"In the excavation of artificial canals as a means for transporting their wood by water to their lodges, we discover, as it seems to me, the highest act of intelligence and knowledge performed by beavers."

-Lewis Henry Morgan, from *The American beaver and his works* (1868)

University of Alberta

Habitat use by the wood frog (*Lithobates sylvaticus* (LeConte, 1825)) within pothole wetlands modified by beaver (*Castor canadensis* Kuhl, 1820) in east-central Alberta

by

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Abstract

Studies of amphibian habitat use often focus on using landscape characteristics to predict occupancy at broad spatial scales, but few have investigated how amphibians use specific habitat features within a wetland, such as the distinct habitat features created by beavers. In pothole wetlands of east-central Alberta, I examined the use of beaver lodges and beaver foraging canals by wood frogs (*Lithobates sylvaticus* (LeConte, 1825)) during breeding, larval development and post-metamorphic dispersal. Early thaw near occupied beaver lodges did not lead to earlier calling in wood frogs, and neither lodges nor canals were attractive oviposition sites compared to unmodified pond margins. Larval wood frogs primarily used unmodified pond margins and beaver canals, and avoided the central open water zone of the pond. Post-metamorphic wood frogs followed canals while dispersing from their natal pond. Thus, beaver canals linked aquatic and terrestrial environments: a potentially important consideration in the design of constructed wetlands.

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Chapter I: General Introduction

Global declines of amphibian populations have been a major concern among conservationists since the late 1980s, partly because these declines are thought to be an early sign of widespread environmental degradation (e.g. wetland loss, barriers to movement between wetlands, invasive species, pathogens, pesticide contamination, etc.) (Barinaga, 1990; Alford and Richards, 1999; Houlahan *et al.*, 2000; Stuart *et al.*, 2004; Alford, 2011). Although there are many contributing factors, habitat loss is among one of the highest ranked threats to anuran amphibians (Hof *et al.*, 2011). The complex life cycle of pond-breeding anurans makes them vulnerable to the loss of terrestrial habitat, aquatic breeding habitat, or to disruption of the migratory pathways between the two (Gibbs, 1998; Lehtinen *et al.*, 1999; Fahrig, 2003; Cushman, 2006). In the prairie pothole region of North America (which includes the southern portions of Canada's Prairie Provinces), 40 to 70% of wetlands have been drained or filled in for agriculture (Whigham, 1999; Dahl, 2000; Bartzen *et al.*, 2010). Such habitat loss, along with the fungal disease chitridiomycosis, will likely continue to be a major threat to amphibians in the southern half of Alberta for at least the next 70 years, as suggested by the global risk assessment maps in Hof *et al.* (2011).

The use of ecosystem engineers, such as beavers (*Castor canadensis* Kuhl, 1820), has been suggested as a means of restoring degraded habitats (Rosemond and Anderson, 2003; Byers *et al.,* 2005); however, outcomes can be difficult to predict because the modifications beavers make to a wetland depend on the characteristics of the surrounding environment (Berkenbusch and Rowden, 2003;

Wright and Jones, 2006). Although many studies identify the habitat characteristics that can be used to predict the presence or absence of amphibian species among ponds at a landscape scale, few have investigated how amphibians use specific habitat features within a pond, and none have addressed how amphibians use the distinct, beaver-created habitat features within a pond. I argue that patterns of breeding, larval habitat use and post metamorphic dispersal of the wood frog (*Lithobates sylvaticus* (LeConte, 1825)) in pothole wetlands are profoundly affected by the distinctive habitat features created by beavers (i.e. lodges and canals).

Jones *et al.* (1994) define an ecosystem engineer as "an organism that directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials". Although beavers can increase habitat for pond-breeding amphibians in stream dominated landscapes (Cunningham *et al.*, 2006; Stevens *et al.*, 2006; Cunningham *et al.*, 2007; Stevens *et al.*, 2007; Karraker and Gibbs, 2009; but see also Hokit and Brown, 2006) there has been very little research on the response of amphibians to beaver modifications located within and adjacent to naturally occurring ponds. When beavers occupy such ponds, they might not build a dam, but often construct a lodge. In wetlands with gradually sloping banks and soft substrates (such as peat, clay, sand, and gravel), beavers also dig extensive foraging canals that radiate away from the pond (Morgan, 1868; Berry, 1923; Butler, 1991; Butler and Malanson 1994; Collen and Gibson, 2001). Although lodge building and canal digging behaviours have been well documented in the literature, there has been little research on the effects on wetland ecosystems of lodges and canals (but see Cowell, 1984; France, 1997; Bromley and Hood, 2013; Hood and Larson, *in review*).

Beavers construct a lodge by piling woody debris and mud into the shape of a rounded cone before burrowing in from underwater and hollowing out a chamber above the water level (Morgan, 1868). Lodges typically protrude about 2 m above the water's surface, are 6 to 18 m in circumference at the waterline, and can have considerable ecological effects (France, 1997). In pothole wetlands of Alberta's dry-mixed wood boreal forest, Bromley and Hood (2013) found that ponds with occupied beaver lodges began thawing earlier near the lodge compared to the rest of the pond and that these occupied lodges were attractive nesting sites for Canada geese (*Branta canadensis* L. 1758). Early thaw near lodges occupied by beavers is probably related to thin ice near these lodges, as observed by Hood and Trefry (*Unpublished data*; see also Figures A.1 and A.2, Tables A.1 through A.3, Appendix A); although the underlying mechanism of this pattern has not been determined, possible mechanisms could include the metabolic heat generated by beavers in the lodge, intentional breaking of ice by beavers, or unintentional disturbance of water and ice caused by beavers entering and exiting the lodge during the winter. In Chapter II of this thesis, I examine how the presence of beavers in a pond affects the call phenology of two spring breeding amphibians, the wood frog and the boreal chorus frog (*Pseudacris maculata* (Agassiz, 1850)) through nocturnal call surveys. In this chapter, I also examine wood frog breeding site selection in relation to beaver lodges and canals.

Beavers are central place foragers, and typically remain within 100 m of water except during dispersal (Jenkins, 1980; Fryxell and Doucet, 1991; Collen and Gibson, 2001). By digging long canals to access foraging areas, beavers are able to extend their aquatic habitat as well (Berry, 1923; Johnston and Naiman, 1987; Butler, 1994). Canals allow beavers to float branches and logs back to their lodge, and also provide a quick escape from terrestrial predators (Johnston and Naiman, 1987; Severud *et al.,* 2011). Beavers also use canals to divert water from neighbouring wetlands or the riparian zone to maintain the depth of a pond (Cowell, 1984; Butler and Malanson, 1994; Hood and Bayley, 2008). Beavers can only dig canals through relatively soft substrates such as clay or sand, and only if the banks of the pond are shallow in slope. Although canals are usually less than 1.5 m wide, they can extend for several hundred metres in length (Butler, 1991; Collen and Gibson, 2001). In Montana, Berry (1923) described a beaver canal that was 340 m long. Also in Montana, Townsend (1953) observed beaver canals up to 108 m in length, and Cowell (1984) observed a beaver canal that was 160 m long in a northern Ontario peatland, which diverted water from one wetland into a neighbouring one, where the beavers had built their lodge. Beaver canals are also found throughout Europe and Asia, as a result of the activities of the Eurasian beaver (*Castor fiber* L., 1758) (Richard, 1967; Wilsson, 1971; Stocker, 1985, in Collen and Gibson, 2001). Although not as thoroughly studied as dams, canals represent a considerable modification of the riparian zone that could affect many wetland species, such as amphibians, and might have implications for ecosystem processes such as energy and nutrient transport between aquatic and terrestrial environments. My examination of oviposition site selection by wood frogs in Chapter II addresses the use of beaver canals as breeding sites. In Chapter III, I explore the use of beaver canals by wood frog tadpoles and some of their invertebrate predators. In Chapter IV, I examine the use of beaver canals as movement corridors for post-metamorphic wood frogs.

I conducted my research at Miquelon Lake Provincial Park (MLPP), approximately 65 km southeast of Edmonton, Alberta, in the Cooking Lake Moraine (Figure A.3 and Table A.4 Appendix A). The moraine is an isolated patch of dry mixed-wood boreal forest (Natural Regions Committee, 2006), and is representative of the boreal transition zone. Upland forests are dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The landscape of MLPP consists of kame and kettle topography with a high density of semi-permanent to permanent pothole-type wetlands, most of which have been modified by beavers through the construction of lodges and foraging canals. The lack of permanent stream connections between ponds and low dissolved oxygen over winter prevents the establishment and persistence of fish populations, but wood frogs, boreal chorus frogs and western tiger salamanders (*Ambystoma mavortium* Baird (1850)) are common in the park.

In this thesis, Chapters II through IV are in the form of self-contained manuscripts. Chapter V synthesizes my findings from Chapters II through IV and how they relate to one another within the context of seasonal use of beaver-modified wetlands by the wood frog. I also discuss the role of beavers as ecosystem engineers in pothole wetlands and how my findings might be applied to the field of wetland construction and restoration. Figures and tables not presented in Chapters II through IV are provided in Appendix A.

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Chapter II: Does the presence of beavers in a pond improve breeding conditions for wood frogs and boreal chorus frogs?

Introduction:

Beavers (*Castor canadensis* Kuhl 1850) are well known as ecosystem engineers, but their ecological effects vary considerably depending on the characteristics of the surrounding environment (Jones *et al.,* 1994; Rosell *et al.*, 2005). Many anuran amphibians benefit from the presence of beavers in stream-dominated landscapes, where beaver ponds provide the only areas of still water where frogs can breed (e.g. Cunningham *et al.,* 2006; Cunningham *et al.*, 2007; Stevens *et al.*, 2007). By building lodges and digging foraging canals, beavers can also have substantial effects even in naturally occurring wetlands where they seldom build dams (e.g. Cowell, 1984; France, 1997). Beavers actively break ice near the entrances to their burrows and lodges in the late fall and early winter (Bromley and Hood, 2013), and thin ice in these areas is maintained throughout the winter (Sidorovich, 1996 in Collen and Gibson, 2001; G. Hood and L. Trefry, *personal communication*; see also Figures A.1 and A.2, and Tables A.1 through A.3, Appendix A), possibly by the metabolic heat produced by beavers within the lodge, or through continued scraping of the underside of the ice, a behaviour employed by ringed seals (*Pusa hispida* (Schreber, 1775)) to maintain their breathing holes (Smith *et al.*, 1991).

In pothole wetlands of Alberta's dry-mixed wood boreal forest, Bromley and Hood (2013) determined that the ice near occupied beaver lodges thawed earlier than the rest of the pond, and these lodges surrounded by water were attractive nesting sites for breeding Canada geese (*Branta canadensis* L., 1758) when they returned in the spring. In these wetlands, beavers also dig long, narrow foraging canals from the pond towards the nearby forest and other ponds- a typical behaviour of beavers in wetlands with soft substrates if the banks are not too steep (Morgan, 1868; Berry, 1923; Stocker, 1985; Butler, 1991). These canals might also affect ice phenology and early spring water temperatures by collecting snowmelt, and might warm faster in spring than the rest of the pond because of their isolation from the larger body of water. All the amphibian species in this region breed in the spring, and their breeding activities might be affected by changes in ice phenology near occupied beaver lodges.

As ectotherms, temperate amphibians face many challenges in northern climates. The wood frog (*Lithobates sylvaticus* (LeConte, 1825)) is a cold-tolerant species, able to breed very soon after ponds thaw, in shaded sites, and further north than any other North American amphibian (Herreid and Kinney, 1967; Russell and Bauer, 2000), but temperature still limits its breeding activities. Air temperature and snowmelt determine the end of hibernation, and ponds must be at least partially ice free before breeding begins (Herreid and Kinney, 1967). Once the eggs are deposited, low temperatures can limit the rate of embryonic development (Herreid and Kinney, 1967). To speed embryonic development, wood frogs breed in communal aggregations, where the egg masses of many females are laid together near the water's surface to absorb warmth from the sun and provide thermal insulation for one another (Seale, 1982). Wood frog breeding sites are typically located in warm, shallow areas of the pond, such as along the north shoreline where solar exposure is maximized (Seale, 1982; Stevens and Paszkowski, 2004).

The boreal chorus frog (*Pseudacris maculata* (Agassiz, 1850)) is also tolerant of cold temperatures, however its range does not extend as far north as that of the wood frog (Russell and Bauer, 2000). Although they begin calling very soon after wood frogs, the breeding patterns of boreal chorus frogs are less understood, because their egg masses are small, often laid on the underside of vegetation and calling occurs over a longer time period (Whiting, 2010). Boreal chorus frogs breed in shallow water around the edge of the pond and probably select sites similar to those favoured by wood frogs. Whiting (2010) noted that chorus frog eggs are sometimes located very close to aggregations of wood frog egg masses. Unlike wood frogs, female boreal chorus frogs lay their eggs in separate clutches spread out around the pond margin (Russell and Bauer, 2000).

Because embryonic development of both species is constrained by water temperature, and because frogs are able to take advantage of small scale habitat features within a pond, I suggest that spatial and temporal breeding patterns of wood frogs and boreal chorus frogs are affected by the small-scale habitat features and ice phenology created by beaver lodges and canals. My first hypothesis was that the early thaw near occupied beaver lodges allows spring breeding amphibians to access open water and begin breeding earlier on ponds with beavers compared to those without. I predicted that both wood frogs and boreal chorus frogs would begin calling earlier on ponds with beavers compared to those without. I also predicted that aggregations of wood frog egg masses would be located near occupied beaver lodges, where early spring water temperature would be elevated relative to other parts of the pond. My second hypothesis was that lodges and canals provide attractive breeding sites for spring breeding amphibians. I predicted that aggregations of wood frog egg masses would be more common along the edge of the lodge and in beaver canals compared to pond margins that were not modified by beavers (hereafter referred to as unmodified pond margins), after accounting for differences in the relative availability of the habitat types.

Methods

Study area

I conducted my research at Miquelon Lake Provincial Park (MLPP), approximately 65 km southeast of Edmonton, Alberta, in the Cooking Lake Moraine (Figure A.3 and Table A.4, Appendix A). The moraine is an isolated patch of dry mixed-wood boreal forest (Natural Regions Committee, 2006), and is representative of the boreal transition zone. The forest is dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The landscape of MLPP consists of kame and kettle topography with a high density of semi-permanent to permanent pothole-type wetlands, most of which have been modified by beavers, through the construction of lodges and foraging canals. The lack of permanent stream connections between ponds and low dissolved oxygen over winter prevents the establishment and persistence of fish populations, but wood frogs, boreal chorus frogs and western tiger salamanders (*Ambystoma mavortium* Baird, 1850) are common in the park. Although both western toads (*Anaxyrus boreas* (Baird and Girard, 1852)) and Canadian toads (*Anaxyrus hemiophrys* (Cope, 1886)) are known to occur in the Cooking Lake Moraine (Russell and Bauer, 2000; Parks Canada, 2011), none were detected at MLPP during my study.

Data collection

To establish which lodges were occupied by beavers, I surveyed lodges in Miquelon Lake Provincial Park (MLPP) in the fall of 2010 to select 11 ponds with beavers and 11 ponds without beavers for study sites (Figure A.3 and Table A.4, Appendix A). Fresh applications of mud on the lodge, a food cache of small, freshly cut twigs from deciduous trees piled in the water near the lodge, and hoar frost forming a chimney on the lodge vent were used as indicators of beaver presence (Dyck and MacArthur, 1993; Hood and Bayley, 2008; Bromley and Hood, 2013).

In spring 2011, I conducted call surveys for amphibians on 11 ponds with lodges occupied by beavers and 11 with only unoccupied lodges to compare the timing of frog breeding between ponds with and without beavers. I visited each pond on every other night, in an alternating order, during a 3 hour period starting at sunset (~2045 h) for 3 weeks following the start of wood frog calling (April 27th to May

16th). Survey locations were typically along the north side of the pond, 5 to 10 m from the shoreline (Stevens and Paszkowski, 2004). For the two largest ponds, 8.86 and 4.97 ha in area, I established multiple survey locations (three and two stations respectively) to cover the area adequately. A 5-minute survey began 1 minute after arriving at the survey location to allow frogs to resume calling after any disturbance caused by the surveyor. Each spatially distinct chorus of frogs on a pond was identified to species and assigned a rank as follows: I- no overlapping calls; II- some overlapping calls but some breaks; III- total overlapping calls, no breaks (Weir, 2001).

To determine where wood frogs were laying their eggs, I marked the approximate location of each rank II and rank III chorus with flagging tape during call surveys in 2011 and 2012. I revisited these sites in daylight at least three times during the calling period to determine if oviposition had occurred. I defined an aggregation of wood frog egg masses to be a group of more than 10 egg masses within 4 m^2, following Seale's (1982) approach, and hereafter I refer to these communal oviposition sites as 'egg aggregations'. I marked the locations of all egg aggregations with a Garmin 62s GPS (±2 m accuracy), and assigned each egg aggregation to a habitat class ("unmodified pond margin"; "lodge"; "canal") based on the characteristics of the nearest shoreline. Unmodified pond margins were identified in the field by wide zones of emergent vegetation and shallow sloping banks facing the pond centre, and from aerial photos as smoothly curving shorelines. Beaver canals were easily distinguished from the unmodified pond margins in the field and from aerial photos by their long, narrow shape, steep banks and perpendicular junction with the pond. During the winter of 2007-08, all beaver lodges in MLPP were surveyed and marked by Bromley and Hood (2013), and more recently constructed lodges were added to this census during beaver occupancy surveys in the winter of 2011-12. Lodge shorelines were easily distinguished in the field by cut and peeled logs protruding from the mound shaped lodge. In aerial photographs, lodges appear distinctly lighter than shorelines unmodified by beavers. Egg aggregations occurring far from shore or in human-modified areas of the wetland could not be assigned to one of these habitat classes, and were not included in the analysis.

I installed three iButton© temperature loggers on each of five ponds with beavers and five ponds without beavers in 2011, to evaluate if the early thaw near occupied beaver lodges (Bromley and Hood, 2013) leads to higher water temperatures in the early spring. One temperature logger was installed in the unmodified pond margin on the north side of the pond at the edge of the emergent vegetation, one was installed in the food cache area near the edge of the lodge, and one was installed in a beaver canal on the north side of the pond, about 5 to 10 m from where the canal meets the pond. Each data logger recorded water temperature once per hour from April 30, when wood frog oviposition began, to May 21, when most eggs had hatched.

Statistical methods

I assigned each pond to a calling category for each night that it was surveyed. Calling categories were defined as follows for wood frogs: “no calling”- no wood frogs heard during the 5-minute survey; “low calling”- only rank I and II choruses; “medium calling”- only one rank III chorus; “high calling”- two or more rank III choruses. These categories were based on the number of rank III choruses, which represent two orders of magnitude more male wood frogs than either a rank I or a rank II chorus (Stevens and Paszkowski, 2004). Because only half the ponds were visited each day, I pooled observations of wood frog calling activity into 2-day time periods for statistical analysis. I included measures of wind (either wind < Beaufort 4 for both days in a 2-day time period, or wind > Beaufort 4 for at least one of the days in a 2-day time period) and minimum air temperature (average of the lowest temperature for each of the 2 days in a time period from Environment Canada’s New Sarepta weather station, 17 km west of MLPP) as covariates in the analysis, because both wind and cold temperature can inhibit calling activity and affect detection of calling that does occur (Stevens and Paszkowski, 2004). I used proportional odds logistic regression to model the probability of occurrence for each wood frog calling category through time using the “MASS” package in Program R (Venables and Ripley, 2002; R Core Team, 2012). I created a set of 12 candidate models, using date (2-day period) and pond area in all models, and combinations of beaver presence/absence, beaver presence/absence by date interaction, wind and minimum air temperature to predict the probability of occurrence of each wood frog calling category (“no calling”; “low calling”; “medium calling”; “high calling”). I used Akaike’s “Information Criterion” (corrected for small sample size, AICc) to select the best model for predicting wood frog calling activity. Models with a Δ AICc ≤ 2 were considered to be equivalent (Burnham and Anderson, 2002).

I used a similar approach for categorizing boreal chorus frog calling activity, although Corn *et al.* (2011) found that boreal chorus frog call ranks were not strongly correlated to abundance of this species, unlike wood frogs. Calling boreal chorus frogs are not as aggregated as wood frogs, making it difficult to differentiate between distinct choruses. Thus, I categorized boreal chorus frog calling activity on a given night as follows: “no calling”- no boreal chorus frogs heard during the 5-minute survey; “low calling”- only rank I and II choruses; “high calling”- at least one rank III chorus. I used proportional odds logistic regression to predict boreal chorus frog calling activity through time, and structured candidate models as previously described for wood frog calling activity. I selected the best model for predicting boreal chorus frog calling activity using AICc, and considered models with a Δ AICc ≤ 2 to be equivalent to the top model (Burnham and Anderson, 2002).

I used a chi-square goodness of fit test to compare the number of times egg aggregations occurred in each habitat class (“unmodified pond margin”; “lodge”; “canal”) versus expected occurrence based on the availability of each habitat class. I used a linear approximation of the available habitat because wood frogs typically breed at the edges of a pond. Where beaver canals were more than 3-m wide (approximately twice the diameter of the largest egg aggregation I observed), I considered each side of the canal to be independently available to breeding wood frogs, and included both sides in my measurements. Where beaver canals were less than 3-m wide, I considered the canal to be a single, linear feature and measured along the centre of the canal. I then measured the remaining sections of pond shoreline that had not been modified by beavers, and measured the length of shoreline provided by beaver lodges on each pond. I multiplied the total number of egg aggregations found in each year by the ratio of the total length of each habitat class (summed across the 21 ponds in which wood frog breeding was detected) to the total length of all habitat classes (summed across the 21 ponds) to generate the number of egg aggregations expected in each habitat class if each of these classes were used equally for oviposition. After significant results, I conducted separate pairwise tests of the three habitat classes, using a Šidák alpha value correction to control family-wise Type I error. I conducted separate analyses for each year of data collection (2011 and 2012).

I used a Friedman test with repeated measures to compare median daily water temperature (the average of the hourly values for a given day) among the three habitat classes from April 30 to May 21 ("muStat" package in R version 2.15.1; Wittkowski and Song, 2012). Several loggers were not recovered due to interference by beavers, and some failed electronically. Only five ponds with data from all three loggers were used for analysis, one with beavers and four without (Pond 47 and Ponds 06, 22, 26, and 32 respectively, see Table A.3, Appendix A).

Results:

Wood frog calling did not begin earlier on ponds with beavers compared to ponds without beavers (Figures 2.1 and 2.2). The best model, according to AICc, included only wind as a predictor of wood frog calling activity in addition to date and pond area which were included in all models (Table 2.1). Three other models (the model that included wind and minimum air temperature; the model that included beaver and wind; and the model that included beaver, wind and minimum air temperature) were considered to be equivalent to the top model. Wind was the only predictor included in all four top models, and in all cases the odds ratio for wind was less than 1. In the top model, the odds ratio for wind was 0.265 (95% confidence interval: 0.148 to 0.464), indicating that when there was no wind, all other factors being equal, wood frog calling activity was about four times more likely to increase by at least one category compared to when there was wind. When beaver presence/absence was included as a predictor of wood frog calling activity, the odds ratio for this variable was less than 1 in both cases (0.779; 0.775 respectively), which suggests that wood frog calling activity is negatively affected by the presence of beavers in a breeding pond, all other factors being equal. However, the 95% confidence interval for this odds ratio overlapped 1 in both models (95% confidence intervals: 0.464 to 1.303; 0.461 to 1.299), thus indicating some uncertainty about the direction of the effect of beaver presence/absence. When minimum air temperature was included as a predictor, its odds ratio was greater than 1 in both models (1.144; 1.360 respectively), which suggests that wood frog calling activity is positively affected by an increase in minimum air temperature, all other factors being equal. However, the 95% confidence interval for this odds ratio overlapped 1 in both cases (95% confidence intervals: 0.921 to 1.424; 0.111 to 1.219), which indicates some uncertainty about the direction of the effect of minimum air temperature.

