Life in a Drawdown Zone: Natural History, Reproductive Phenology, and Habitat Use of Amphibians and Reptiles in a Disturbed Habitat

by

Kelly Boyle
B.Sc., University of Toronto, 2004

A Masters Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

University of Victoria

Supervisory Committee

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Dr. John Dower, Departmental Member
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Virgil Hawkes, Additional Member
(LGL Limited Environmental Research Associates)

Abstract

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Canada is the second highest producer of hydroelectric energy in the world. Nearly 50 of the hydroelectric reservoirs in the country have a capacity larger than 1 billion m^3. Despite the great number and extent of hydropower developments in Canada and around the world, relatively little is known about how dams and their operations influence terrestrial and semi-aquatic wildlife. Reservoirs at northern latitudes are characterized by large fluctuations in water level, which create modified shorelines called drawdown zones. To evaluate the impact of these disturbances on amphibians and reptiles, I conducted visual encounter surveys at two sites in the drawdown zone of Kinbasket Reservoir, near Valemount, B.C. From April to August of 2010 and 2011, I documented the habitat use, reproductive phenology, and body condition of two amphibian species (*Anaxyrus boreas* and *Rana luteiventris*) as well as the growth, movements, diet, and distribution of one species of garter snake (*Thamnophis sirtalis*). At two sites in the drawdown zone, *A. boreas* and *R. luteiventris* were present for the duration of the summer and utilized several ponds for reproduction. The presence and abundance of *Rana luteiventris* eggs were generally associated with ponds that had higher mean temperatures, higher mean pH, and the presence of fish. In 2010, there was sufficient time for amphibian breeding and metamorphosis to occur before the reservoir inundated the drawdown zone, but low precipitation levels in that year led to desiccation of many breeding ponds. In 2011, high rainfall and snowmelt led to early inundation of breeding ponds, and thousands of tadpoles were presumably swept into the reservoir. Gravid *Thamnophis sirtalis* were found at just one of two sites in the drawdown zone, but both sites were frequented by foraging individuals of this species. *Anaxyrus boreas* appears to be the primary prey of *T. sirtalis* in the drawdown zone. An improved understanding of how the amphibians and reptiles at Kinbasket Reservoir have persisted in this highly disturbed environment may be vital to their conservation — the activation of a new generating unit at Mica Dam in 2014 will alter the pattern and timing of reservoir inundation for the first time since it was constructed 40 years previously.

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Acknowledgements

Thank you first of all to my mentor and supervisor, Pat Gregory. I count myself lucky to have been a part of your lab. I'm so grateful for your encouragement, guidance, and occasional teasing, which always came exactly when I needed it most. Thank you for giving me the freedom to try things the wrong way first (or in your words, giving me "just enough rope to hang [myself] with"). I've really loved graduate school and I think I have you to thank for that.

Thank you also to my committee members, Dr. Geraldine Allen, Dr. John Dower, and Virgil Hawkes, for your advice and encouragement along the way. Virgil gave me the opportunity to work with LGL Limited environmental research associates and to secure an Industrial NSERC scholarship. This research was possible because of his ambition to put a grad student in the Valemount Peatland. I was also supported by the University of Victoria's President's Research Scholarship and by the Department of Biology, especially Eleanore Blaskovich, who was always willing to stop whatever she was doing to answer my random questions.

Thank you to my parents (all four of you) for whole-heartedly supporting my gypsy lifestyle and my passion for wildlife biology. Knowing that I have your love and support makes even the most frustrating days tolerable.

My field assistant and friend, Nicole Genton, was with me every day for two field seasons. We shed blood, sweat, and tears of laughter in the drawdown zone, and I am truly grateful for her dedication to this project.

Many other friends and loved ones provided me with great laughs, food, shelter, and/or an empathetic ear, including: Ashley Thomson, Crystal Porter, Sheena Rosentreter, Erin Marshall, Stefanie van Huystee, Leanne Peixoto, Katie Bell, and Graham Dixon-MacCallum. Thank you also to Gordon and Ann Carson for sharing your local knowledge of Valemount and opening your home to two snake-catching, sun-tanning girls from Victoria. Finally, thank you to Ian Swan for bringing so much sunshine into my life.

CHAPTER 1 - INTRODUCTION

INTRODUCTION

Global energy use has increased by 70% since 1971 and continues to increase by 2% per year (World Energy Council, 2007). Growing populations and developing economies demand an increase in energy production, but our current dependence on fossil fuels is detrimental to the environment and to global climate patterns (e.g. Vitousek, 1994; Houghton, 2005). To cope with these realities, many governments are turning to the production of renewable energy. As of 2005, renewable energy accounted for 1/5th of the energy produced worldwide, 87% of which was derived from hydropower (World Energy Council, 2007).

Hydroelectricity is a relatively inexpensive and naturally replenished energy source, making it a popular alternative to energy derived from finite resources such as coal and oil. However, hydropower is not without its drawbacks. Dams constructed to harness river energy effectively create lakes where rivers used to be, consequently altering natural water and sediment flows, disturbing natural flood regimes and influencing erosion patterns (Booth, 1998). These impoundments also obstruct migration pathways for native fish (Nilsson and Berggren, 2000), create habitat for invasive species (Rahel and Olden, 2008), and destroy valuable riparian habitat (Nilsson and Berggren, 2000). Upstream of a dam, existing riparian habitats are frequently inundated with water, and new riparian areas are created where none previously existed (Nilsson and Berggren, 2000). In addition, water levels of reservoirs fluctuate significantly when water is released for generation of energy, resulting in greatly modified shorelines (Baxter, 1977; Nilsson et al., 1991).

Hydroelectric reservoirs at northern latitudes typically store water during and after spring flooding, with peak water levels occurring in late summer. Water is released during the fall and winter months, when power is most needed, with the lowest water levels occurring in the winter (Lindström, 1973). The affected areas, subject to frequent inundation and desiccation, are commonly referred to as “drawdown zones”. Depending on the size of a reservoir, drawdown zones may encroach upon or completely encompass pre-existing riparian areas. Given that riparian habitats are home to a diverse array of species (Naiman et al., 1993) and facilitate the movement of matter, energy and organisms (Tabacchi et al., 1990; Tabacchi et al., 1998), reservoir operations likely influence a wide variety of organisms and ecological processes. The influence of river impoundment and reservoir operation on fish and invertebrates is well-studied (e.g. McAfee, 1980; Bain et al. 1988; Taylor et al. 2001; Falke and Gido, 2006; McEwen and Butler, 2010), but relatively little is known about the effects of reservoirs on terrestrial wildlife (for exceptions see Barclay, 1976; Smith and Peterson, 1991; Crivelli et al. 1995; Lind et al., 1996; Brandau and Araujo, 2008).

Due to their relatively low vagility, amphibians and reptiles are particularly vulnerable to such habitat disturbances. Most amphibians are aquatic breeders and require suitable wetland habitat for mating, oviposition and larval growth. Wetlands also provide foraging and dispersal habitat, as well as shelter and overwintering sites. The negative effects of habitat alteration on amphibian populations (Cushman, 2006) may be compounded by disease (Berger et al., 1998; Pounds et al. 2006), climate change (Kieseker et al. 2001; Pounds, 2001; Reading, 2007) and environmental pollution (Rouse et al. 1999; Sanzo and Hecnar, 2006). These effects can cascade through ecosystems because amphibians provide an important food source for other predators, including many species of snakes (e.g. Arnold and Wassersug, 1978; Rossman et al. 1996; Tuttle and Gregory, 2009). The persistence of some populations of garter snakes (*Thamnophis*) may in fact be dependent on the presence of amphibians (Jennings et al. 1992; Matthews et al. 2002). For snakes living at northern latitudes (where the active season is short), the consequences of reduced abundance of amphibian prey may be intensified. The effects of low prey density during a single active season could linger in subsequent years, given that snakes are primarily capital breeders (Gregory, 1996). *Thamnophis* spp. living at high latitudes typically mate immediately after emergence from hibernation (Aleksiuk and Gregory, 1974). Very little time exists for acquisition of resources prior to yolk formation and ovulation; therefore a female's reproductive output is largely dependent on her nutritional state at emergence from hibernation (Gregory, 1996). Because hibernating snakes are aphagic, the nutritional state of an emerging female is presumably most influenced by her condition immediately prior to entering hibernation. Ultimately, a very small window of time exists for capital breeding reptiles to acquire enough resources to reproduce in the subsequent year, particularly at high latitudes. Gravid females often eat little to nothing (e.g. Gregory et al. 1999), further decreasing the time in which they can forage prior to hibernation. Should the availability of amphibian prey be limited by habitat disturbances such as reservoir operation, the consequences to reproductive females (and ultimately the entire local population) may be great.

Given the important role that amphibians and reptiles play in the flow of energy and nutrients in ecosystems (Pough, 1980), especially between aquatic and terrestrial environments, threats to these species have potentially serious ramifications. Increasing attention has been given to the conservation of amphibians and reptiles worldwide (e.g. Gibbons et al. 2000; Keisecker et al. 2001; Pounds, 2001; Sodhi et al. 2008), but surprisingly little is known about how they are affected by reservoir development and operation. Brandao and Araujo (2008) observed substantial declines in abundance and species richness of amphibians, both during and following reservoir formation along the Tocantins River in central Brazil. Lind et al. (1996) showed that egg and larval survivorship of pond breeding amphibians were negatively affected by habitat loss and altered water levels downstream of a dam. However, the long-term effects of reservoir operations on amphibians and reptiles remain unclear. The need to understand the potential consequences is great, as hydroelectric development is set to increase around the world. Recent estimates predict a ten-fold increase in hydropower development in Africa, a three-fold increase in Asia, and a doubling in South America (World Energy Council, 2007). An improved understanding of how the amphibians and reptiles at Kinbasket Reservoir have persisted in this disturbed environment may be vital to their conservation; in October of 2014, BC Hydro will activate the first of two new generating units at the Mica Dam. These 500 MW generating units are expected to alter the timing of reservoir inundation and subsequently increase the extent of reservoir disturbance for the first time since its construction in 1974.

