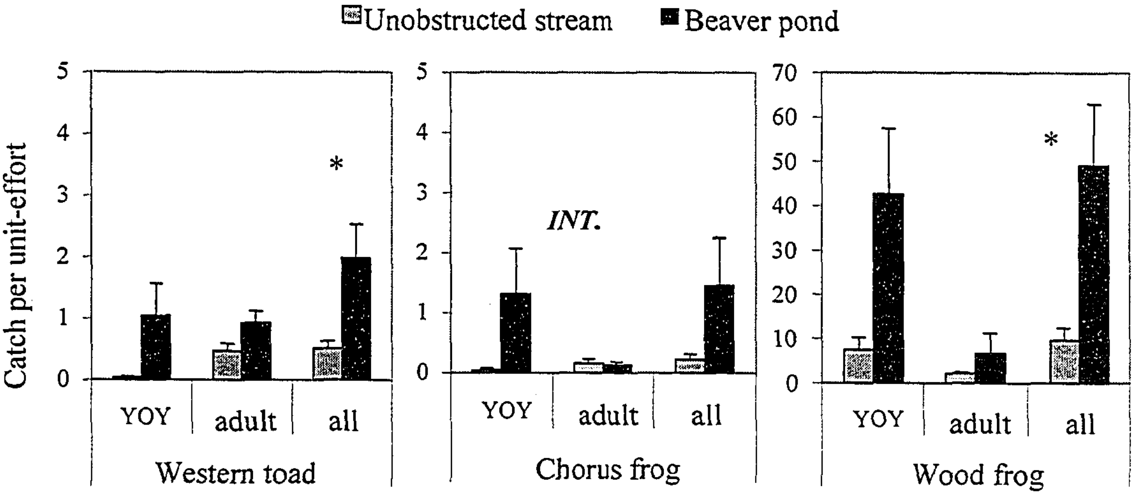

Figure 4:3. Pitfall trap data for three anuran species as mean (±SE) catch per-unit effort [CPUE= (total captures x 100 days)/ (trap nights x number of pitfall traps)] of post-metamorphic young-of-year (YOY) and adult (age-1+) on nine pairs of unobstructed streams and beaver ponds. Trapping was conducted from July 10 to August 15, 2001 in the Boreal Foothills of Alberta. At $P < 0.05$, split-plot ANOVAs indicated that total CPUE of western toad and wood frog was higher on beaver ponds versus unobstructed stream (*), and that the effect of stream type was dependent on age class (*INT.*) for the boreal chorus frog.

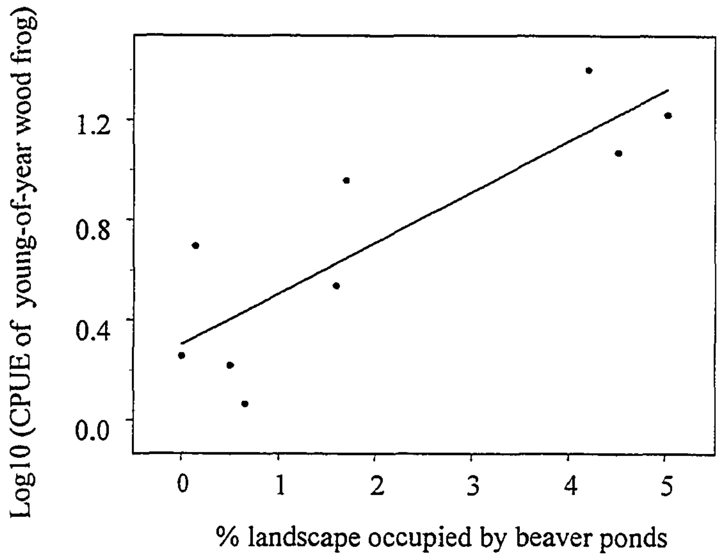

Figure 4:4. Scatterplot with a linear least square smoother of % landscape occupied by beaver ponds (within 500 m) versus log10 transformed catch per unit-effort [CPUE= (total captures)/ (trap nights x number of pitfall traps)] of young-of-year wood frog on nine unobstructed streams in west-central Alberta (y = 0.304 +0.203x).

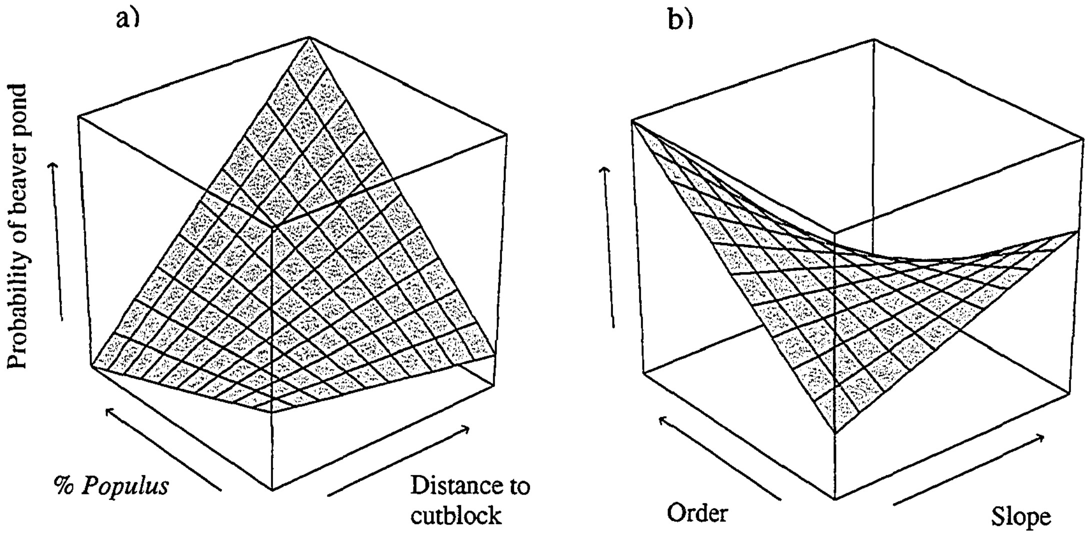

Figure 4:5. The interacting effects of % nearby *Populus* x distance to nearest cutblock (a), and stream order x slope (b) on the presence of beaver ponds on small streams in the Boreal Foothills that were assessed in a generalized linear model. Percent *Populus* was determined from a 100 m radius of stream location and for non-beaver pond area only. Cutblocks were of varying age since logging (1-100 yrs); however most were cut within 20 yrs (75% of total area harvested) and comprised of *Populus* trees under 5 m in height (72% of total area harvested). Stream order and slope were calculated using a digital elevation model.

Chapter 5. 'Older is Better': Beaver Ponds on Boreal Streams as Breeding Habitat for the Wood Frog*

Abstract.— Succession of stream ponds mediated by beaver (*Castor canadensis*) damming and foraging in riparian zones may contribute to changes in amphibian populations. I examined use of beaver ponds by the wood frog (*Rana sylvatica*) in a network of boreal streams in west-central Alberta, Canada by quantifying relations between breeding populations estimated from call surveys with pond age and riparian canopy cover, and by comparing an index of juvenile recruitment to metamorphosis estimated with pitfall traps between new (<10 yrs) and old (>25 yrs) beaver ponds. I also conducted an in-pond enclosure experiment to determine whether differences in physicochemical conditions of new versus old ponds influenced larval performance. Regression and AIC model-averaging indicated that both density and calling intensity of male wood frogs at beaver ponds were negatively related to percent riparian canopy cover and positively related to pond age; however, the best *a priori* statistical models included riparian canopy cover rather than pond age as a significant covariate. Reduced riparian canopy and greater abundance of submergent vegetation, thermal degree days, and dissolved oxygen concentrations were noted in old ponds compared to newly formed ponds. While survival of larval wood frogs in enclosures did not differ between pond age classes, growth and development rates in old ponds were greater than in new ponds. In addition to warmer water in old ponds, results from a laboratory experiment suggest that higher concentrations of dissolved oxygen characteristic of old ponds can enhance larval growth rates. Older beaver ponds may support more breeding wood frogs because of adult selection for open canopy ponds and associated larval environments favourable for high rates of juvenile recruitment. Forest management that protects beaver and their food supplies may also promote healthy populations of boreal amphibians.

5:1 INTRODUCTION

Succession through disturbance of habitats and displacement of individuals is a fundamental ecological process influencing the dynamics of animal populations (e.g., Connell and Slatyer 1977, Johnson 1992, Skelly et al. 1999). In the boreal forest, the

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*Under review as Stevens et al. (2005) in Journal of Wildlife Management (submitted April 29, 2005) effects of succession on the structure of plant communities are evident at a variety of spatial and temporal scales and are driven predominantly by wildfire (reviewed in Johnson 1992). Less understood is the role of stream succession resulting from beaver (*Castor canadensis*) that disturb or alter water flow by constructing dams on streams (Naiman et al. 1988, Schlosser and Kallemyn 2000). Densities of beaver dams can exceed 16 per km on small streams in boreal landscapes (Naiman et al. 1988, Hillman 1998), and their occurrence may influence the distribution and abundance of aquatic organisms. Species with life cycles constrained to streams and responsive to habitat fragmentation and changes in physicochemical conditions may be affected negatively by beaver damming (Gresswell 1999, Schlosser and Kallemyn 2000). In contrast, species that utilize ponds for breeding and disperse across land during post-metamorphic stages, such as many species of amphibians, may benefit from the construction of dams on streams if newly created ponds create environments favourable for high larval survival (Gill 1978). Few researchers have addressed this hypothesis (but see Gill 1978). Beaver ponds may support low densities of predatory fish because dams restrict their movements (Schlosser and Kallemyn 2000) and are often built on small, ephemeral streams (Naiman et al. 1988, Barnes and Mallik 1997), which support low diversity and abundance of fish (Vannote et al. 1980). Beaver ponds also have a high likelihood of water permanency which insures sufficient time for development of larval amphibians (Gill 1978) but may also provide habitat for predatory fishes and macroinvertebrates (Schlosser and Kallemyn 2000). In turn, felled trees and submergent vegetation within beaver ponds (France 1997, Ray et al. 2001) create a heterogeneous environment that offers diverse refuges from predators for amphibian eggs and larvae (France 1997, Babbitt and Tanner 1998).

Anuran amphibians are known to display high variation in population sizes (Alford and Richards 1999, Hannon et al. 2002, Green 2003), and given the global scale of recorded extinctions and recent declines in amphibian numbers because of human development (Houlahan et al. 2000, Alford and Richards 1999, Alford et al. 2001), an understanding of natural variation in amphibian densities represents an important component for ensuring their conservation. A potentially important mechanism on created ponds is 'inertia' where a population can increase through annual episodes of pond colonization, successful reproduction and individuals exhibiting site fidelity, resulting in a larger pool of potential breeders with each subsequent year (Gill 1978). Forest succession can also affect long-term dynamics of populations and lead to either local extirpation in closed-canopy ponds (Skelly et al. 1999) or opportunistic, wholesale shifting of breeding populations to other habitats with less overhead canopy (Petranka et al. 2004). These may be responses to suboptimal pond conditions for developing larvae under closed canopies that reduce light, thermal inputs, and primary production (Werner and Glennemeier 1999, Skelly et al. 2002). Larval amphibians may be affected similarly by the same factors in newly established beaver ponds that have intact riparian canopies relative to the reduced canopy cover of older ponds created by extensive foraging by beaver (Donkor and Fryxell 1999, Barnes and Mallik 2001) or by tree-death caused by flooding of riparian zones.

First objective of the present study was to determine the extent that breeding populations of the wood frog (*Rana sylvatica* LeConte) were influenced by differences in temporal and successional features on a network of beaver-obstructed streams in the boreal forest of west-central Alberta, Canada. I predicted that older ponds would be characterized by lower levels of riparian canopy cover and support more calling wood frogs because of inertia mechanisms and habitat selection by breeding adults. The second objective was to examine factors influencing population dynamics of wood frog at beaver ponds of varying age by identifying breeding ponds with high-quality conditions that were potential source habitats for metapopulations (Gill 1978, Marsh and Trenham 2001). High-quality conditions include those that promote high larval survival and rapid larval development which decreases vulnerability to predation and environmental perturbations. In a subset of newly formed (<10 yrs) and older (>25 yrs) beaver ponds, I quantified variation in physicochemical characteristics for these sites and generated an index of recruitment rates for newly metamorphosed juveniles for these sites using pitfall traps. I also completed a split-plot experiment using field enclosures to identify key breeding habitats for the wood frog by comparing larval performance between pond-age classes. I predicted that larval performance measured as survival, development rate, and growth rate would be higher in older beaver ponds because they receive more light under reduced overhead canopies and are therefore characterized by elevated thermal regimes, and a more abundant algal food base. Higher light levels in older ponds may result in higher dissolved oxygen concentrations owing to increased levels of photosynthesis by algae and submerged macrophytes. Thus, I also completed a short-term laboratory experiment to examine the extent that growth and development of larval wood frogs were influenced by varying concentrations of dissolved oxygen.

5:2 STUDY AREA

Field work was conducted near Lodgepole, Alberta (53° 06' N-115° 19' W) within the Lower Boreal-Cordilleran eco-region. This eco-region supports a forest dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh), white spruce (*Picea glauca* Voss), black spruce (*Picea mariana* Mill.) and lodgepole pine (*Pinus contorta* Dougl., Strong and Leggat 1992). Anthropogenic activities in the region include those of the petroleum and forestry sector (Stevens et al. 2005). The topography is rolling and has created a landscape dominated by networks of low-to-moderate gradient (first to fourth order) streams but relatively few basin (non-beaver) wetlands or ponds (Strong and Leggat 1992, Stevens et al. 2005). The climate in the Lower Boreal-Cordilleran eco-region is relatively dry with a mean total annual precipitation = 464 mm and cold with mean annual temperatures near 0°C and mean temperature May through August = 12.8°C (Strong and Leggat 1992).

The amphibian fauna in my study area consists of the wood frog, boreal chorus frog (*Pseudacris maculata* Agassiz), and western toad (*Bufo boreas* Baird and Girard) (Stevens and Paszkowski, unpublished data). I chose to focus on the wood frog because it is the most abundant species in the region (Roberts and Lewin 1979, Stevens and Paszkowski, unpublished data), and occurs throughout the boreal forest (Conant and Collins 1998). The species' life cycle includes a 50-60 d larval aquatic stage (Herreid and Kinney 1967, Stevens and Paszkowski, unpublished data) followed by a 4-6 yr post-metamorphic, largely terrestrial phase (Leclair et al. 2000). At sexual maturity, individuals return to ponds from hibernation sites for an explosive and synchronized breeding season in early May (e.g., Seale 1982, Stevens and Paszkowski 2004).