Boreal chorus frogs did not call earlier on ponds with beavers than on ponds without beavers (Figures 2.3 and 2.4). The best model, according to AICc, included only wind as a predictor of boreal chorus frog calling activity in addition to date and pond area which were included in all models (Table 2.2). In the top model, the odds ratio for wind was 0.382 (95% confidence interval: 0.209 to 0.682), thus indicating that when there was no wind, all other factors being equal, boreal chorus frog calling activity was about three times more likely to increase by at least one category compared to when there was wind. The top model was considered equivalent to the model that included beaver in addition to the variables included in the top model as predictors of boreal chorus frog calling activity. The odds ratio for beaver in this model was 0.706 (95% confidence interval: 0.412 to 1.206), which suggests that boreal chorus frog calling activity is negatively affected by the presence of beavers in a breeding pond. However, the 95% confidence interval for this odds ratio overlaps 1, which indicates some uncertainty about the direction of the effect of beaver on boreal chorus frog calling activity.

Most wood frog egg aggregations were located along the unmodified pond margins in both 2011 and 2012 (Figure 2.5) and wood frogs tended to avoid north aspect shorelines (Figure A.4, Appendix A). Although some egg aggregations were located along the edge of a lodge and in beaver canals, this was not a common occurrence. In 2011, I found forty wood frog egg aggregations in the unmodified pond margins, none along the edges of beaver lodges, four in beaver canals, and four that could not be assigned to one of these three habitat classes because of their central location in the pond. The observed frequencies of wood frog egg aggregations in the three habitat classes was significantly different than would be expected based on availability ($\chi^2 = 11.321$, $df = 2$, $p < 0.001$). Egg aggregations were no more or less common along the edge of beaver lodges compared to the unmodified pond margins ($\chi^2 = 2.418$, $df = 1$, $p = 0.120$, corrected $\alpha = 0.017$) or beaver canals ($\chi^2 = 0.444$, $df = 1$, $p = 0.505$, corrected $\alpha = 0.017$). However fewer than three of the forty-four egg aggregations included in the analysis were expected to occur in the lodge habitat class based on availability, and such a small expected value violates one of the assumptions of this statistical test. There were significantly fewer egg aggregations in beaver canals compared to the unmodified shoreline than would be expected based on availability ($\chi^2 = 13.212$, $df = 1$, $p < 0.001$, corrected $\alpha = 0.017$).

In 2012, I found thirty-four wood frog egg aggregations in the unmodified pond margins, one along the edge of a beaver lodge, three in beaver canals, and four that could not be assigned to any of these groups. The observed frequencies of wood frog egg aggregations in the three habitat classes was significantly different than would be expected based on availability ($\chi^2 = 12.594$, $df = 2$, $p = 0.002$). Egg aggregations were no more or less common along the edge of beaver lodges compared to the unmodified pond margins ($\chi^2 = 0.527$, $df = 1$, $p = 0.468$, corrected $\alpha = 0.017$), or beaver canals ($\chi^2 = 1.003$, $df = 1$, $p = 0.317$, corrected $\alpha = 0.017$). However, fewer than two of the thirty-eight egg aggregations included in the analysis were expected to occur in the lodge habitat class based on availability, and such a small expected value violates one of the assumptions of this statistical test. I found significantly fewer wood frog egg aggregations in beaver canals than would be expected based on availability ($\chi^2 = 11.960$, $df = 1$, $p = 0.001$, corrected $\alpha = 0.017$).

On five ponds, I was able to recover data from the temperature loggers set in all three habitat classes. In 2011, from April 30, when wood frogs began breeding, to May 21, when most eggs had hatched, median water temperatures were similar in unmodified pond margins, lodge margins, and beaver canals (Figure A.5, Appendix A; $\chi^2 = 4.234$, $df = 2$, $p = 0.120$). Because data could only be recovered from one of the temperature loggers located at the food cache of a lodge with beavers, I was unable to make statistical comparisons of early spring water temperature between the food caches of lodges with and without beavers. The water temperatures recorded at the food cache of the lodge that was occupied by beavers were higher than the average for sites without beavers, but were no warmer than the site along the unmodified pond margin for that pond. However, because of the sample size, this pattern cannot be extrapolated to other sites.

Discussion:

Contrary to my expectations, I cannot conclude that either wood frogs or boreal chorus frogs call earlier on ponds with beavers than on ponds without beavers. The margins of all ponds thawed several days before frogs began calling, and in some cases the whole pond was ice free before frogs began calling, which suggests that the onset of calling for both species was not limited by the presence of open water. Likewise, as both these species hibernate in terrestrial habitats, the initial onset of calling might be more closely tied to soil temperatures and snow depth which determine the end of hibernation. My results suggest that wind has a negative effect on the calling activity of both wood frogs and boreal chorus frogs, which is consistent with the results of Steelman and Dorcas (2010) who investigated the effect of weather conditions on *Pseudacris crucifer* (Wied-Newied, 1838), *Pseudacris feriarum* (Baird, 1854) and *Lithobates sphenocephalus* (Cope, 1886) in the North Carolina piedmont. Wind can limit the ability of surveyors to detect choruses, but based on my observations, wind also directly reduces calling activity. A few days after wood frogs had established rank III choruses at locations that were consistent from one visit to the next (May 1 and 2, 2011**)** there was a period of high winds (May 3 and 4, 2011), that corresponded with the drop in calling activity recorded for the fifth time period (Figure 2.1). Many chorus sites that had been ranked as III in the previous survey visit were still active, however, calling was recorded at a rank I or II level. Male frogs may reduce their calling activity during periods of wind over Beaufort force 4 because calls, which are energetically expensive, are only audible to females over a very short distance (Dorcas and Foltz, 1991).

The presence of beavers in a pond may also have had a negative effect on calling activity, and by inference breeding activity, for both wood frogs and boreal chorus frogs, but beaver presence was not a strong predictor for either species. Pond area (over a range of sizes from 0.22 to 8.86 ha) also had a negative effect on calling activity, perhaps because small ponds in this size range thaw faster and might warm up more quickly than larger ponds. Although I selected ponds in a narrow size range for the two treatment groups (with and without beavers), the average area of study ponds with beavers was somewhat larger than study ponds without beavers (1.78 and 1.05 ha respectively). Such a difference might reflect a regional pattern: Hood and Bayley (2008) determined that the presence of beavers in the Cooking Lake Moraine contributed to a greater area of open water in pothole wetlands during drought years. However, the mean area of my study ponds with and without beavers did not differ significantly (*t*-test (unequal variances): $t = 0.896$, $df = 20$, $p = 0.195$).

Although the ice near occupied beaver lodges might thaw earlier than other parts of the pond (Bromley and Hood, 2013), this area was not an attractive oviposition site for wood frogs. In two years of surveys, I only observed a single wood frog egg aggregation situated along the edge of a lodge, and this lodge was not occupied by beavers. The area near a beaver lodge tends to be deeper than the rest of the pond, as beavers excavate the pond bottom (Hood and Bayley, 2008), and by the time wood frogs began breeding, most of the shallow margins of study ponds were ice free. Bromley and Hood (2013) also observed that lodges occupied by beavers were less likely to be connected to the mainland than lodges that were not occupied by beavers. Although Canada geese can readily access island lodges, wood frogs migrating to breeding ponds would be unlikely to cross ice to reach a beaver lodge when shallow pond margins were already thawed. The steeply sloping banks of an occupied beaver lodge also tend to lack submerged and emergent vegetation, so eggs laid in this area could very easily drift and sink into relatively deep water where they would absorb less solar radiation and where decomposing sediments might reduce dissolved oxygen leading to a reduction in hatching success.

Wood frogs avoided breeding in beaver canals, preferring to situate their egg aggregations along the unmodified pond margins, in shallow water where the stems of submerged and emergent vegetation were used to support egg masses near the water's surface. When egg aggregations were laid in canals, they were often located near the intersection of the canal and the pond. Only one relatively small egg aggregation was located mid-way along the canal in each year (29 m and 16 m from the unmodified shoreline of the pond in 2011 and 2012 respectively). These two egg aggregations contained 11 and 54 egg masses respectively, compared to average egg aggregation sizes of 84 egg masses in 2011 and 115 egg masses in 2012. Eggs laid in beaver canals were able to complete development in both years (*personal observation*), thereby demonstrating that wood frogs can successfully breed in beaver canals, even if they are not optimal sites.

Although I did not detect a difference in water temperature between the unmodified shoreline and beaver canals, I often observed ice at the bottom of canals in early spring, where it had been covered by spring snow melt and shaded by overhanging grasses and sedges from the previous year's growth. If canals are colder than unmodified pond margins, eggs laid in canals might suffer slower development or reduced hatching success, but this was not addressed in my study.

Likewise, my study did not address the long-term effects of canals on pond hydrology (e.g. drought resistance), which some authors have suggested could be considerable, even after beavers have abandoned a pond (Cowell, 1984; Hood and Bayley, 2008).

In many cases, I observed wood frog egg aggregations at roughly the same location in both years, consistent with Seale's (1982) observations of wood frog egg aggregations in seasonal ponds in Pennsylvania. Both male and female frogs are probably involved in selecting these sites, and multiple cues may be used at different spatial scales. According to Sinsch (2006), amphibians orient and navigate to and from breeding sites by integrating acoustic, magnetic, mechanical, olfactory and visual cues.

Anurans have been known to use olfactory cues to orient towards their breeding pond, however the role of conspecific olfactory cues in anuran navigation within a pond has not been well studied (Sinsch, 2006). Howard (1980) observed that male wood frogs were uniformly distributed around small breeding ponds at the beginning of the breeding season, but within a few days males were clustered around the sites where oviposition had occurred. Once oviposition sites were established, Howard (1980) noted that calling activity increased as males from around the pond moved towards the communal egg aggregation site, probably using acoustic cues to do so, because male wood frogs are attracted to the sounds of a conspecific chorus (Bee, 2007). By transplanting wood frog egg masses within a pond, Howard (1980) was able to induce wood frogs to lay eggs at a breeding site that had not been used for several years, but Seale (1982) was unable to induce frogs to lay eggs in a deep, cold part of the breeding pond by the same method. Visual and olfactory cues associated with the presence of egg masses appear important for the small scale selection of an oviposition site, but these cues are not sufficient to induce frogs to lay eggs in unsuitable sites.

Male wood frogs breeding for the second or third time might remember where breeding activity was concentrated in previous years and could relocate these sites using visual cues such as tree silhouettes or shoreline features (Sinsch, 1992). Once a chorus of older males was established, the smaller males breeding for the first time could use this as an acoustic beacon to find their way to the chorus site (Bee, 2007). Most of my study ponds had multiple chorus sites associated with distinct egg aggregations. Although Howard and Kluge (1985) found little evidence to suggest that female wood frogs were able to choose their mates, females may be able to choose between chorus sites based on acoustic cues, as Sinsch (1992) determined was the case for female natterjack toads (*Epidalea calamita* (Laurenti, 1768)).

Although ice tends to thaw earlier near occupied beaver lodges than the rest of the pond (Bromley and Hood, 2013), the presence of beavers in a pond does not affect the timing of calling for either wood frogs or boreal chorus frogs. The steeply sloping banks of beaver lodges and canals are not as attractive to breeding wood frogs as the shallower water of the unmodified pond margins. Because wood frogs do not compete for individual breeding sites, many wood frogs can breed in a small area. Thus, alteration of pond habitats by beavers is unlikely to limit (or increase) the number of frogs that are able to breed on a pond.

Tables and Figures

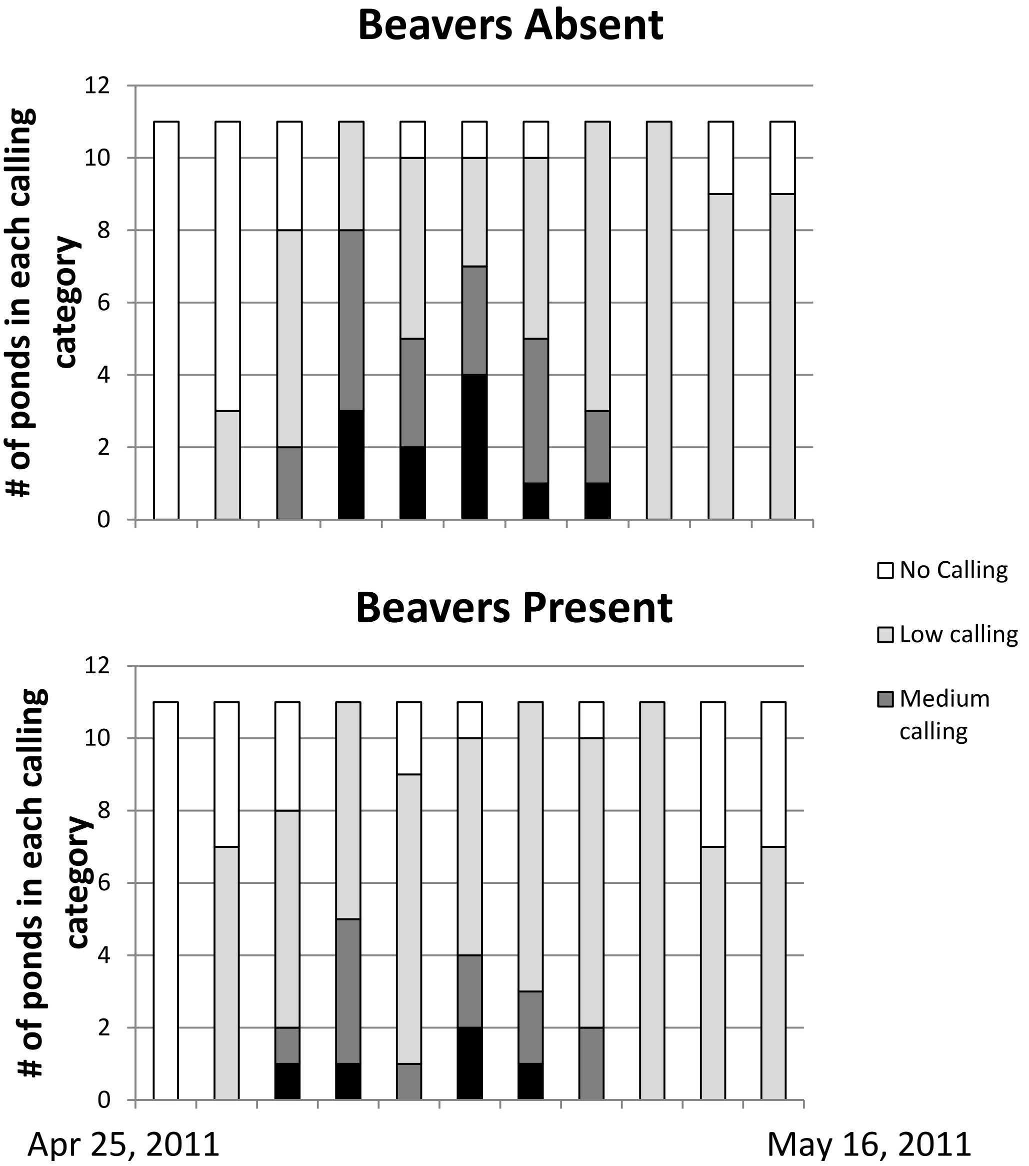

Figure 2.1. Wood frog calling activity through time for 11 ponds with beavers and 11 ponds without beavers in Miquelon Lake Provincial Park, AB from April 25 to May 16, 2011 (“no calling” = no wood frogs heard; “low calling” = only rank I or rank II choruses; “medium calling” = only one rank III chorus; and “high calling” = two or more rank III choruses).

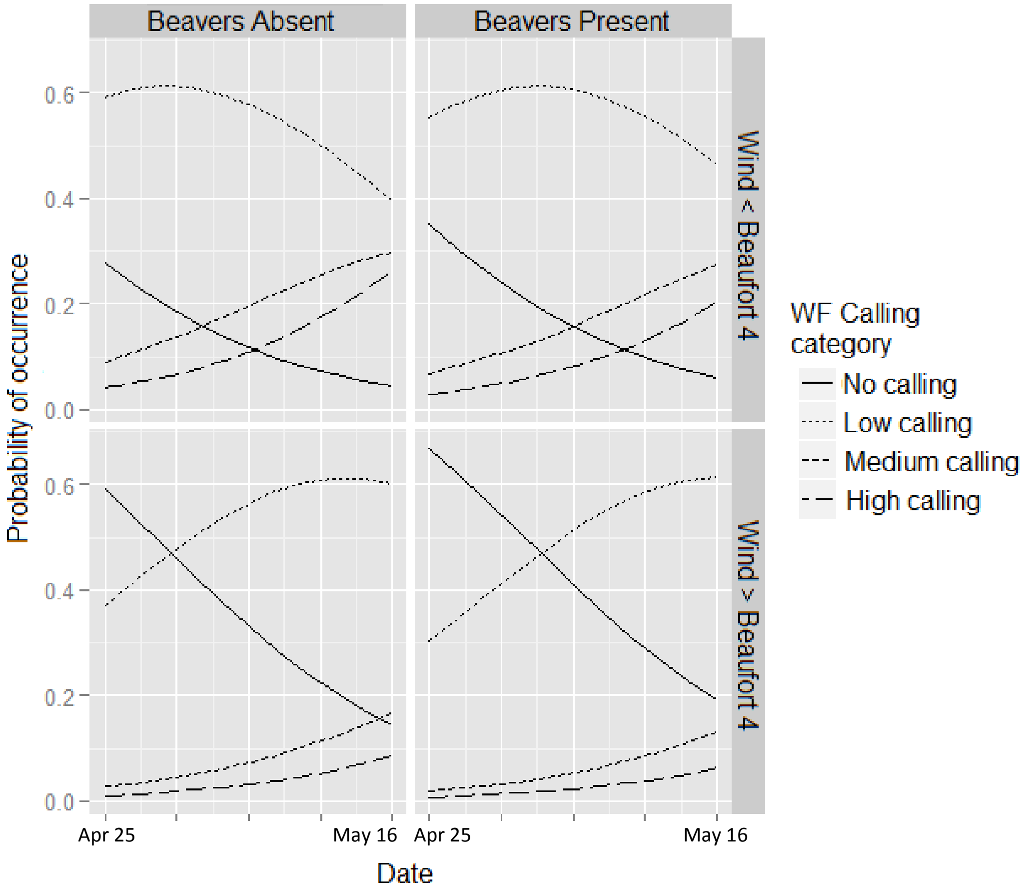

Figure 2.2. Probability of occurrence for the four wood frog calling categories through time as predicted by ordinal logistic regression, with and without beaver present and at two levels of wind (with or without at least one day in a time period with wind > Beaufort 4) from 11 ponds with beavers and 11 ponds without beavers in Miquelon Lake Provincial Park, AB from April 25 to May 16, 2011.

Table 2.1. Model selection results assessing the effect of beaver presence/absence (B) on wood frog calling activity from 11 ponds with beavers and 11 ponds without beavers in Miquelon Lake Provincial Park, AB, using ordinal logistic regression models to predict wood frog calling category (“no calling” = no wood frogs heard; “low calling” = only rank I and/or rank II choruses; “medium calling” = only one rank III chorus; and “high calling” = two or more rank III choruses) based on date (D, included in all models) and pond area (A, included in all models), with wind (W) and minimum air temperature (T).

Model	Factors	Log likelihood	k	AICc	Δi	wi	$e^{(-0.5\Delta i)}$	Evidence Ratio
1	**D+W+A**	**-251.8**	**4**	**515.75**	**0.00**	**0.31**	**1.00**	**1.000**
2	**D+W+T+A**	**-251.0**	**5**	**516.39**	**0.63**	**0.23**	**0.73**	**1.371**
3	**D+B+W+A**	**-251.3**	**5**	**516.95**	**1.20**	**0.17**	**0.55**	**1.820**
4	**D+B+W+T+A**	**-250.6**	**6**	**517.58**	**1.83**	**0.13**	**0.40**	**2.493**
5	D+B+B*D+W+A	-250.9	6	518.16	2.40	0.09	0.30	3.327
6	D+B+B*D+W+T+A	-250.1	7	518.80	3.04	0.07	0.22	4.583
7	D+T+A	-261.0	4	534.24	18.48	0.00	0.00	10307.221
8	D+B+T+A	-260.6	5	535.50	19.74	0.00	0.00	19382.484
9	D+A	-262.9	3	535.94	20.18	0.00	0.00	24115.507
10	D+B+B*D+T+A	-260.2	6	536.91	21.16	0.00	0.00	39310.717
11	D+B+A	-262.5	4	537.18	21.42	0.00	0.00	44868.891
12	D+B+B*D+A	-262.1	5	538.59	22.83	0.00	0.00	90764.641
** Sums **						1	3.1988	

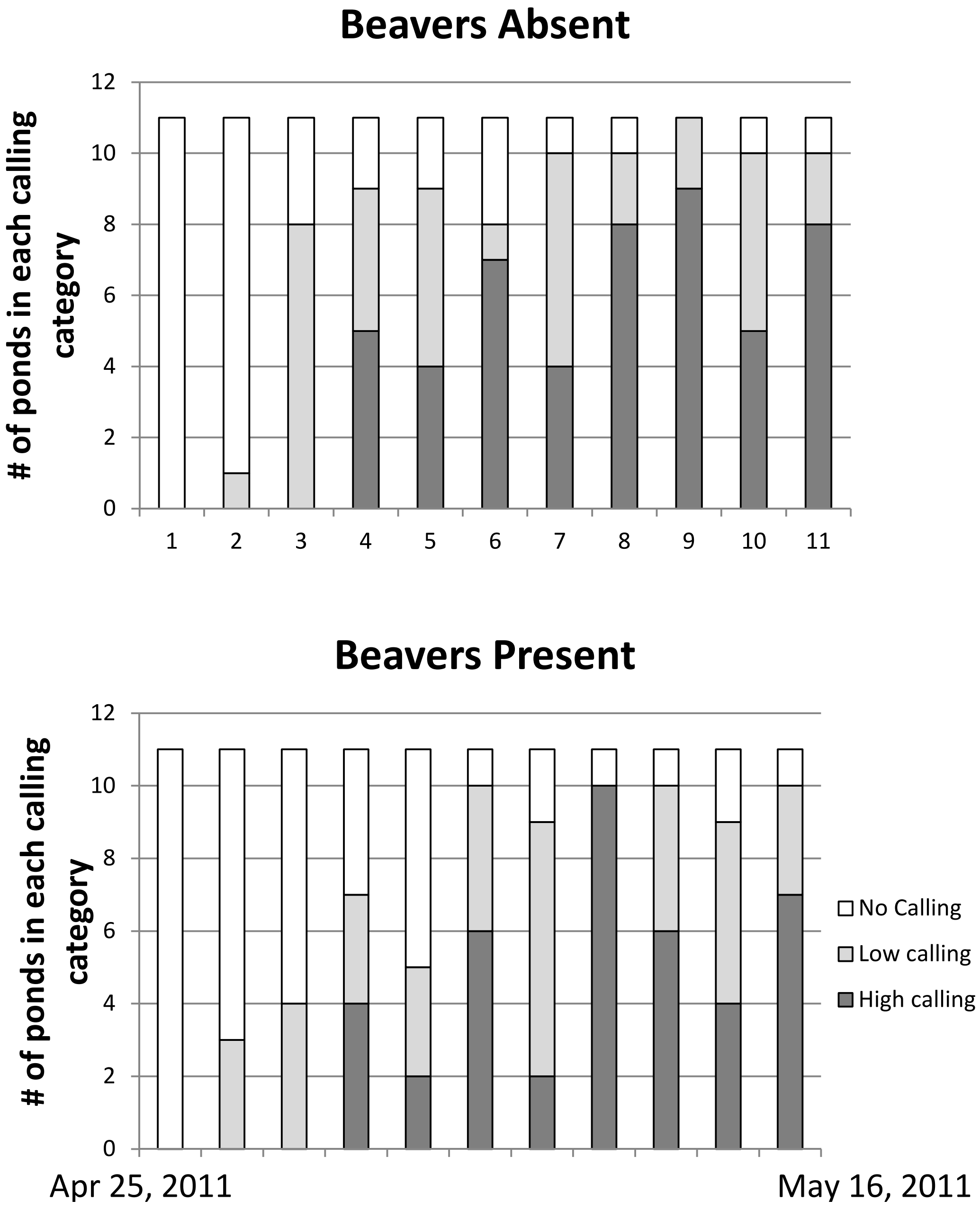

Figure 2.3. Boreal chorus frog calling activity through time for 11 ponds with beavers and 11 ponds without beavers in Miquelon Lake Provincial Park, AB from April 25 to May 16, 2011 ("no calling" = no boreal chorus frogs heard; "low calling" = only rank I or rank II choruses; "high calling" = at least one rank III chorus).