In 2008, BC Hydro implemented an 11-year monitoring program for amphibians and reptiles, to investigate the effects of reservoir operations on these taxa and their habitat (Hawkes and Tuttle, 2010). The program includes two hydroelectric reservoirs in the Columbia River basin: Kinbasket Reservoir and Arrow Lakes Reservoir. My research incorporates several objectives of BC Hydro's long-term monitoring at Kinbasket (conducted by LGL Limited environmental research associates), while also addressing more specific questions about the ecology of amphibians and reptiles in the drawdown zone. The particular objectives of my research were as follows:

(1) Determine which species of amphibians and reptiles utilize the drawdown zone in the Canoe Reach of Kinbasket Reservoir.
(2) Identify amphibian and reptile life history stages associated with habitat use in the drawdown zone.
(3) Determine amphibian phenology, especially reproduction and development, relative to yearly reservoir inundation.
(4) Identify the habitat characteristics associated with amphibian breeding locations in the drawdown zone.

STUDY SITES

In response to the burgeoning post-WWII economy and rapid population growth, Canada and the United States of America signed the Columbia River Treaty in 1964. This international agreement required cooperative development and operation of dams along the Upper Columbia River, for the purposes of flood control and energy generation (Sewell, 1966). As a result of the treaty, three dams were constructed along the Canadian portion of the Columbia River: Mica, Duncan and Arrow (the latter now Hugh-Keenleyside). The Mica Dam was constructed in 1973 and is the northern-most dam on the Columbia River. Its impoundment, Kinbasket Reservoir, is 216 km long and has a licensed storage volume of 12 MAF (Million Acre Feet) (BCHydro, 2007a). On average, the water line of the reservoir is approximately 725 m above sea level (ASL) in early spring and approximately 750 m ASL in late summer (Hawkes and Tuttle, 2010).

LGL Limited environmental research associates (LGL) identified several sites in the drawdown zone of Kinbasket Reservoir with habitat suitable for amphibians and reptiles (Hawkes et al., 2011; Figure 1). I collected data from two of these sites: the Valemount Peatland and Ptarmigan Creek. Both are located at the northern end of the reservoir, in a narrow valley referred to as Canoe Reach. The Valemount Peatland is the northern-most site, located where the Canoe River enters the reservoir. The Peatland is a large wetland, characterised by a series of ponds (~50, depending on the amount of rainfall and snowmelt in a given year), springs and marsh-like areas (Figure 2). It is a remnant of a large fen that was adjacent to the Canoe River prior to the construction of Mica Dam (Ham, 2010). The Peatland is approximately 450 hectares in area, spans ~7 m in elevation (748 - 755 m ASL), and is typically not inundated by the reservoir until mid to late August. Only the lower elevations of the Peatland are regularly inundated, and the complexity of vegetation at this site generally increases with elevation (Hawkes et al., 2007). A relatively large amount of coarse woody debris (CWD) was not removed from the drawdown zone after it was cleared in the 1970s and much of it remains in the Peatland today. Yearly inundation of the area often lifts and moves this CWD (e.g. large tree trunks) around the wetland, occasionally creating small pools where trees once rested and blocking shorelines and streams that were previously unobstructed (pers. obs.). Recent research also suggests that the Peatland is threatened by erosion resulting from wave-action and reservoir drawdown (Ham, 2010). This highly dynamic environment is where the majority of my data were collected.

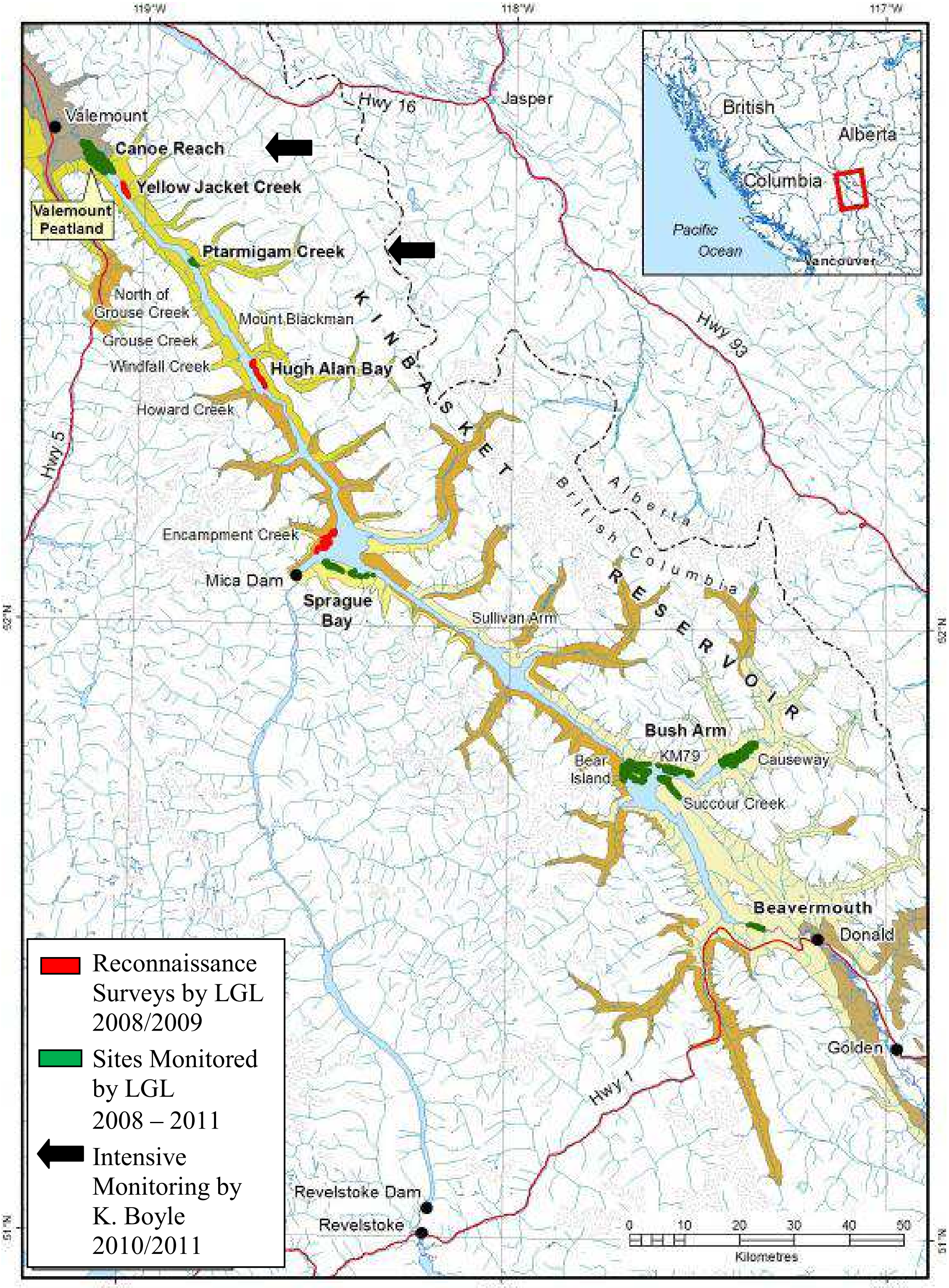

Figure 1. Location of Kinbasket Reservoir and amphibian and reptile survey sites in the drawdown zone. Sites marked in green are surveyed by LGL Limited environmental research associates as part of BC Hydro's long-term monitoring project (CLBMON-37). Black arrows indicate the location of my study sites. Figure is modified from Hawkes et al. (2011).