5:3 METHODS

In April 2001, I randomly selected 15 beaver-obstructed stream reaches (mean length = 190 m ± 11.9 SE) representing various ages since damming from within the North Saskatchewan and Pembina River drainages (approximately 200 km^2 landscape). Most stream reaches (11 of 15) were located >1 km from each other to minimize potential non-independence of ponds; four reaches were 0.5–1.0 km from others being studied. These smaller distances may allow some movement of wood frogs between ponds and preclude genetic differentiation between populations (Berven and Grudzien 1990, Newman and Squire 2002), but probably prevent the large number of migrants needed if immigration is to play a meaningful role in local recruitment and population dynamics (Newman and Squire 2002, Petranka et al. 2004). Thus, all 15 stream reaches were treated as independent units in habitat-use analyses. Each reach consisted of 1-6 consecutive beaver ponds that flooded areas ranging from 0.17-1.84 ha for a total number of 54 beaver ponds in 2001 and 52 beaver ponds in 2002. The lower number of ponds in 2002 reflected beaver activity and changing water levels during late summer of 2001 in 2 stream reaches that resulted in the consolidation of 2 ponds on each reach. A beaver dam also broke on a large beaver pond during an intense rain storm in late summer 2001 and remained partially damaged in spring 2002, creating a flooded area substantially smaller than the previous year (0.05 ha in 2002 versus 0.35 ha in 2001).

Wood frog call surveys

To estimate the number of breeding wood frogs in beaver ponds, I conducted 5 call surveys in 2001 and 2002 (Weir 2001) beginning each year when ice cover receded from all ponds in May and ending when no calling males were recorded at ponds in early June (Stevens and Paszkowski 2004). All surveys were conducted at night within a 3-hr window starting 0.5 hr after sunset and were completed under optimal weather conditions (i.e., light or no rain, Beaufort Wind Scale <4, air temperature >5 C). Each survey comprised a 180° point count for 5 min that covered pond habitat extending <75 m from a survey station. Most ponds in my study were relatively small and had 1 survey station, whereas, I established 2 stations on 3 ponds because of their large size (>0.5 ha) and elongated shape. Call data from these 2 stations were pooled during a survey. To minimize disruption of reproductive activity, surveys were conducted 7-10 m from the pond margin and from the south side of the pond where there was often no calling. Observers first identified each chorus that was a spatially distinct aggregation of calling males that quickly responded to each other's calls but were less responsive to and unsynchronized with other choruses. Next, observers counted individuals in Rank-1 and 2 choruses. Rank 1 indicates no overlap in calls and the number of individuals can be reliably estimated, and a Rank 2 suggests some overlap in calls and the number of males can be estimated (but less accurately than for Rank-1 choruses). Analyses were conducted using two estimates of the breeding population size measured as the highest density of calling males and the highest recorded calling intensity of males per pond over the first three surveys for 2001 and surveys 2-4 for 2002. These surveys were chosen because they included periods when the numbers of recorded Rank-2 and 3 choruses peaked, and thus I felt they most accurately measured maximum reproductive activity (Stevens and Paszkowski 2004). For calculation of male densities in ponds where a Rank-3 chorus consisting of unknown numbers was encountered, I assigned a value of 59 males to that group. This value was based on analyses described in Stevens and Paszkowski (2004) that combined data from multiple call surveys with counts of egg masses, and then used a conservative male to female ratio of 1:1 to determine the average number of males in a Rank 3 chorus. Although translating call-ranks into actual numbers of animals is an attractive proposition, the estimated number of males in a Rank-3 chorus does vary across ponds (8-157 males; Stevens and Paszkowski 2004), and is also dependent on the ratio of males to females, which was not actually recorded in Stevens and Paszkowski (2004). Thus, I generated a second index of abundance of breeding wood frogs that was less quantitative than the first but more conservative, by calculating the average of the maximum rank on a pond across 3 surveys conducted during the peak breeding period.

Environmental variables

Beaver pond age, riparian canopy cover and other local habitat and landscape attributes known to affect amphibian distributions were assessed for all study ponds. Aerial photographs (1:15,000-40,000, 10 sets between 1969 and 2000) were used to estimate pond age, calculated as the mean of the age of the earliest photograph where a pond was absent and the age of the next temporal sequence of photographs where the pond was present. The mean number of years between sets of photographs was 3.6 (range

2-5 yrs). None of the study ponds were present on the landscape in 1969. Riparian canopy cover adjacent to beaver ponds, which was composed primarily of *Populus* spp., was estimated using a spherical densiometer after trees leafed out for all ponds in spring 2002. The mean of measurements taken at 4 cardinal directions at 10 m intervals along the pond margin was assigned to each pond. There were no obvious changes in riparian canopy structure between the 2 study years so I assigned riparian canopy cover values from 2002 to the same ponds surveyed in 2001 for analyses. Pond area was visually estimated on grid paper using distances marked with flagging tape every 10 m along the pond perimeter as a guide. Area of larger ponds (>0.5 ha) was confirmed through GIS and interpretation of aerial photographs (1:15000) taken in 2000. The presence or absence of fish was determined using minnow traps with 2 traps set per 0.1 ha for 24 hrs in 15 ponds during summer 2001 and all ponds (n = 52) in summer 2002. Only one of the ponds sampled in both years changed in fish-occupancy status between years. Therefore, fish data collected in 2002 were assigned to the same ponds examined in 2001 for analyses. Finally, using GIS tools and geo-referenced, spatially-corrected aerial photographs (1:15,000) taken in 2000, I calculated percent landscape occupied by ponds within 250 m of each study pond because evidence suggest that pond population-demographics can be influenced by nearby populations for some amphibian species (Marsh and Trenham 2001, Newman and Squire 2001, Petranka et al. 2004). I also calculated percent landscape in forest cover (<250 m) for each study pond as a possible index of terrestrial habitat quality for post-metamorphic amphibians (Vesely and McComb 2002, Vasconcelos and Calhoun 2004).

Mixed-effect modelling

I used linear mixed effects (LME) models (Crawley 2002) in combination with an information-theoretic approach that ranked and weighted *a priori* models (Burnham and Andersen 2002) to assess the fixed effects of riparian canopy cover and beaver pond age on calling wood frog density under a pseudo-replicated design of beaver pond clusters on stream reaches and 2 years of population data per pond (random effect formula = ~1|stream reach/beaver pond). These models incorporated covariates such as fish occurrence to improve model fit. Pond area was included in all models because preliminary observations indicated it influenced abundance of breeding male wood frogs strongly. In contrast, percent landscape in forest cover was excluded from models because it was correlated ($r > 0.5$) with riparian canopy cover and beaver pond age (Table 5:1). Also, studies have indicated that the presence of forestry cutblocks has minimal impacts on amphibian movements and non-breeding (terrestrial stage) numbers in the western boreal forest (Constible et al. 2001, Hannon et al. 2002). I found percent riparian canopy cover and beaver pond age to be moderately correlated (Table 5:1), and therefore, created 2 sets of *a priori* models such that each of these predictors was examined separately (Table 5:2). Each set consisted of 4 models with a unique combination of habitat covariates. All covariates were also assessed in univariate models (Table 5:2). The response variable, either estimated wood frog density or calling intensity, was log-transformed to approximate normality. All relationships were examined for non-linearity's using scatter-plots (Figure 5:1). I used Akaike's Information Criterion (AIC) as a basis to select models (Burnham and Andersen 2002). The best model had the smallest AIC value (AIC_{min}). I drew primary inference from this model and others within 2 units of AIC_{min} (Burnham and Andersen 2002). I also calculated Akaike weights (w_i) to assess evidence supporting each model and to estimate the relative importance of parameters through model averaging; a robust method that reduces model selection bias (Burnham and Andersen 2002).

Characteristics of new and old beaver ponds

In a subset of ponds surveyed for calling wood frogs, I quantified variation in water chemistry parameters, and compared performance of larval wood frogs through an enclosure experiment on 5 new ponds (<10 yrs of age since damming) and 5 old ponds (>25 yrs of age since damming). One old pond and 2 new ponds were examined during 30 May-2 July 2002, and 4 old ponds and 3 new ponds were examined during 7 June-9 July 2003. The 10 experimental ponds were distributed on 7 low-order watersheds and separated by >250 m and by at least 2 intervening ponds. All experimental ponds had dams upstream of their location with the exception of two old beaver ponds receiving unobstructed headwater streams. Water chemistry parameters included pH, turbidity, dissolved organic carbon (DOC), total phosphorous (TP), total nitrogen (TN), and water column Chlorophyll *a* (phytoplankton). These were measured from a 500 ml water sample in the littoral zone on 2 collection dates (11 June and 5 July for 2002, and 13 June and 25 June for 2003) and were examined at the University of Alberta Limnology Laboratory using standard methods. For each water chemistry parameter, the average value of 2 collection dates was assigned to each pond per year for analysis. Biomass of benthic algae (periphyton) in the littoral zones were measured using 2 1-cm diameter acrylic rods planted <2 m from enclosures for 30 days (Goldsborough et al. 1986). On each rod, a 10 cm section located below the surface of the water for the entire experiment was examined for Chlorophyll *a* (µg/cm) using an ethanol extraction method and measured on a spectrophotometer. The average value of the 2 rods was calculated for analyses.

Water temperature degree-days (= average daily temperature x days of enclosure experiment) was also estimated for the 10 ponds using HOBO data loggers that recorded water temperature adjacent to enclosures and 10 cm below the pond surface every 30 min. Dissolved oxygen (DO, mg/L) was measured using a HACH field kit on 29 June and 4 July in 2002, and on 16 June and 27 June in 2003. During each date, 2 samples of water were taken during the afternoon from 2 littoral locations in each pond and assessed with an AccuVac ampul and colour comparator. One DO value was assigned to each pond as the mean of the 4 accumulated readings during the respective year. Levels of in-pond beaver activity and the relative abundance of submersed vegetation per pond were also estimated during late June 2002 and 2003 because of their possible influence on pond conditions, particularly turbidity and dissolved oxygen through photosynthesis, respectively. Beaver activity was measured as the number of runs (or paths) exiting the pond that showed exposed mud divided by the length of the entire shoreline. The submergent vegetation estimate was based on 2 sweeps taken at 10-m intervals along the pond margin in 0.3-1.0 m of water in zones lacking floating or emergent vegetation. Each sweep was made with a 4-pronged garden hoe raking 2 m in the lower water column parallel to and just above the pond bottom. The amount of vegetation was coded as 0 = none, 1 = some (1-2 individual plants), and 2 = extensive (>2 individual plants). The mean score for all sweeps on a beaver pond was then assigned to that site. Although individual species of plants were not identified or quantitatively assessed, *Potamogeton* spp. was most common.

In-pond enclosure experiment

I compared survival, growth and development of larval wood frogs stocked in 10 experimental beaver ponds using enclosures (4 per pond) under a split-plot design that included a nested and replicated (1-time) food augmentation treatment within ponds to determine whether the abiotic environment itself or the abiotic environment mediated by food resources affected larval performance in new versus old sites. Enclosures were constructed of rectangular (0.62 x 0.62 x 0.76 m) wood frames with nylon window screen on all sides. Enclosures were placed in the littoral zone with 18 L of benthic, organic matter added to each enclosure to emulate natural food conditions at the start of the experiment (6 June 2002 and 30 May 2003). Two egg masses were collected in early spring each year and held under similar environmental conditions in enclosures in one pond until larvae hatched and were free-swimming. These larvae were added to enclosures at a density of 68 per m^3 (20 per enclosure) and at mean snout-vent length = 4.6 mm ± 0.1 SE, mean mass = 0.012 mg ± 0.001 SE, and mean Gosner stage = 24.6 ± 0.03 SE. Following the onset of the experiment, quantities of Purina rabbit chow were added to food-augmented enclosures based on a feeding schedule similar to Werner and Glennemeier (1999). Specifically, I added 7 g at day 0 and 7, 10 g at day 13, and 14 g at day 19, 24, and 29. At the end of the experiment (day 32), I immediately measured mass, and larval development stage of surviving larvae. All larvae were nearing metamorphosis (Gosner stage 36-40).

Mean development rate (Gosner stage/day), growth rate (mg/day) of surviving larvae, and percent survival per enclosure in experimental ponds, and in the food-augmented and non-augmented enclosures during 2002 and 2003 were analyzed with a split-plot ANOVA (Crawley 2002, Quinn and Keough 2002). My model was larval performance = pond age x food augmentation x year + Error (beaver pond/food augmentation). Tests for skewness and kurtosis suggested that the latter two response variables required a log and arcsine transformation, respectively, to satisfy assumptions of normality for ANOVA.

Dissolved oxygen experiment

Because reduced canopy cover on older ponds might result in higher levels of submergent vegetation and photosynthesis in these sites, I compared growth (mass and SVL) and development rates of later stage larvae under low DO and high DO conditions for 11 days at the University of Alberta Aquatic Facility. Each treatment was replicated 8-times using plastic containers. Mean concentrations of DO in the low treatment = 2.81 mg/L ± 0.14 SE, and high treatment = 7.03 mg/L ± 0.1 SE, and were measured daily with a YSI Model 85 DO Meter. Concentrations of DO were regulated through use of air stones that delivered low-levels (single streams of bubbles) of atmospheric air for high DO containers and low-levels of nitrogen for low DO containers at water temperatures near 17° C. Each container held 2 larvae and 16 L of water so that the densities = 125 tadpoles per m^3. Larvae were from the same egg masses used for the in-pond enclosure study. Conditions of larvae at the start of the lab experiment were assessed by measuring a small sample (n = 15) of similar-sized larvae from the same egg masses. The measured larvae were not added to containers. These individuals had a mean SVL = 10.1 mm ± 1.1 SE, mass = 0.25 g ± 0.01 SE, and Gosner stage = 28.6 ± 0.1 SE. All containers were cleaned daily with a fine-mesh net prior to addition of food (rabbit chow at 15% body mass). At the end of the experiment (day 11), all animals were euthanized and preserved in ethanol for later measurements of size. For analyses, the average value of growth and development rates of surviving larvae per container were used to assess differences between low and high treatments with a Student's *t*-test.