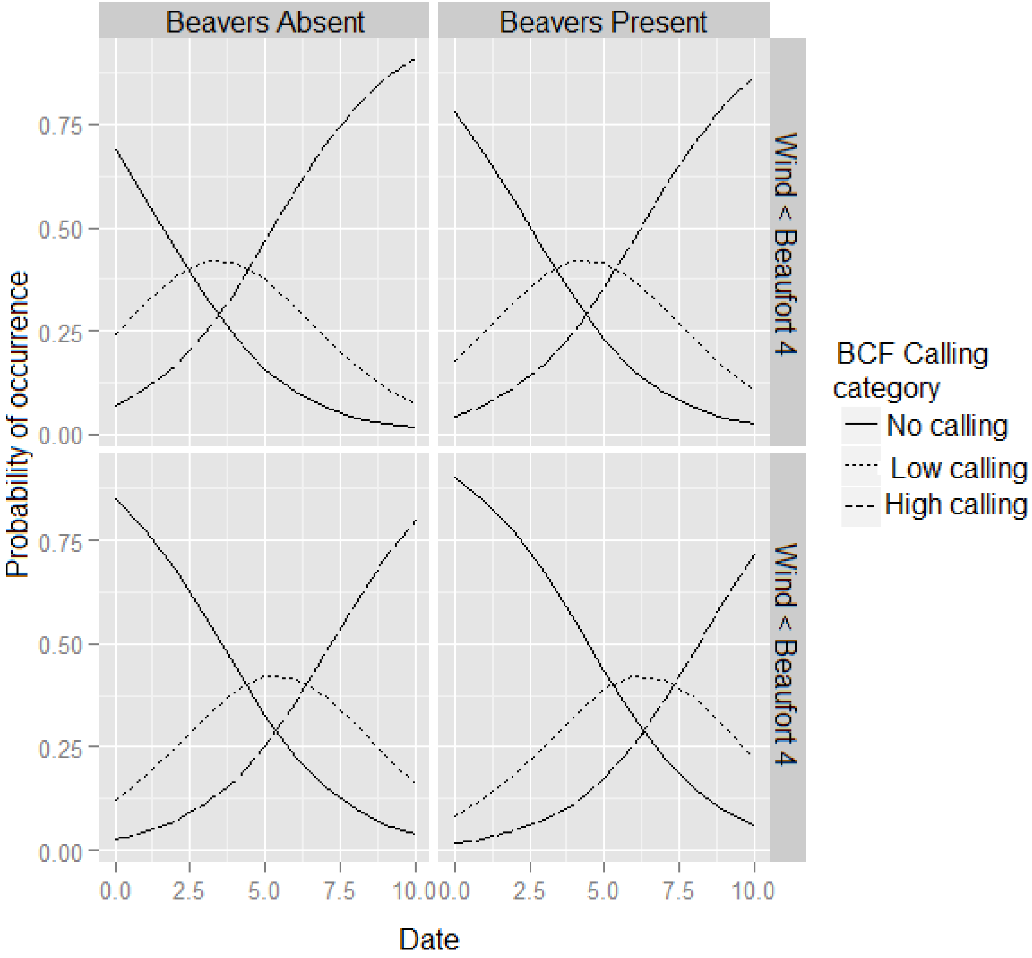

Figure 2.4. Probability of occurrence for the three boreal chorus frog calling categories through time as predicted by ordinal logistic regression, with and without beaver present and at two levels of wind (with or without at least one day in a time period with wind > Beaufort 4) from 11 ponds with beavers and 11 ponds without beavers in Miquelon Lake Provincial Park, AB from April 25 to May 16, 2011.

Table 2.2. Model selection results assessing the effect of beaver presence/absence (B) on boreal chorus frog calling activity from 11 ponds with beavers and 11 ponds without beavers in Miquelon Lake Provincial Park, AB, using ordinal logistic regression models to predict boreal chorus frog calling category ("no calling" = no boreal chorus frogs heard; "low calling" = only rank I and/or rank II choruses; "high calling" = at least one rank III chorus) based on date (D), with wind (W) and minimum air temperature (T) as sampling covariates and pond area (A) as a site specific covariate included in all models.

Model	Factors	Log likelihood	k	AICc	Δi	wi	$e^{(-0.5\Delta i)}$	Evidence Ratio
1	**D+W+A**	**-210.1**	**4**	**430.43**	**0.00**	**0.35**	**1.00**	**1.000**
2	**D+B+W+A**	**-209.3**	**5**	**430.92**	**0.48**	**0.27**	**0.79**	**1.273**
3	D+W+T+A	-210.1	5	432.51	2.08	0.12	0.35	2.824
4	D+B+B*D+W+A	-209.3	6	432.97	2.54	0.10	0.28	3.556
5	D+B+W+T+A	-209.3	6	433.01	2.57	0.10	0.28	3.622
6	D+B+B*D+W+T+A	-209.3	7	435.09	4.65	0.03	0.10	10.242
7	D+T+A	-213.6	4	437.43	6.99	0.01	0.03	32.990
8	D+B+T+A	-212.8	5	437.99	7.55	0.01	0.02	43.623
9	D+A	-215.5	3	439.19	8.75	0.00	0.01	79.552
10	D+B+A	-214.7	4	439.70	9.27	0.00	0.01	102.802
11	D+B+B*D+T+A	-212.8	6	440.01	9.57	0.00	0.01	119.756
12	D+B+B*D+A	-214.7	5	538.59	11.26	0.00	0.00	277.987
** Sums **						1	2.8704	

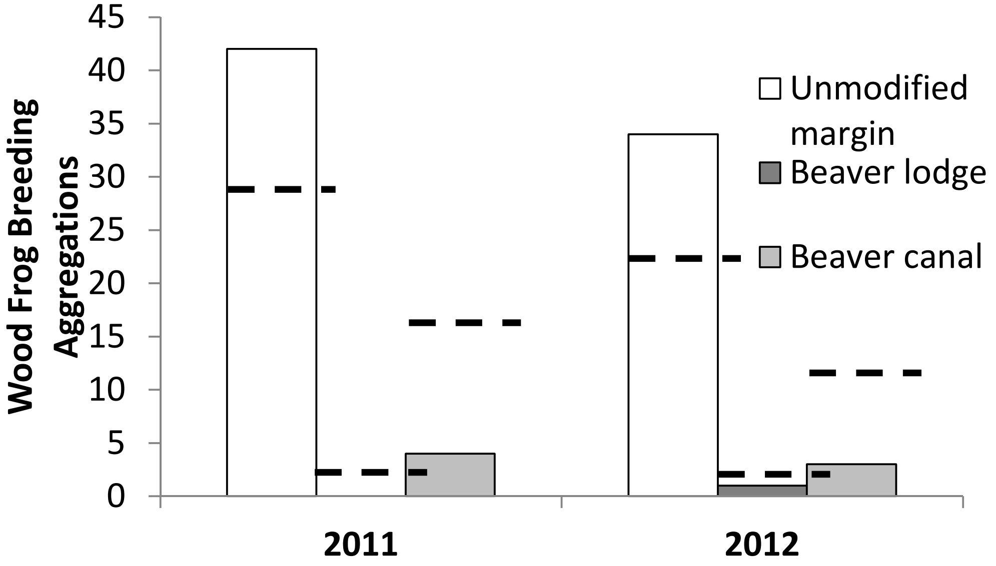

Figure 2.5. Frequency of occurrence of aggregations of wood frog egg masses along the unmodified pond margins, beaver canals, and beaver lodges from 21 ponds in Miquelon Lake Provincial Park, AB. Expected frequencies, based on the relative availability of each habitat type are shown in dashed lines.

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Chapter III: Beaver canals provide habitat for tadpoles and their aquatic insect predators

Introduction:

Wood frogs (*Lithobates sylvaticus*) grow faster as larvae than as post-metamorphic frogs (Werner, 1986) by taking advantage of the warm, productive waters of the pond margins (Hutchinson, 1957; Alford, 1999; Porej and Hetherington, 2005; Strayer and Findlay, 2010). However, survival to metamorphosis is often very low in wood frog larvae as is the case for many other pond breeding anurans (Herreid and Kinney, 1966; Alford, 1999; Govindarajulu and Anholt, 2006) and intraspecific competition for food is widely assumed to be an important contributing factor (Licht, 1967; Skelly and Kiesecker, 2001). Tadpoles commonly feed on periphyton (Altig *et al.*, 2007) which grows on the submerged portions of emergent and submerged vegetation, although they also feed opportunistically on soft-bodied invertebrates, carrion and plant detritus (Petranka and Kennedy, 1999; Hunte-Brown, 2006; Whiles *et al.,* 2006; Whiting, 2010), all of which tend to be abundant around the edges of a pond. Tadpoles might not use the deeper central part of the pond which lacks emergent vegetaion (hereafter referred to as the 'open water zone') because of cooler temperatures and lower availability of food resources and refuges from predators.

The shorelines of many permanent and semi-permanent wetlands in North America's Prairie Pothole Region have been extensively modified by beavers

(*Castor canadensis* Kuhl, 1820), but the effects of beavers on larval anurans in these wetlands have not been studied. Although best known for damming streams (Naiman *et al.*, 1986; Jones *et al.*, 1994), beavers occupying ponds with gently sloping banks and soft substrates (e.g. clay or sand) often dig long foraging canals towards adjacent forest cover (Morgan, 1868; Berry, 1923; Stocker, 1985; Butler, 1991). Beaver canals may provide additional habitat for tadpoles by extending a pond's shoreline; however, canals differ from the pond margins that have not been modified by beavers (hereafter referred to as 'unmodified pond margins'). Canals often exceed 200 m in length, but they are rarely more than 1 m wide and emergent vegetation does not usually grow on their nearly vertical banks (Morgan, 1868; Collen and Gibson, 2001; Hood and Larson, *in review*). In contrast, the unmodified margins of pothole wetlands tend to slope gradually (approximately 2º), allowing emergent vegetation to grow in a fringe, often several metres wide, around the edge of a pond (*personal observation*). Because canals appear to share characteristics of both unmodified pond margins and the open water zone, I hypothesized that canals provide larval wood frogs with habitat that is intermediate in quality to that of unmodified pond margins and the open water zone. I predicted that wood frog tadpoles would be most abundant in the unmodified pond margins, followed by beaver canals, and the open water zone.

Water temperature might indirectly contribute to tadpole mortality by affecting primary productivity and larval development rates. Based on observations reported in Chapter II, I hypothesized that beaver canals are not as warm as other shallow inshore areas of the ponds. I predicted that, during the period of wood frog larval development, water temperature would be highest in the unmodified pond margins, followed by beaver canals and the open water zone.

Predation also contributes to the high mortality rate of larval wood frogs and other anurans (e.g. Herreid and Kinney, 1966). In the dry mixed-wood boreal forest of Alberta, Hood and Larson (*in review*) found that aquatic macroinvertebrates belonging to the predator functional feeding group (e.g. water striders (Gerridae) and whirligig beetles (Gynirindae)) were more abundant in beaver canals compared to the edge of emergent vegetation along the unmodified shorelines. However, larger invertebrate predators capable of preying on tadpoles (e.g. predacious diving beetles and anisopteran nymphs) were not well represented in Hood and Larson's study, although these taxa might be expected to use beaver canals preferentially, as documented for the smaller members of this functional feeding group. I hypothesized that beaver canals provide favourable habitat to large-bodied predacious insects capable of preying on tadpoles. I predicted that these species would be most abundant in beaver canals, followed by unmodified pond margins and the open water zone.

Methods:

Study area

I conducted my research at Miquelon Lake Provincial Park (MLPP), approximately 65 km southeast of Edmonton, Alberta, in the Cooking Lake Moraine (Figure A.3 and Table A.4, Appendix A). The moraine is an isolated patch of dry mixed-wood boreal forest (Natural Regions Committee, 2006), and is representative of the boreal transition zone. The forest is dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The landscape of MLPP consists of kame and kettle topography with a high density of semi-permanent to permanent pothole-type wetlands, most of which have been modified by beavers, through the construction of lodges and foraging canals. The lack of permanent stream connections between ponds and low dissolved oxygen over winter prevents the establishment and persistence of fish populations, but wood frogs, boreal chorus frogs (*Pseudacris maculata* (Agassiz, 1850)) and western tiger salamanders (*Ambystoma mavortium* Baird (1850)) are common in the park. The 14 ponds used in this study ranged from 0.24 to 2.28 hectares in area and were all less than 2.5 m maximum depth (Table A.4, Appendix A).

Data collection

I collected tadpoles from a single overnight set of 15 Gee© minnow traps (20 cm diameter funnels with 2 cm diameter entrances) in each of 14 beaver-modified ponds from June 1 to July 7, 2011 (Ponds 01, 02, 09, 11, 12, 20, 23, 26, 32, 35, 36, 40, 47, and 62; Figure A.3 and Table A.4, Appendix A). In each pond, I set five traps systematically in each of three habitat classes (“unmodified pond margin”; “beaver canal”; “open water”). Unmodified pond margins were identified from aerial photos as smoothly curving shorelines, and in the field by wide zones of emergent vegetation and shallow sloping banks facing the pond centre. Beaver canals were easily distinguished from the unmodified pond margins from aerial photos and in the field by their long, narrow shape, steep banks and perpendicular junction with the pond. I defined the open water zone as the area of the pond lacking emergent vegetation. The locations of my traps were constrained by the availability of beaver canals, and I used a systematic approach to selecting sites. I selected five beaver canals over 20 m in length, one located in each cardinal direction from the pond centre and the fifth located where there was the largest distance between the first four sampling sites. I set these traps in the canal halfway between the end of the canal and its junction with the pond, with the trap's entrances oriented parallel to the bank of the canal. Trap sites in unmodified pond margins were located within approximately 10 m of the mouth of the selected canals at the edge of emergent vegetation, and I oriented the entrances of these traps parallel to the shoreline. One open water trap site was located approximately in the pond centre, and the remaining four were set about halfway between the pond centre and the edge of the emergent vegetation in each cardinal direction. I did not orient the entrances to traps set in the open water zone in any specific direction. Traps were set at the surface where possible to give captured amphibians access to atmospheric oxygen. When a trap was recovered after the overnight trapping period, it was immediately emptied into a 20-litre bucket filled with water. Captured tadpoles were counted as they were moved to a second bucket before they were released at their initial capture location.

I measured water depth at each trap site and used a 0.5 m by 0.5 m quadrat to record the percent cover and height of emergent and submerged vegetation (both living and dead) as well as the percent cover of woody debris. I included fully submerged plants as well as the submerged portions of emergent vegetation in measurements of submerged vegetation. I was unable to evaluate vegetation structure at most open water sites, because of the depth and turbidity of the water, so these sites were not included in the analysis. To compare water temperature between beaver canals, the unmodified pond margins and the open water, I installed three iButton temperature loggers on each of five ponds, a subset of the 14 ponds in which tadpoles were trapped (Ponds 12, 20, 26, 32 and 47, see Table A.4, Appendix A). I installed one temperature logger in the unmodified pond margin on the north side of the pond at the edge of the emergent vegetation, one in a beaver canal on the north side of the pond halfway between the end of the canal and its junction with the pond, and one roughly in the pond centre. Each temperature logger recorded water temperature hourly from May 22 to July 20, which coincided with the larval development period for wood frogs in the study ponds.

I also captured aquatic invertebrates in minnow trap sampling (described above), and several of these groups were capable of predating on wood frog tadpoles (Herreid and Kinney, 1966; Clifford, 1991; Govindarajulu and Anholt, 2006; Michel and Adams, 2009). Large bodied predacious insects were identified in the field to the lowest feasible taxonomic group as follows: *Dytiscus alaskanus* Balfour-Browne, 1944 (larvae > 40 mm and adults >25 mm total length); and anisopteran nymphs (>20 cm total length) according to keys developed by Clifford (1991).

Statistical analysis

I compared catch-per-unit-effort (CPUE, number of individuals per overnight set of five traps) for wood frog tadpoles among the three habitat classes (unmodified pond margins, beaver canals, and open water zone) using a generalized linear model fitting a negative binomial distribution. After significant results, I compared the 95% confidence intervals of the means for each habitat class to determine which classes were different. I used the same methods for comparisons of CPUE of predacious insects among habitat classes, and conducted these analyses in Program R (version 2.15.1, R Core Team, 2012).

I standardized habitat variables (percent cover and height of both emergent and submerged vegetation, along with water depth and percent cover of woody debris) by subtracting the sample mean from each observed value and dividing by the standard deviation and used principal components analysis to compare visually between trap sites in beaver canals and the unmodified pond margins (70 trap sites in each habitat class). I tested for differences in these six characteristics between canals and unmodified pond margins using multi-response permutation procedures (MRPP) with a Euclidean distance measure (because of negative values in the standardized data), as this approach does not rely on assumptions of multivariate normality (Mielke and Berry, 2001). I conducted these analyses using PC-ORD 6.0 (McCune and Mefford, 2011). I compared daily water temperature (the average of hourly values for a given day) between unmodified pond margins, beaver canals and the open water zone using a Friedman test with repeated measures in the "muStat" package in R version 2.15.1 (R Core Team, 2012; Wittkowski and Song, 2012).

Results:

CPUE of wood frog tadpoles in the unmodified pond margins was similar to that of beaver canals, whereas CPUE in open water was considerably lower (Figure 3.1, $D_2 = 17.925$, $p < 0.001$; Table A.5, Appendix A). Based on the 95% confidence intervals of the means for each habitat class, CPUE of wood frog tadpoles in beaver canals was significantly higher than that of the open water zone, but not significantly different from that of the unmodified shorelines. Although mean CPUE in the unmodified pond margins was somewhat higher than that of the open water zone, the 95% confidence intervals for these two habitat classes overlapped to a small extent (Figure 3.1).

Trap sites in unmodified pond margins were similar to trap sites in beaver canals in terms of height and cover of emergent and submerged vegetation, water depth, and cover of woody debris (Figure A.6, Appendix A); the two habitat classes did not differ significantly ($A = -0.003$, $p = 0.937$). Median water temperatures in all three habitat classes were comparable during the period of wood frog larval development, although maximum water temperatures in the unmodified pond margins were somewhat lower than in beaver canals and open water sites during periods of warm weather (Figure A.7, Appendix A). Although habitat class had a significant effect on mean daily water temperature ($\chi^2 = 18.113$, $df = 2$, $p < 0.001$), I was unable to determine which habitat classes differed using post hoc tests.

Mean CPUE of larval *D. alaskanus* was highest in the unmodified pond margins and in beaver canals, whereas mean CPUE in open water sets was low (Figure 3.2, $D_2 = 15.090$, $p < 0.001$; Table A.6, Appendix A). Based on the 95% confidence intervals of the means, I found that CPUE of larval *D. alaskanus* in beaver canals was significantly higher than in the open water zone, but did not differ significantly from CPUE in unmodified pond margins. Although mean CPUE in the unmodified shorelines was somewhat higher than that of the open water zone, there was a small amount of overlap in the 95% confidence intervals for these two habitat classes (Figure 3.2). Mean CPUE of adult *D. alaskanus* in the unmodified pond margins was slightly lower than in beaver canals, whereas CPUE was considerably lower in the open water zone (Figure 3.2, $D_2 = 17.855$, $p < 0.001$; Table A.7, Appendix A). Based on 95% confidence intervals of the means, CPUE of adult *D. alaskanus* in beaver canals did not differ significantly from CPUE in unmodified pond margins, but CPUE for both of these habitat classes was significantly higher than for the open water zone (Figure 3.2). Anisopteran nymphs tended to be caught more often in beaver canals compared to the unmodified pond margins and the open water zone (Figure 3.2), however this trend was not significant ($D_2 = 5.053$, $p = 0.080$; Table A.8, Appendix A).

I also captured adult dytiscid beetles less than 20 mm total length (e.g. *Agabus, Graphoderus* and *Ilybius spp.*), but these beetles were considered too small to prey on large wood frog tadpoles. Adults of *Hydrochara* spp. were also captured, but these beetles are unlikely to prey on tadpoles because they are scavenging omnivores (Clifford, 1991). Results for small dytiscids and *Hydrochara* are included in Appendix A (Figure A.8, Tables A.9 and A.10). In several of the study ponds, I observed belostomatid water bugs (*Lethocerus americanus* (Leidy, 1847)) which are capable of preying on wood frog tadpoles (Clifford, 1991); however I did not capture this species in minnow traps.

Discussion:

Pond margins tend to be more biologically productive than deeper open water zones, which lack emergent vegetation (Hutchinson, 1957). These productive areas within a pond are attractive to larval anurans in temperate regions, where relatively warm water temperatures speed development (Noland and Ultsch, 1981; Porej and Hetherington, 2005), and my results are consistent with this pattern. Wood frog tadpoles were much more abundant around the margins of the pond than in the deeper pond centre. Tadpoles used beaver canals as well as unmodified pond margins, and their abundance was similar between these two habitat classes. The additional tadpole habitat provided by beaver canals could reduce negative effects of overcrowding of larvae, which are often assumed to limit populations of pond breeding anurans (Alford, 1999). However, I did not collect data on survivorship, size, or developmental rates of tadpoles in each of the three habitat classes.

The steep banks and linear shape of canals suggest that they offer a distinctly different habitat from unmodified pond margins. However, I did not find any difference between trap sites in beaver canals and those in unmodified pond margins, at least for the limited set of habitat characteristics that I measured.

Although beaver canals do not support extensive growth of emergent vegetation, the sedges and grasses that overhang the canal's banks create underwater vegetation structure, with stems and leaves that extend above and below the water surface. Such vegetation was included as emergent vegetation during habitat surveys, even though it was not rooted underwater. The small size of the quadrats I used (only 0.25 m^2) is likely only adequate for characterising the area immediately around trap sites, and my data might not represent the full range of conditions offered by each habitat type. As a result, my comparison of the habitat characteristics of trap sites in beaver canals and the unmodified pond margins may not offer a full comparison of the characteristics of these two habitat classes.