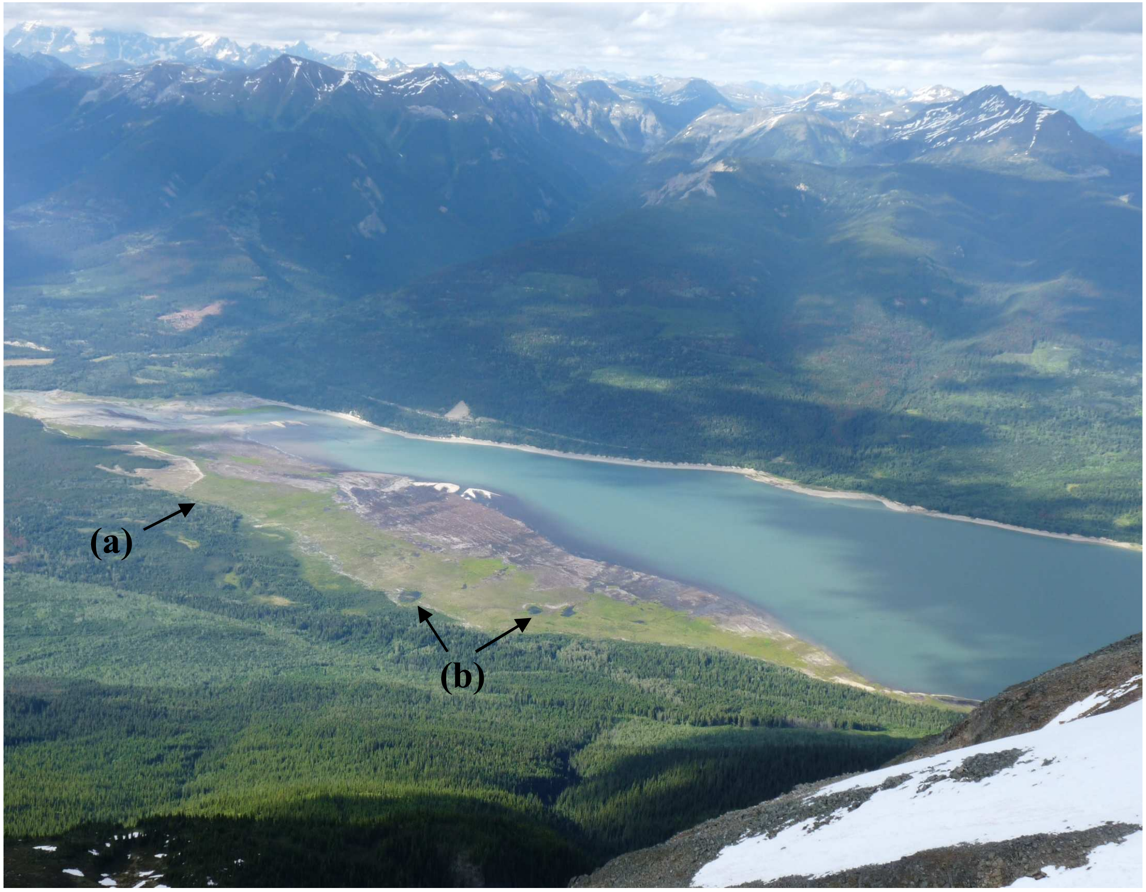

Figure 2. View of the Valemount Peatland, Kinbasket Reservoir, and the Selwyn Range of the Rocky Mountains from the summit of Canoe Mountain (to the south). The high water marks of the drawdown zone are clearly visible by the marked change in vegetation from marsh to trees (a). Several large ponds in the Peatland are visible as well (b). Photo was taken on July 23, 2010.

Ptarmigan Creek is located ~40 km south of the Peatland, on the reservoir's eastern shoreline. This site consists of a single perched, spring-fed pond, approximately 0.95 ha in area (Figure 3). It is surrounded by fast-growing sedge and flood-tolerant plant species and is completely inundated by the reservoir by mid to late July of each year. The pond is immediately adjacent to the East Canoe Forest Service Road, which was subject to light summer traffic during the years this study was conducted (a maximum of 1-2 vehicles were observed using the road on a given day of surveying the site). However, during periods of local logging activity, the road is likely subject to heavier traffic. This periodic human disturbance may influence the behaviour and survivorship of amphibians and reptiles at Ptarmigan Creek, but it cannot be accounted for within my two-year study. A small, clear, spring-fed pond (referred to as the “Ditch pond”) is located on the opposite side of the road, but is not within the drawdown zone.

Figure 3. Wetland at the Ptarmigan Creek site, viewed from the south end of the pond. Photo was taken on May 25, 2010.

Cranberry Marsh is a Ducks Unlimited wildlife sanctuary located several kilometres to the north of Kinbasket Reservoir. This large (~110 hectares) man-made wetland was surveyed in 2010, as a potential reference site for this study. However, efforts to locate amphibians and their eggs at this site were greatly impeded by thick shoreline vegetation and large amounts of duckweed and algae on the water surface. In addition to low visibility, the water level decreased dramatically during the spring, and the marsh was completely dry in most areas by June. I later learned that this dramatic desiccation was partly due to problems with the design and construction of the wetland. While I persevered for the duration of the field season, insufficient data (for amphibians or garter snakes) were obtained from this site to make worthwhile comparisons to populations at Kinbasket Reservoir. However, the site was used by breeding Western Toads (*Anaxyrus boreas*), and some data for this species will be reported here.

GENERAL METHODS

With the help of a summer field assistant, I conducted visual encounter surveys at the Valemount Peatland, Ptarmigan Creek, and Cranberry Marsh, in 2010 and 2011. Surveys were conducted at all three sites from April 27th to August 26th in 2010, and at the Peatland and Ptarmigan Creek sites from April 27th to August 14th in 2011. Cranberry Marsh was visited just twice in 2011, to capture and measure young-of-the-year Western Toads. Search effort (minutes spent searching over a measured distance, often a pond perimeter) and weather conditions were carefully recorded each day. Amphibians and garter snakes were captured opportunistically, by hand or dip net. Inevitably, many escaped, but their locations, behaviour, and life stage were noted. Hand-captured amphibians were sexed, weighed, measured (snout-urostyle length) and photographed for individual identification upon recapture. Captured garter snakes were also sexed, weighed and measured (head width, snout-vent length, and tail length). Additionally, each garter snake was palpated to locate and remove recently eaten prey, which was identified and then fed back to the snake. The abdomens of gravid females were gently massaged to count the number of eggs carried. Prior to their release, each garter snake was uniquely marked by the removal of one or more scales on the ventral side of its tail. GPS locations of each species observation were used to identify potential habitat associations in the drawdown zone. In particular, egg observations allowed for analyses of amphibian habitat use, due to their high detectability and fixed location in the drawdown zone. Morphometric data were used to estimate the body condition of individuals in each population. Recaptures of unique individuals provided information about the growth rates and movement patterns of garter snakes and anurans.

CHAPTER 2 – NATURAL HISTORY OF AMPHIBIANS AND REPTILES IN THE DRAWDOWN ZONE OF KINBASKET RESERVOIR

INTRODUCTION

Natural history studies investigate the ethology and ecology of organisms in their natural settings (Greene, 1994). Careful documentation of species interactions, abundance, distribution, and behaviour in a natural setting is necessary for conservation efforts (Greene, 1994) and conceptual advancements in biology (Arnold, 2003). However, the likelihood that a species can be observed in its “natural” environment has steadily diminished as human disturbances extend into even the most remote areas of the planet. Nearly three-quarters of the habitable land on the planet is disturbed in some way (Hannah et al., 1994). Temperate biomes, in particular, are among the most highly disturbed areas of the planet (Hannah et al, 1995). Wildlife in these areas is influenced by ever-present anthropogenic disturbances such as habitat fragmentation, pollution, and introduction of invasive species — common side-effects of industrial development and urbanization. To quantify the effects of human disturbances on wildlife populations, researchers often rely on population estimates made before and after a disturbance, or on estimates made across a range of disturbance levels (Gill et al., 1996). However, it can be difficult to attribute species’ behaviours, adaptations, or population fluctuations to a particular disturbance pattern or event, because pre-disturbance data are not always available. In spite of this limitation, it remains important to document the natural history of species in disturbed habitats and to compare them with the same species in more natural settings. Studying populations that have persisted in spite of extensive human disturbance may provide insight into the environmental conditions or life-history traits that have aided in their persistence. Alternatively, such populations may suffer from decreased abundance (Fahrig and Rytwinski, 2009), reduced reproductive success (e.g. Fort and Otter, 2004) or increased prevalence of disease (e.g. Friggens and Beier, 2010), among other things. The mere presence of a species in a disturbed area does not indicate that it is unaffected by its altered habitat and the importance of monitoring these populations should not be underestimated.

Amphibians and reptiles are arguably the most threatened vertebrates on the planet (Gibbons et al., 2000; Stuart et al., 2004). Members of these two taxa often occupy similar habitats, have relatively low vagility, and are highly vulnerable to habitat destruction (Gibbons et al., 2000). Amphibians are especially vulnerable to habitat alterations, due to their reliance on both aquatic and terrestrial habitats. In turn, animals that prey on amphibians, including many bird and snake species, are vulnerable to these changes. Researchers have attributed the decline of amphibian and reptile populations around the world to a multitude of human-facilitated disturbances, including: habitat fragmentation, ultraviolet radiation, acidification, invasive species, disease, pollution, and climate change (see Gibbons et al., 2000 and Gardner, 2001 for reviews). With the exception of a few studies (Jones, 1988; Lind et al., 2006; Brandau and Araujo, 2008), the role of river impoundment in amphibian and reptile declines has been largely overlooked.

I spent 8 months, over two summers, in the drawdown zone of Kinbasket Reservoir, near Valemount, B.C., to document the presence of amphibians and reptiles and to investigate their natural history. I studied the distribution, body condition, movement, growth, and food habits of individuals in the drawdown zone. Although these data cannot be directly attributed to reservoir construction or operation, they may help to identify potential consequences of life in the disturbed areas of a hydroelectric reservoir. For instance, the body condition (variation from expected mass for a given length) of an animal can reflect its quality of habitat (Sztatecsny and Schabetsberger, 2005), prey availability (Pope and Matthews, 2002), and degree of environmental stress (Reading, 2007), among other things. Individual growth rates can also be influenced by extrinsic factors, such as prey availability (Bronikowski and Arnold, 1999) or environmental temperature (Angiletta et al., 2004). Should the amphibians and garter snakes living within the drawdown zone be negatively impacted by reservoir operations in one or more of these aspects, they may be characterized by poorer body condition or reduced growth relative to populations at undisturbed sites. Diet and movement data provide information about foraging and migration behaviours (e.g. Larsen, 1987; Mazerolle, 2001), which in turn reflect energy requirements and expenditures (Peterson et al., 1998; Carfagno and Weatherhead, 2008). Ultimately, I intended to document the natural history of amphibian and reptile species in the drawdown zone and to identify potential conservation concerns, should they exist.

METHODS

Study Species

Initial surveying efforts by LGL (Hawkes and Tuttle, 2010) identified two species of garter snake and three amphibian species occurring in the Canoe Reach of Kinbasket Reservoir: Common Garter Snakes (*Thamnophis sirtalis*), Western Terrestrial Garter Snakes (*Thamnophis elegans*), Western Toads (*Anaxyrus boreas*), Columbia Spotted Frogs (*Rana luteiventris*), and Long-toed Salamanders (*Ambystoma macrodactylum*). All but the Western Toad are currently yellow-listed in British Columbia, which means their populations appear to be secure for now. Western Toads are classified as Special Concern at both the provincial and national level (B.C. Conservation Data Centre, 2012).