Pitfall trapping

At a subset of experimental ponds (2 new beaver ponds and 2 old beaver ponds), I employed pitfall traps and drift fences covering 20% of riparian shorelines to provide an index of the rate of juvenile recruitment to metamorphosis in ponds. On each pond, 10-18 pitfall traps were placed in pairs along drift fences; each fence had 1 trap at each end. The drift fence was a polyethylene sheet 5 or 10 m long, 30 cm wide and partly buried in the soil. All fences were approximately 5 m from, and parallel to, the shoreline of each pond. The pitfall trap was a 7.6 L black plastic bucket with a plastic funnel (Stevens and Paszkowski 2005). A small quantity of moss was added to the bottom of traps to keep animals moist. A stick of 1.0 cm diameter was also added to each trap to enable small mammals to escape (Perkins and Hunter 2002). Pitfall traps were opened from 10 July-15 August in 2001 and from 15 July-19 August in 2002, and checked every 3-4 days. Captured wood frogs were marked by clipping one toe, weighed, measured and identified to age class: juveniles or young-of-year had remnants of a larval tail or SVL <27 mm, sub-adults or sexually immature individuals had an SVL = 27-40 mm, and adults an SVL >40 mm (LeClair et al. 2000, Stevens and Paszkowski, unpublished data). All anurans were released 5-10 m from their point of capture. Trapping results for wood frogs were converted to catch per unit-effort = (total captures x 100) / (trap nights x number of pitfall traps).

5:4 RESULTS

Calling wood frogs

On average, beaver ponds surveyed for calling wood frogs were relatively small ($\bar{x} = 0.18$ ha ± 0.04 SE, Table 5:1), of moderate age ($\bar{x} = 17.6$ yrs ± 1.2 SE, range = 2.5-31 yrs) with moderately intact riparian canopy cover ($\bar{x} = 24\%$ ± 2.0 SE, range = 1-53%, Table 5:1). Pearson correlation analyses of beaver pond age, pond area, percent riparian canopy cover, percent landscape in forest cover and percent landscape occupied with ponds indicated three moderate-to-high correlations at beaver ponds ($r > 0.5$): a negative correlation between pond age and both percent riparian canopy cover and percent landscape in forest cover, and a positive correlation between percent riparian canopy cover and percent landscape in forest cover (Table 5:1). Fish (brook stickleback, *Culaea inconstans*) occurred in 19 of 57 ponds.

Based on the number of male wood frogs counted in Rank 1 and 2 choruses and values assigned to Rank 3 choruses (59 individuals), male wood frogs were abundant at beaver ponds with a total of 1537 individuals estimated from 52 ponds in 2001 and 2019 estimated from 54 ponds in 2002. On average, after pooling data from both years, beaver ponds supported a mean density of 146 wood frogs per ha ± 27 SE. Regression analyses showed that the same three LME models did equally well at explaining both density and calling intensity of male wood frogs in beaver ponds: 1) riparian canopy cover with pond area as a covariate (AIC_{min}), 2) riparian canopy cover with pond area and landscape occupied by ponds as covariates, and 3) riparian canopy cover with pond area and fish occurrence as covariates (Table 5:2). These three LME models also provided strong empirical support for an effect of riparian canopy cover on wood frog density (sum of weights = 0.85) and wood frog calling intensity (sum of weights = 0.89). The model-averaged parameter estimate of riparian canopy cover and its unconditional standard error indicated a negative relation between riparian canopy cover and wood frog density (Table 3, Figure 5:1), and between riparian canopy cover and wood frog calling intensity (Table 5:3). In contrast, there was a positive relationship between beaver pond age and wood frog density (Table 5:3, Figure 5:1), and between beaver pond age and wood frog calling intensity (Table 5:3).

Larval performance

Of the suite of physicochemical variables measured at the experimental ponds, riparian canopy cover, thermal degree days, density of active beaver runs, water turbidity, abundance of submergent vegetation and concentrations of dissolved oxygen differed ($P < 0.05$) between new and old ponds based on Student's *t*-test (Table 5:4). Older ponds had fewer active beaver runs and both lower levels of turbidity and riparian canopy cover, and a higher number of thermal degree days, abundance of submergent vegetation and concentration of dissolved oxygen. In addition, concentrations of total phosphorous were 16 times higher in new ponds than in old ponds ($P = 0.064$).

Survival rates of larval wood frogs in pond enclosures were high (overall mean = 90.9%, range = 60-100%) and statistically unaffected by year (2002, 2003), pond age, and food augmentation in my split-plot ANOVAs (Figure 5:2). In contrast, larval growth rates were affected by year ($F_{1,6} = 11.4$, $P = 0.014$), pond age ($F_{1,6} = 14.1$, $P = 0.009$) and food addition ($F_{1,6} = 48.5$, $P < 0.001$). Larval growth rates were 16.6% higher in 2002 than 2003, 21% higher in older ponds, and 20.9% higher in enclosures that received rabbit chow compared to non-augmented enclosures (Figure 5:2). Similarly, larval development rates were affected by year ($F_{1,6} = 20.6$, $P = 0.004$), pond age ($F_{1,6} = 10.7$, $P = 0.017$), and food addition ($F_{1,6} = 19.3$, $P = 0.005$). Development rates were 13.8% faster in 2002 than 2003, 11.5% higher in older ponds, and 4.2% higher in enclosures with added food compared to those without. There appeared to be no interaction among treatments in larval performance ($P > 0.10$).

For the laboratory experiment, larval wood frogs in containers had an overall survival rate = 84%. Four of the five larvae that died were in two containers in the low DO treatment on day 4 (possibly because of faulty valves that created toxic levels of N_2 and turbulence). Growth rates, but not development rates of surviving larvae were influenced significantly by dissolved oxygen concentrations (*t*-test, $P < 0.05$, Figure 5:3).

Larvae reared in the high dissolved oxygen treatment were heavier (23%) than those reared in the low dissolved oxygen treatment ($t_{12} = 2.87$, $P = 0.014$).

Post-metamorphic wood frogs

Pitfall traps captured a total of 2024 juveniles, 24 sub-adults and 60 adults at two new beaver ponds and two old beaver ponds during approximately 35 days in summer 2001 and 2002. There were no recaptures during my study. Based on mean catch per unit-effort (CPUE), pitfall traps at ponds pooled from 2001 and 2002 combined, yielded considerably more juvenile wood frogs at old ponds (55.31 CPUE ± 11.63 SE) than at new ponds (6.58 CPUE ± 3.93 SE) but similar number of sub-adults at old ponds (0.44 CPUE ± 0.06 SE) as at new ponds (0.43 CPUE ± 0.23 SE). Slightly more adult wood frogs were captured at old ponds (1.22 CPUE ± 0.24 SE) versus new ponds (0.82 CPUE ± 0.26 SE) (Figure 5:4). On average, the estimated rate of juvenile recruitment to metamorphosis was higher in old ponds (55.3 juveniles per adult captured) versus new ponds (8 juveniles per adult captured).

5:5 DISCUSSION

My study describes breeding distributions and larval environments for an anuran amphibian on beaver-obstructed streams in a boreal ecosystem, and builds on amphibian research heavily biased towards lower latitudes in North America (but see Herreid and Kinney 1966, 1967, Roberts and Lewin 1979, Leclair et al. 2000, Constible et al. 2001, Hannon et al. 2002). Results for breeding populations measured using multiple call-surveys (Nelson and Graves 2004, Stevens and Paszkowski 2004) showed that older beaver ponds supported more wood frogs. Larval growth and development rates in experimental enclosures were also higher in old ponds (>25 yrs) versus new ponds (<10 yrs), and likely due to pond succession, mediated by beaver foraging and possibly flooding of riparian zones due to beaver activity, that resulted in reduced canopy cover on older ponds. Pitfall trapping, which provided an index of juvenile recruitment to metamorphosis, suggested that older beaver ponds offer high-quality breeding habitats and were potential population sources (Gill 1978).

Inertia and habitat selection

I propose that larger breeding populations of wood frogs occurred on older beaver ponds in my study primarily through selection by breeding adults for conditions, such as warm water, that are an outcome of an open canopy around ponds. Riparian canopy cover was strongly and negatively related to wood frog densities, and this relation was considerably stronger than the one between pond age and wood frog densities. Inertia may also influence the size of breeding population at a pond through site fidelity and the cumulative effects of previous years of colonization and successful reproduction (Gill 1978). Although strong philopatric behaviour might enhance inertia effects, the wood frog populations in my study probably exhibit weak site fidelity as suggested by the small increases in wood frog numbers on older ponds in Figure 5:1. In addition, beaver ponds may be too temporary and short in duration (beaver ponds = 10-25 yrs, Gill 1978) for northern populations of wood frogs that reach sexual maturity slowly (>5 yrs; LeClair et al. 2000). Thus, the chance that the same pond is standing for breeders from the third generation associated with that pond is small. My results also confirm genetic research showing that wood frog populations have inherent tendencies to disperse from their pond of origin (Newman and Squire 2002, but for a contrary view see Berven and Grudzien 1990). The network of streams linked to beaver ponds may facilitate dispersal of wood frogs by offering relatively intact forest canopies and appropriate microclimates for foraging and summer refugia (Seburn et al. 1997, Vasconcelos and Calhoun 2004). Although I did not observe wood frogs breeding in unobstructed streams, trapping results indicated that juvenile and adult wood frogs commonly used streamside terrestrial habitat (Stevens et al. 2005).

Even if the wood frog in my study exhibited strong site fidelity I may be unable to detect strong effects of inertia on population sizes because the age of ponds examined in my study spanned only 33 yrs versus 100 yrs in Gill (1978). Pitfall trapping on newly formed ponds in my study suggested low juvenile recruitment for these ponds, and therefore inertia would not affect sizes of breeding populations until pond conditions improved and sufficient years had elapsed for offspring to return as breeding adults. However, more accurate estimates of recruitment using data from egg counts and drift fences that completely surround ponds are needed to confirm low juvenile recruitment patterns on new ponds. My method of using 10 sets of archival aerial photographs between 1969 and 2000 to estimate pond age may also result in poor detection of inertia-effects because these photographs do not reveal temporary periods of pond collapse and pond instability that could have reduced past juvenile recruitment, and thus affected sizes of breeding populations recorded at ponds during my study.

Results from my call surveys revealed a strong relation between riparian canopy cover and the size of breeding populations of wood frogs at beaver ponds. Similarly, Skelly et al. (1999) examined species turnover at temporary ponds in a successional north-temperate forest (540 ha forest reserve) in Michigan, USA, and found that two-thirds of the populations present at open-canopy ponds during 1967-1974 were absent or extirpated on the same ponds that were under closed canopies by 1988-1992. However, none of the 14 species monitored during the study had disappeared from the reserve, and growing evidence suggests that amphibians can choose breeding sites opportunistically (Resetarits and Wilbur 1989, Hopey and Petranka 1994) and that populations can shift from one site to another in response to the condition of the pond (Petranka et al. 2004). Female treefrogs (*Hyla chrysoscelis*) and wood frogs are known to avoid ponds experimentally stocked with fish capable of consuming larval amphibians (Resetarits and Wilbur 1989, Hopey and Petranka 1994). Similarly, wood frogs in Pennsylvania select warmer sites for oviposition compared with adjacent cooler areas within ponds (Seale 1982). Results from my study showed that increased densities of wood frogs in old versus new ponds coincided with significant differences in water physicochemistry. Old ponds were warmer, less turbid and contained higher concentrations of dissolved oxygen than their newly formed counterparts. Thus, the ability to choose a breeding pond may be an important mechanism affecting population sizes of boreal anurans and this mechanism may be responsive to variations in the structure of overhead canopy (Werner and Glennemeier 1999, Skelly et al. 2002) and the effect of beaver foraging on pond-side vegetation (Donkor and Fryxell 1999, Barnes and Mallik 2001).

Larval performance

Our mesocosm-based field experiment demonstrated that wood frog larvae grew and developed faster in old versus new beaver ponds, possibly because older ponds had, on average, 71% less riparian canopy cover contributing to a 3 C increase in water temperature. These trends are comparable to 84% less canopy cover and 5 C warmer temperatures in a study of closed versus open canopy ponds in the Yale-Myers Forest, Connecticut (Skelly et al. 2002). Better larval performance in older beaver ponds in our study also coincided with considerably more submergent vegetation and twice the concentrations of dissolved oxygen, and less in-pond beaver activity resulting in less turbid water in old sites. I caution, however, that observed differences in physicochemistry between pond age classes could be a result of alternative explanations such as landscape position of ponds. On average, stream order was smaller for old ponds ($\bar{x} = 1.6 \pm 0.4$ SE) versus new ponds ($\bar{x} = 2.4 \pm 0.24$ SE) (C. E. Stevens and C. A. Paszkowski, unpublished data), and may affect water temperatures through the pond morphometry it creates after flooding. Older ponds were also in landscapes with less forest cover (Table 1), possibly due to a combination of tree-felling by beaver, forestry cutblocks, roads and oil well clearings, resulting in warmer water temperatures of in-flowing streams (Johnson and Jones 2000, Melina et al. 2002). However, groundwater in-flows and the absence of beaver ponds upstream of two old ponds holding enclosures (see methods) may moderate their responses to nearby human activities (Melina et al. 2002). Higher turbidity levels in new ponds could also be a result of nearby human activities, although their influence on water turbidity may be minimal as newer ponds occurred in landscapes with more forest cover. It is unclear why old and new beaver ponds had similar levels of periphyton and water column Chlorophyll *a* despite open canopy conditions on old ponds that can result in higher within-pond rates of primary production (see Skelly et al. 2002). One possibility is that high phosphorous levels in new beaver ponds increased primary production and offset decreased growth associated with receiving less light (Bayley and Prather 2003). Regardless, the lack of interaction between treatments (food augmentation and pond age) suggested that food was not more limiting in new ponds compared to old ponds and that abiotic conditions were the primary determinants of larval performance.

It is well known that elevated temperature can enhance performance of larval amphibians by facilitating enzyme reactions and increasing metabolic rates (Herreid and Kinney 1967, Noland and Ultsch 1981). I expect that the higher water temperatures in old ponds increased wood frog development and growth as has been suggested previously (also see Herreid and Kinney 1967). My results from a laboratory microcosm experiment also showed that larval wood frogs reared in high concentrations of dissolved oxygen attained larger mass than those reared in low concentrations of dissolved oxygen (Figure 5:3). Similarly, larvae reared in mesocosms within old ponds that supported moderately high levels of dissolved oxygen exceeded that in new ponds that contained substantially lower levels of dissolved oxygen (Table 5:4). Taken together, my results suggest that differences in dissolved oxygen could contribute to observed variance in the performance of larval wood frogs. While the underlying mechanisms are not well understood, concentrations of dissolved oxygen below 4 mg/L, similar to levels measured in new beaver ponds, have been shown to increase bobbing rates of larval leopard frogs (*R. pipiens*) with developing lungs (Gosner stage 37-43, Wassersug and Seibert 1975). Thus, the ability to sustain normal aerobic metabolism through the skin and gills may be compromised by nearly hypoxic conditions that could either, slow growth directly or reduce energy allocations to growth because of increased energetic demands of swimming near the surface to obtain sufficient oxygen.