Beaver canals could act as ecological traps for tadpoles if predation risk is higher in canals than along unmodified pond margins. Although there was no difference in the abundance of larval and adult *D. alaskanus* between beaver canals and the unmodified pond margin, the confined environment of a beaver canal could make tadpoles more vulnerable to predation. Larval *D. alaskanus* are flexible predators, able to switch from an active searching strategy to a sit-and-pursue strategy depending on the characteristics of their surroundings (Michel and Adams, 2009). These predators may not show a clear preference for beaver canals over the unmodified pond margins if they can compensate behaviourally for differences between these two habitat classes. Anisopteran nymphs, however, are exclusively sit-and-pursue predators and tended to be more abundant in canals than the unmodified pond margins, and although this pattern was not significant, the *p*-value of 0.080 (generalized linear model) suggests a trend. Canals could be attractive hunting areas for anisopteran nymphs because the confined nature of beaver canals would force groups of tadpoles and other prey animals to pass close to nymphs perched on the dead grasses and sedges that hang into the water along the edges canals.

My research documents the importance of pond margins as habitat for larval anurans in natural wetlands. The design of constructed wetlands is an important factor in determining amphibian abundance, and Shulse *et al.* (2010) recommended that such wetlands should be fish-free, well vegetated and should include shallow areas in order to effectively compensate for lost amphibian habitat. Although many wetland compensation guidelines focus on the area of wetlands lost, there is often no mention of the perimeter of these wetlands (e.g. Water Resources Commission, 1993; Alberta Water Council, 2008). Even if there is no net loss of area, a net loss of wetland margins can still occur if the shoreline of the compensation wetland is less complex than that of the original wetland, or if the loss of several small wetlands is compensated for by the construction of one large wetland. My results suggest that the loss of wetland perimeter is worthy of consideration in compensation efforts, in addition to wetland area.

Tables and Figures

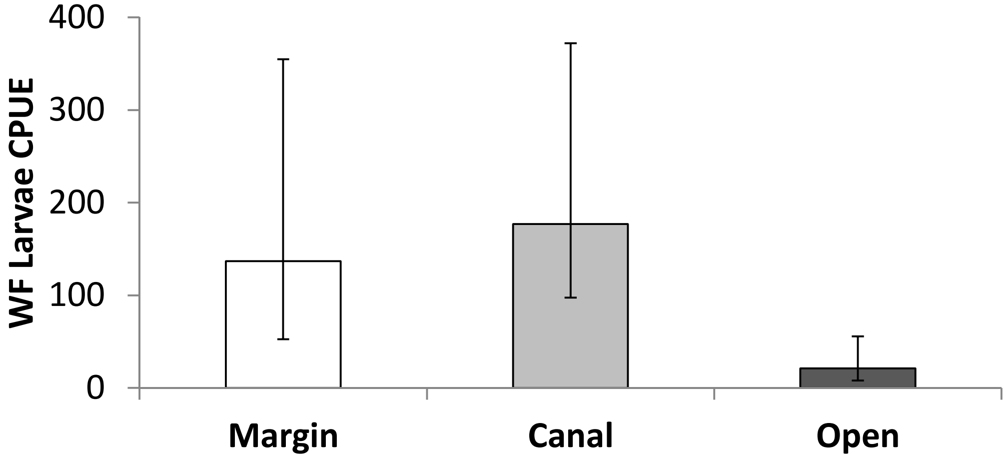

Figure 3.1. Mean number of wood frog tadpoles caught in unmodified pond margins, beaver canals, and the open water zone from one overnight set of five minnow traps per habitat class in 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB between June 1and July 7, 2011. Error bars represent the 95% confidence interval.

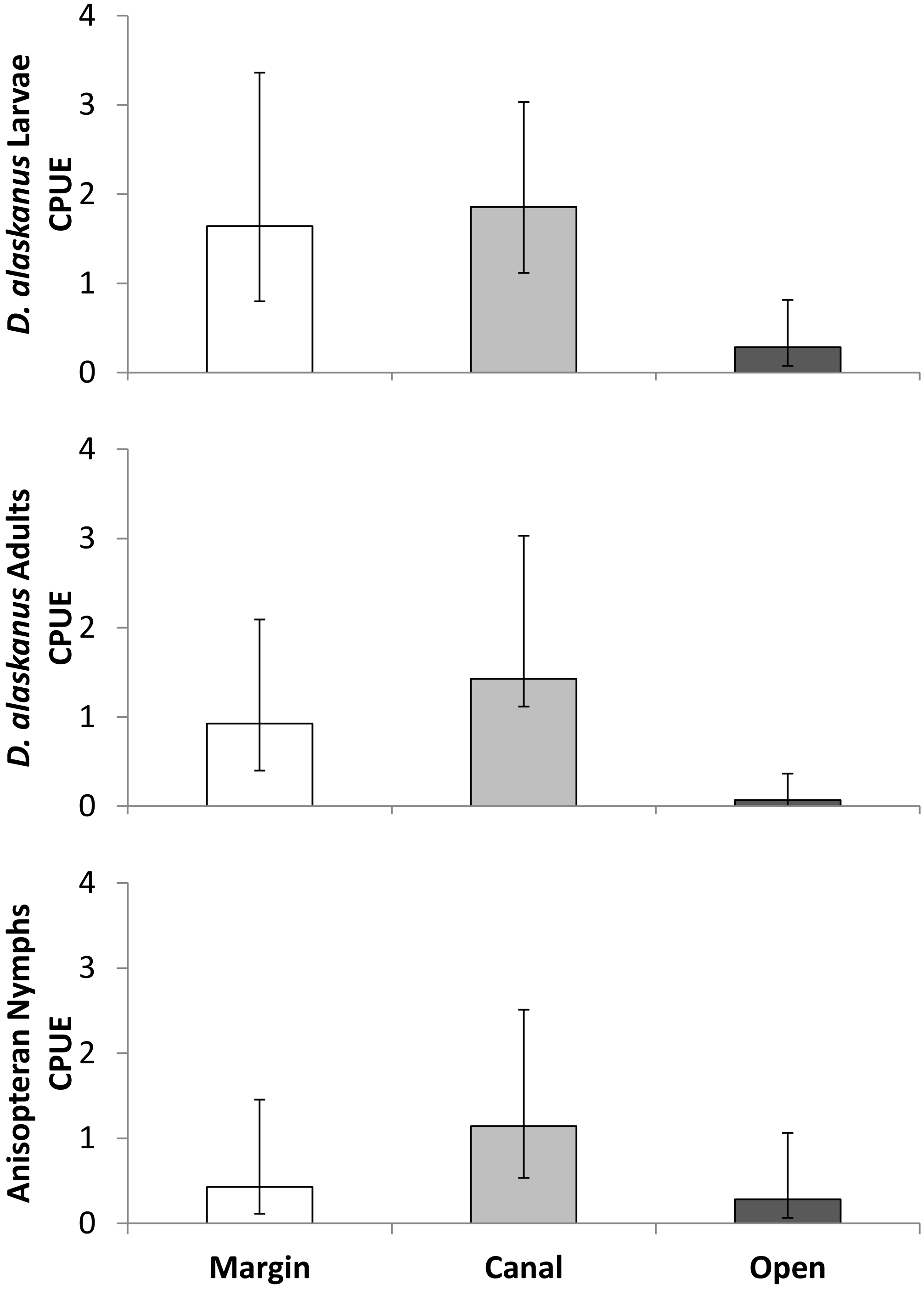

Figure 3.2. Mean number of individuals of three groups of predatory insects caught in unmodified pond margins, beaver canals, and the open water zone from one overnight set of five minnow traps per habitat class in 14 beaver-modified ponds in Miquelon Lake Provincial Park, between June 1 and July 7 2011. Error bars represent the 95% confidence interval.

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Chapter IV: Post-metamorphic wood frogs follow beaver canals during dispersal.

Introduction:

Beavers (*Castor canadensis* Kuhl, 1820) are recognized for their ability to modify their surroundings (Jones *et al.*, 1994). Although best known for damming streams, beavers occupying naturally occurring ponds can also have considerable effects. Beavers are central place foragers (Jenkins, 1980; Collen and Gibson, 2001), and they often dig long canals from their lodges to distant foraging areas, if the substrate is soft and the banks of the pond are not too steep (Berry, 1923; Richard, 1967; Wilsson, 1971). Beavers use these canals to float branches and logs back to their lodge and to escape from terrestrial predators (Johnston and Naiman, 1987; Severud *et al.,* 2011).

Canal digging behaviour by beavers has been well documented in the literature, but in most cases there is little more than a description of the canals. Morgan (1858) provides one of the earliest written descriptions of beaver canals from Michigan, which reached up to 200 m in length. In Montana, Berry (1923), observed one beaver canal that was 340 m, Townsend (1953), also in Montana, reported canals up to 108 m in length and in a northern Ontario peatland, Cowell (1984) observed a 160 m long beaver canal. The Eurasian beaver (*Castor fiber* L., 1758) has also been known to dig canals, as observed in France by Richard (1967) and in Switzerland by Stocker (1985, in Collen and Gibson, 2001). Such observations demonstrate the widespread occurrence of this behaviour, and give some indication of the magnitude of the alterations made to a wetland, yet there has been very little research on how beaver canals affect wetland ecosystems. Canals can alter wetland hydrology, either by diverting water from one pond to another (Butler and Malanson, 1994; Cowell, 1984) or by more efficiently directing surface water into isolated ponds (Hood and Bayley, 2008). Although they may not garner as much attention as dams, canals do represent a considerable modification of the riparian zone that could affect many wetland species, including amphibians.

Pond-breeding amphibians are efficient vectors of energy and nutrient transport between aquatic and terrestrial environments because of their two-stage lifestyle, efficient conversion of ingested food to body mass and the high primary productivity of shallow, warm wetlands in which they breed (Burton and Likens, 1975; Pough, 1980; Davic and Welsh, 2004; Regester *et al*., 2006; Unrine *et al*., 2007). These animals use both aquatic and terrestrial habitats and depend on connectivity between the two to complete their life cycle. Several studies have identified watercourses and ephemeral streams as attractive movement corridors for amphibians (e.g. Eaton, 2007; Okonkwo, 2011), and movement patterns of post-metamorphic frogs may also be affected by the foraging canals that beavers dig through riparian areas.

In this study, I focus on how beaver canals are used by wood frogs (*Lithobates sylvaticus* (LeConte, 1825)), an abundant and widely distributed amphibian throughout the forested regions of Canada and the north-eastern United States

(Russell and Bauer, 2000). Wood frogs breed communally in late April and early May, very soon after ice has retreated from their breeding ponds. Metamorphosis begins in mid-July of the same summer, and young of the year (YOY) frogs typically disperse to nearby upland deciduous forest or shrub cover where they will overwinter (Russell and Bauer, 2000). During one active season, YOY wood frogs typically move further from the pond than adults in spite of their small size. Bellis (1965) observed average total movements of 100 m for YOY versus 11 m for adult wood frogs in a Minnesota peat bog, and Newman and Squires (2001) reported average total movements of 314 m for YOY versus 118 m for adults in pothole wetlands in North Dakota.

Post-metamorphic movements of YOY wood frogs appear to be on a similar scale to the length of beaver canals reported in the literature. In Maine, Calhoun, *et al.* (2005) suggested that most YOY wood frogs disperse less than 230 m from the edge of their natal pond. In the mixed-wood boreal forest of Alberta, MacDonald *et al.* (2006) observed that YOY wood frogs were most abundant within 100 m of the shore of small lakes, but that YOY wood frogs were encountered at upland sites 400 to 600 m from the lakeshore. YOY wood frogs are vulnerable to dehydration while moving towards forested upland habitat, and commonly follow moist corridors during post-metamorphic movements (Gibbs, 1998; Eaton, 2007; Okonkwo, 2011). By providing moist movement corridors through the riparian sedge meadow that surrounds most of my study ponds, beaver canals might facilitate YOY frog movement from their natal pond to upland forest cover. Although the sedge meadow may not be the driest environment a juvenile frog will face, the high density of sharp sided sedge stems in the riparian meadow in July and August may further impede movement. If beaver canals do help YOY wood frogs disperse into the upland forests, these canals could alleviate density dependent effects of overcrowding that can occur in the terrestrial environment following metamorphosis (Harper and Semlitsch, 2007; Patrick *et al.,* 2008; Berven, 2009).

The purpose of my study was to determine how post metamorphic movement patterns of YOY wood frogs are affected by beaver canals. I hypothesized that YOY wood frogs in my study sites show typical patterns of dispersal to uplands following metamorphosis (Hypothesis 1), and I predicted net movement away from breeding ponds from mid-July to the end of August. As they disperse, I hypothesized that YOY wood frogs follow beaver canals through the riparian meadow towards terrestrial feeding and overwintering habitats in nearby deciduous forests (Hypothesis 2). I predicted that dispersing YOY wood frogs would be relatively more abundant on beaver canals compared to the shoreline where it was not modified by beavers (hereafter referred to as the unmodified shoreline). I also predicted that dispersing YOY wood frogs would be encountered more often near beaver canals than in the adjacent riparian meadow. I also hypothesized that beaver canals improve YOY wood frog survival, and that this is reflected in the relative abundance of breeding female wood frogs at a pond (Hypothesis 3). I predicted that the relative abundance of breeding females would increase with the density of beaver canals on a pond. Although beaver canals could also provide additional sites for female wood frogs to lay eggs, canals are not attractive oviposition sites and aggregations of wood frog egg masses were rarely found in beaver canals in my study ponds (Chapter II).

Methods:

Study area

I conducted research in Miquelon Lake Provincial Park (MLPP), which is approximately 65 km SE of Edmonton, Alberta in the Cooking Lake moraine (Figure A.3 and Table A.4, Appendix A). This region is comprised of dry-mixed wood boreal forest surrounded by aspen parkland, although much of the parkland has been converted to agriculture (Natural Regions Committee, 2006). The moraine consists of kame and kettle topography, with many isolated basin ponds. The forest is dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) with an understory of beaked hazelnut (*Corylus cornuta* Marshall), Saskatoon berry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem) and scattered patches of white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marshall). Ponds are surrounded by riparian meadows which are dominated by sedges (*Carex spp.*) and reed canary grass (*Phalaris arundinacea* L.), often with a fringe of cattail (*Typha latifolia* L.) or giant bulrush (*Schoenoplectus spp.*) around the pond edge, and scattered willow (*Salix spp.*) in the meadow. Ponds used in this study range from 0.24 to 8.86 ha in area, 43 to 1290 µg/L total phosphorus (TP), 1580 to 3900 µg/L total nitrogen (TN) and are less than 2.5 m maximum depth (Table A.4, Appendix A). These ponds are semi-permanent to permanent water bodies (Class IV and V wetlands according to Stewart and Kantrud, 1971), and their levels fluctuate from year to year. No fish have been encountered in the past five years of sampling, and it is unlikely that any of the study ponds supports a population of fish due to low dissolved oxygen over winter and very little connectivity between ponds. Wood frogs, boreal chorus frogs (*Pseudacris maculata* (Agassiz, 1850)) and western tiger salamanders (*Ambystoma mavortium* Baird (1850)) are common in the park.

Data collection

To address Hypotheses 1 (that YOY wood frogs disperse from their natal pond following metamorphosis) and Hypothesis 2 (that dispersing YOY wood frogs follow beaver canals), I captured recently metamorphosed wood frogs using drift fences constructed on two beaver canals on each of four ponds in 2011 and added two more ponds in 2012 for a total of six ponds. I selected canals over 30 m in length, and on opposite sides of the pond where possible, because wood frogs do not disperse evenly in all directions from their natal pond (Patrick, 2007). Each array consisted of three 4.5-m long fences set perpendicular to the canal, with each fence divided into three equal sections by 50-cm projections of fence material (Figure 4.1). Fence 1 was set 20 m towards the pond from the end of surface water in the canal, Fence 2 at the end of surface water in the canal, and Fence 3 20 m beyond the end of surface water in the canal, where either a moist ditch or a faint beaver-foraging trail was present. Fences were checked almost daily from July 28 to September 1 in 2011 and on weekdays from July 16 to August 30 in 2012. I started checking fences earlier in 2012 because wood frog breeding occurred about a week earlier than in 2011, which could have caused metamorphosis to commence earlier as well. Two surveyors checked fences in the morning, from about 0630 to 1100 h, when frogs were slow moving because of low temperatures and vegetation was typically still moist from the previous night's dew. From one visit to the next, I alternated the order in which I visited arrays, as well as the order that sections within a fence were checked in order to eliminate bias. Both sides of the fence were checked simultaneously, and all frogs within 50 cm of the main fence were counted and assigned to a size class. Wood frogs were considered to be YOY if their snout to urostyle length (SUL) was less than 27 mm and to be adults that had overwintered at least once if their SUL was greater than or equal to 27 mm (Okonkwo, 2011; MacDonald, 2006).

I also addressed Hypothesis 2 (that dispersing YOY wood frogs follow beaver canals) using time-constrained visual encounter surveys along the shorelines of 14 ponds from July 13 to August 26, 2011 and from August 2 to 31, 2012. Two observers walked the entire shoreline of these ponds and recorded the number of wood frogs (YOY if SUL < 27 mm, adult if SUL ≥ 27 mm) seen on the unmodified shoreline and on beaver canals. Canals were easily distinguished from the unmodified shoreline in the field based on their long, narrow shape, steep banks and perpendicular junction with the unmodified shoreline. To avoid counting individual frogs more than once on canal transects, surveys were performed from the junction with the pond to the end of the canal, with one observer on either side of the canal. Transects were timed, and counts corrected for search time in both the unmodified shoreline and beaver canals. Total length of unmodified shoreline transects on a pond ranged from 206 to 729 m, and total length of beaver canal transects on a pond ranged from 166 to 905 m.

Differences in CPUE can reflect differences in either relative abundance or detection probability (Mazerolle *et al.*, 2007; Schmidt and Pellet, 2010). To determine the probability of detecting YOY wood frogs in both beaver canals and the unmodified shoreline, I conducted visual searches for life size models of YOY wood frogs (hereafter referred to as 'frog decoys'), a similar approach to that of Williams and Berkson (2004) and Saul (2008). I constructed frog decoys using biodegradable play-dough: water, white flour, salt and cream of tartar, and added cocoa powder to achieve a pale brown colour. Decoys were approximately 2.5 cm long, with shallow ridges running along the body (Figure 4.2). Three small black beads were glued to the head region to simulate eyes, at least one of which would be visible however the decoy was placed. Half of a wooden toothpick was inserted into the hind end of the decoy to mimic a leg. All decoys were baked in an over at 200º C for 3 hours to dry the dough and improve durability in moist environments. I deployed 15 decoys randomly along a 3-m wide and 15-m long transect (consistent with the highest densities of YOY frogs observed) in late August 2012, the same time of year that visual transect surveys for live frogs were conducted. Transects were established using a 15-m throw bag, and decoys were tossed on to the transect from a few metres to one side to avoid trampling vegetation. The streamlined shape of the decoys allowed them to penetrate thick vegetation and come to rest at or near the ground. Two surveyors, naïve to the location and number of decoys, were allowed up to 4 minutes to search the transect, which resulted in a similar pace to that of visual encounter surveys for live frogs. We conducted searches for decoys on 26 transects in each habitat type on three ponds (6, 10 and 10 transects per pond as dictated by pond size). Searches were timed, and the proportion of frog decoys recovered was corrected for search time, standardized to 4 minutes.

To address Hypothesis 3 (that breeding females are relatively more abundant on ponds with high densities of beaver canals), I conducted call surveys from April 27 to May 16 in 2011 and from April 20 to May 2 in 2012 on 22 beaver-modified ponds to determine where wood frogs were breeding. I revisited chorus sites during daylight and counted the number of egg masses as an estimate of the number of breeding females, as a female wood frog lays a single egg mass each year (Russell and Bauer, 2000). Aggregations of wood frog egg masses (> 10 egg masses within 4 m^2; Seale, 1982) were revisited at least three times after breeding began. Amphibian populations can fluctuate from one year to the next, so I took the average of the total number of egg masses on a given pond as an estimate of the relative abundance of breeding female wood frogs for that pond. I used pond perimeter as a measure of the available habitat at each pond, because wood frogs predominantly use pond margins in both breeding and larval development (Russell and Bauer, 2000; Alford, 1999; Porej and Hetherington, 2005; Chapters II and III of this thesis).

To address how primary productivity might differ between these ponds, and possibly affect growing conditions for larval wood frogs, I collected a water sample from each pond on June 20, 2011. These samples were processed by the

University of Alberta Biogeochemical Analytical Lab to determine total nitrogen (Flow Injection Analysis using a Lachat QuikChem 8500 FIA automated ion analyzer), total phosphorous (Flow Injection Analysis using a Lachat QuikChem 8500 FIA automated ion analyzer) and chlorophyll-a (using a Shimadzu RF-1501 spectrofluorophotometer) as measures of primary productivity in each of these ponds. I used Quantum GIS version 1.7.4 Wroclaw (Quantum GIS Development Team, 2011) and an orthographic aerial photo (0.25-m pixel size) from 2007 (when water levels were similar to 2011 and 2012) to determine the density of canals on each of these ponds (number of canals per metre of shoreline, measured at 1:250 scale).

Statistical analysis

To test Hypothesis 1 (that YOY wood frogs disperse from their natal pond following metamorphosis), I compared the total number of wood frog encounters between the front (pond facing) and back (forest facing) sides of the fence using a chi-squared test goodness of fit test to determine if there was net movement of YOY wood frogs away from the pond. I also encountered adult wood frogs on drift fences, and I used a separate chi square goodness of fit test to determine if there was net movement by adults towards or away from the pond from mid-July to the end of August. I conducted separate analyses for each year.

Using data collected from drift fences, I tested Hypothesis 2 (that dispersing YOY wood frogs follow beaver canals) using a generalized linear model with repeated measures, fitting a negative binomial distribution to test the effect of fence section (a discrete measure of distance from the canal) on the weekly encounter rate of YOY wood frogs, after accounting for differences between arrays (eight in 2011 and twelve in 2012) and weeks (five in 2011 and six in 2012). For this analysis, I combined the number of YOY wood frogs encountered on both sides of the fence for each section and pooled by week to reduce the number of zeros in the dataset. I conducted separate tests for each fence (Fence 1, Fence 2, and Fence 3) in each year (2011, 2012) using the "MASS" and "stats" packages in Program R version 2.15.1 (Venables and Ripley, 2002; R Core Team, 2012). Following significant results ($\alpha = 0.05$), I used 95% confidence intervals to determine which fence sections differed.

I also tested Hypothesis 2 using the data collected from shoreline visual encounter surveys. I calculated the relative abundance of YOY wood frogs by dividing CPUE by detection probability, *p(D)*, which was calculated based on data generated by decoy searches and using the following equation:

$$p(D) = \frac{N\ decoys\ recovered}{Search\ time\ in\ seconds} \times \frac{240\ seconds}{Search\ time\ in\ seconds}$$

Relative abundance of YOY wood frogs was compared between canal and shoreline habitats using a Wilcoxon rank sum test, with data paired by pond ($n = 14$, $\alpha = 0.05$) using the "stats" package in Program R version 2.15.1 (R Core Team, 2012). I conducted separate analyses for each year.