The Common Garter Snake (*T. sirtalis*) is a wide-ranging generalist predator that occurs in a variety of environments across North America. It is commonly associated with wetland habitats, where it preys on amphibians, fish, leeches, and small birds and mammals (Matsuda et al., 2006). However, Common Garter Snakes are capable of travelling great distances to meet their requirements for foraging and overwintering habitat (Gregory and Stewart, 1977), and are not strictly associated with wetlands.

The Western Terrestrial Garter Snake (*T. elegans*) is also wide-ranging and is very similar to the Common Garter Snake in its general ecology. Both species prey heavily on metamorphic anurans when they are available (Arnold and Wassersug, 1978; Kephart and Arnold, 1982; Jennings et al., 1992), but *T. elegans* will shift to alternative forms of prey more readily than *T. sirtalis* (Kephart and Arnold, 1982).

The Western Toad (*A. boreas*) is found throughout the province of British Columbia. It is an explosive, communal breeder that prefers shallow, ephemeral ponds. Females lay up to 12,000 eggs in a single clutch and offspring metamorphose and emerge from ponds *en masse*, where they make easy prey for birds and garter snakes (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978; Matsuda et al., 2006). Juveniles and adults overwinter in terrestrial habitats, inside squirrel middens, peat hummocks, natural crevices, or other locations below the frost-line (Bull, 2006; Browne and Paszkowksi, 2010).

Columbia Spotted Frogs (*R. luteiventris*) are highly aquatic and rarely stray far from the shorelines of ponds and streams. They breed, forage, and overwinter in aquatic habitats, and may be found at very high latitudes (up to 60° 01’ N in the Yukon Territory; Slough and Mennell, 2006) and altitudes (up to 3,000 m above sea level in Montana; Maxell et al., 2006, as cited by Patla and Keinath, 2005). Reproductive females lay a single egg mass in early spring, containing ~ 400 to 1500 eggs (Nussbaum et al., 1983; Boyle, unpublished data). Although Columbia Spotted Frogs will breed communally, tadpoles do not aggregate and metamorphose *en masse*, as Western Toads do.

Long-toed Salamanders (*A. macrodactylum*) are widely distributed throughout British Columbia, and are the only urodele found in the northern interior of the province (Matsuda et al., 2006). Like most ambystomatid salamanders, they are primarily nocturnal and spend most of their time underground or under cover of logs, rocks or other debris (Faccio, 2003). Long-toed Salamander eggs are laid in shallow ponds and lakes, either singly or in small clumps.

Visual Encounter Surveys

I conducted visual encounter surveys from late April to mid-August in 2010 and 2011, between the hours of 7 am and 8 pm. Local weather conditions were recorded at the start and end of each survey, as well as once at mid-day, using a Kestrel 4500 Weather Meter. This handheld device records wind speed, air temperature, and percentage humidity. Percentage cloud cover and recent rainfall were also noted. Total precipitation and mean daily temperatures at Mica Dam were obtained from Environment Canada's National Climate Data and Information Archive (Environment Canada, 2012). I conducted most of my visual encounter surveys along the perimeter of ponds, streams and marshes at the Valemount Peatland and at Ptarmigan Creek. However, I also conducted regular transect surveys in drier habitat, to capture garter snakes and dispersing frogs or toads. In 2011, I placed 40 plywood boards (24" x 24") and 40 asphalt roof tiles (24" x 24") along 6 transects that spanned the width of the Peatland, in an effort to increase capture rates of garter snakes. Maps were created in ArcGIS 10 using ortho photos provided by BC Hydro. Elevation data (1 m contour lines) and some shapefiles were shared with me by LGL Limited environmental research associates.

Amphibians were captured by hand or dip net, weighed to the nearest 0.1g using a Nexxtech mini digital scale, and measured from snout-to-urostyle (SUL). I counted all amphibian eggs at each site and monitored them until they hatched. All ponds were revisited throughout the field season to record the Gosner stage of developing tadpoles (Gosner, 1960) and to capture juveniles and adults. GPS locations were recorded for each individual or egg observation. I also photographed each adult and large juvenile Columbia Spotted Frog or Western Toad that was captured. These photos were used to create unique "fingerprints" from individual dorsal spot patterns, using the Interactive Individual Identification System (I^3S Manta v. 2.1; Van Tienhoven et al., 2007). This free photo-identification software was designed for identification of individual Ragged Tooth Sharks, but has since been used for a variety of other taxa, including seadragons (Martin-Smith, 2011), salamanders (Moldowan and Tattersall, 2011), and lizards (Sacchi et al., 2010). Average daily movements of recaptured anurans were estimated by dividing the distance between capture locations by the total number of days that had passed in that time. These values reflect minimum average daily movements of individuals because it is unlikely that they moved in straight lines, as assumed by this method. Growth rates (mm/day) were estimated by dividing the total change in body length by the number of days that had passed since the frog was last captured. For individuals that were recaptured multiple times over the sampling period, I used the first and last measurements only. If frogs were recaptured after a hibernation period, only those days that were part of the typical active season (April 15 to September 15) were included in estimates of growth rate.

Garter snakes were hand captured, sexed, weighed, measured (total length and snout-vent length), and marked by clipping a unique combination of subcaudal scutes (Blanchard and Finster, 1933). Each garter snake observation was marked by handheld GPS. The abdomens of gravid female snakes were gently palpated to estimate the number of offspring carried. Although not all eggs ovulated will develop into offspring (Fitch, 1965), this measure generally provides a reliable estimate of litter size (Farr and Gregory, 1991). Captured individuals were also palpated to force regurgitation of recent prey items, which were identified to species where possible. Recaptures of garter snakes provided information on growth and movement rates, via the same methods described for frogs (above). In addition to estimating mean growth rates for this species, I also compared the growth of males and females. The growth rate of garter snakes is negatively correlated with body size (Bronikowski and Arnold, 1999; Stanford and King 2004). However, an analysis of covariance (ANCOVA) could not be used to compare growth rates of the sexes, due to issues of non-linearity in my data set. Instead, I used a non-parametric method to test for sex-differences in growth rate (Tuttle and Gregory, 2012). I regressed the rank value of the response (growth increment) on the rank values of the dependent variables (interval length and initial snout-vent length), and used a student’s t-test to compare the mean residuals of males and females. Only those snakes that were recaptured after an interval of 10 days (minimum) were included in growth estimates, to ensure that time for growth was allowed.

Due to the variable sample sizes available for each species in a given year or at a given site, I conducted several different body condition analyses. For Common Garter Snakes, I compared the body condition of adults/juveniles at the Valemount Peatland and at Ptarmigan Creek. Due to sex-related differences in Common Garter Snake body condition (Gregory, 2011) and disparate sample sizes, I used mass data from non-feeding male garter snakes only. I also compared the body condition of young-of-the-year (YOY) Western Toads between years at the Valemount Peatland (i.e. 2010 vs. 2011) and between three sites: the Valemount Peatland, Ptarmigan Creek, and Cranberry Marsh. For Columbia Spotted Frogs, I compared the body condition of adult/juvenile individuals captured at the Valemount Peatland in 2010 to those captured in 2011. Anurans of both sexes were used in these analyses. I used an analysis of covariance (ANCOVA) to test for differences in mass relative to body length, with mass as the response variable, site (or year) as the main effect, and body length as a covariate. Site comparisons were performed using body size data from both years and recaptures were excluded from all analyses to avoid pseudoreplication. Mass and length measurements were natural-log transformed (Green, 2001). All statistical analyses were performed using Program R. Figures were created in Microsoft Excel and Program R.

RESULTS

Weather conditions

In 2010, spring conditions arrived early. Relatively little snow (Figure 4) and higher than average temperatures were recorded in January, February, and March (Figure 5). The summer was also drier than average, as 254.6 mm of rain fell between April 1 and August 31. The 30-year average amount of rainfall during these months is 353.5 mm (Figure 4). In 2011, the opposite occurred. Close to 7 m of snowfall was recorded at Kinbasket Reservoir (nearly three metres more than the previous year and one more than average). Lower than average temperatures were recorded during the first three months of 2011 and summer rainfall was close to average levels. Welch’s t-tests revealed that it was significantly warmer in March ($t(39) = 3.09$, $p = 0.003$) and April ($t(48) = 2.93$, $p =$

0.005) of 2010 than in 2011, but no significant differences were detected for the remaining months of the active season (May: t(58) = -0.22, p = 0.823; June: t(56) = -1.73, p = 0.088; July: t(32) = 1.26, p = 0.216; August: t(55) = 0.39, p = 0.695).