Similar enclosure studies in temporary ponds under open and closed canopies from eastern North America suggest that differences in dissolved oxygen and water temperatures play a large role in the performance of larvae for other populations of the wood frog, and also for larvae of the leopard frog, American toad (*Bufo americanus*) and spring peeper (*Pseudacris crucifer*) (Werner and Glennemeier 1999, Skelly et al. 2002). However, the relative effect of varying food quality on larval performance in natural ponds remains inconclusive. A wide variety of algal and benthic resources can occur in wetlands and ponds, and their relative importance for larval development is poorly understood (but see Kupferberg et al. 1994, Skelly and Golon 2002).

Conclusions and management implications

My study was one of the first to investigate the ecology of a boreal anuran in beaver ponds. Specifically, I found that changes to the riparian canopy, possibly through beaver herbivory, strongly affected sizes of breeding populations at beaver ponds, and we propose that wood frogs select older beaver ponds for rearing larvae. Older beaver ponds may be good breeding habitats because these sites provided larvae with warm and highly oxygenated environments that, according to the literature and results from our experiments, can enhance development and growth rates (Herreid and Kinney 1967, Noland and Ultsch 1981). Faster development and growth of larvae may, in turn, increase the overall production of newly metamorphosed juveniles through reduced exposure to aquatic predators in older ponds (Wilbur 1980, Smith 1983). Enhancing the longevity of beaver colonies and the occurrence of old ponds on the landscape may ensure source habitats for amphibians and the persistence of amphibian metapopulations. This may be achieved through the protection of beaver food items from forestry activities, such as large stems of *Populus* spp. in riparian zones (Donkor and Fryxell 1999, Barnes and Mallik 2001). The development of management plans based on the habitat needs of beaver may thus aid in the conservation of boreal amphibians.

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Table 5:1. Mean (SE) and Pearson correlation matrix for habitat and landscape characteristics of beaver ponds sampled for wood frog populations during 2001 and 2002 in west-central Alberta.

	Mean (SE)	Range	Pond age	Pond area	Canopy cover	Land. in forest cover
Pond age (yrs)	17.6 (1.18)	2.5–31	--	--	--	--
Pond area (ha)	0.18 (0.04)	0.01–1.48	0.16	--	--	--
% Riparian canopy cover	23.8 (1.97)	0.88–53.3	-0.56^{***}	-0.27^{*}	--	--
% Landscape^{+} in forest cover	77.5 (1.63)	50.5–94.5	-0.78^{***}	-0.17	0.63^{***}	--
% Landscape^{+} occupied by ponds	7.0 (0.83)	0.13–32.5	0.082	0.29^{*}	-0.26	-0.35^{**}

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*Significant at alpha = 0.05; **Significant at alpha = 0.01; ***Significant at alpha = 0.001

$^{+}$areas within 250 m of study ponds

Note: Characteristics were based on 57 ponds, 49 of which were stable and similar in area between 2001 and 2002, 1 pond from 2001 collapsed to a much smaller size in 2002, and 4 ponds from 2001 merged to 2 ponds in 2002.

Table 5:2. Akaike's Information Criterion (AIC) ranking of a *priori* mixed-effect models consisting of pond age or riparian canopy cover with covariates explaining variation in density of calling wood frogs and calling intensity in beaver ponds in west-central Alberta.

	Density of Males				**Calling Intensity**			
	LL	AIC	Δ AIC	w_i*	*LL*	AIC	Δ AIC	w_i*
Univariate Models								
Pond age	-128.2	266.4	16	0	41.24	-72.5	24.2	0
Riparian canopy cover	-122.8	255.5	5.1	0.03	46.9	-83.8	12.9	0
Area	-130.1	270.3	19.9	0	47.24	-84.5	12.2	0
Fish occurrence	-132.8	275.6	25.2	0	38.36	-66.7	30	0
% landscape occupied by ponds	-133	276.1	25.7	0	38.16	-66.3	30.4	0
Pond Age Models								
& Area	-125.1	262.2	11.8	0	49.84	-87.7	9	0
& Area, fish occurrence	-124.4	262.8	12.4	0	50.36	-86.7	10	0
& Area, % landscape occupied by ponds	-125.1	264.1	13.7	0	49.94	-85.9	10.8	0
& Area, fish occurrence, % landscape occupied by ponds	-124.3	264.6	14.2	0	50.49	-85	11.7	0
Canopy Cover Models								
& Area	-119.2	250.4	0	0.42	54.34	-96.7	0	0.45
& Area, fish occurrence	-119.1	252.3	1.9	0.16	54.41	-94.8	1.9	0.18
& Area, % landscape occupied by ponds	-118.6	251.3	0.9	0.27	54.79	-95.6	1.1	0.26
& Area, fish occurrence, % landscape occupied by ponds	-118.6	253.1	2.7	0.11	54.87	-93.7	2.9	0.10

*Akaike weight: probability that the current model (i) is the best model among those considered.

Table 5:3. Coefficient estimates and 95% CI for habitat variables from linear mixed effects models explaining variation in the log-transformed density of calling wood frogs and calling intensity in beaver ponds in west-central Alberta.

	Density of Males		**Calling Intensity**	
Covariate	Coefficient estimate[+]	95% CI	Coefficient estimate[+]	95% CI
% Riparian canopy cover	-0.036	-0.05 to -0.019*	-0.062[++]	-0.095 to -0.028*
Pond age	0.036	0.007 to 0.065*	0.065[++]	0.004 to 0.126*
Pond area	1.15	0.291 to 2.018*	0.3	0.14 to 0.46*
Fish occurrence	-0.088	-0.58 to 0.405	-0.019	-0.117 to 0.08
% Landscape occupied by ponds	-0.018	-0.056 to 0.019	-0.003	-0.011 to 0.005

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*CI does not include zero.

[+] Based on model averaging and AIC weights (see Table 5:2).

[++] Change per 10 units.

Table 5:4. Comparisons of mean (SE) physical-chemical features in new (<10 yrs) and old (>25 yrs) beaver ponds that held enclosures for larval wood frogs in 2002 and 2003.

Environmental parameters	New (n = 5)		Old (n = 5)		t_8	P
Physical						
Canopy cover (%)	35.7	(2.9)	10.4	(3.3)	3.09	0.015*
Pond area (ha)	0.16	(0.04)	0.4	(0.14)	-1.17	0.276
Submergent vegetation index (0-2)	0.02	(0.02)	1.45	(0.19)	-14.6	<0.001*
Active beaver runs (#/km)	247	(30.6)	132	(23.2)	2.44	0.041*
Chemical						
Conductivity (µmhos/cm)	319	(50.2)	272	(39.5)	0.763	0.467
Dissolved organic carbon (mg/L)	21.6	(2.1)	21.3	(2.1)	0.087	0.933
Dissolved oxygen (mg/L)	4.9	(0.9)	10.5	(0.6)	-3.84	<0.005*
Periphyton chlorophyll *a* (µg/cm)	0.09	(0.03)	0.05	(0.01)	1.78	0.113
pH	7.6	(0.14)	7.8	(0.09)	-1.03	0.335
Total nitrogen (µg/L)	987	(158)	923	(60.3)	0.109	0.916
Total phosphorous (µg/L)	112	(14.5)	69.8	(11)	2.15	0.064**
Turbidity (NTU)	13.5	(3.9)	3.2	(0.9)	3.62	0.007*
Water colour (mg/L Pt)	124	(22.3)	105	(19.1)	0.496	0.633
Water column chlorophyll *a* (µg/L)	4.7	(2.0)	6.0	(1.49)	-0.944	0.373
Water temperature (degree days)$^{+}$	752	(22.7)	850	(19.8)	-3.26	0.012*

*Significant at alpha = 0.05, **Significant at alpha = 0.10

$^{+}$Calculated for duration of enclosure experiment

Note: *P*-values reflect differences between pond age classes for log-transformed parameters in a *t*-test.

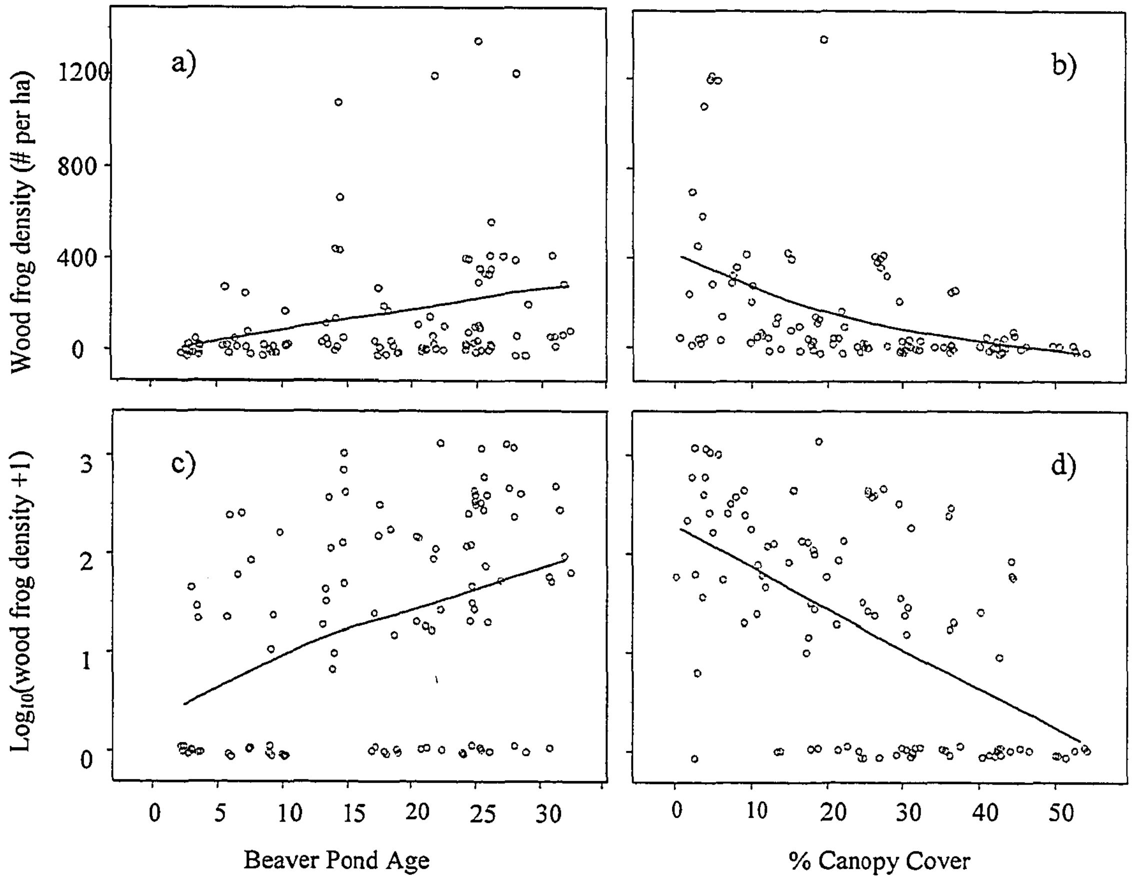

Figure 5:1. Scatter plots fit with spline smoothers (3 df in SPLUS) for beaver pond age (a, c) and percent riparian canopy (b, d) against non-transformed (a, b) and log10 transformed (c, d) indices of breeding wood frog density per pond (106 observations pooled from all beaver ponds surveyed during 2001 and 2002). Density estimates for each pond were based on the maximum number of calling males (with values for Rank 3 choruses assigned 59 males) recorded from 3 survey periods in May of each year.

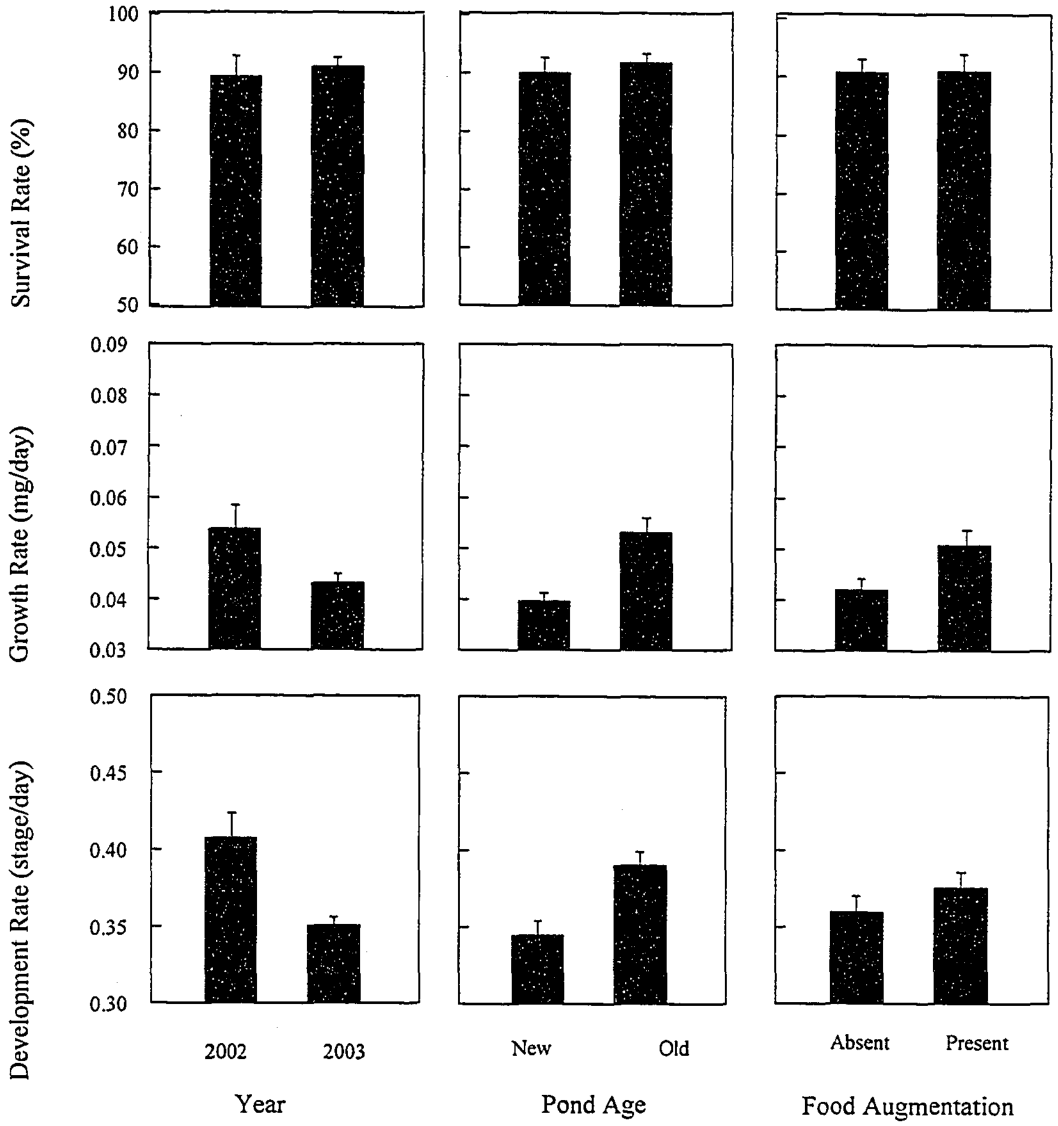

Figure 5:2. Mean ± SE survival (%), growth rate (mg/day) and development rate (Gosner stage/day) of larval wood frogs in 2002 and 2003, with and without food augmentation in 40 enclosures in 5 new (<10 yrs) and 5 old (>25 yrs) beaver ponds. The food augmentation treatment was nested and replicated once within ponds.