To test Hypothesis 3 (that breeding females are relatively more abundant on ponds with high densities of beaver canals), I compared 16 candidate linear models for predicting the relative abundance of breeding female wood frogs on a pond using Akaike's "Information Criterion" (corrected for small sample sizes, AICc). All models included pond perimeter as a measure of the amount of habitat available for use by both terrestrial and aquatic stages of the wood frog life cycle. Three models were based on the assumption that relative abundance of breeding females is limited by conditions faced by larval wood frogs, and included a measure of primary productivity from 2011 water samples, either total nitrogen, total phosphorous, or chlorophyll-a. Three models were based on the assumption that relative abundance of breeding females is limited by conditions in the terrestrial environment and included distance to the nearest neighbouring shoreline, average width of the riparian meadow ($Rw = \surd(\text{Pond Perimeter}^2/(4\pi^2)+\text{Riparian Area}/\pi) - \text{Pond Perimeter}/\pi$), or both. A null model including only pond perimeter (pond size) and a global model including all variables (based on the hypothesis that the relative abundance of breeding female wood frogs is limited by conditions in both the terrestrial and aquatic environment) were also constructed. The remaining eight models were identical to the previous ones, but included the density of beaver canals (number of canals per metre of shoreline) as an additional predictor of wood frog abundance. I considered models to be equivalent if Δ AICc ≤ 2 (Burnham and Anderson, 2002).

Results:

In 2011, I encountered 3,273 YOY and 71 adult wood frogs on eight drift fence arrays over the 5 week sampling period and in 2012, I encountered 1,200 YOY and 208 adult wood frogs on 12 drift fence arrays over the 6 week sampling period. In both years, the total number of YOY wood frogs encountered on drift fences in a given day declined over the sampling period (Figure A.9, Appendix A) and YOY wood frogs were encountered significantly more often on the side of the fence facing the pond compared to the side of the fence facing away from the pond (2011: $\chi^2 = 11.146$, $df = 1$, $p < 0.001$; 2012: $\chi^2 = 25.628$, $df = 1$, $p < 0.001$; Figure 4.3). However, there was no difference in the number of adult wood frogs encountered on the side of the fence facing the pond compared to the side of the fence facing away from the pond in either 2011 ($\chi^2 = 0.352$, $df = 1$, $p = 0.553$) or 2012 ($\chi^2 = 0.296$, $df = 1$, $p = 0.586$).

In 2011, YOY wood frogs were encountered more often at the end of the fence set in the canal for the Fences 1 and 2, but the encounter rate was more uniform along Fence 3 (Figures 4.4). At Fence 1 (20 m towards the pond from the end of water in the canal) and Fence 2 (at the end of water in the canal), YOY wood frogs were encountered more often at the section of the fence closest to the canal than at either of the other two sections (Fence 1: $D_2 = 79.791$, $p < 0.001$; Table A.11; Fence 2: $D_2 = 130.338$, $p < 0.001$; Table A.12, Appendix A). At Fence 3 (20 m beyond the end of water in the canal), there was an effect of distance from canal on the weekly number of YOY encountered ($D_2 = 9.116$, $p = 0.010$; Tables A.13,

Appendix A), but I was unable to determine which fence sections differed, as there was overlap in the 95% confidence intervals of all three sections.

In 2012, the total number of YOY wood frog encounters was lower, but the patterns were similar to those observed in 2011: YOY wood frogs were more commonly encountered at the canal end of Fences 1 and 2, but encounter rates were uniform along Fence 3 (Figure 4.5). At Fence 1, YOY wood frogs were encountered significantly more often at the fence section closest to the canal compared to the section farthest from the canal ($D_2 = 68.553$, $p < 0.001$; Table A.14, Appendix A). At Fence 2, although there was a significant effect of distance to canal on the number of YOY wood frog encounters ($D_2 = 36.069$, $p < 0.001$; Table A.15, Appendix A), I was unable to determine which fence sections differed based on the 95% confidence intervals of the means. There was no difference in the weekly number of YOY wood frogs encountered among the three sections of Fence 3 ($D_2 = 0.962$, $p = 0.618$; Table A.16, Appendix A).

In both 2011 and 2012, the pattern of higher encounter rate of YOY wood frogs at the end of Fences 1 and 2 set in the beaver canal was most pronounced in the first weeks of the sampling period, but the same trend was observed in later weeks, as the number of frogs encountered declined. Adult wood frogs were also encountered more commonly at the section of the fence closest to the canal in both years; however, I did not perform any statistical comparisons of the encounter rate of adult wood frogs among fence sections because of low weekly catch numbers. YOY wood frogs were also encountered more often at Fence 1 compared to Fence 2, and more often at Fence 2 compared to Fence 3 in both

2011 and 2012. Such a pattern is typical of drift fences (of equal length) set at increasing distances from the breeding pond, and could be the result of frogs spreading out as the perimeter of their dispersing front increases with distance from the pond, as well as the possibility that some individuals may not reach the more distant fences.

During visual encounter surveys of pond shorelines, 6,015 YOY and 366 adult wood frogs were observed in 2011, and 380 YOY and 316 adults in 2012. In both years, YOY wood frogs were relatively more abundant on beaver canals than on the unmodified shoreline. In 2011, median relative abundance of YOY wood frogs was nine times higher than on the unmodified shoreline (Figure 4.6; $V = 105$, $n = 14$, $p < 0.001$). In 2012, median relative abundance of YOY wood frogs was six times higher than on the unmodified shoreline (Figure 4.7; $V = 91$, $n = 14$, $p = 0.013$). Detection probability of frog decoys was slightly higher on transects in the unmodified shoreline (mean $p(D) = 0.45$) compared to beaver canals (mean $p(D) = 0.35$) and this difference was marginally significant (paired t-test: $t = 2.000$, $df = 25$, $p = 0.056$, Figure A.10, Appendix A).

Adult wood frogs were also more commonly observed on beaver canals than on the unmodified shoreline in both 2011 and 2012 (Figure A.11, Appendix A). No adult wood frogs were observed at one pond in 2011, and on a different pond in 2012; these ponds were removed from analyses. In 2011, median relative abundance of adult wood frogs was 26 frogs per hour on canals and only 6 frogs per hour on the unmodified shoreline ($V = 91$, $n = 13$, $p < 0.001$). In 2012, median relative abundance of adult wood frogs was 45 frogs per hour on canals and only 18 frogs per hour on the unmodified shoreline (V= 79, n = 13, p = 0.017).

The relative abundance of breeding female wood frogs, as estimated from egg mass counts and averaged between 2011 and 2012, tended to increase with the density of beaver canals on a pond (Figure A.12, Appendix A). The best model for predicting the abundance of breeding female wood frogs only included distance to nearest neighbouring shoreline (with a positive coefficient) in addition to pond perimeter (Table A.17, Appendix A). The AICc scores of three other models were within two points of the top model: the model that included only pond perimeter (with a negative coefficient); the model that included total phosphorous (with a negative coefficient) in addition to pond perimeter; and the model that included the density of beaver canals (with a positive coefficient).

Discussion:

In both years YOY wood frogs were more commonly encountered on the side of the fence facing the pond compared to the side facing the uplands, thereby supporting Hypothesis 1. I concluded that these frogs were dispersing to upland habitats from their natal pond when I encountered them. Although total catch of YOY wood frogs declined gradually from late July to the end of August in 2011, the decline was much more abrupt in the second week of sampling in 2012 (Figure A.8, Appendix A). Such a pattern could reflect mass emigration of YOY wood frogs after a synchronised metamorphosis, but could also be explained by a gradual decline in activity as dictated by weather conditions or high mortality of

YOY after metamorphosis. The number of adult frogs encountered on drift fences also declined over the sampling period, which would be consistent with frogs moving less as conditions become drier over the last half of summer as I did not find evidence of directional movement, either towards or away from the pond, by adults.

The results of both drift fence surveys and shoreline visual encounter surveys support Hypothesis 2. On drift fences, YOY wood frogs were encountered more often on beaver canals compared to the adjacent riparian meadow, if there was water present in the canal. The number of frogs encounters also declined with distance from the breeding pond. However, differences in drift fence captures may not reflect relative abundance if for example, animals are moving at different rates along the canal and through the adjacent riparian meadow (Willson and Gibbon, 2010) and the presence of surface water could reduce dehydration stress or allow frogs to move more quickly through the dense, sharp-sided vegetation of the riparian meadow. At a broader spatial scale, on visual encounter surveys of the entire pond shoreline, YOY wood frogs were many times more abundant on beaver canals compared to the unmodified shoreline, indicating that these frogs are attracted to beaver canals during post-metamorphic movements from their natal pond to upland habitats. By using decoys to quantify detection probability, I can be confident that these patterns reflect a real difference in relative abundance, and not merely a difference in the number of frogs seen.

Adult wood frogs also appear to use beaver canals preferentially over the unmodified shoreline in the late summer, but I did not find strong evidence for directional movement by adults, either towards or away from the pond in mid to late summer. Regosin *et al.* (2002) suggested that male wood frogs will overwinter close to the breeding pond, in order to begin calling as soon as possible after spring thaw, and Eaton (2007) observed adult wood frogs in boreal Alberta migrating towards breeding ponds in August, at the same time as post-metamorphic frogs were dispersing away from the pond. Adult migration towards the pond may take place before I began my drift fence sampling in late July, or may occur in the spring, when I was not monitoring drift fences. Adult frogs are not as vulnerable to dehydration as YOY, but may still be using beaver canals as a way to maintain access to water. Migrating adults could also be using beaver canals as landmarks to find their way to breeding ponds.

Migrating anurans rely on many sensory cues to find their way to breeding sites, including olfactory, visual and acoustic cues. Acoustic cues, such as male vocalizations, are only effective once a breeding chorus is established and can only be heard over a relatively short distance (Sinsch, 2006). Berven (1982) found that adult wood frogs transplanted from Virginia to ponds in Maryland did not show the same homing response towards breeding sites as did the resident frogs that had developed and metamorphosed in these ponds, which suggests that wood frogs learn their migratory routes early in life. Heemeyer and Lannoo (2012) determined that individual crawfish frogs (*Lithobates areolatus* (Baird and Girard, 1852)) repeatedly used an almost identical, convoluted path to move between breeding and overwintering sites. Repeatedly using such circuitous paths suggests that crawfish frogs are not capable of path integration (dead reckoning) to find the most direct path back to the breeding pond after overwintering, and instead rely on piloting by a sequence of landmarks learned during dispersal. If wood frogs also rely on landmarks rather than dead reckoning to find their way back to the breeding pond, then by following beaver canals as YOY, frogs could be using these as landmarks to follow during future migrations as adults.

Although YOY wood frogs are attracted to beaver canals during post-metamorphic dispersal, I do not have direct evidence that they benefit from using these corridors. Density dependent mortality of YOY wood frogs can be high immediately after metamorphosis (Patrick *et al.*, 2008; Berven, 2009), and beaver canals might improve YOY survival by assisting recently metamorphosed frogs in dispersing away from their natal pond. If recruitment plays a larger role than immigration in determining the abundance of females breeding on a pond, then higher YOY survival would be reflected in the number of females returning to breed on their natal pond. Wood frogs are typically a very philopatric species, and Berven and Grudzien (1990) determined that 82% of frogs returned to their natal pond to breed in the Shenandoah Mountains of Virginia. In a deciduous woodland in Pennsylvania, Meier (2007) found that all YOY wood frogs returned to their natal pond to breed, even though distances between ponds were only 35 – 185 m. Wood frogs are capable of dispersing several kilometres, and those breeding on ponds separated by up to 5.5 km show little genetic differentiation (Berven and Grudzien, 1990; Newman and Squire, 2001; Squire and Newman, 2002; Vasconcelos and Calhoun, 2004). However, such genetic connectivity can be maintained with as few as one individual moving between ponds per generation (Crow and Kimura, 1970), and the abundance of breeding female wood frogs at a pond is usually assumed to be driven by recruitment more than immigration and emigration (e.g. Stevens *et al.*, 2006).

Although higher YOY survival would be reflected in female relative abundance, this is not the only possible explanation for the positive correlation between the density of beaver canals and the relative abundance of breeding females. Beaver canals could provide habitat for larval wood frogs, alleviating negative density dependent effects on growth and survival to metamorphosis (Skelly and Kiesecker, 2001; Berven, 2009; Chapter II of this thesis). Therefore, higher relative abundance of breeding female wood frogs in ponds with a greater density of beaver canals could be the results of more larvae surviving to metamorphose, and thus more females returning to breed on their natal pond. Alternatively, the weak correlation between relative abundance of breeding female wood frogs and the density of beaver canals might not reflect a direct causal relationship. When beaver-modified ponds experience low water levels as a result of hydrologic succession, the basin shoreline is reduced while the number of beaver canals typically does not change as the canals are also dug into the bottom of shallow parts of the pond. As a result, the density of beaver canals would be expected to increase as a pond accumulates sediment, or loses water due to climatic shifts. Such a pond may present favourable conditions for wood frogs including warm, shallow water, that are not the result of a high density of beaver canals. Stevens *et al.* (2006) determined that adult wood frog relative abundance (based on call ranks) and juvenile recruitment (based on pitfall trap captures on drift fences covering 20% of the pond shoreline) was higher on old beaver ponds compared to new ones, and attributed this result to both hydrologic succession of the pond and reduced canopy cover resulting from years of beaver foraging.

A future study could test if there is a causal relationship between beaver canals and wood frog abundance by monitoring the relative abundance of breeding females on ponds before and after filling in the beaver canals. Ideally these ponds would be more than 1000 m from the nearest breeding site so that the relative abundance of female wood frogs reflects recruitment rather than immigration or emigration. Because wood frogs can live for about 5 years in Alberta (Russell and Bauer, 2000), monitoring would have to be continued for many years after experimental manipulations before any effect on the relative abundance of breeding female frogs would be detectable. Because of the cost and time involved with this approach, an alternative would be to compare relative abundance of breeding female wood frogs between ponds modified by beaver canals and ponds that have not been modified in this way. However, the study sites used would have to be carefully selected to control for other factors that could affect the relative abundance of wood frogs, including area, perimeter, depth, nutrient concentrations and characteristics of the terrestrial environment, such as vegetation structure and distance to nearest neighbouring wetland.

Tables and Figures

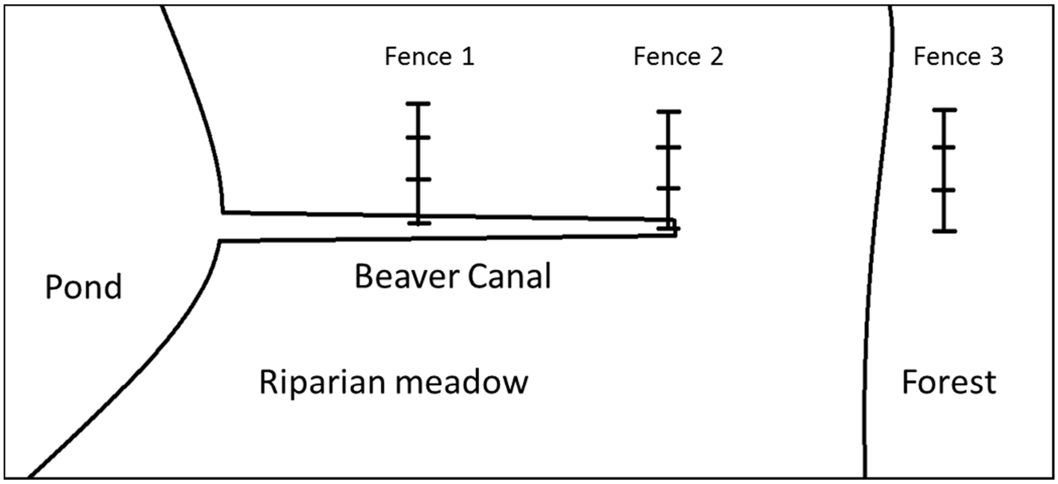

Figure 4.1. Diagram of the layout of drift fence arrays installed on two beaver canals on each of four ponds in 2011 and six ponds in 2012 in Miquelon Lake Provincial Park, AB. Each fence was 4.5 m long and divided into three equal sections by 50 cm projections of fence material. Fences were made of 90 cm wide landscaping fabric buried 15 cm into the soil.

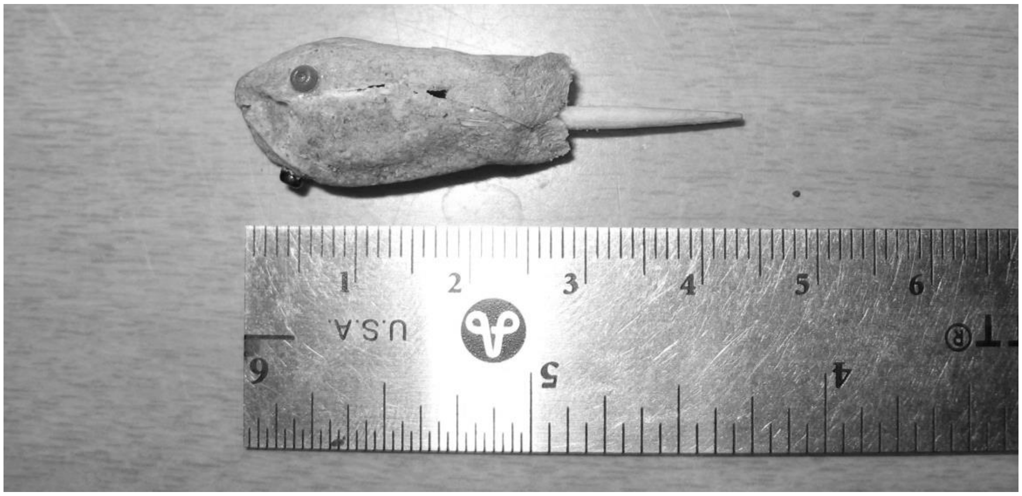

Figure 4.2. An example of a frog decoy (SUL = 28 mm) used to determine the detectability of YOY wood frogs in beaver canals and unmodified shorelines in Miquelon Lake Provincial Park, in late August , 2012. A third bead (not visible) was glued to the other side of the decoy's head, and the half toothpick mimics a leg.

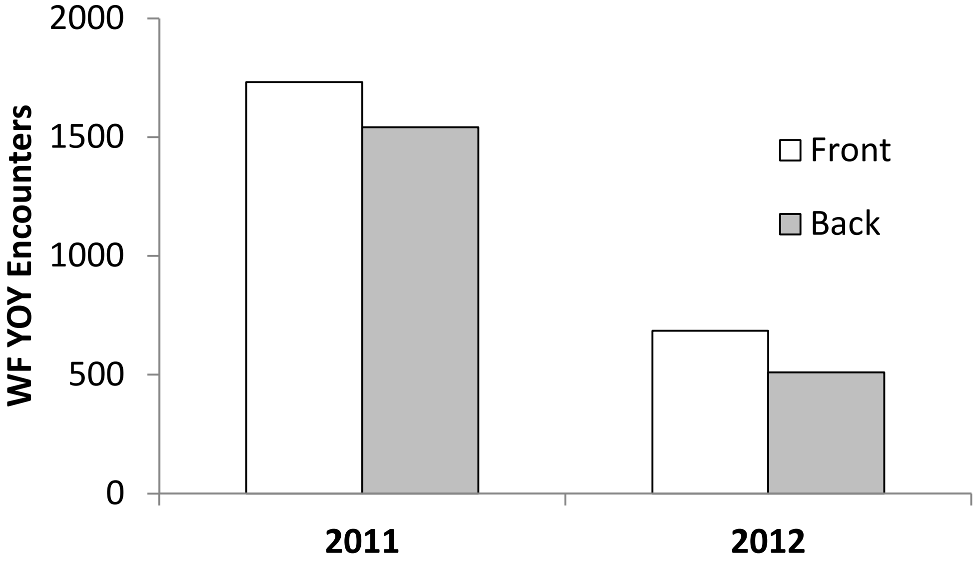

Figure 4.3. Total number of wood frog YOY encountered on the side of drift fences facing the pond (front) and the side facing away from the pond (back) on eight drift fence arrays in 2011 (Jul. 28 to Sept. 1) and 12 arrays in 2012 (Jul. 16 to Aug. 30), in Miquelon Lake Provincial Park, AB.

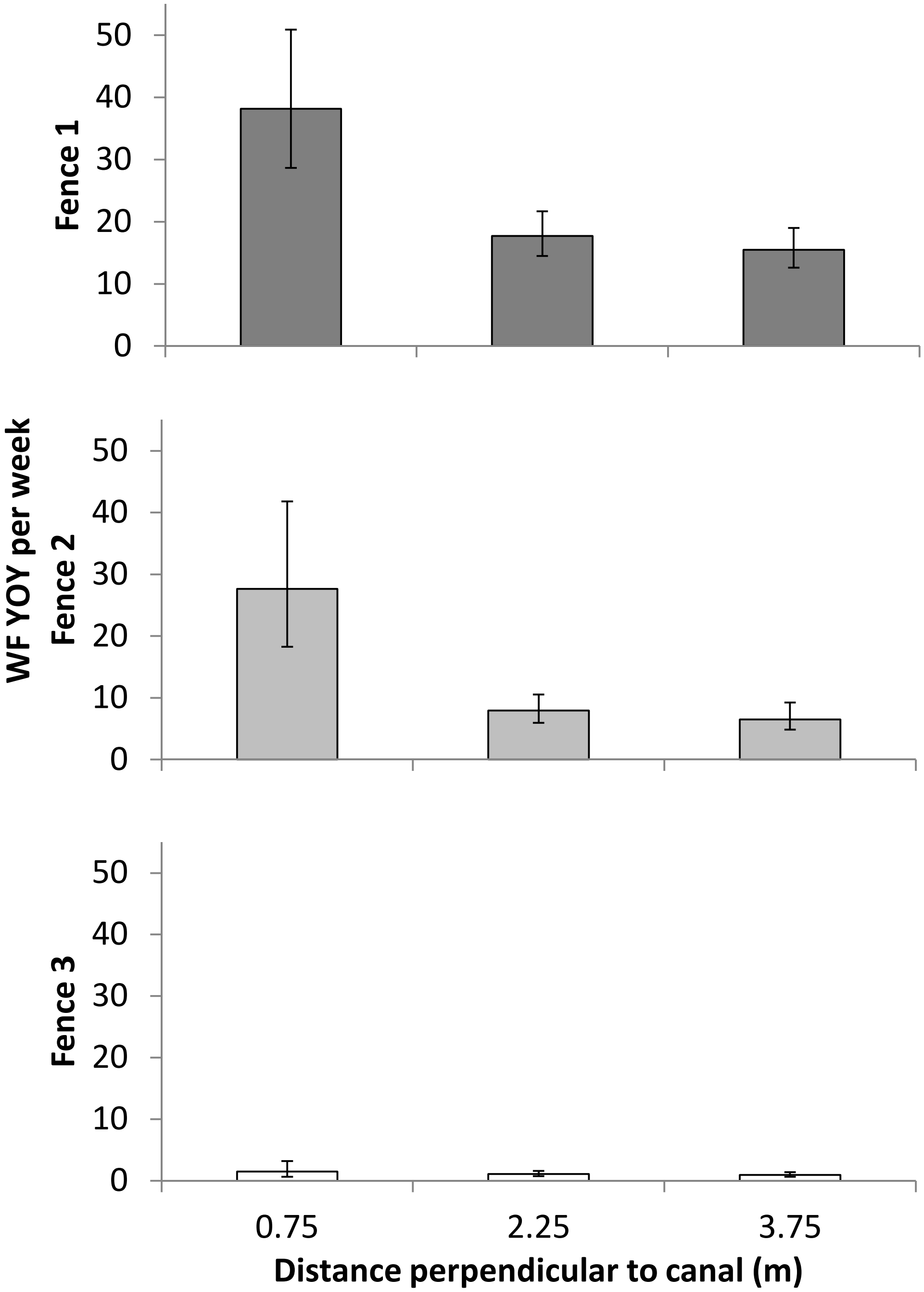

Figure 4.4. Mean number of wood frog young-of-the-year captured per week, at three distances perpendicular to the beaver canal (error bars represent 95% confidence intervals). Drift fences were located 20 m before the end of water in the canal (Fence 1), at the end of the canal (Fence 2), and 20 m beyond the end of the canal (Fence 3) on two canals in each of four ponds in Miquelon Lake Provincial Park, AB and monitored from late-July to the beginning of September, 2011.