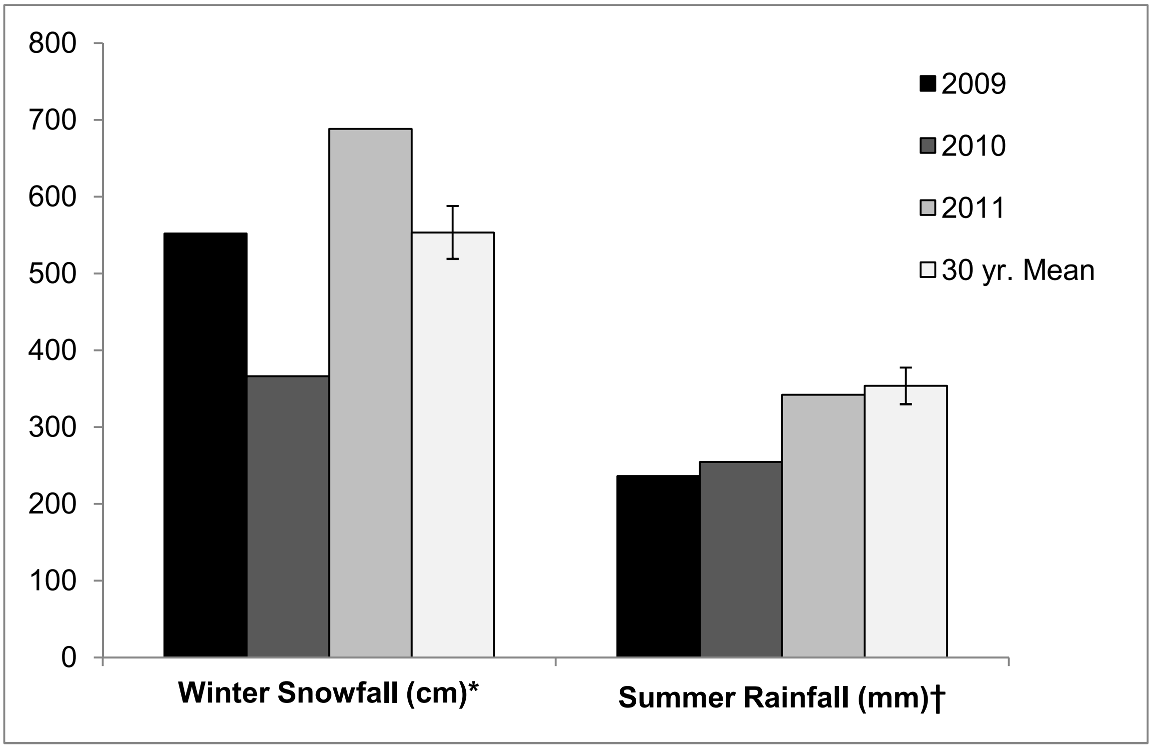

Figure 4. Total precipitation recorded at the Mica Dam in 2009, 2010, and 2011. The 30 year mean (1971 – 2000) is included for comparative purposes. *Winter Snowfall was recorded in centimetres from September 1 of the previous year to March 31 of the plotted year. □Summer Rainfall was recorded in millimetres, from April 1 to August 31 of the plotted year. Bars represent the standard error of the mean. Data were obtained from Environment Canada's National Climate Data and Information Archive.

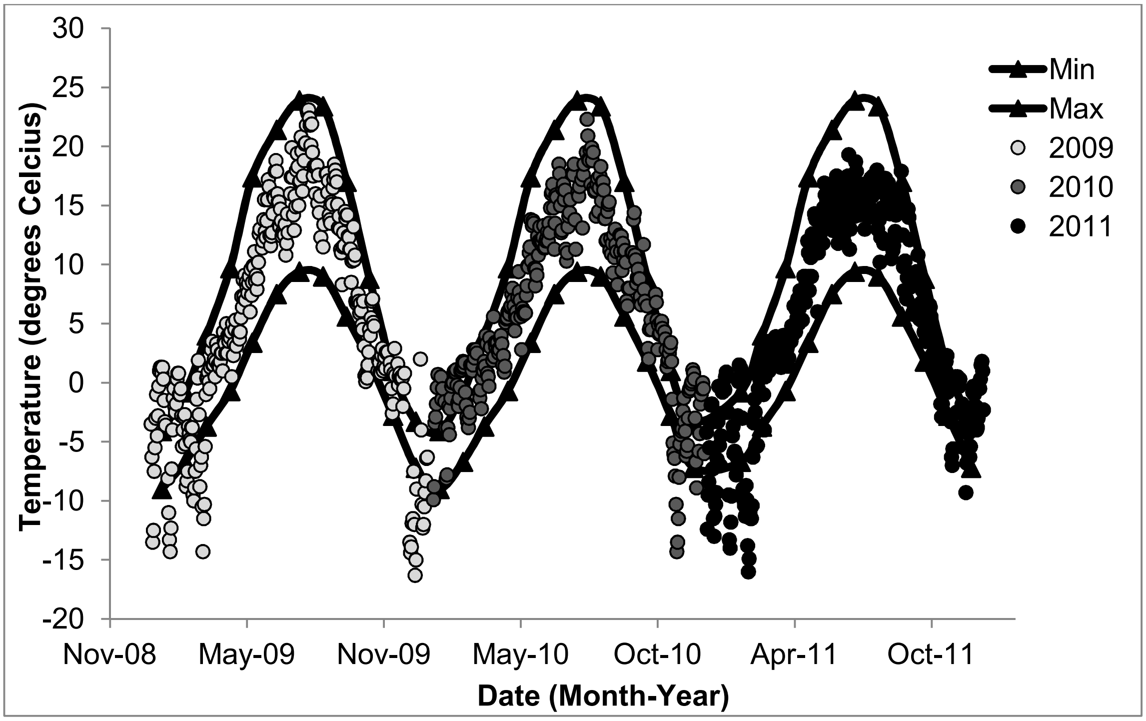

Figure 5. Daily temperatures recorded at Mica Dam in 2009, 2010 and 2011. Mean minimum and maximum monthly temperatures were averaged over a thirty year period (1971 – 2000). Data were obtained from Environment Canada's National Climate Data and Information Archive.

Species Observations

I documented three amphibian species and one species of garter snake in the Canoe Reach of Kinbasket Reservoir: the Columbia Spotted Frog, Western Toad, Long-toed Salamander, and Common Garter Snake. Western Terrestrial Garter Snakes were not detected in the drawdown zone at the Valemount Peatland or at Ptarmigan Creek. The placement of cover boards across the Peatland in 2011 did not increase capture rates of garter snakes. A juvenile Common Garter Snake was found beneath an asphalt cover board in mid-June, but no other snakes were detected under cover boards for the remainder of the year. Tables 1 and 2 summarize the species observations at each site in the drawdown zone, by life stage.

Table 1. Total numbers of unique individuals observed and/or captured at the Peatland, by species and life stage. RALU = *Rana luteiventris*, ANBO = *Anaxyrus boreas*, AMMA = *Ambystoma macrodactylum*, THSI = *Thamnophis sirtalis*. n/a = not applicable

YEAR	**SPECIES**	**Adult/Juvenile**		**YOY/Neonate**		**Larvae**	**Egg Masses/ Strings**
		Observed*	Captured	Observed*	Captured	Observed	Observed
2010	RALU	137	55	46	31	~135	183
	ANBO	12	7	1576	335	~10,000	~100
	AMMA	1	1	0	0	0	0
	THSI	42	22	11	8	n/a	n/a
2011	RALU	227	71	23	9	~225	160
	ANBO	87	17	1720	246	~7000	~134
	AMMA	3	3	1	1	6	89
	THSI	48	32	0	0	n/a	n/a
TOTAL	RALU	364	126	69	40	360	343
	ANBO	99	24	3296	581	~17000	~234
	AMMA	4	4	1	1	6	89
	THSI	90	54	11	8	n/a	n/a

*Observed counts include individuals that were seen, but missed, and also those that were captured.

Table 2. Total numbers of unique individuals observed and/or captured at Ptarmigan Creek, by species and life stage. RALU = *Rana luteiventris*, ANBO = *Anaxyrus boreas*, AMMA = *Ambystoma macrodactylum*, THSI = *Thamnophis sirtalis*.

YEAR	**SPECIES**	**Adult/Juvenile**		**YOY/Neonate**		**Larvae**	**Egg Masses/ Strings**
		Observed*	Captured	Observed*	Captured	Observed	Observed
2010	RALU†	10	2	0	0	0	0
	ANBO	33	8	38	33	~7000	~70
	AMMA	0	0	0	0	0	0
	THSI	40	25	1	1	x	x
2011	RALU†	18	10	0	0	12	1
	ANBO	39	11	4450	174	~26,000	~357
	AMMA	0	0	0	0	0	0
	THSI	85	68	0	0	x	x
TOTAL	RALU	28	12	0	0	12	1
	ANBO	72	19	4488	207	~33,000	~427
	AMMA	0	0	0	0	0	0
	THSI	125	93	0	1	x	x

*Observed numbers include individuals were seen, but missed, and also those that were captured. † Many Columbia Spotted Frog observations were made upland of the drawdown zone, in the "Ditch Pond".

Species Distributions

Valemount Peatland

Columbia Spotted Frogs were widespread at the Peatland and were observed at ponds across the entire site. In 2011, Columbia Spotted Frog egg masses were commonly found in exactly the same locations they had been in the previous year. These frogs exhibited strong fidelity to breeding ponds and locations within those ponds (see Chapter 3 for further discussion). Western Toads bred in fewer ponds than Columbia Spotted Frogs (Figure 6) and were observed less frequently (with the exception of young-of-the-year toads when they emerged from their natal ponds). Western Toads also demonstrated strong breeding pond fidelity, but the location of egg strings within these ponds was variable. Long-toed Salamanders were observed infrequently (Tables 1 and 2) and at only 4 ponds in the Peatland.