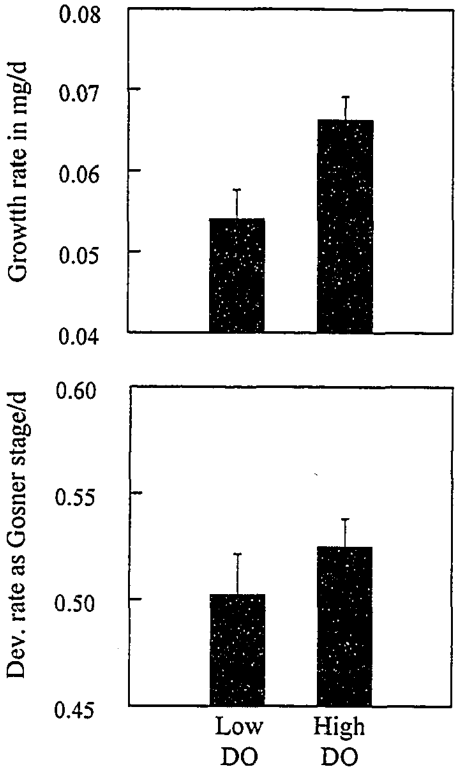

Figure 5:3. Mean ± SE growth rate (mg/day) and development rate (Gosner stage/day) of larval wood frogs held in 6 containers with low dissolved oxygen (DO) and in 8 containers with high DO containers for 11 days under laboratory conditions. Concentrations of DO in the low treatment = 2.7 mg/L and high treatment = 7.0 mg/L.

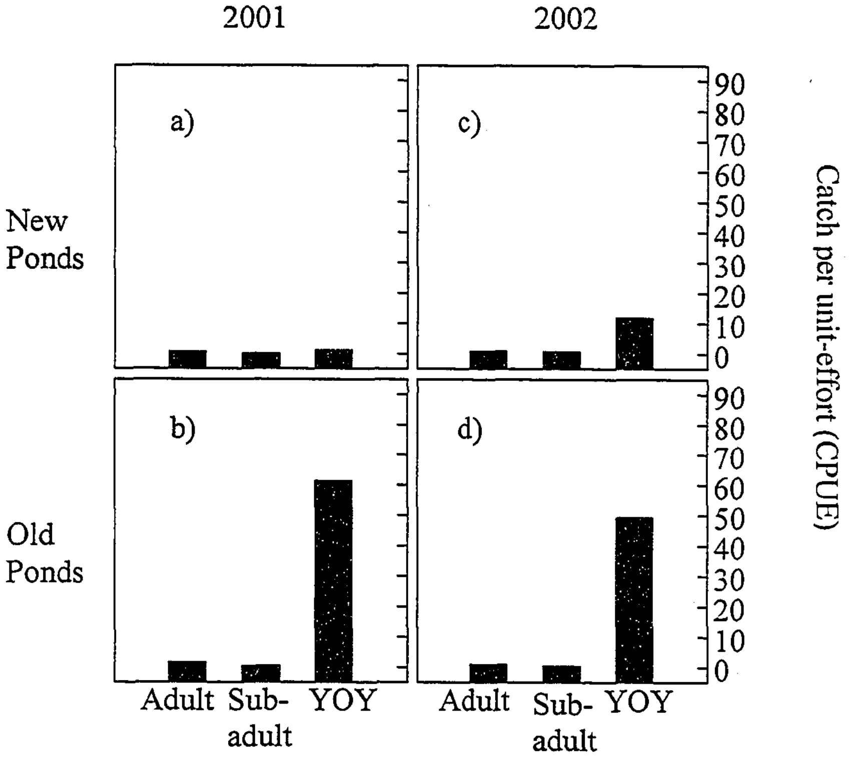

Figure 5:4. Wood frogs (adults, sub-adults and YOY) captured with pitfall traps and drift fences on 2 new and 2 old beaver ponds measured as mean catch per unit-effort = (total captures x 100) / (trap nights x number of pitfall traps) for 2001 (a, b) and 2002 (c, d). Trapping periods were 10 July-15 August in 2001 and 15 July-19 August in 2002.

Chapter 6. Status of the Western Toad and its Use of 'Borrow Pits' in the Foothills of West-Central Alberta*

Abstract.—Populations of western toad (*Bufo boreas*) have declined or disappeared from much of the species' southern range in the U.S. To assess distributions and densities of the western toad in the foothills of west-central Alberta, Canada, I conducted visual surveys of 130 natural waterbodies in watersheds of the Pembina and North Saskatchewan Rivers in early and late summer 2000. Encounter rates were consistently low throughout the study area (0.2-0.3 toads/hr), one-tenth the rate for the co-occurring wood frog (*Rana sylvatica*), and nearly one-third the value reported in the literature for a toad population in south-western British Columbia during the late 1970s. Large-scale pitfall trapping of breeding and non-breeding sites during 2001 and 2002 showed differing age structures between wood frog and western toad populations, and that recruitment of newly metamorphosed juveniles in western toad populations was low. On potential breeding ponds, more age-1+ toads were captured than young-of-year toads, and the difference in numbers between age classes was greater on 'borrow pits' (human-created roadside ponds) compared to beaver ponds indicating that borrow pits might be population sinks providing poor larval habitat. Borrow pits had either dried prior to juvenile emergence or had oligotrophic to mesotrophic waters compared to eutrophic states in beaver ponds. Pond creation as a management strategy or product of road construction may put western toad populations at risk of decline in the foothills of Alberta.

6:1 INTRODUCTION

Since the late 1980s there have been numerous accounts of declining and disappearing amphibian population and species in various parts of the globe (for example, Alford and Richards 1999; Houlahan and others 2000; Green 2003; Stuart and

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*Under review as Stevens et al. (2005) in Northwestern Naturalist (submitted June 27, 2005) others 2004). Stuart and others (2004) contend that amphibian species are more threatened and are declining more rapidly than either bird or mammal species. In western North America, one of the most threatened species of amphibian is the western toad (*Bufo boreas*), which has been red-listed by the IUCN (Hammerson and others 2004). Populations have declined or disappeared in many regions of the species' southern range in the U.S., including the southern Rocky Mountains (Carey 1993; Livo and Yeakely 1997; Corn 2000), and California's Sierra Nevada and Central Valley (Drost and Fellers 1996; Fisher and Shaffer 1996). Declines have been linked to disease, such as chytridiomycosis (Muths and others 2003), UV radiation (reviewed in Blaustein and others 1998, but see Licht 2003, Corn and Muths 2004) and synergistic effects of UV radiation with pathogens and climate change on developing embryos and larvae (Kiesecker and others 2001). However, the ecology and status of the western toad throughout much of the northern portion of its range in western Canada is relatively unknown with the exception of reported declines on southern Vancouver Island in British Columbia (Davis and Gregory 2003), and a possible (easterly) range expansion in central Alberta (Eaton and others 1999).

Habitat degradation or alteration (for example, draining of wetlands, forest fragmentation) is a major cause of amphibian declines (Blaustein and others 1994; Wake 1998; Alford and Richards 1999; Semlitsch 2002; Corn 2000). In British Columbia and Alberta, forested regions have become increasingly disturbed and fragmented by agriculture, logging, energy extraction and roads associated with such activities. A common practise during road-building is dredging of adjacent land for gravel and soils to raise roads above wet areas. The resulting 'borrow pit' often fills with water attracting breeding anuran amphibians (Bunnell and Zampella 1999; Graham 2002). There are numerous anecdotal accounts of amphibians using ditches or dugouts as breeding habitat; however, few studies have determined whether anthropogenic ponds are population sinks or sources (habitats with low or high rates of juvenile recruitment; see DiMauro and Hunter 2002). Such assessments are relevant to projects that create wetlands, a practice in compensatory mitigation that is often poorly monitored (Lichko and Calhoun 2003).

The first objective of the present study was to assess the status of the western toad in the foothills of the Rocky Mountains in west-central Alberta by comparing visual encounter rates with: 1) rates reported for an apparently 'healthy' (non-declining) population in British Columbia; and 2) rates for a widespread co-occurring anuran (*Rana sylvatica*) that has generally healthy populations throughout Canada and northern United States. My second objective was to describe the size distribution and age structure of a peripheral population of the western toad (Russell and Bauer 2000) in a landscape under high-use by forestry and energy sectors, and to compare juvenile recruitment of western toads and wood frogs captured with pitfall traps on borrow pits versus naturally occurring ponds. Mechanisms underlying trends were examined through a comparison of physiochemical parameters (e.g., hydroperiod, primary production) between the two pond types.

6:2 METHODS

My study was conducted in the foothills (Boreal-Cordilleran Ecoregion) of west-central Alberta (Figure 6:1). The North Saskatchewan River bordered the southern and eastern range of my study area which extended northward to the Pembina River and westward to the Rocky Mountains. At lower elevations (lower foothills; 500-1150 m), the Boreal Foothills supports a forest dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* Voss), and lodgepole pine (*Pinus contorta* Dougl.) (Beckingham and others 1996). At higher elevations (upper foothills; 900-1500 m), the forest is dominated by conifers with lodgepole pine being the most prevalent species. The climate throughout the region is relatively dry (total annual precipitation = 464-538 mm). Mean temperature May through August at lower elevations = 12.8°C, and at higher elevations = 11.5°C.

Visual Surveys & Toad Status

To describe the distribution and status of western toad relative to wood frog in my study area, I conducted visual surveys of 130 natural aquatic habitats in four regions: 1) Marshy Bank Ecological Reserve, a relatively pristine watershed of the Cardinal River in the upper foothills; 2) Nordegg, a large area that encompasses watersheds of Nordegg River, Blackstone River, and Shunda Creek with moderate levels of forestry and energy activity; 3) Dismal Creek, a mid-point between the upper and lower foothills in the Pembina River watershed with moderate amounts of industrial activity; and 4) Lodgepole, a region of low-order watersheds flowing to the North Saskatchewan and

Pembina River, which is under intense land-use by energy and forestry sectors. For example, these industries have built over 240 km of roads to drill 446 oil and gas wells and to harvest trees from approximately 10% of the Lodgepole region (14 548 ha; Stevens and others 2005). Aquatic habitats included low-order unobstructed streams (n = 51), small lakes and ponds (1-10 ha; n = 14), oxbows on higher-order stream (n = 11), beaver ponds (beaver-obstructed streams; n = 36), seasonal marshes (wetlands dominated by emergent vegetation cover; n = 7) and peatlands (bryophyte-dominated wetlands with no open water; n = 11). A greater number of stream-linked habitats was sampled than other types because the rolling topography created a landscape dominated by networks of low-to-moderate gradient streams (first to fourth order) with numerous beaver ponds, but relatively few basin wetlands or ponds (Stevens and others 2005). At each site, two 200-meter transects were installed along shorelines using flagging tape. Transects in a pair were adjacent and parallel to one another, and on opposing shorelines for streams and lakes, or separated by 10-25 m when on peatland.

Along transects, visual surveys (Crump and Scott 1994) were conducted during an early summer period (23 June-27 July, 2000) and late summer period (28 July-1 September, 2000) to determine site occupancy and encounter rates for the western toad and wood frog. The majority of habitats were sampled during both these periods (n = 93). Early and late summer dates (approximately) reflect periods before and after the emergence of newly metamorphosed individuals. Surveys were conducted between the hours of 1000 hr and 1900 hr, and during relatively good weather (>15°C). During a survey, one observer would slowly search the ground or shoreline edge using a search radius of 1.5 m for the length of the 200 m transect. On average ($s_{\bar{x}}$), a survey of a pair of transects on a site lasted for 0.76 (0.02) hrs per one person. I assumed detection probabilities were high (>0.70) for both the wood frog and western toad as observed in other studies (Corn and others 2004). Dip-nets assisted with capturing amphibians and identifying individuals to species.

Pitfall Trapping & Toad Recruitment

In 2001 near Lodgepole, AB (Figure 6:1), I first documented the age structure of the western toad and wood frog associated with non-breeding sites (unobstructed stream reaches and temporary wetlands), and breeding sites (ponds) combined using pitfall traps and drift fences (Table 6:1). Sites were classified as 'non-breeding' or 'breeding' depending on whether a calling anuran was recorded on that site during multiple visits in spring of the trapping year (see methods described in Stevens and others 2005). In 2001 and 2002, I also examined juvenile recruitment to metamorphosis for anuran species on beaver ponds and borrow pits (Table 6:1). Study sites were distributed among 10 spatial clusters (or blocks) on a 200 km^2 landscape. Sites within a cluster were within 50-900 m of other sites in that cluster, whereas sites from different clusters were >1 km from one another. Nine of the 10 clusters included 1-4 beaver ponds, one unobstructed stream reach and 1-2 temporary wetlands or borrow pits; the tenth cluster consisted of three beaver ponds and one borrow pit only. In 2001, pitfall traps were opened on 15 beaver ponds, nine unobstructed stream reaches, six borrow pits and five temporary wetlands from 10 July–15 August. In 2002, I closed pitfall traps on unobstructed stream reaches and temporary wetlands and focused trapping efforts on 21 beaver ponds and five borrow pits from 15 July -19 August.