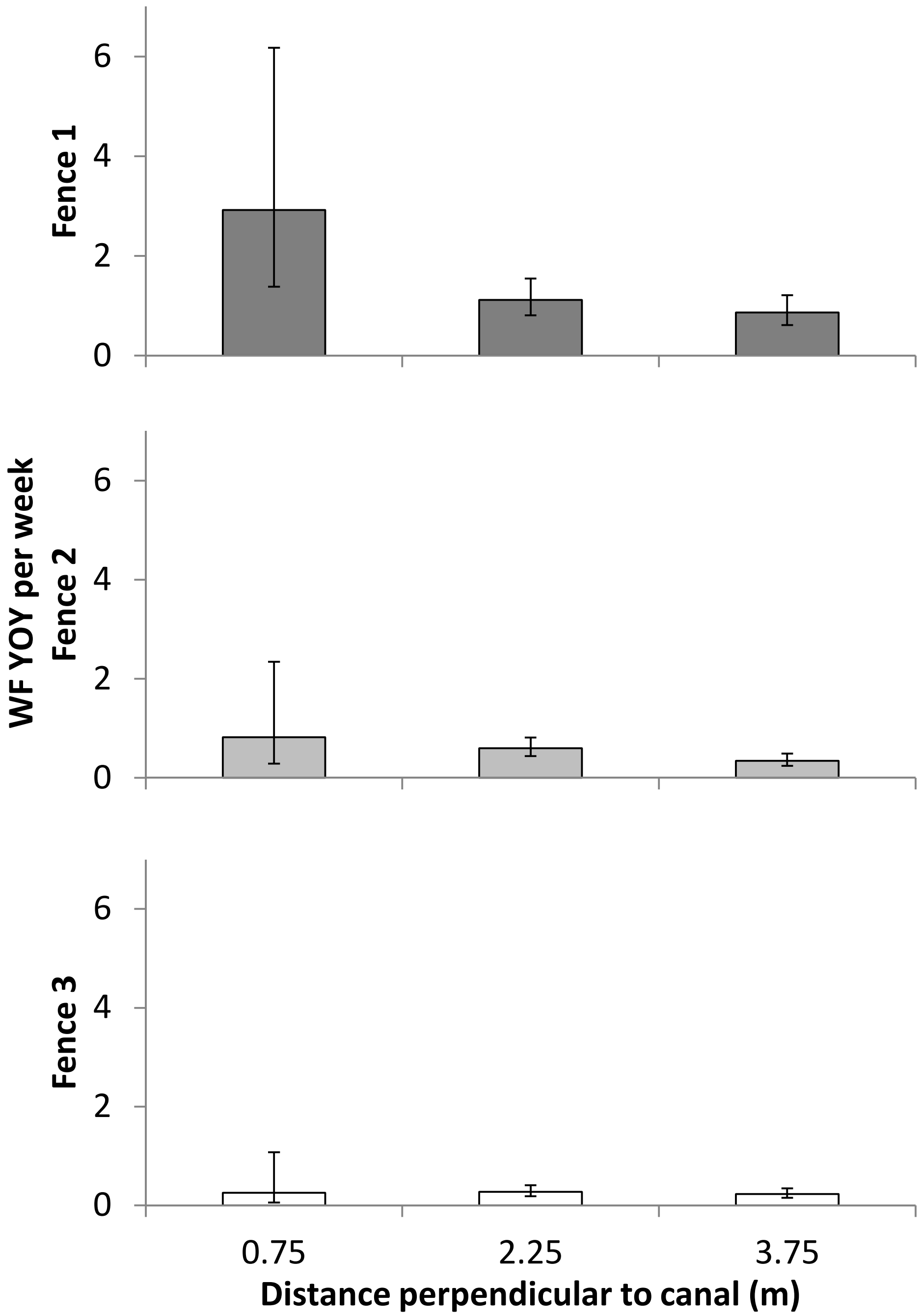

Figure 4.5. Mean number of wood frog young-of-the-year captured per week, at three distances perpendicular to the beaver canal (error bars represent 95% confidence intervals). Drift fences were located 20 m before the end of water in the canal (Fence 1), at the end of the canal (Fence 2), and 20 m beyond the end of the canal (Fence 3). These arrays were set on two canals in each of six ponds in Miquelon Lake Provincial Park, AB and monitored from mid-July to the end of August, 2012.

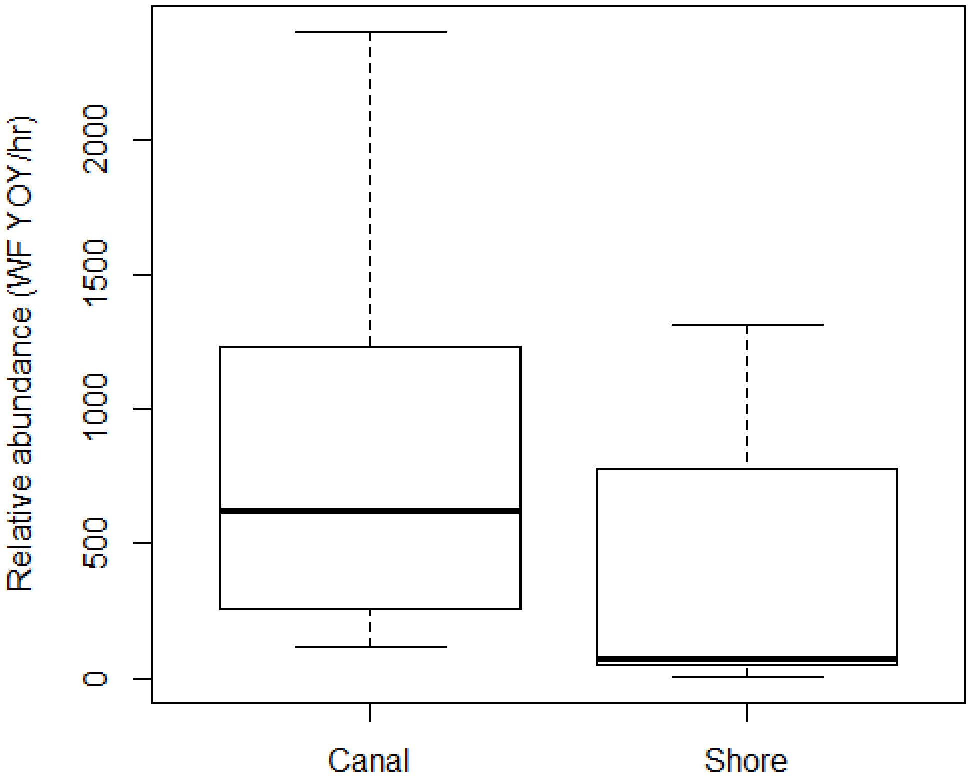

Figure 4.6. Boxplot showing mean and interquartile range of YOY wood frog relative abundance (CPUE/p(D)) in beaver canals and the unmodified shoreline from a single visual encounter survey of all beaver canals and unmodified shoreline on each of 14 ponds in Miquelon Lake Provincial Park, AB, July and August 2011.

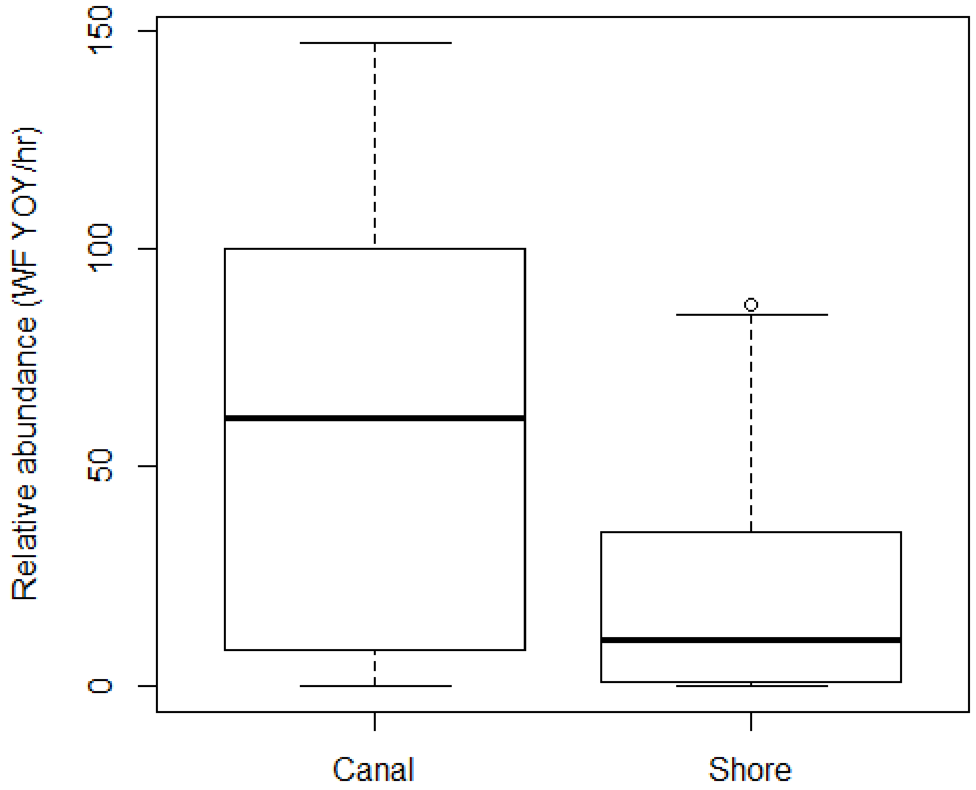

Figure 4.7. Boxplot showing mean and interquartile range of YOY wood frog relative abundance (CPUE/p(D)) in beaver canals and the unmodified shoreline from a single visual encounter survey of all beaver canals and unmodified shoreline on each of 14 ponds in Miquelon Lake Provincial Park, AB, August 2012.

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Chapter V: Summary and conclusions

Amid growing concern over widespread amphibian declines, there is a need to develop innovative strategies to conserve these species. Although many studies have identified the habitat characteristics that determine amphibian occupancy among ponds (e.g. Laan and Verboom, 1990; Pope *et al.*, 2000), few have investigated how amphibians use specific habitat features within a pond, and to the best of my knowledge my study is among the first to address how amphibians at various stages of their life cycle use the habitat features created by beavers (*Castor canadensis* Kuhl, 1820) within ponds. I determined that patterns of wood frog (*Lithobates sylvaticus* (LeConte, 1825)) breeding, larval habitat use and post-metamorphic dispersal in pothole wetlands are profoundly affected by the small scale habitat features created by beaver canals and lodges. Wood frog adults avoided laying their eggs in beaver canals or near lodges, but tadpoles were attracted to both beaver canals and the unmodified pond margins. After metamorphosis, YOY wood frogs followed beaver canals as they moved toward upland forest habitats (Figure 5.1).

Wood frogs typically lay eggs in communal aggregations along the north shoreline of ponds, in shallow water, and supported by submerged vegetation (Russel and Bauer, 2000; Chapter II). In this way, egg masses are kept near the surface where insolation and black body effects keep the eggs warmer than the surrounding water and speed embryonic development (Herreid and Kinney, 1967; Seale, 1982; Stevens and Paszkowski, 2004; Chapter II). Beaver lodges and foraging canals are rarely used by wood frogs for oviposition (Chapter II), perhaps because of their steeply sloping banks and relatively deep water. Beaver foraging may contribute to reduced canopy cover and warmer temperatures in the pond as a whole (Skelly and Freidenburg, 2000; Stevens *et al.*, 2006), but this effect was not addressed by my study. Most of my study ponds were surrounded by a fringe of wet meadow and low prairie about 20 m wide, and these ponds probably would not have an overhead canopy regardless of beaver foraging.

After eggs hatch, wood frog tadpoles spend from 50 to 60 days in the pond (Russell and Bauer, 2000). Anuran larvae often face intense intraspecific competition for food resources, which can negatively affect survival and size at metamorphosis (Russell and Bauer, 2000; Alford, 1999; Skelly and Kiesecker, 2001; Whiting, 2010) and cold water temperatures can also limit the rate of development (Herreid and Kinney, 1967; Skelly and Freidenburg, 2000; Stevens *et al.,* 2006). Wood frog tadpoles primarily use pond margins, possibly to take advantage of warmer temperatures or more abundant food resources (Noland and Ultsch, 1981; Porej and Hetherington, 2005). In my study sites, tadpoles were as abundant in beaver canals as they were along unmodified pond margins (Chapter III). Canals may alleviate negative density-dependent effects of overcrowding by providing near shore habitat if suitable food resources are also present, but I did not address the availability of tadpole food sources. Aquatic insects capable of predating on tadpoles were also present in beaver canals, although these predators were not any more abundant in canals than along the unmodified pond margins.

The confined environment of canals might make tadpoles particularly susceptible to predation, but I did not address this possibility.

In mid-July, wood frog tadpoles undergo metamorphosis and begin to move away from the pond towards upland forests, where they forage and overwinter. Metamorphosis is fairly synchronous, resulting in high densities of YOY wood frogs near the pond. These newly metamorphosed frogs must disperse to terrestrial feeding areas to reduce intraspecific competition, but are especially vulnerable to water loss because their small bodies have a higher surface area to volume ratio than those of the larger adults. YOY wood frogs often follow moist movement corridors during dispersal (Eaton, 2007; Okonkwo, 2011). Eaton (2004) suggested that water and deciduous forest have very low resistance to wood frog movement, but that areas with closely packed plant stems and a lack of canopy cover can make movement difficult. To reach the deciduous forest surrounding my study ponds, frogs had to traverse a wide riparian meadow which lacked a shrubby canopy, at a time of year when thistles, sharp sided sedges and grasses were prominent and the weather was typically hot and dry. By following beaver canals, dispersing frogs can stay near water while moving a considerable distance from the pond towards the closed canopy deciduous forest where they can move more freely. Exceptional individuals may disperse from their natal pond to breed on ponds over 1 km away (Berven and Grudzien, 1990; Newman and Squires, 2001; Smith and Green, 2005), and marked wood frogs in the mixed-wood boreal forest have been observed in upland habitat as far as 400 m from their natal pond in the spring following metamorphosis (C. Paszkowski, *personal* *communication*). However, such movement represent exceptional individuals, while the distance that most newly metamorphosed wood frogs travel before overwintering for the first time is much less. For example, in Maine, Calhoun, *et al.* (2005) found that most YOY wood frogs remain within 230 m of their natal pond. If most YOY wood frogs overwinter for the first time within several hundred metres of their natal pond, beaver canals, which commonly exceed 200 m in length, could provide these frogs with movement corridors for much of the distance to overwintering sites.

Beavers occupying pre-existing ponds have different effects on their surroundings than beavers inhabiting lotic systems. Beaver dams create barriers on streams while canals dug by beavers can enhance connectivity between separate wetlands (Cowell, 1984; Collen and Gibson, 2001). Jones *et al.* (1994) define an ecosystem engineer as "an organism that directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials", and suggest that ecosystem engineers with a large impact on their surroundings are those with large per capita impacts, living at high densities, over large geographic areas, for a long time, producing durable structures and affecting many resource flows. Applying these criteria to the impacts of beavers in pothole wetlands, I argue that beavers have large impacts on their surroundings resulting from their construction of foraging canals and lodges.

Networks of foraging canals that more than double the amount of shoreline edge are a considerable modification to the riparian zone (Johnston and Naiman, 1987, Hood and Larson, *in review*). These networks represent the work of a colony of beavers, usually made up of two adults, two yearlings, and sometimes a pair of two year olds if they have not yet dispersed (Svensden, 1989). Canal networks are probably the result of construction and maintenance efforts across multiple generations of beavers, as is the case for large dams (Butler, 1991). Beaver colonies are present in high densities in Miquelon Lake Provincial Park, where beavers have built lodges and foraging canals on almost every pond (Bromley and Hood, 2013). At the time of this study, MLPP hosted approximately one occupied beaver lodge and six unoccupied lodges per square kilometre. Although they were extirpated from much of east-central Alberta by the late 1800s as a result of intense trapping, subsequent management and reintroductions have allowed beavers to recolonize much of their former geographic range, as is the case throughout much of North America (Naiman, *et* al. 1986; Naiman *et al.* 1988; Hood and Bayley, 2008).

Beaver canals likely persist for decades after beavers have ceased maintaining them (Naiman *et al*., 1988), and in my study area, several ponds that had not been occupied by beavers for several years still had very clearly defined canals. These canals affect the availability of resources within and among wetlands by altering hydrology (Johnston and Naiman, 1987; Cowell, 1984) and possibly make ponds more resistant to drying during droughts, as reported for landscapes where beavers were present versus absent (Hood and Bayley, 2008). Occupied beaver lodges facilitate early spring thaw, and provide attractive nesting sites for Canada geese (*Branta canadensis* L. 1758) (Bromley and Hood, 2013). Canals also contribute to shoreline complexity, providing unique habitats within ponds for larval anurans and aquatic macro-invertebrates (Chapter III; Hood and Larson, *in review*) and provide connectivity between aquatic and terrestrial environments by facilitating the movement of post-metamorphic wood frogs from the pond to upland forests (Chapter IV). According to criteria put forward by Jones *et al.* (1994), beavers should be considered ecosystem engineers with large impacts on their surroundings as a result of their construction of foraging canals and lodges, even in pothole wetlands where beavers seldom build large dams, if they build dams at all.

As beavers continue to expand into their former range, land managers should be aware of their impacts and ecological roles in novel environments (Zav'yalov *et al.*, 2010). Land managers can use beaver canals as a means of identifying likely movement corridors for wood frogs, and perhaps other amphibians. My findings are also relevant to the restoration of degraded wetlands, and the design of constructed wetlands. The use of ecosystem engineers, like beavers, has been suggested as a means of restoring degraded wetland habitats (e.g. Rosemond and Anderson, 2003; Byers *et al.*, 2006), and based on my results, I suggest that this strategy might be of use even in pothole wetlands where beavers might not build dams. If beavers cannot be allowed in a constructed or restored wetland, their canals could be mimicked to achieve the same functional linkage between aquatic and terrestrial habitats. As Wright and Jones (2006) suggested, the impacts of ecosystem engineers, such as beavers, varies depending on their surroundings. If the use of beavers in wetland restoration becomes more common, managers should be aware of how the impacts of beaver differ among various types of aquatic systems and integrate these differences into their planning.

Figures

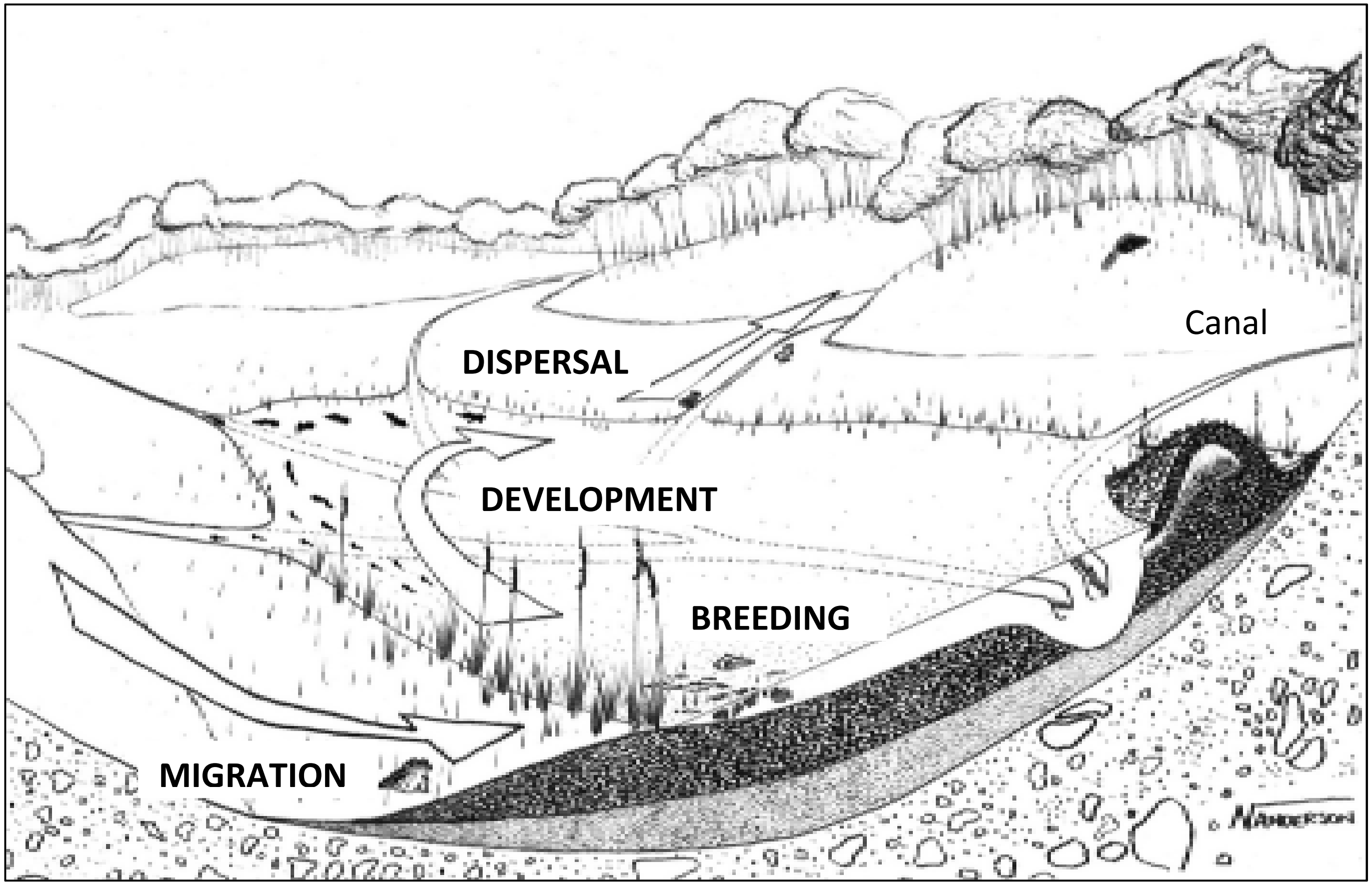

Figure 5.1. Wood frog habitat use in a beaver-modified pothole wetland from breeding site selection in early spring (Chapter II of this thesis), larval development through to midsummer (Chapter III), to post-metamorphic dispersal in late summer and early fall (Chapter IV).