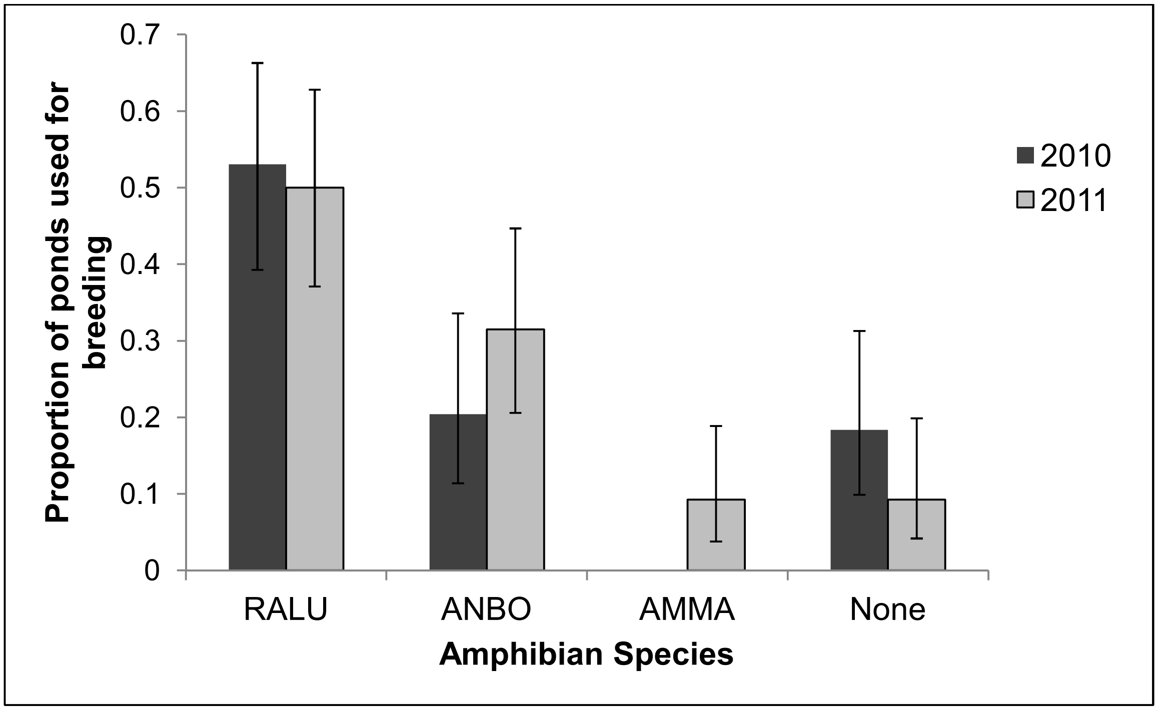

Figure 6. The proportion of ponds in the Valemount Peatland used for breeding by Columbia Spotted Frogs (RALU), Western Toads (ANBO) and Long-toed Salamanders (AMMA), in 2010 and 2011. "None" refers to the ponds where no breeding activity was detected. Bars represent the Wilson score 95% confidence intervals for a binomial distribution.

The majority of Common Garter Snakes were found around a single pond in the Peatland. At 753 m ASL, this pond is not regularly inundated by the reservoir (see Chapter 3 for details). Most anurans in the Valemount Peatland were observed between 751 and 753 m ASL (Figures 7 and 8). However, Western Toads bred in ponds at lower elevations, and many young-of-the-year toads were observed at 749 m ASL in 2010 (Figures 9 and 10). In 2011, I was unable to survey the Peatland at 749 or 750 m ASL for young-of the-year anurans because the reservoir inundated these areas before metamorphosis was complete (see Chapter 3).

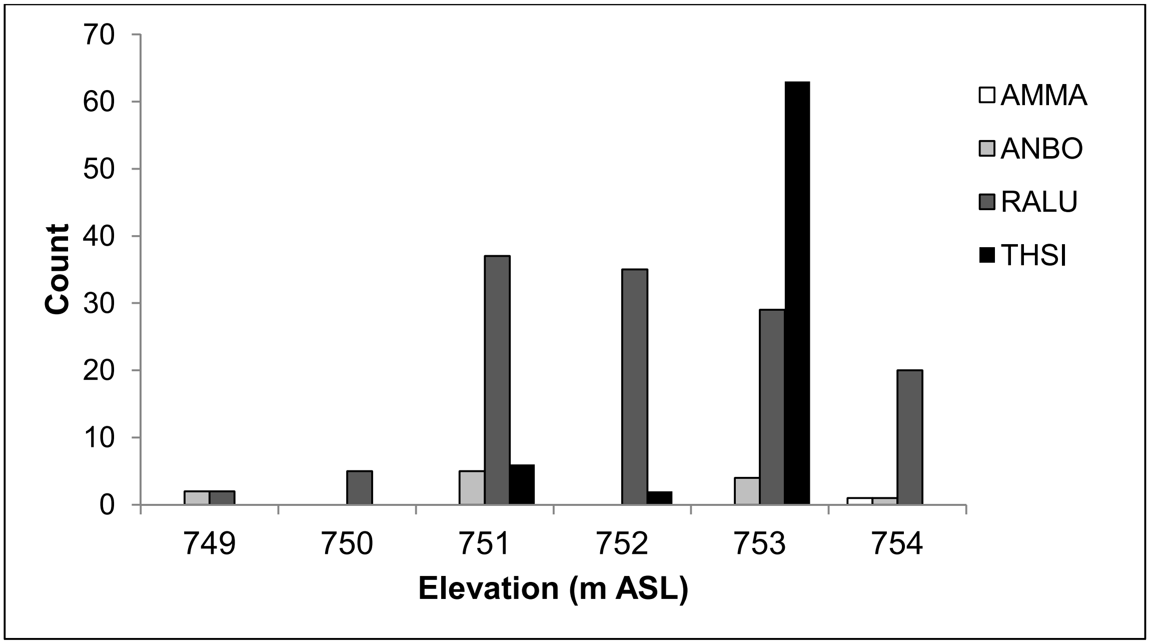

Figure 7. Total number of adults and juveniles observed in the Valemount Peatland in 2010, by species and elevation. Long-toed Salamander (*Ambystoma macrodactylum*) = AMMA, Western Toad (*Anaxyrus boreas*) = ANBO, Columbia Spotted Frog (*Rana luteiventris*) = RALU, and Common Garter Snake (*Thamnophis sirtalis*) = THSI.

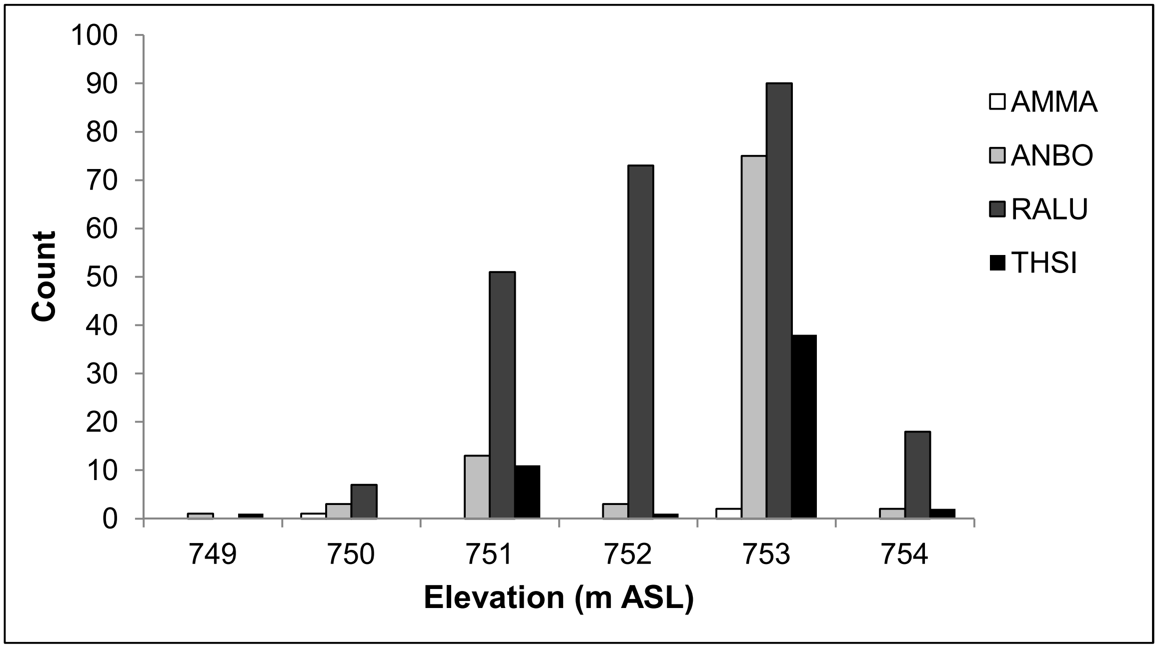

Figure 8. Total number of adults and juveniles observed in the Valemount Peatland in 2011, by species and elevation. Long-toed Salamander (*Ambystoma macrodactylum*) = AMMA, Western Toad (*Anaxyrus boreas*) = ANBO, Columbia Spotted Frog (*Rana luteiventris*) = RALU, and Common Garter Snake (*Thamnophis sirtalis*) = THSI.