Pitfall traps (Stevens and Paszkowski 2005) were 7.6 L plastic buckets fitted with plastic funnels; installed in pairs along drift fences such that one trap was placed at each end of a fence. The drift fence was a polyethylene sheet 5 or 10 m long, 30 cm high, partly buried in the soil and installed 3-7 m from water but parallel to a shoreline edge or unobstructed stream. Approximately 20% of the shoreline associated with each pond or wetland (area range = 65-7250 m^2) and unobstructed stream (200 m reach) had an adjacent drift fence to capture amphibians. Beaver ponds had 6-20 pitfall traps per site, temporary ponds had 4-12 traps, borrow pits had 6-20 traps, and all unobstructed stream reaches had 16 traps per site. Traps were checked every 2-5 days. Captured anurans were marked by clipping one toe, weighed and measured for snout-vent length (SVL) and identified to age class. Individuals were identified as young-of-year (YOY or juvenile) if they had remnants of a larval tail or were smaller than the largest individual with a tail bud: SVL <27 mm for the wood frog, and SVL <23 mm for the western toad. For age-1+ amphibian, I classified captured individuals as adults versus sub-adults if they were larger than the smallest recorded sexually mature male for that species: wood frog = 40 mm and western toad = 45 mm. Wood frogs were mature males if they had swollen thumbs (n = 135) and western toads were mature males if they elicited a release call when pressure was applied under forelimbs ($n = 85$). All anurans were released 5-10 m from their point of capture. For presentation of results, trapping data were converted to catch per unit-effort (CPUE) = (total captures x 100 days)/ (trap nights x number of pitfall traps).

Abundance of post-metamorphic western toad and wood frog (both young-of-year and age-1+ individuals) was compared between pond types and study years with linear mixed-effect (LME) models in SPLUS (Crawley 2002). Abundance was measured as log10-transformed CPUE in the model, which included habitat type (0 = borrow pit, 1 = beaver pond), age (0 = young-of-year, 1 = age-1+) and year (0 = 2001, 1 = 2002). The cluster or random effects included both landscape location and study site to account for potential spatial and temporal autocorrelation among the measured response. Quality of fit of the model was assessed by visually assessing plots of standardized residuals against fitted values.

Pond Characteristics

To investigate potential mechanisms underlying habitat-use patterns of western toad, I measured physiochemical characteristics of the beaver ponds and borrow pits sampled for amphibians with pitfall traps. First, aerial photographs (1: 15,000-40,000 scale, 11 sets between 1959 and 2000) were used to estimate age of beaver ponds and borrow pits, calculated as the midpoint of the age of the earliest photograph where a pond was absent and the age of the next temporal sequence of photographs where the pond was present. Five of six borrow pits were approximately 38-yrs old (created between 1959 and 1969). The sixth borrow pit was approximately 27.5-yrs old (created between 1973 and 1976). As a correlate of pond temperature and primary production (Skelly and others 2002), riparian canopy cover adjacent to ponds was estimated using a spherical densiometer after trees leafed out for all ponds in late spring 2002. The mean of measurements taken at four cardinal directions at 10-m intervals along the pond margin was assigned to each pond. Pond area was estimated using marked distances on each pond (flagging tape every 10 m along the perimeter). There were no obvious changes in riparian canopy structure or area of ponds between 2001 and 2002. In early June of 2001, multiple depth measurements were taken every 10 m from the centre of ponds and streams. Percent open water was visually estimated for all sites during this time. All ponds were assessed as dry or not dry in early July of each year prior to the emergence of young-of-year. The presence or absence of predatory fish was determined using minnow traps with two traps set per 0.1 ha for 24 hrs in all ponds during summer 2001 and 2002.

Water chemistry parameters included standard measurements of conductivity and pH, as well as those that attenuate solar radiation: water turbidity, water colour, and dissolved organic carbon (DOC) (Palen and others 2002). Both total phosphorous (TP) and water column chlorophyll-*a* (phytoplankton) were measured as indicators of primary production and trophic state of ponds (Kalff 2002). All parameters were measured from a 500 ml water sample in the littoral zone collected on two dates at the study ponds (22 July 2001 and 5 July 2002) and were analyzed at the University of Alberta Limnology Laboratory. The relative abundance of submersed vegetation was also estimated during late June 2002 because of its possible influence on pond conditions, including habitat structure and dissolved oxygen through photosynthesis. This estimate was based on two sweeps taken at 10 m intervals along the pond margin. Each sweep was made by raking a 4-pronged garden hoe for 2 m in the lower water column parallel to and just above the pond bottom. All samples were taken in 0.3-1.0 m of water and in zones lacking floating or emergent aquatic vegetation. The amount of vegetation was coded as 0 = none, 1 = some (1-2 stems), and 2 = extensive (>2 stems). The mean score for all sweeps on a pond was then assigned to that site.

Habitat variables were compared on beaver ponds versus borrow pits with t-tests on log10 transformed pond age, area, canopy cover, % open water, and pond depths; whereas mean values of water chemistry parameters and the submergent vegetation index were fit with 90% confidence intervals on beaver ponds and borrow pits because two of the six borrow pits were dry in early July of each year leaving my study design with a small sample size for statistical tests. I accepted significance at the 5% level for all tests.

6:3 RESULTS

Toad Status

During summer 2000, 222 visual surveys of 130 aquatic sites in west-central Alberta resulted in records for a total of 582 anuran amphibians. Of these amphibians, 44 were western toads representing a small fraction of observations (8%) compared to 524 wood frogs (90% of observations). The remaining 2% of observations were of boreal chorus frogs (14 individuals). Approximately 174 hours of visual surveys recorded 0.3

western toads/hr and 3 wood frogs/hr. Western toad and wood frog occurrence rates on sites surveyed during the early summer period ($n = 120$) were: western toad = 13% sites occupied, and wood frog = 63% sites occupied. Occurrence rates for sites surveyed again during the late summer period ($n = 102$) were lower for both the western toad (8%) and wood frog (60%).

Based on presence-absence data from the early and late summer surveys combined, the site occurrence of western toad was slightly higher on sites in Dismal Creek (23%) compared to sites in Lodgepole (17%), Marshy Bank (14%) and Nordegg (11%). The rate of encounter for western toad during visual surveys was also relatively similar among the four study areas (0.2-0.3 toads/hr) (Figure 6:1). In addition, site occurrence rates of western toad among surveyed habitat types were low. The western toad most commonly occurred on beaver ponds (25% occurrence), followed by oxbows and peatland (both 18%), unobstructed streams (12%), pond or small lake (7%) and marsh habitat (0%). In contrast to the western toad, wood frog encounter rates were higher in lower versus upper foothill locations (Figure 6:1); wood frog occurrence was highest on sites in Lodgepole (94%), moderately high in Dismal Creek (69%) and Nordegg (67%), and lowest on sites in Marshy Bank (14%). During the summer, wood frog occurrence appeared to be associated with standing water representing typical breeding sites (pond or small lake = 86%, beaver pond = 83% and oxbow = 82%) rather than non-breeding habitats (unobstructed streams = 51% and peatland = 55%).

Toad Recruitment

Pitfall trapping recorded 4179 wood frogs and 186 western toads on breeding and non-breeding aquatic habitats with an effort of 19662 trap days from July 11-August 15, 2001. Of wood frog captures, 5% were classified as breeding adults, 5% were sub-adults, and 90% were identified as young-of-year; whereas for the western toad, 46% of those captured were adults, 24% were sub-adults and 30% were young-of-year (Figure 6:2). The number of captures per age category was significantly dependent on species according to a Pearson chi-squared test ($X^2 = 599$, $P < 0.001$). There were no recaptures of western toads and few recaptures of wood frogs: 2 adults and 11 young-of-year. The mean SVL of age-1+ wood frogs was 39.4 mm (maximum = 63.5) and of age-1+ western toads was 52.7 mm (maximum = 82).

On potential breeding sites, western toads were recorded on 94% of beaver ponds and 50% of borrow pits surveyed in 2001, and on 100% of beaver ponds and borrow pits surveyed in 2002. Wood frogs were recorded on all beaver ponds and borrow pits during both study years. My mixed-effect model indicated that for western toad, CPUE was higher for age-1+ versus YOY toads, and related to both the interacting effects of pond type and age class, and of study year and age class ($P < 0.05$; Table 6:2). A simple plot of pond type against CPUE suggests that the number of captured age-1+ toads was much greater than captured YOY toads on borrow pits, but only marginally greater than YOY toads on beaver ponds (Figure 6:3). In 2002, the number of captured age-1+ toads greatly exceeded YOY toads, whereas in 2001, there were similar levels of abundances between age classes (Figure 6:3). In contrast to the western toad, CPUE of wood frogs was higher for YOY than for age-1+ individuals ($P < 0.05$; Table 6:2, Figure 6:3). There was also a non-significant trend of an overall higher CPUE of wood frogs on beaver ponds than on borrow pits ($P = 0.084$; Table 6:2, Figure 6:3). CPUE of wood frogs was unrelated to study year ($P > 0.05$; Table 6:2).

Pond Characteristics

In my study, borrow pits and beaver ponds had similar areas, levels of canopy cover and percent open water ($P > 0.05$) but differed in pond age and water depth (Table 6:3). Borrow pits were significantly older and shallower than beaver ponds ($P < 0.05$). As noted, two of the six borrow pits were dry by early July of each study year. Based on the remaining study ponds, concentrations of chlorophyll-*a* were considerably lower on borrow pits than beaver ponds in 2001, and on average, 2-6 times lower in borrow pits during my study. Reduced concentrations of total phosphorous were also noted on borrow pits versus beaver ponds in 2001 and 2002 (Table 6:3). On average, borrow pits had oligotrophic to mesotrophic states (mean TP = 26.8 µg/L; mean chlorophyll *a* = 3.4 µg/L) whereas beaver ponds had eutrophic waters (mean TP = 100.5 µg/L; mean chlorophyll *a* = 11.5 µg/L) (Kalff 2002). Water clarity also varied across pond types (Table 6:3). Compared to beaver ponds, borrow pits had lower levels of DOC (in 2001 only) and turbidity (in 2001 and 2002); however, water colour was similar between beaver ponds and borrow pits during both study years. Fish were not observed in borrow pits whereas brook stickleback (*Culaea inconstans*) were recorded in 6 of 15 beaver ponds in 2001 and again in the same ponds the following year. Conductivity (overall range = 105-804 µS/cm) and pH levels (overall range = 6.6-10.3) in both beaver ponds and borrow pits were indicative of freshwater conditions and neutral to slightly basic water during the study (Table 6:3) (Kalff 2002).

6:4 DISCUSSION

My visual surveys suggested that the western toad occurs at low densities relative to the wood frog in the foothills of west-central Alberta, and that the low site occupancy rates that I documented are comparable to those of contemporary populations in the southern Rocky Mountains (Corn and others 2004), and further north in Jasper National Park, Canada (Stringer 2004). In contrast, western toads were relatively common on southern Vancouver Island in the late 1970s, and encountered 2-3 times more often during visual surveys than in my study (Davis and Gregory 2003). Populations have since been extirpated on that part of Vancouver Island, possibly because of habitat loss and fragmentation (for similar cases see Corn 2000; Semlitsch 2002) or disease such as *Saprolegnia* spp. introduced through stocking of rainbow trout (*Oncorhynchus mykiss*) (Kiesecker and Blaustein 1997). Stocking of ponds and lakes is also common practice throughout Alberta including the Nordegg region of my study area (Nelson and Paetz 1992), but to my knowledge, there have been no reported population declines of western toads or adverse effects of stocking on their populations in the province. However, there is a paucity of long-term data on western toads in Alberta so it is difficult to say whether my encounter rates are lower than historical values. I suggest that populations of western toads are naturally both small in size and sparsely distributed in west-central Alberta because my surveys showed consistently low visual encounter and site occupancy rates throughout a large section of the foothills encompassing watersheds of the Pembina and North Saskatchewan Rivers and both an ecological reserve that was relatively remote and pristine, and a landscape under intense use by industry.

Large-scale trapping efforts on breeding and non-breeding habitats near Lodgepole, AB showed that populations of western toad were not only smaller in size than that of wood frog but that they may be structured differently with relatively few newly metamorphosed individuals and sub-adults in the population. Varying age structures could be an artefact of sampling biases and partial fencing of ponds that missed toad movements in streams (Adams and others 2005) or aggregations of emerging juvenile toads in riparian zones (Black and Black 1969). However, during three years of pitfall trapping in my study area, no visual observations of western toads in ponds or streams were made outside of the breeding season, and only one observation of a large group of newly metamorphosed toads was made adjacent to a pond by C. E. Stevens. Although varying age structures between species could reflect differences in survivorship of young-of-year to adulthood, I propose that toad populations in the foothills are characterized by lower rates of juvenile recruitment than wood frog populations. Few young-of-year toads were captured relative to adult toads even though potential recruitment was high. For example, up to 20000 eggs have been observed in a string deposited by a female toad (Maxell and others 2002) compared to 1000 eggs in a mass deposited by a female wood frog (C. E. Stevens, personal observation). Even if I consider the fact that more cohorts may be in the adult age category for the western toad than for the wood frog because they are generally longer-lived amphibians (for example, 8 vs. 5 yrs; C. A. Paszkowski, unpublished data), my results still show the western toad was unsuccessful at breeding when the wood frog was successful. Varying rates of juvenile recruitment between species also coincided with observed differences in anuran densities (also see Beebee and others 1996) and site occurrence rates indicating that western toad occurred at low densities and on few sites surveyed in the foothills possibly because of low rates of juvenile recruitment in ponds.

Beaver ponds are the predominant pond type in the study area and are used extensively by breeding wood frog and occasionally by breeding western toad (this study, also see Stevens and others 2005), however, many beaver ponds are relatively deep ($\bar{x}$ = 1.5 m), and small (<1.5 ha) with high canopy cover (up to 50%), and possibly avoided by western toads because of poor larval conditions such as cold water temperatures (Noland and Ultsch 1981; Banks and Beebee 1988). Borrow pits being an alternative pond type on the landscape are on average shallower than beaver ponds, and possibly attractive to a breeding toad as a warmer site for developing embryos and larvae. In addition, western toads may select borrow pits for their relatively clear water allowing embryos to obtain higher levels of solar radiation and faster development rates. The ability of anurans to choose a breeding pond among available sites based on environment is well documented

(Seale 1982; Hopey and Petranka 1994). For example, wood frog in Pennsylvania select warmer sites within ponds for oviposition compared with adjacent cooler areas (Seale 1982). Why the western toad and not wood frog was more abundant on borrow pits than on beaver ponds is unclear but could reflect varying selection strengths for shallow or clear water between species.