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Appendix A

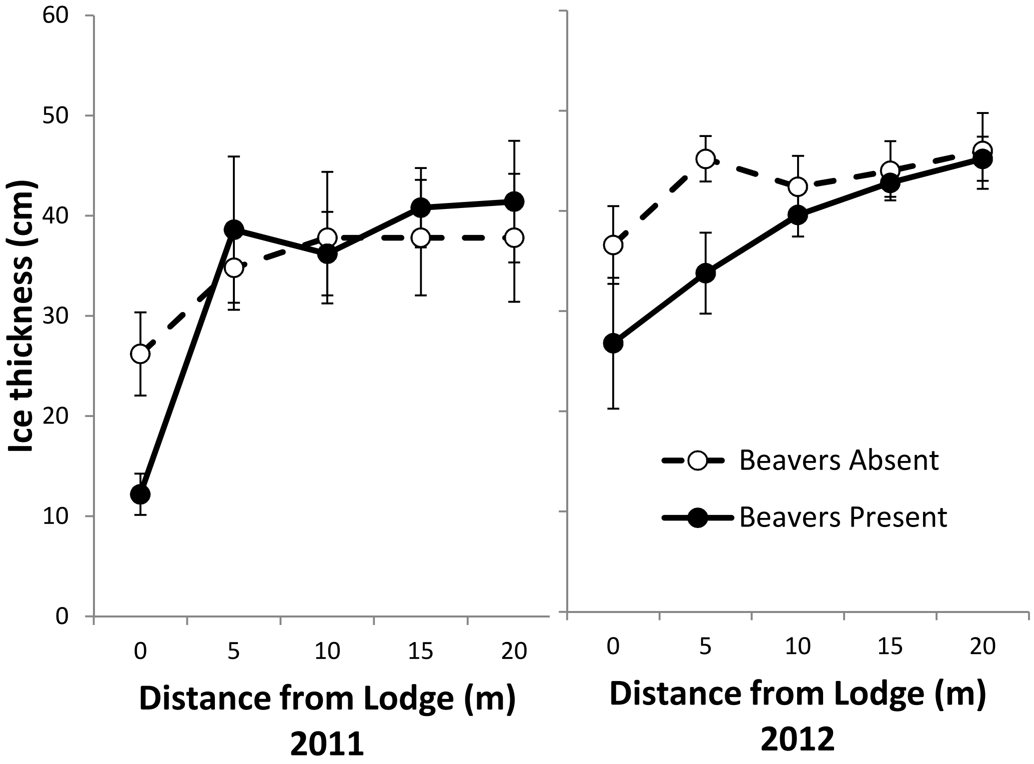

Figure A.1. Ice thickness versus distance from the beaver lodge for five lodges with and five lodges without beavers, sampled from late January to early February in 2011 and 2012 at Miquelon Lake Provincial Park, AB.

Table A.1. Results of a two way ANOVA blocked by lodge, on the effect of beaver occupancy on ice thickness along 20 m transects from the lodge, using 5 lodges with beavers and 5 without in Miquelon Lake Provincial Park, AB in late January and early February 2011. Tukey's Honestly Significant Difference tests of pairwise comparisons of ice thicknesses are presented below. The highlighted cells refer to contrasts between lodges with and without beavers, the cells above and to the right of the highlighted ones refer to contrasts between distances for lodges with beavers, and those to the left and below the highlighted cells refer to contrasts between distances for lodges without beavers.

Source	***df***	**SS**	**MS**	***F* ratio**	***p*-value**
Distance	4	2941	735	16.919	<0.001
Beaver	1	14	14	0.311	0.581
Beaver*Distance	4	574	144	3.301	0.023
Lodge	8	4194	524	12.062	<0.001
Error	32	1391	44		
Total	99	9114			

Pairwise comparisons:	0 m	5 m	10 m	15 m	20 m
0 m	$p = 0.055$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
5 m	$p = 0.565$	$p = 0.995$	$p > 0.999$	$p > 0.999$	$p > 0.999$
10 m	$p = 0.185$	$p = 0.999$	$p > 0.999$	$p = 0.981$	$p = 0.958$
15 m	$p = 0.185$	$p = 0.999$	$p > 0.999$	$p = 0.999$	$p > 0.999$
20 m	$p = 0.185$	$p = 0.999$	$p > 0.999$	$p > 0.999$	$p = 0.997$

Beavers Present

Beavers Absent

Beavers Present vs. Absent

Table A.2. Results of a two way ANOVA blocked by lodge, on the effect of beaver occupancy on ice thickness along 20 m transects from the lodge, using five lodges with beavers and five without in Miquelon Lake Provincial Park, AB in late January and early February 2012. Tukey's Honestly Significant Difference tests of pairwise comparisons of ice thicknesses are presented below. The highlighted cells refer to contrasts between lodges with and without beavers, the cells above and to the right of the highlighted ones refer to contrasts between distances for lodges with beavers, and those to the left and below the highlighted cells refer to contrasts between distances for lodges without beavers.

Source	***df***	**SS**	**MS**	***F* ratio**	***p*-value**
Distance	4	1128	282	7.782	<0.001
Beaver	1	338	338	9.330	0.005
Beaver*Distance	4	252	63	4.494	0.001
Lodge	8	1302	163	1.738	0.166
Error	32	1159	36		
Total	99				

Pairwise comparisons:	0 m	5 m	10 m	15 m	20 m
0 m	$p = 0.270$	$p = 0.707$	$p = 0.054$	$p = 0.007$	$p = 0.001$
5 m	$p = 0.441$	$p = 0.121$	$p = 0.873$	$p = 0.379$	$p = 0.121$
10 m	$p = 0.873$	$p = 0.999$	$p = 0.999$	$p = 0.997$	$p = 0.894$
15 m	$p = 0.641$	$p > 0.999$	$p > 0.999$	$p > 0.999$	$p > 0.999$
20 m	$p = 0.322$	$p > 0.999$	$p = 0.993$	$p > 0.999$	$p > 0.999$

Beavers Present

Beavers Absent

Beavers Present vs. Absent

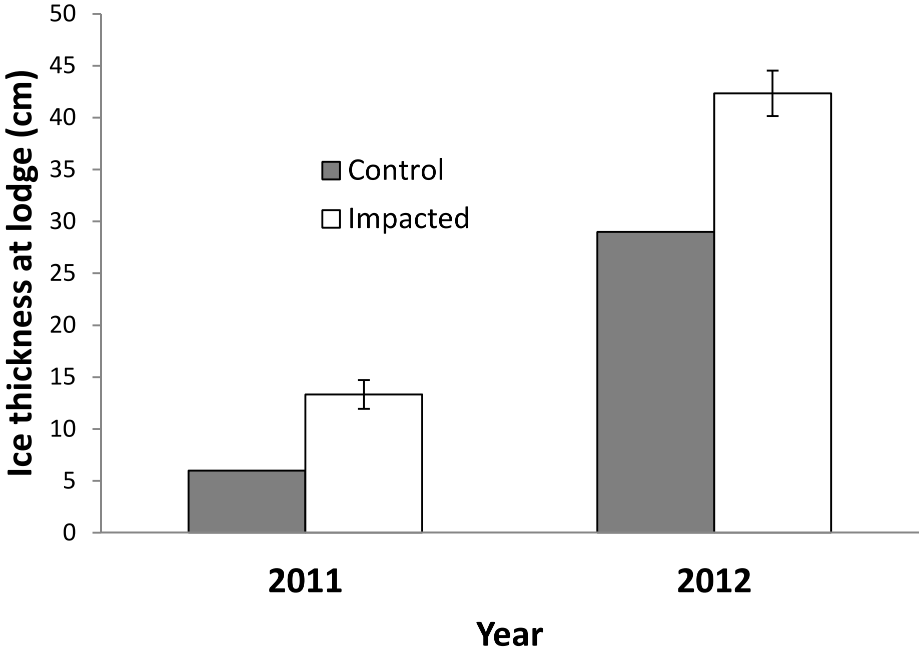

Figure A.2. Modified Before-After Control-Impact analysis of the effect of beaver abandoning a lodge on ice thickness at the food cache of one lodge with beavers in both years and three lodges that had beavers in 2011, but were abandoned in 2012 in Miquelon Lake Provincial Park, AB.

Table A.3. Results of a before-after/control-impact analysis of the effect of beaver presence on ice thickness at the food cache of one lodge with beavers in both years and three lodges that had beavers in 2011, but were abandoned in 2012 in Miquelon Lake Provincial Park, AB.

Source	***df***	**SS**	**MS**	***F* ratio**	***p*-value**
BA	1	1512.5	1512.5	49.590	0.020
CI	1	160.2	160.2	5.251	0.149
BA*CI	1	13.5	13.5	0.443	0.574
Lodge	2	2.3	1.2	0.9632	0.963
Error	2	61.0	30.5		
Total	7	1749.5			

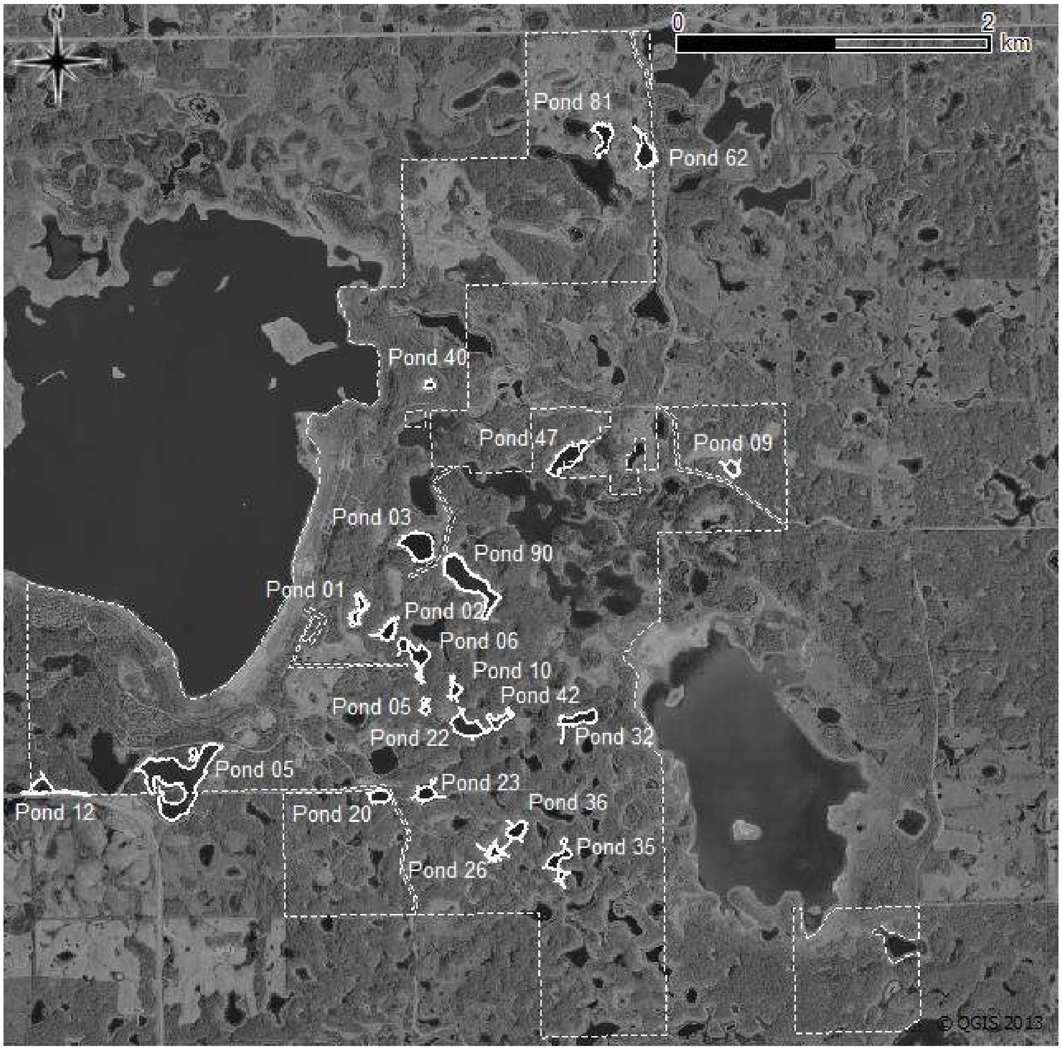

Figure A.3. Map of Miquelon Lake Provincial Park, AB with park boundaries represented by a dashed line and study ponds outlined in white on a 2007 aerial photo.

Table A.4. Physical characteristics of the 22 ponds in Miquelon Lake Provincial Park, AB, that were used in this study, and the types of amphibian data that were collected from each of the 22 study ponds. Four temperature loggers (one each in the unmodified pond margins, beaver canals, food caches and open water zones) on ponds 05, 06, 12, 20, 22, 23, 26, 32, 47, and 90. Call surveys and egg mass counts were performed on all 22 ponds in both 2011 and 2012, but no breeding was detected on pond 90 in both years, and it was not included in determining relative habitat availability for wood frog oviposition. Both tadpole trapping and shoreline visual encounter surveys for YOY wood frogs was conducted on ponds 01, 02, 09, 11, 12, 20, 23, 26, 32, 35, 36, 40, 47 and 62. Two drift fence arrays were constructed on beaver canals of ponds 01, 02, 35 and 36 in 2011, with the addition of ponds 23 and 36 in 2012. Locations are provided in projection system NAD83 Alberta 3TM reference meridian 114.

Pond ID	Northing	Easting	Area (m2)	Perimeter (m)	Riparian Width (m)	Nearest neighbour shore (m)	Canal count	Total canal length (m)	Total N (µg/L)	Total P (µg/L)	Chl a (µg/L)	Secchi depth (cm)	pH	Conductivity (µS)	TDS (ppm)	Salinity (ppm)	2011 Beaver	2012 Beaver
1	74490	5902029	6000	469.7	19.6	157.5	28	670.0	2960	191	3.76	58	7.36	1208	840	601	0	0
2	74677	5901890	7100	372.3	25.1	60.6	22	545.6	2140	48	2.74	>66	7.73	992	703	480	0	0
3	74873	5902443	29600	768.0	23.4	90.4	10	245.6	2560	61	0.89	96	7.82	1627	1150	810	0	0
5	73365	5900954	88600	2400.0	6.0	39.8	8	73.4	2370	158	2.23	127	7.92	1300	924	638	1	1
6	74836	5901758	13300	643.3	13.8	4.9	13	552.5	2300	133	3.85	>104	8.04	1147	813	564	0	0
9	76879	5902943	5600	357.6	11.7	47.7	20	353.5	2020	389	2.31						1	0
10	75102	5901534	4200	411.6	13.4	103.7	17	335.2	2040	112	2.14	81	7.5	500	355	238	0	0
11	74907	5901414	2200	334.4	8.8	136.8	13	182.6	3240	467	1.56	65	7.72	1273	900	620	1	0
12	72445	5900889	13200	978.9	2.7	30.0	7	90.2	2040	504	2.19	62	7.21	1054	748	507	1	1
20	74620	5900842	8300	376.2	4.1	26.5	12	67.1	1856	356	1.94	77	7.22	930	659	451	1	1
22	75170	5901276	14100	689.2	10.8	49.7	16	289.6	3900	1290	3.28						0	0
23	74910	5900852	8200	363.0	33.0	167.3	16	306.7	1580	49	5.3	108	7.36	1069	759	516	0	0
26	75358	5900474	2900	254.0	41.4	125.5	27	745.7	2200	140	2.49	86	7.34	1241	879	600	0	0
32	75908	5901343	12600	588.7	17.4	89.8	25	332.1	2340	54	3.51						0	0
35	75746	5900423	13900	939.6	11.0	30.7	26	245.8	2220	260	3.87	91	7.42	1247	885	603	1	1
36	75504	5900614	7400	372.5	21.6	125.5	25	380.7	2700	83	2.55	120	7.54	1420	1010	693	1	0
40	74942	5903474	2400	205.9	21.6	163.8	7	63.2	6400	253	3.36	24	4.98	656	462	310	0	0
42	75397	5901326	6100	449.7	9.6	49.7	5	73.1	3780	765	11.02						1	1
47	75813	5903005	22800	788.6	7.6	43.2	17	111.3	3190	120	1.57	154	7.19	1347	956	653	1	1
62	76325	5904965	14900	662.2	29.7	166.1	22	265.8	2250	43	1.57						0	0
81	76063	5905075	12200	580.3	24.5	48.6	10	111.5	2440	125	7.83						1	1
90	75157	5902227	49700	1330.0	16.2	72.7	15	254.0	5280	313	3.04						1	1

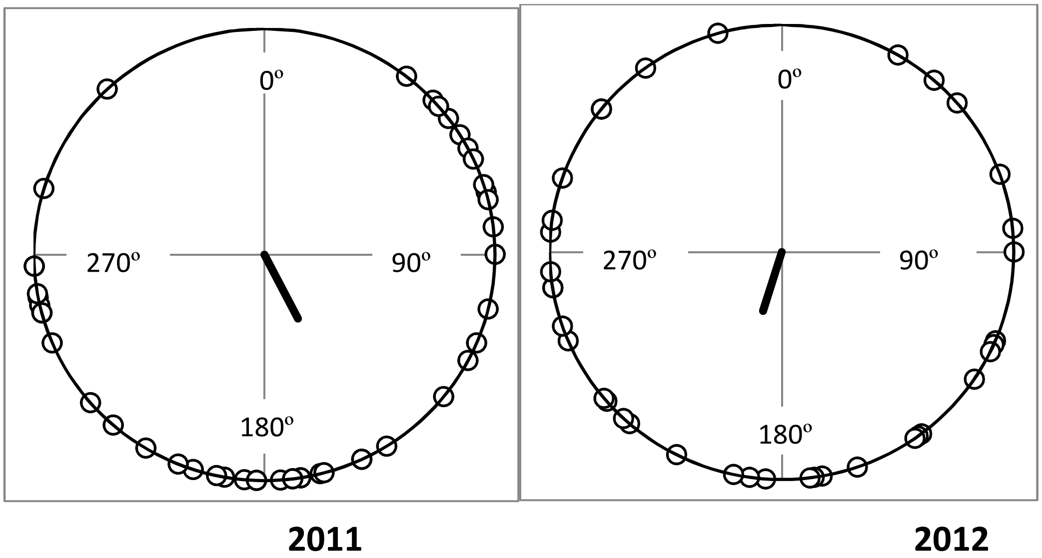

Figure A.4. Mean shoreline aspect of aggregations of wood frog egg masses on 21 ponds in Miquelon Lake Provincial Park, AB in both 2011 (ā = 153º, z = 4.642, n = 46, $p < 0.01$) and 2012 (ā = 197º, z = 2.7262, n = 37, $0.05 < p < 0.10$).

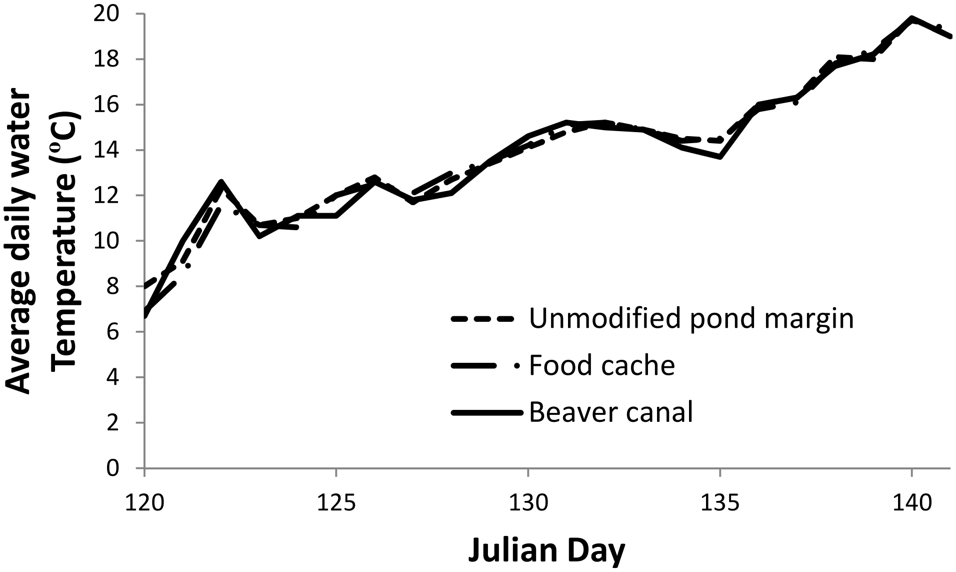

Figure A.5. Median water temperature from iButton temperature loggers set in unmodified pond margin, food cache (adjacent to the lodge) and beaver canal sites in five ponds (one with beavers and four without) in Miquelon Lake Provincial Park, AB from April 30, 2011 when wood frogs began laying eggs to May 21, 2011 when most eggs had hatched.

Table A.5. Results of a generalized linear model using a negative binomial link function, testing for differences in the number of wood frog tadpoles caught in one overnight set of five minnow traps in the unmodified pond margins, five traps in beaver canals, and five traps in the open water zone from 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Habitat class	2	17.295	<0.001
Residual	39	50.446	
Total	41	67.741	

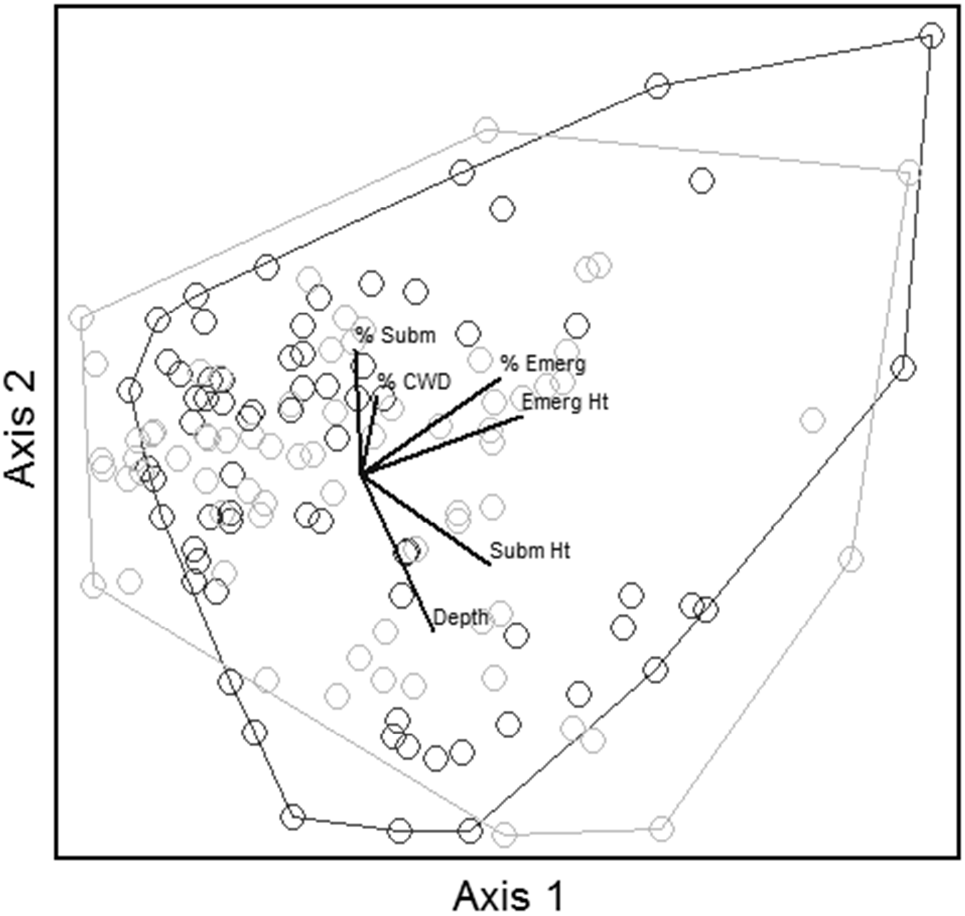

Figure A.6. Principal components analysis of standardized ($(x_i - \overline{x})/s$) depth, % cover and height of emergent vegetation, % cover and height of submerged vegetation, % cover of coarse woody debris from 0.25 m^2 quadrats at five tadpole trapping locations each in beaver canals (black) and the unmodified pond margin (grey) of 14 ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011. Axis 1 explains 27.0 % of the variance, Axis 2 explains 20.6% of the variance.