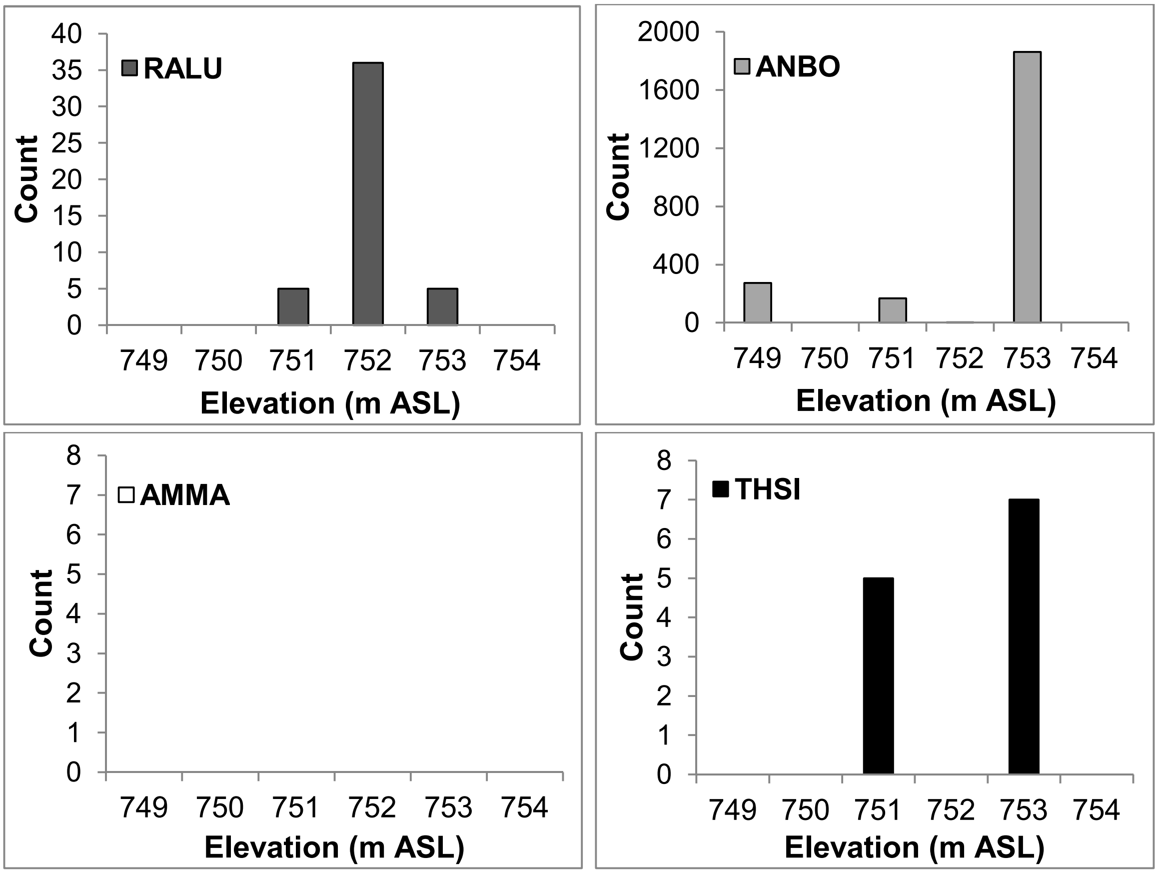

Figure 9. The total number of young-of-the year/neonates observed in the Valemount Peatland in 2010, by species and elevation. Upper left panel: RALU = *Rana luteiventris* (Columbia Spotted Frog), Upper Right: ANBO = *Anaxyrus boreas* (Western Toad); Bottom Left: AMMA = *Ambystoma macrodactylum* (Long-toed Salamander); Bottom Right: THSI = *Thamnophis sirtalis* (Common Garter Snake). No young-of-the-year Long-toed Salamanders were observed in 2010.

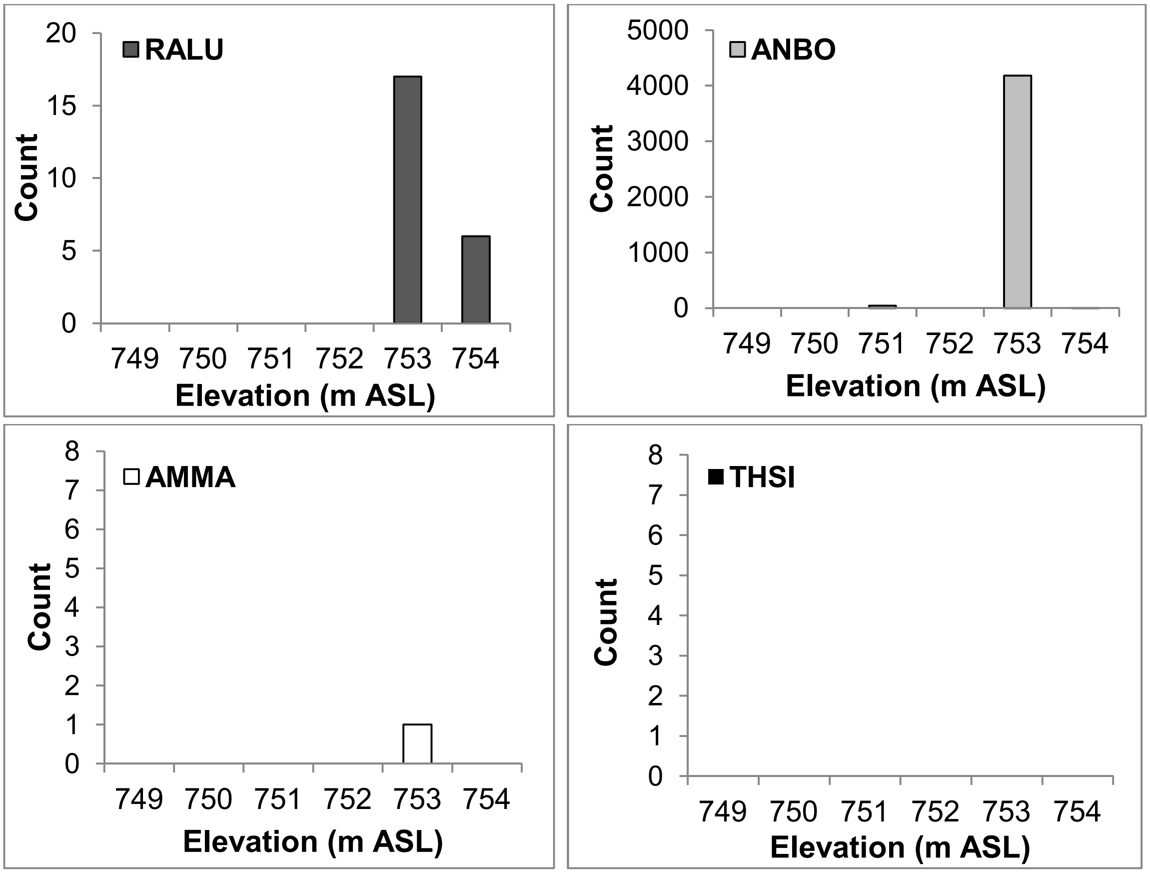

Figure 10. The total number of young-of-the year/neonates observed in the Valemount Peatland in 2011, by species and elevation. Upper left panel: RALU = *Rana luteiventris* (Columbia Spotted Frog), Upper Right: ANBO = *Anaxyrus boreas* (Western Toad); Bottom Left: AMMA = *Ambystoma macrodactylum* (Long-toed Salamander); Bottom Right: THSI = *Thamnophis sirtalis* (Common Garter Snake). No neonate Common Garter Snakes were observed in 2011.

Ptarmigan Creek

Ptarmigan Creek consists of a small vegetated area (31.4 Ha; Hawkes et al., 2007) and a single pond (0.95 Ha; Hawkes and Tuttle, 2012), and has a much steeper elevation gradient than the Valemount Peatland. Nearly all species observations at this site were made within a 100 metre radius. A description of the elevational distribution of each species at Ptarmigan Creek would not be very informative. Common Garter Snakes and Western Toads were regularly found in the drawdown zone here, but Long-toed Salamanders were not detected in either year. Columbia Spotted Frogs were rarely observed in the drawdown zone (only four Columbia Spotted Frogs in two field seasons). The majority of Columbia

Spotted Frog observations at this site (Table 2) were made at a small, spring-fed ditch pond (~37 m^2) that is upland of the drawdown zone. One Columbia Spotted Frog egg mass was observed in the ditch pond in 2011.

Body Size

Valemount Peatland

Morphometric data suggest that Columbia Spotted Frogs in the Peatland can be sorted by snout-urostyle length into three size classes: young-of-the-year (5 – 30 mm), juvenile (30 – 50 mm), and adult (50 – 80 mm). Although low recapture rates prevented the analysis of individual growth patterns (see below), cohort growth patterns were detected in 2010 (Figure 11). In 2011, most of the Columbia Spotted Frogs captured were from the largest size class; therefore cohort growth patterns were not apparent (Figure 12). Outside the breeding season, sexes could not be reliably distinguished. Therefore, I have not attempted to report on them separately here.

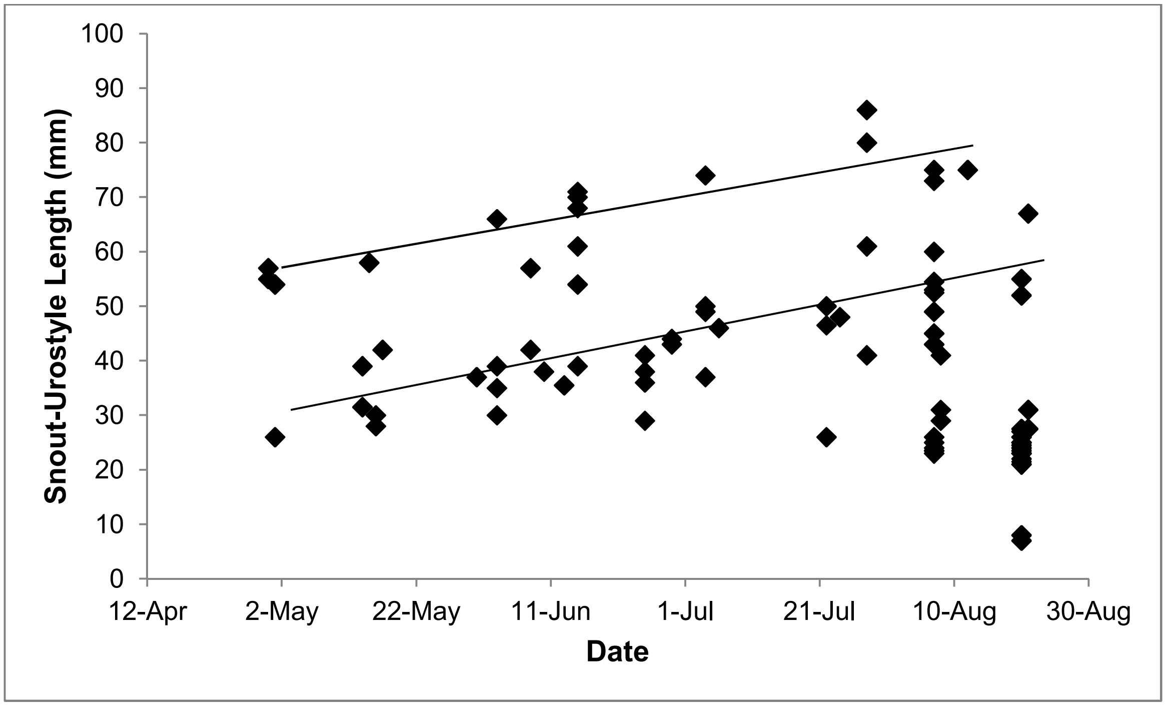

Figure 11. Snout-urostyle lengths for all captured Columbia Spotted Frogs (*Rana luteiventris*) at the Valemount Peatland in 2010. Trend lines are hand-drawn and are intended to highlight separate size classes and their apparent growth over the study period.