Unfortunately, whatever the cue might be that attracts western toad to a particular pond may be disadvantageous for developing embryos and larvae in borrow pits. Pitfall trapping captured more age-1+ individuals than young-of-year on the study ponds, and the difference between the two age classes was greater on borrow pits compared to beaver ponds suggesting that borrow pits were particularly poor larval environments. The fact that two of the six borrow pits had short hydroperiods and dried prior to emergence partly explains why I recorded few young-of-year on these sites. Others have noted early pond drying and extensive larval mortality in anthropogenic ponds formed during industrial forest-management activities (Dimauro and Hunter 2002). However, of the two borrow pits that dried early in my study, calling western toads were heard on one pond during 2001 only (C. E. Stevens, personal observation) suggesting that borrow pits were not always sinks because adults had a tendency to avoid shallow sites. In contrast, C. E. Stevens observed calling toads on the four borrow pits with longer hydroperiods during each study year even though these sites had lower levels of primary production than beaver ponds, and oligotrophic states that may limit available algal-food resources for developing larvae (also see Banks and Beebee 1988). Borrow pits also had clearer water that can result in increased levels of UV-B radiation and higher mortality rates for exposed embryos (Blaustein and others 1998; Kiesecker and others 2001). However, DOC concentrations in borrow pits (near 10 mg/L) should attenuate all damaging levels of UV-B at water depths where western toads deposit their eggs (Morris and others 1995; Palen and others 2002).

In summary, I found that western toad populations occur at low densities and at few waterbodies in the foothills of west-central Alberta, and that juvenile recruitment to metamorphosis is either inherently low in western toad populations or is low because of poor conditions for larval development in breeding ponds currently available in the region. Consistent with the notion that species with high potential for increase (*r*) exhibit yearly fluctuations in population size (for example, Green 2003), I recorded yearly fluctuations in juvenile recruitment for the western toad but not the wood frog. Adult toads encountered on ponds in my study may be a product of at least one previous year of high juvenile recruitment and that such reproductive events may be sufficient to maintain the persistence of local populations. However, the creation of borrow pits might negatively impact populations of western toad in the foothills by creating attractive breeding sites for adult toads but unfavourable environments for developing larvae and embryos resulting in a potential population sink (also see Dimauro and Hunter 2002). I recommend additional research with adequate representation of borrow pits in the foothills to examine whether they are indeed ecological traps for amphibians and that resource managers and engineers should avoid constructed ponds or at least create them at depths and in soil types that maintain adequate hydroperiods and nutrients.

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Table 6:1. Mean value ($s_{\bar{x}}$) of habitat characteristics for beaver ponds, borrow pits, temporary wetlands and unobstructed streams surveyed for amphibians in the foothills of west-central Alberta. *P*-values were based on a *t*-test and reflect habitat differences between beaver ponds and borrow pits only.

	Potential breeding habitat†				Non-breeding habitat†	
	Beaver pond, $n = 21$	Borrow pit, $n = 6$	t_{25}	P	Temporary wetland, $n = 5$	Unobstructed stream, $n = 9$
Area (m^2)	2091 (492)	1355 (569)	1.17	0.253	1933 (590.9)	NA*
Pond age (yrs)	17 (2)	26 (2)	-2.89	0.008	NA	NA
% Canopy cover	21.8 (2.8)	37.3 (8.3)	-1.28	0.213	51.7 (5.6)	NA**
% Open water	69 (6.7)	53 (12.5)	0.286	0.777	0 (0)	100 (0)
Max. depth (cm)	146 (10)	56 (17)	5.95	<0.001	15.8 (5.5)‡	39.2 (6.5)

NA = not available

* Mean ($s_{\bar{x}}$) stream order = 2.3 (0.4)

**Intact riparian zones unaffected by beaver

†Breeding status determined using call surveys (Stevens and others 2005)

‡All temporary wetlands were dry by July 7 of each study year

Table 6:2. Results from a linear mixed-effect model predicting log10-transformed catch per unit-effort (CPUE) of western toad and wood frog on breeding ponds near Lodgepole, AB. The model included habitat type (0 = borrow pit, 1 = beaver pond), age (0 = YOY, 1 = age-1+), year (0 = 2001, 1 = 2002), and random effects (i.e., landscape location and study site), which accounted for potential spatial and temporal autocorrelation among the measured response.

Species	Covariate	df	*t*-value	*P*-value
Western toad	Habitat type	16	-0.132	0.897
	Age class	62	5.41	<0.001
	Study year	62	-0.5908	0.557
	Habitat *x* age	62	-2.831	0.006
	Age *x* study year	62	2.971	0.004
Wood frog	Habitat type	16	1.841	0.084
	Age class	64	-5.713	<0.001
	Study year	64	0.0663	0.947

Note: Non-significant interactions were dropped from final models.

Table 6:3. Mean values (90% CI's) of habitat features including water chemistry and submergent vegetation on beaver ponds and borrow pits in the foothills of west-central Alberta. Water samples were taken on 20 July 2001 and 5 July 2002 and analysed using standard methods. The submergent vegetation index was based on sweeps with a garden hoe in late June 2002 and a ranking of vegetation levels (i.e., 0, 1, and 2).

2001	Beaver pond ($n = 14$)	Borrow pits ($n = 4$)
Total phosphorous (µg/L)	96.2 (67.8, 124)*	20.2 (16.9, 23.4)*
Chlorophyll-*a* (µg/L)	14.77 (5.75, 23.8)*	2.33 (0.8 , 3.86)*
Dissolved organic carbon (mg/L)	17 (15.1, 18.9)*	9.8 (4.8, 14.8)*
Water colour (mg/L Pt)	84.2 (65.1, 103)	114 (-48.2, 275)
Turbidity (NTU)	7.12 (4.57, 9.67)*	2.48 (2.36, 2.59)*
Conductivity(µS/cm)	343 (272, 414)	200 (82, 317)
pH	8.13 (7.91, 8.35)*	9.23 (8.38, 10.1)*
2002	Beaver pond ($n = 21$)	Borrow pits ($n = 4$)
Total phosphorous (µg/L)	103 (78.6, 129)*	33.5 (1, 66)*
Chlorophyll-*a* (µg/L)	9.35 (5.2, 13.5)	4.38 (-0.98, 9.74)
Dissolved organic carbon (mg/L)	20.3 (18.7, 21.9)	13.4 (-0.19, 26.9)
Water colour (mg/L Pt)	104 (86.8, 122)	37.9 (-13.3, 89.1)
Turbidity (NTU)	10.2 (6.49. 13.8)*	2.5 (-0.8, 5.8)*
Conductivity(µS/cm)	325 (270, 379)	303 (34.3, 573)
pH	7.5 (7.4, 7.7)†	8.6 (7.4, 9.7)
Submergent vegetation index	0.91 (0.66, 1.18)	1.21 (0.25, 2.19)

*non-overlapping 90% confidence intervals between pond types

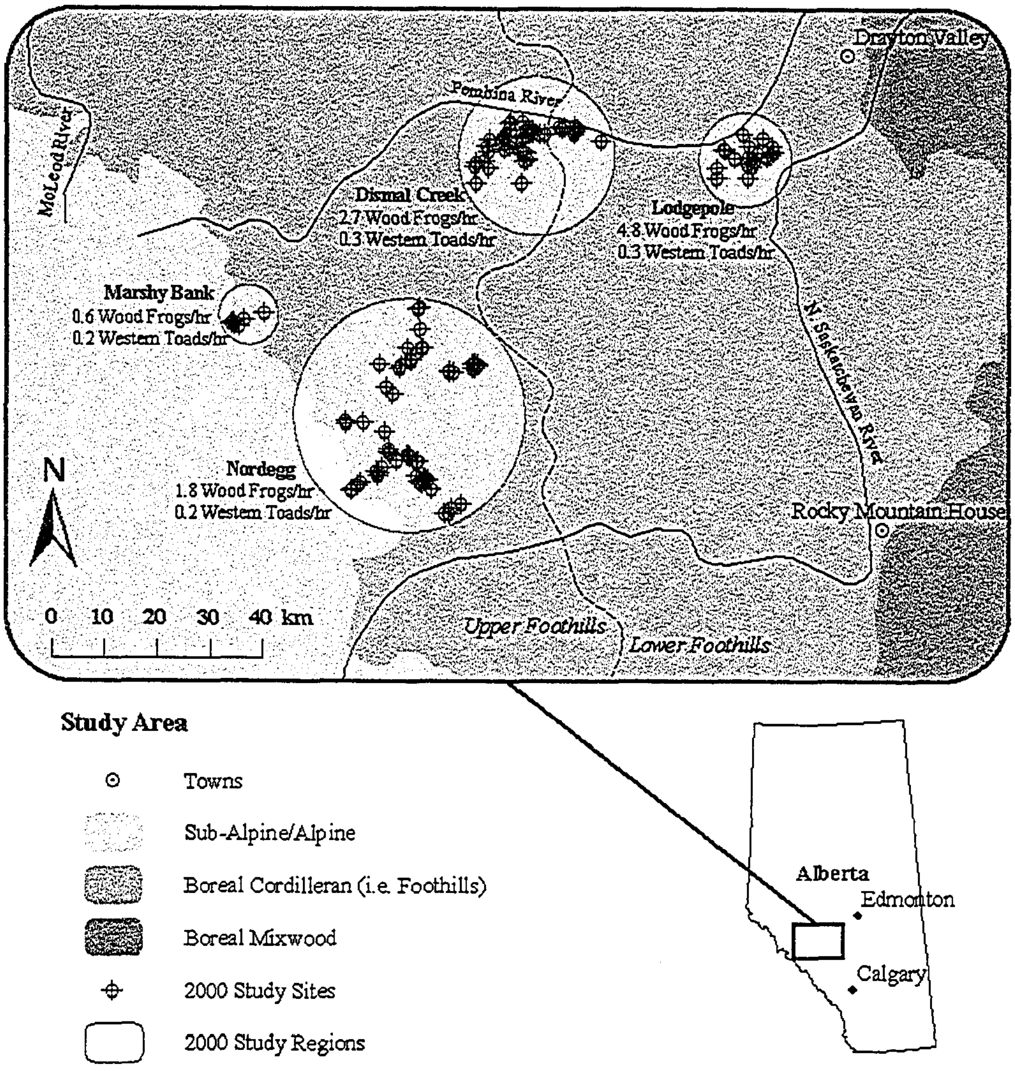

Figure 6:1. Study regions (Marshy Bank, Nordegg, Dismal Creek and Lodgepole) and aquatic sites (n = 130) that were assessed for the presence of western toad and wood frog with visual surveys in the foothills (Boreal Cordilleran eco-region) of west-central Alberta. Most sites were sampled twice; once during an early summer period and again during the late summer of 2000. In total, 174 hrs of surveys recorded 524 wood frogs and 44 western toads.

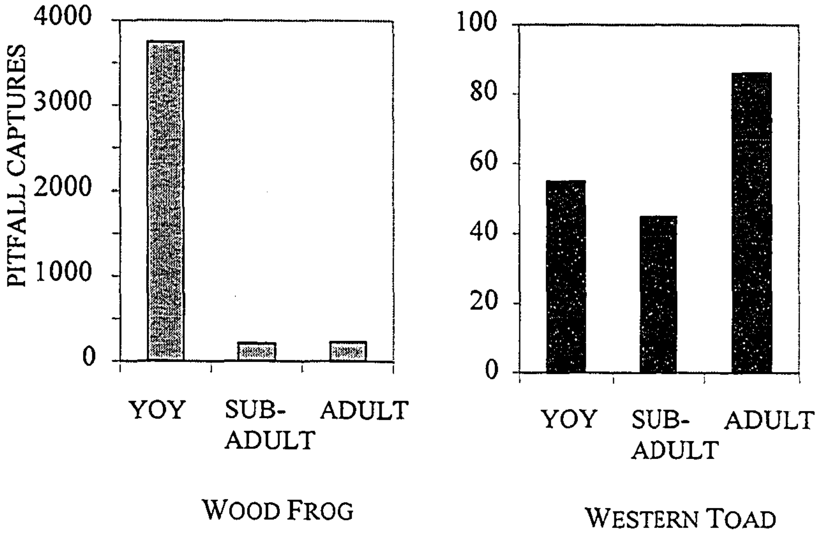

Figure 6:2. Total pitfall captures for wood frog and western toad on beaver ponds (n = 15), borrow pits and temporary wetlands (n = 11) and unobstructed streams (n = 9) near Lodgepole, AB (approximately 200 km^2 study area) in the Boreal Foothills. Total effort = 19 662 trap days from 11 July 2001 to 15 August 2001. See text for classification of age categories.

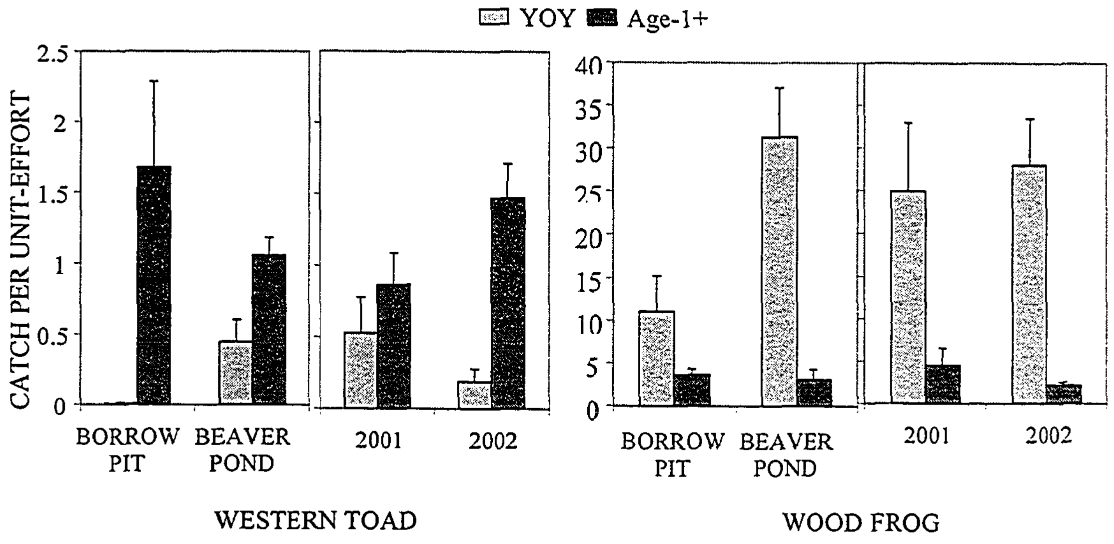

Figure 6:3. Mean (s$\bar{x}$) catch per-unit effort (CPUE per 100 days) of young-of-year (YOY) versus age-1+ western toad and wood frog on 15 beaver ponds and six borrow pits (roadside ponds created by humans) in 2001, and on 21 beaver ponds and four borrow pits in 2002. Trapping dates were 11 July to 15 August in 2001, and 15 July to 19 August in 2002. See methods for classification of young-of-year (YOY) and age-1+ amphibians.