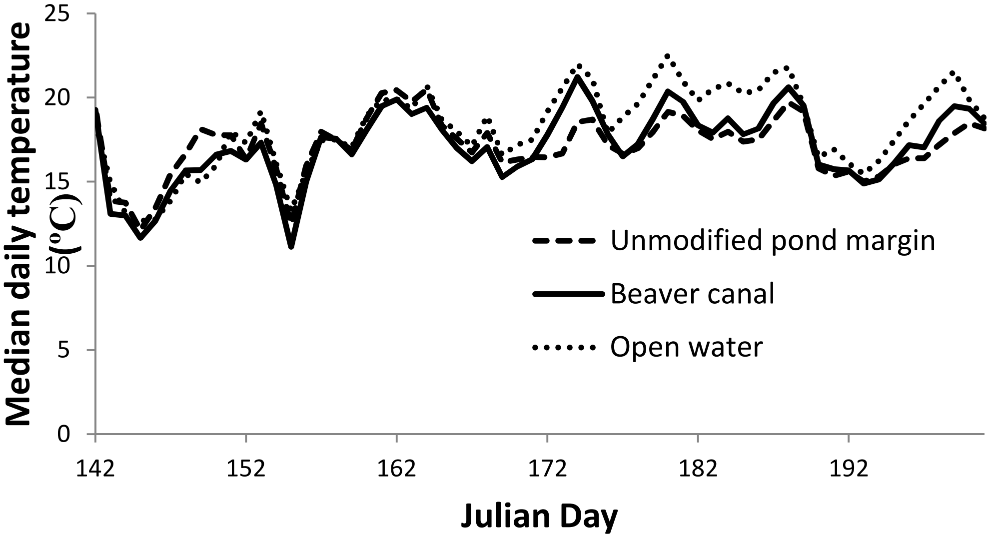

Figure A.7. Median daily temperature of unmodified pond margin, beaver canals, and open water zones of five ponds during the period of wood frog larval development (May 22 to July 20, 2011).

Table A.6. Results of a generalized linear model using a negative binomial link function, testing for differences in the number of larval *Dytiscus alaskanus* caught in one overnight set of five minnow traps in the unmodified pond margins, five traps in beaver canals, and five traps in the open water zone from 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011. Pairwise comparisons between habitat classes were conducted using multiple Wilcoxon tests and a Bonferroni correction.

Source	***df***	**Δ Deviance**	***p*-value**
Habitat class	2	15.09	<0.001
Residual	39	42.534	
Total	41	57.624	

Table A.7. Results of a generalized linear model using a negative binomial link function, testing for differences in the number of adult *Dytiscus alaskansus* caught in one overnight set of five minnow traps in the unmodified pond margins, five traps in beaver canals, and five traps in the open water zone from 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Habitat class	2	17.855	<0.001
Residual	39	34.899	
Total	41	52.754	

Table A.8. Results of a generalized linear model using a negative binomial link function, testing for differences in the number of Anisopteran nymphs caught in one overnight set of five minnow traps in the unmodified pond margins, five traps in beaver canals, and five traps in the open water zone from 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Habitat class	2	5.053	0.080
Residual	39	33.879	
Total	41	38.931	

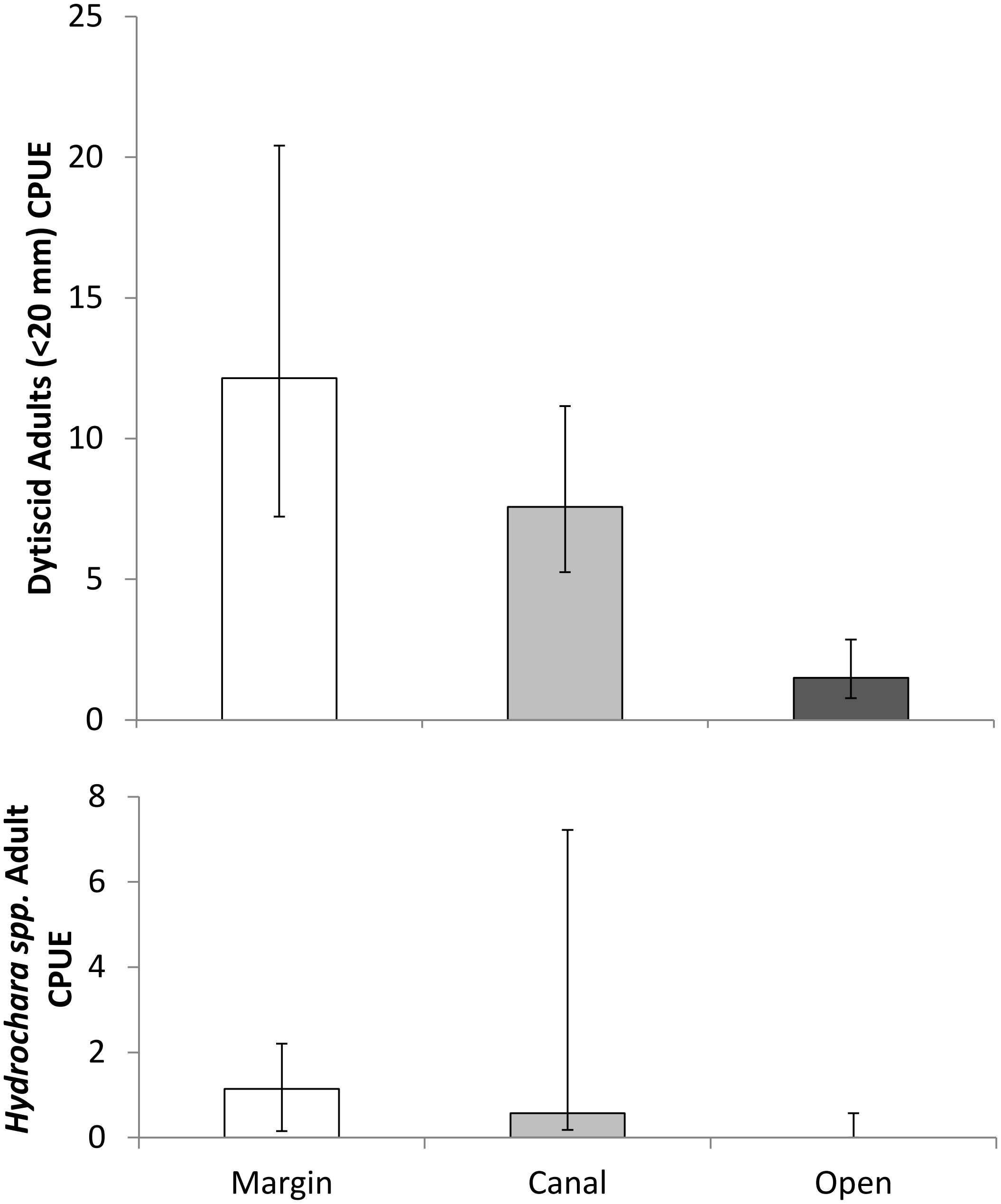

Figure A.8. Mean number of individuals of adult Dytiscid water beetles less than 20 mm total length and adult *Hydrochara* beetles caught in unmodified pond margins, beaver canals, and the open water zone from one overnight set of five minnow traps per habitat class in 14 beaver-modified ponds in Miquelon Lake Provincial Park, between June 1 and July 7 2011. Error bars represent the 95% confidence interval.

Table A.9. Results of a generalized linear model using a negative binomial link function, testing for differences in the number of adult Dytiscid water beetles less than 20 mm total length caught in one overnight set of five minnow traps in the unmodified pond margins, five traps in beaver canals, and five traps in the open water zone from 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Habitat class	2	43.604	<0.001
Residual	39	51.021	
Total	41	94.626	

Table A.10. Results of a generalized linear model using a negative binomial link function, testing for differences in the number of adult *Hydrochara* beetles (Family: Hydrophilidae) caught in one overnight set of five minnow traps in the unmodified pond margins, five traps in beaver canals, and five traps in the open water zone from 14 beaver-modified ponds in Miquelon Lake Provincial Park, AB, between June 1 and July 7, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Habitat class	2	9.008	0.011
Residual	39	17.768	
Total	41	26.776	

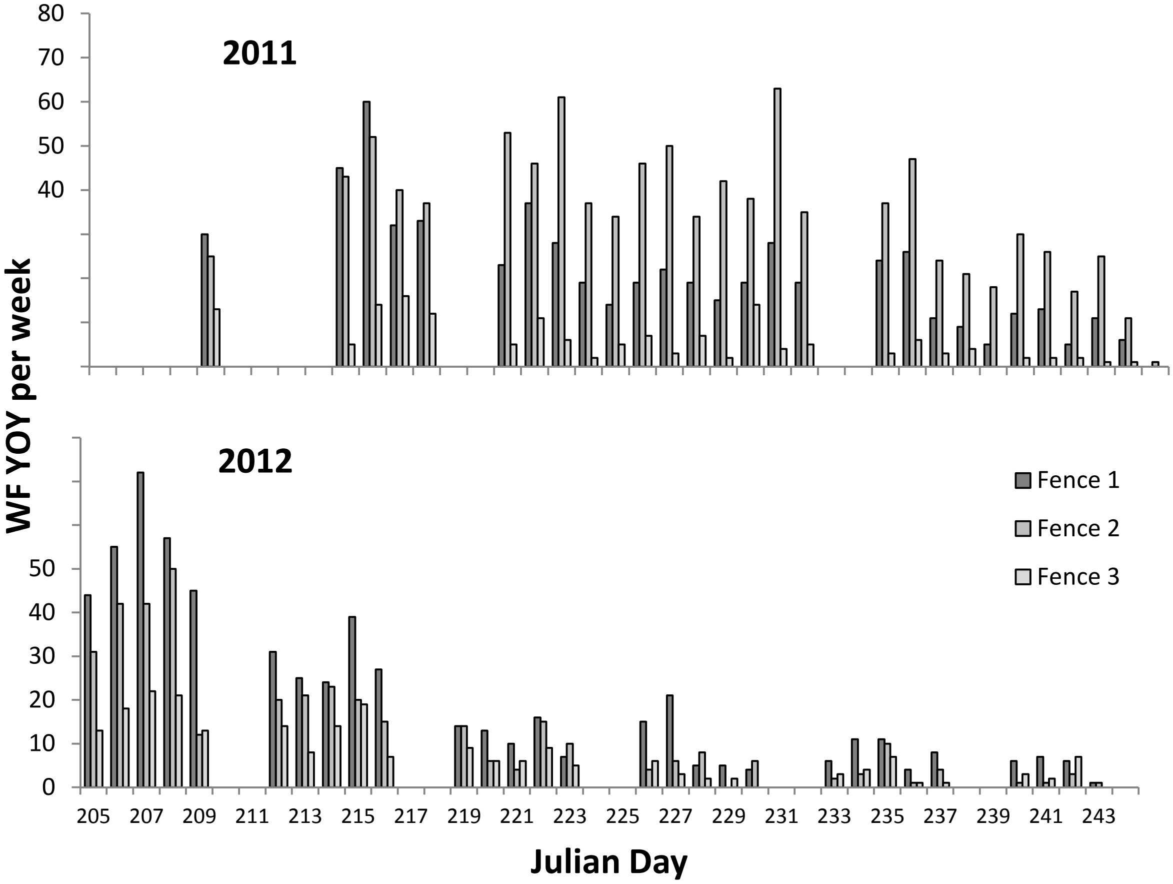

Figure A.9. Total daily catch of YOY wood frogs from drift fences set on beaver canals of four ponds in 2011 and six ponds in 2012 in Miquelon Lake Provincial Park, AB.

Table A.11. Results of a generalized linear model using a negative binomial link function, showing the effect of distance from canal on the relative abundance of young-of-the-year wood frogs on drift fences set 20 m before the end of the canal (Fence 1), on 8 canals in Miquelon Lake Provincial Park, AB, from the end of July to the beginning of September, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Section	2	79.791	<0.001
Week	4	104.973	<0.001
Array	7	106.119	<0.001
Residual	106	136.68	
Total	119	427.56	

Table A.12. Results of a generalized linear model using a negative binomial link function, showing the effect of distance from canal on the relative abundance of young-of-the-year wood frogs on drift fences set at the end of the canal (Fence 2), on 8 canals in Miquelon Lake Provincial Park, AB, from the end of July to the beginning of September, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Section	2	130.338	<0.001
Week	4	114.074	<0.001
Array	7	98.087	<0.001
Residual	106	121.95	
Total	119	464.45	

Table A.13. Results of a generalized linear model using a negative binomial link function, showing the effect of distance from canal on the relative abundance of young-of-the-year wood frogs on drift fences set 20 m beyond the end of the canal (Fence 3), on 8 canals in Miquelon Lake Provincial Park, AB, from the end of July to the beginning of September, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Section	2	9.116	0.010
Week	4	108.237	<0.001
Array	7	120.896	<0.001
Residual	106	123.11	
Total	119	361.36	

Table A.14. Results of a generalized linear model using a negative binomial link function, showing the effect of distance from canal on the relative abundance of young-of-the-year wood frogs on drift fences set 20 m before the end of the canal (Fence 1), on 12 canals in Miquelon Lake Provincial Park, AB, from mid-July to the end of August, 2012.

Source	***df***	**Δ Deviance**	***p*-value**
Section	2	68.553	<0.001
Week	5	146.930	<0.001
Array	11	149.306	<0.001
Residual	197	212.18	
Total	215	576.97	

Table A.15. Results of a generalized linear model using a negative binomial link function, showing the effect of distance from canal on the relative abundance of young-of-the-year wood frogs on drift fences set at the end of the canal (Fence 2), on 12 canals in Miquelon Lake Provincial Park, AB, from mid-July to the end of August, 2012.

Source	***df***	**Δ Deviance**	***p*-value**
Section	2	36.069	<0.001
Week	5	198.436	<0.001
Array	11	247.442	<0.001
Residual	197	187.08	
Total	215	669.02	

Table A.16. Results of a generalized linear model using a negative binomial link function, showing the effect of distance from canal on the relative abundance of young-of-the-year wood frogs on drift fences set 20 m beyond the end of the canal (Fence 3), on 12 canals in Miquelon Lake Provincial Park, AB, from mid-July to the end of August, 2011.

Source	***df***	**Δ Deviance**	***p*-value**
Section	2	0.962	0.618
Week	5	77.829	<0.001
Array	11	152.603	<0.001
Residual	197	180.36	
Total	215	411.76	

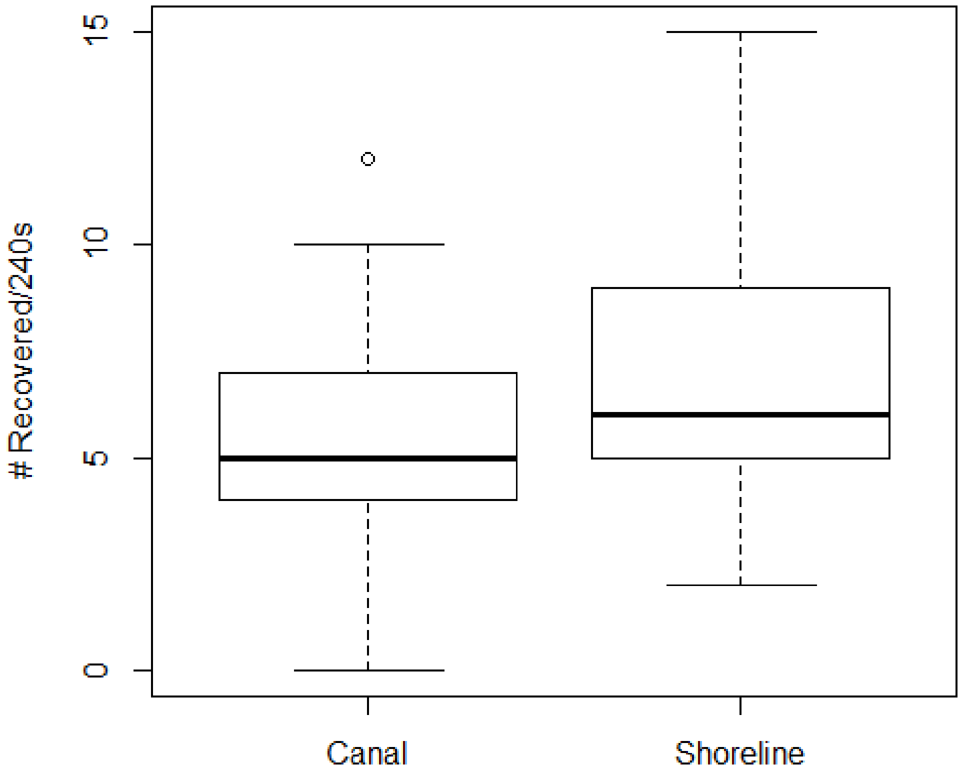

Figure A.10. Boxplot showing mean and interquartile range of the number of frog decoys recovered out of 15 decoys placed on 15 m transects set in beaver canals and unmodified shorelines. Two naïve searchers walked transects within 5 minutes, and completed 26 pairs of transects at Miquelon Lake Provincial Park, AB in August 2012.

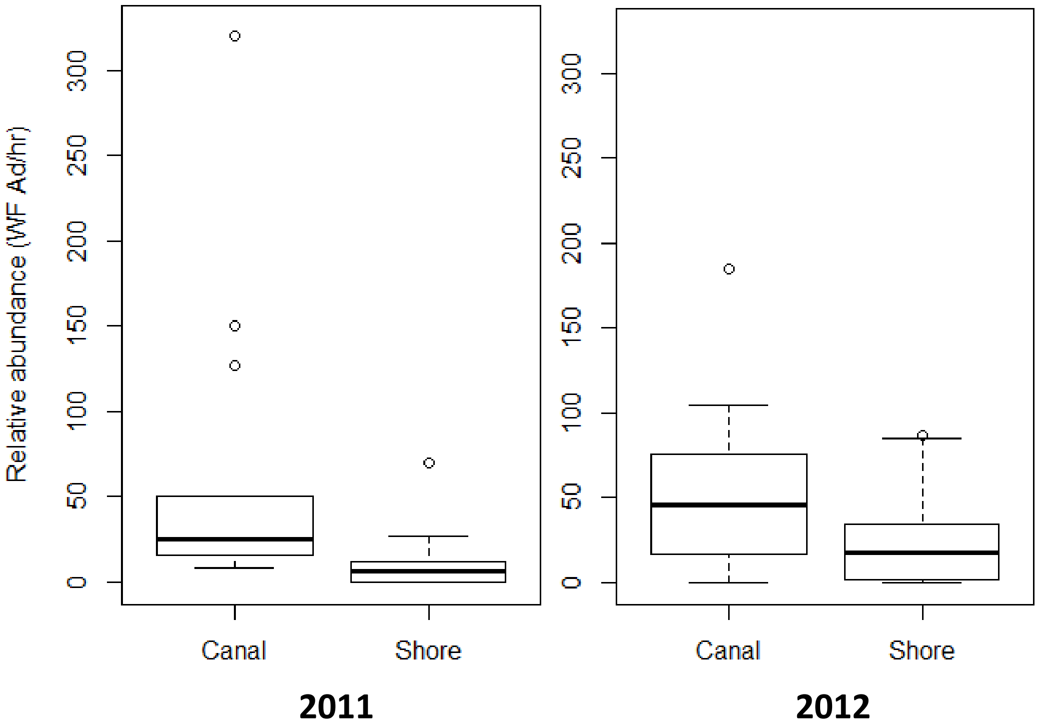

Figure A.11. Boxplots showing mean and interquartile range of relative abundance of adult wood frogs along visual encounter transects of beaver canals and unmodified shorelines conducted in July and August 2011 and August 2012 on 13 ponds in Miquelon Lake Provincial Park, AB.

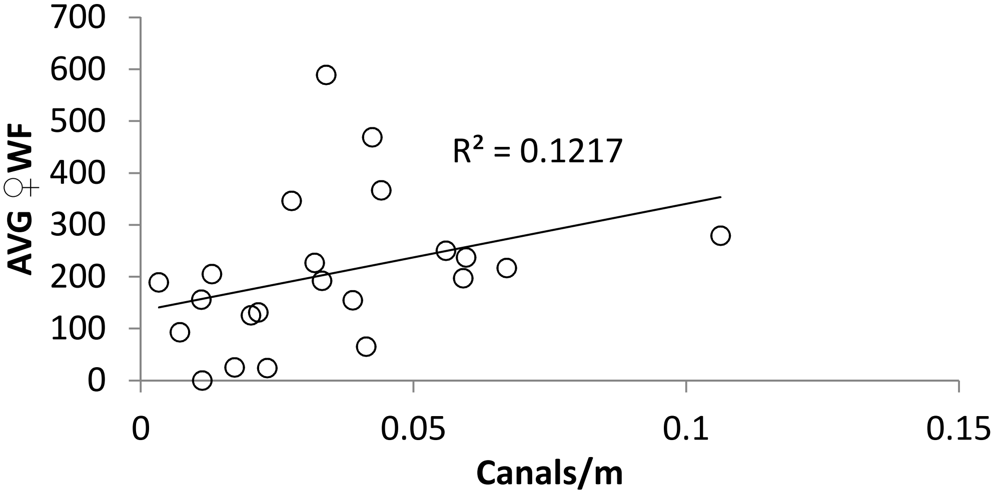

Figure A.12. Relative abundance of breeding female wood frog (average of 2011 and 2012 egg mass counts) versus density of beaver canals in the riparian meadow, for 21 ponds in Miquelon Lake Provincial Park, AB.

Table A.17. AICc values for candidate models predicting the relative abundance of breeding female wood frogs from 22 beaver-modified ponds in Miquelon Lake Provincial Park, AB. TN = Total nitrogen (2011); P = Pond perimeter; Cm = Density of beaver canals; Nn = Nearest neighbouring shoreline; Rw = Riparian width; TP = Total phosphorous (2011); Chla = Chlorphyll-a (2011).

Model	Factors	Log likelihood	k	AICc	Δi	wi	$e^{(-0.5\Delta i)}$	Evidence Ratio
1	**Nn+P**	**-141.40**	**4**	**285.15**	**0.00**	**0.37**	**1.00**	**1.000**
2	**P**	**-141.99**	**3**	**285.32**	**0.17**	**0.23**	**0.92**	**1.087**
3	TP+P	-141.65	4	285.65	0.51	0.15	0.78	1.288
4	BC+P	-142.35	4	287.05	1.90	0.10	0.39	2.582
5	TN+P	-142.83	4	288.01	2.86	0.03	0.24	4.174
6	Chla+P	-142.91	4	288.18	3.03	0.02	0.22	4.546
7	BC+Nn+P	-142.22	5	288.18	3.04	0.02	0.22	4.565
8	Rw+Nn+P	-142.40	5	288.54	3.40	0.02	0.18	5.465
9	BC+TP+P	-142.43	5	288.61	3.46	0.02	0.18	5.648
10	Rw+P	-143.35	4	289.05	3.90	0.02	0.14	7.022
11	BC+TN+P	-142.90	5	289.54	4.40	0.00	0.11	9.009
12	BC+Rw+P	-143.23	5	290.20	5.05	0.00	0.08	12.503
13	BC+Chla+P	-143.35	5	290.44	5.29	0.00	0.07	14.113
14	BC+Rw+Nn+P	-143.18	6	291.96	6.82	0.00	0.03	30.200
15	Rw+Nn+TN+TP+Chla+P	-144.20	8	299.47	14.33	0.00	0.00	1290.121
16	BC+Rw+Nn+TN+TP+Chla+P	-144.68	9	304.37	19.22	0.00	0.00	
** Sums **						1	3.5606	