Chapter 7. General Conclusion

My thesis represents scientific contributions to the field of ecology and amphibian biology by addressing technical, ecological and conservation-based questions at multiple scales and in laboratory and field settings. The ecological information on boreal amphibians within my thesis can be used as part of conservation strategies to maintain biodiversity in Alberta and boreal ecosystems of North America. In brief, I design an effective technique to trap boreal anurans and show that data collected from anuran call surveys can be a good indicator of reproductive success (Chapters 2-3). I propose that beaver be part of a surrogate species approach for amphibian conservation (Chapter 4) and that succession of beaver ponds contribute to natural fluctuations in amphibian populations on boreal streams (Chapter 5). I also suggest that the status of the western toad in the foothills of west-central Alberta is comparable to other populations in the Rockies but that human created ponds (i.e., borrow pits) may put the western toad at risk in the Boreal Foothills (Chapter 6). Chapters 2-6, and the results within, advance our knowledge of amphibian ecology and conservation biology because they provide new information on amphibian population dynamics and their use of beaver ponds (but see Gill 1978, Russell et al. 1998), and habitats in the boreal forest. The ecology of amphibians in the boreal forest is a particularly understudied field in the literature (but see Herreid and Kinney 1966, 1967, Roberts and Lewin 1979, Leclair et al. 2000, Constible et al. 2001, Hannon et al. 2002).

Amphibian use of beaver ponds

Beaver are ecological engineers that change the physicochemical properties of streams through dam construction (Naiman et al. 1986, Naiman et al. 1988, Snodgrass and Meffe 1998, Schlosser and Kallemyn 2000), and can therefore influence local populations and communities of fishes (Snodgrass and Meffe 1998, Schlosser and Kallemyn 2000) and birds (Brown et al. 1996, McCall et al. 1996) because of these changes. In Chapter 4, results from call surveys suggest that beaver damming on small streams may increase populations of the wood frog, boreal chorus frog and western toad in the Boreal Foothills of Alberta through creation of breeding habitat (also see Chapter

3). Russell et al. (1998) found that more post-metamorphic anurans occur in riparian zones on beaver ponds versus unobstructed streams in North Carolina, USA. Also in Chapter 4, my results from pitfall trapping show that the wood frog and boreal chorus frog had high rates of juvenile recruitment on beaver ponds (i.e., young-of-year outnumbered adults) possibly because the study sites, which were on 1^{st}-3^{rd} order streams, infrequently contained predatory fish (i.e., 28% of ponds surveyed), and the only species present was the small-bodied brook stickleback (*Culaea inconstans*). Beaver ponds were also characterized by a relatively stable seasonal hydroperiod: only one pond (of 54) surveyed for calling anurans disappeared due to dam collapse during the larval period in 2 years of study (Chapter 4; also see Gill 1978, Schlosser and Kallemyn 2000).

As noted in Chapters 2 and 4, very few newly metamorphosed toads were captured in pitfall traps due to either shortcomings in sampling techniques or the larval environment in beaver ponds studied in 2001-2003. Partial fencing of ponds could have missed toad movements in streams (Adams and others 2005) or large aggregations of emerging juvenile western toads in riparian zones (Black and Black 1969). However, during 3 years of pitfall trapping in my study area, no visual observations of western toads in ponds or streams were made outside of the breeding season, and only one observation of a large group of newly metamorphosed toads was made adjacent to a pond. A more likely explanation for low number of captures may be that my study design and sample size was ineffective at measuring toad populations because this species occurs at relatively low densities and few sites in the Boreal Foothills (Chapter 6). Although beaver ponds may be poor environments producing few juvenile toads, the fact that this species occurs in an eco-region where beaver ponds are the predominant breeding habitat suggests that at the very least some ponds are population sources within the region (Chapter 4 and 5).

Chapter 5 is, to my knowledge, the first study to describe the distribution and abundance of a boreal anuran on beaver ponds and addressed whether succession of stream ponds mediated by beaver damming and foraging in riparian zones could contribute to changes in amphibian populations. Estimates of breeding populations indicated that beaver pond age was positively correlated with wood frog densities. I propose that larger breeding populations occurred on older sites primarily through selection by breeding adults for open canopy pond conditions (e.g., warm water) because riparian canopy cover was strongly and negatively related to wood frog densities, and that this relation was considerably stronger than the direct relationship between pond age and wood frog densities. I may have been unable to detect a strong effect of pond age (i.e., evidence for population inertia) because the variation in pond age that I could examine in my landscape was too short (33 yrs). In addition, low rates of juvenile recruitment were recorded on newly formed ponds (<10 yrs), which may have resulted in few offspring returning as breeding adults until pond conditions improved. Results in Chapter 5 show that increased densities of wood frogs in old versus new ponds coincided with reduced canopy cover and significant differences in water physicochemistry. Older ponds had lower levels of riparian canopy cover and increased water temperatures, and more submergent vegetation in less turbid water and higher concentrations of dissolved oxygen. In addition, my mesocosm-based field experiment demonstrated that wood frog larvae grew and developed faster in old (<10 yr) versus new (>25 yr) beaver ponds. Thus, in choosing a breeding pond, frogs may be responding to variations in the structure of overhead canopy (1-53%) that affect larval performance (also see Resetarits and Wilbur 1989, Hopey and Petranka 1994).

My mesocosm experiment also suggests that food was not more limiting in new ponds compared to old ponds and that abiotic conditions were the primary determinants of larval performance. I expect that the higher water temperatures in old ponds increased wood frog development and growth as has been suggested previously (Herreid and Kinney 1967, Noland and Ultsch 1981). In addition, results from a short-term laboratory experiment in Chapter 5 suggest that differences in dissolved oxygen could also contribute to observed variance in the performance of larval wood frogs between pond age classes. The ability to sustain normal aerobic metabolism through the skin and gills may be compromised by near hypoxic conditions in new ponds thus directly slowing growth or reducing energy allocations to growth because of increased energetic demands of swimming near the surface to obtain sufficient oxygen (Wassersug and Seibert 1975, Noland and Ultsch 1981). Thus, wood frog select older beaver ponds for rearing larvae because these sites provide larvae with warm and well-oxygenated environments that, according to the literature and results from my experiments, can enhance development and growth rates. This, in turn, may have increased the overall production of newly metamorphosed juveniles in older ponds by reducing exposure to predatory invertebrates (e.g., Smith 1983, Berven 1990).

Conservation of boreal amphibians

Results from Chapter 4 indicate that beaver may serve as a surrogate species aiding amphibian conservation. Specifically, the presence of beaver may be a good indicator of the presence of anuran amphibian populations on boreal streams because breeding wood frog, boreal chorus frog and western toad were recorded only in association with beaver dams (also see Russell et al. 1998). The presence of beaver on small streams was easily monitored through delineation of beaver ponds with aerial photography (also see Slough and Sadleir 1977, Howard and Larson 1985, Johnston and Naiman 1990). The beaver also has a particularly large role in maintaining amphibian populations in the Boreal Foothills of Alberta since the majority of standing water on the landscape was created by beaver flooding of small streams (94% of total area of standing water in 1997). Interestingly, observations of aerial photographs prior to 1960 suggest that beaver ponds were scarce on the study landscape, if at all present suggesting that populations of anuran amphibians in the boreal foothills may have undergone dramatic changes in size over time, and that present numbers of beaver ponds may be indicative of a successful recovery of amphibians from near extirpation. Thus, detailed examination of temporal changes in the abundance of beaver ponds will be considered for future publication of material related to Chapter 4.

To maintain or promote breeding habitat for amphibians in regions such as the Boreal Foothills, forestry planning should incorporate landscape-use patterns of beaver. In Chapter 4, I found that the probability of beaver pond occurrence was positively associated with elevation (also see Sun et al. 2000), and also with intermediate levels of stream flow. Consistent with the latter hydrological relationship, a New England study identified wide, slow-moving streams as beaver habitat (Howard and Larson 1985), whereas a study in the Boreal Shield characterized beaver habitat as small, fast-moving streams (Barnes and Mallik 1997). I also found that beaver pond occurrence on stream was negatively related to nearby cutblocks. Future publication of Chapter 4 will reconsider the definition of forestry cutblocks by using young cutblocks only (<67 yrs) versus all historical cutblocks in the habitat models. Such an analysis may show stronger relationships between beaver pond occurrence on streams and proximity to nearby cutblocks.

Also in Chapter 4, I propose that forestry activities that alter stand composition and age have the potential to impact beaver foraging and the persistence of colonies and associated amphibian populations, particularly on low-order streams. Not only are ponds on low-order streams potentially better breeding sites than those on high-order streams because of lower abundance and diversity of predatory fish on these sites (Vannote et al. 1980, Snodgrass and Meffe 1998), these habitats also receive no, or minimal, riparian buffers from logging (i.e., prescribed zones of uncut trees adjacent to a water body that are the sole remnant of older-aged stands; Lee et al. 2004). To reduce forestry impacts on beaver and amphibian populations, I recommend buffer widths of 20 m around established beaver ponds to maintain food supplies within distances travelled by foraging beaver (Johnston and Naiman 1990, Donkor and Fryxell 1999, Barnes and Mallik 2001) and wider buffers on potential pond sites that account for flooding after dam establishment. I also recommend that forest managers use maps that identify existing beaver ponds, as well as future potential sites of ponds from predictive spatial models.

Although Chapter 4 suggests that beaver create breeding habitat for western toad, breeding densities were relative low on beaver-obstructed streams (12 males/km) compared to the wood frog (702 males/km) and boreal chorus frog (195 males/km). These results warranted further investigation of the regional status of the western toad, particularly because this species has been red-listed by the IUCN (*Bufo boreas*; Hammerson et al. 2004). In addition, the ecology and status of the western toad throughout much of the northern portion of its range in western Canada is relatively unknown with the exception of reported declines on southern Vancouver Island in British Columbia (Davis and Gregory 2003), and a possible (easterly) range expansion in central Alberta (Eaton et al. 1999). In Chapter 6, I suggest that populations of the western toad are naturally both small in size and sparsely distributed in west-central Alberta because my surveys show consistently low visual encounter and site o ccupancy rates throughout a large section of the foothills encompassing watersheds of the Pembina and North Saskatchewan Rivers, and both an ecological reserve that was relatively remote and pristine, and a landscape under intense land-use by industry. My pitfall trapping data suggests that the creation of borrow pits as a product of road construction in industrial landscapes might negatively impact populations of western toads in the foothills by creating attractive breeding sites for adult toads but unfavourable environments for developing larvae and embryos resulting in a potential population sink and regional decline in numbers (Chapter 6; also see Dimauro and Hunter 2002).

Future research

Although there are many ecological topics, hypotheses and arguments presented in Chapters 2-6 that require testing and additional research, some should have higher priority because of current information gaps and their relevance to the conservation of amphibians in Alberta. For example, I recommend additional baseline research on the ecology of the western toad (IUCN red-listed species; Hammerson et al. 2004) in the Alberta foothills and Canadian Rocky Mountains, including more work on beaver ponds predicting patterns of occurrence with new mixed-modelling tools (Allen and Weale 2005). The effectiveness of call surveys in estimating the abundance of breeding western toads on a pond also requires additional testing as some populations in the Rocky Mountains do not call when breeding (Conant and Collins 1998). Research on factors that limit population sizes and questions related to site fidelity and dispersal might also shed light on why the western toad is susceptible to decline in some regions and not others (Green 2003).

A second area worthy of future work is on inertia as a mechanism underlying population size of species that are associated with temporarily dynamic habitats such as beaver ponds. Gill (1978) was the first to propose such a hypothesis in the amphibian literature. Specifically, he suggested that older ponds supported larger populations of breeding newts in the Shenandoah Mountains, Virginia, USA because of homing behaviour (i.e., efts colonized ponds every year, survived to reproductive maturity and faithfully returned to the same pond to breed year after year). Unfortunately, site fidelity characteristics of boreal species are largely unknown and few researchers have addressed inertia mechanics in amphibian ecology even though it may be a useful concept in measuring the success of restoration or habitat mitigation projects (see Petranka et al. 2003).

I recommend more work on amphibians and beaver ponds related to the GIS results in Chapter 4. For example, the finding that beaver select wide, slow-moving streams or small, fast-moving streams for pond creation due to their intermediate level of flow (also see Howard and Larson 1985, Barnes and Mallik 1997) has implications for amphibian populations if assemblages containing predatory fish species occur more commonly on ponds associated with higher-order streams (Snodgrass and Meffe 1998). The observation that beaver pond occurrence was negatively related to nearby cutblocks also requires additional mechanistic study because of the lack of research on forestry impacts on beaver.

Summary

Worldwide, amphibians are more threatened and are declining more rapidly than either birds or mammals: 32% of amphibian species, 12% of birds, and 23% of mammals (Stuart et al. 2004). The problem is complex and there is no easy solution (e.g., Collins and Storfor 2003). My research will contribute to an increased ability to detect declines, elucidate underlying mechanisms of population fluctuations, and build on our capacity to manage and conserve amphibian populations. Given that industrial activity continues to expand in Alberta and the Boreal Forest, conservation biologists and wildlife managers are challenged by the goal of preventing amphibian declines observed in other regions of the world. We also face a lack of conservation remedies for a large number of amphibian declines (48% of those globally threatened; Stuart et al. 2004). These species will inevitably go extinct if mechanisms underlying their declines are not quickly understood. The integrity and general health of many ecosystems may also be irreversibly impaired if declines are part of a larger problem and indication of environmental decay (Vitt et al. 1990).

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