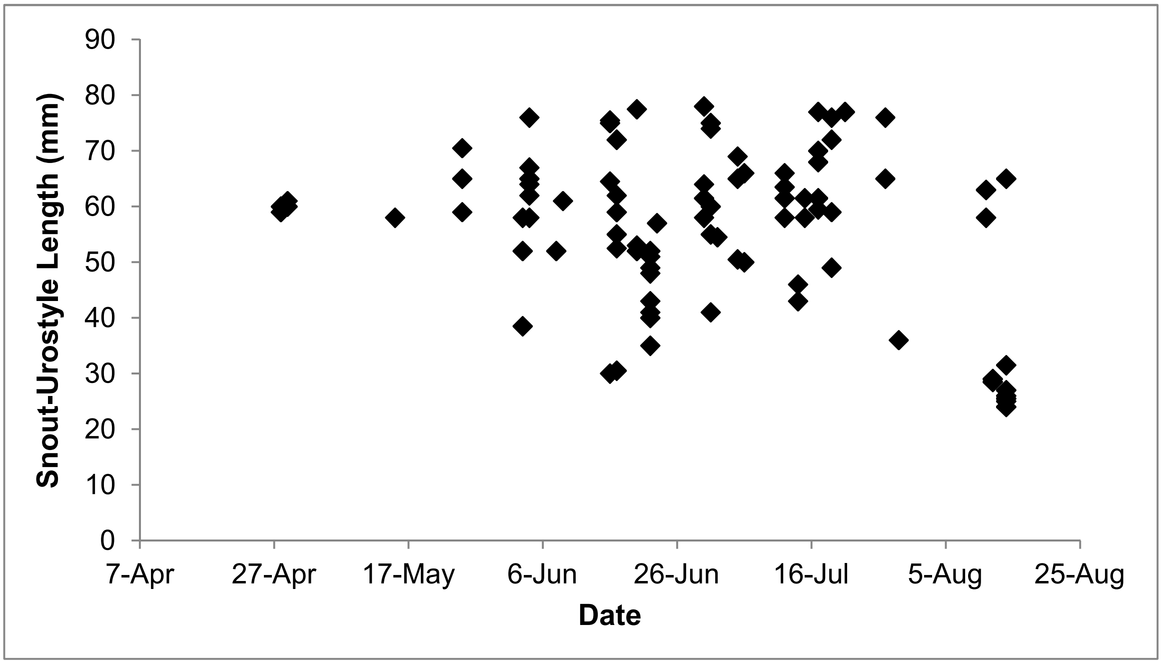

Figure 12. Snout-urostyle lengths for all captured Columbia Spotted Frogs (*Rana luteiventris*) at the Valemount Peatland in 2011.

Western Toads were captured less frequently than Columbia Spotted Frogs at the Valemount Peatland. With the exception of three individuals captured in 2011, all toads were classified as adult (65 to 110 mm SUL) or young-of-the-year (10 to 20 mm SUL). The virtual absence of juveniles (25 to 60 mm SUL) suggests that Western Toads do not utilize the drawdown zone at all stages of their life cycle (Figures 13 and 14).

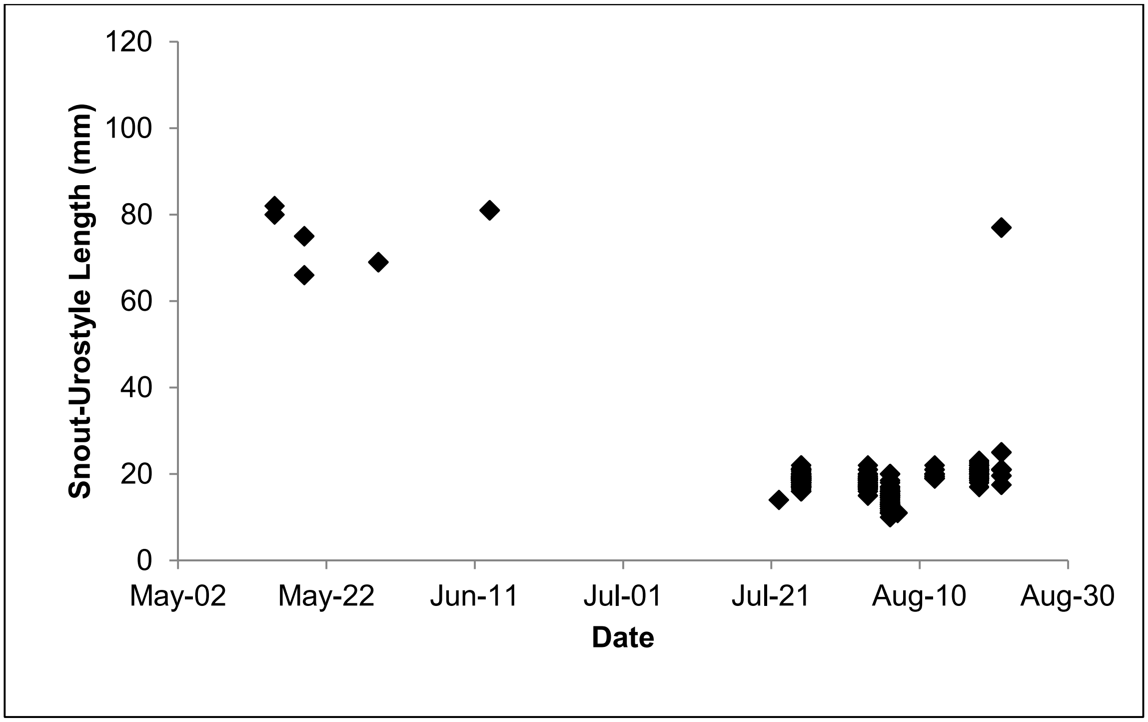

Figure 13. Snout-urostyle lengths for all captured Western Toads (*Anaxyrus boreas*) at the Valemount Peatland in 2010.

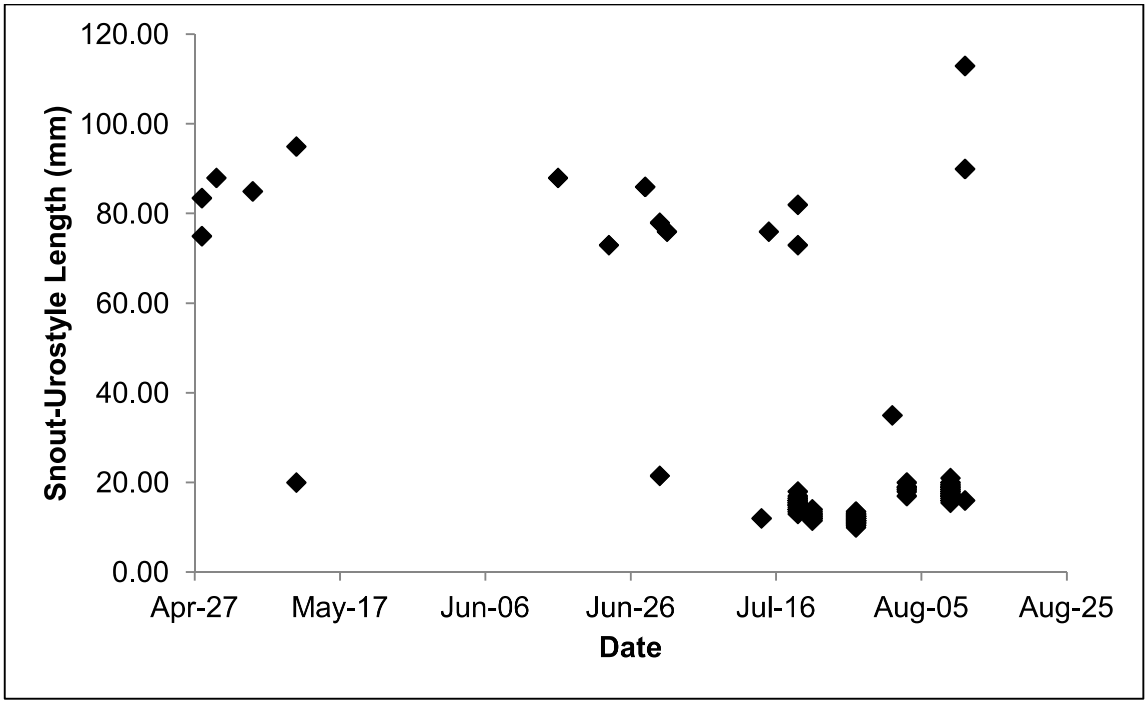

Figure 14. Snout-urostyle lengths for all captured Western Toads (*Anaxyrus boreas*) at the Valemount Peatland in 2011.

The Common Garter Snakes at the Valemount Peatland are among the biggest on record (Figure 15; for comparison see Fitch, 1965; Stewart, 1968; Whittier and Crews, 1990; Gregory and Larsen, 1993; Matsuda et al., 2006). Female snout-vent lengths ranged from 219 to 956 mm and males ranged from 229 to 640 mm. Neonates were between 191 and 220 mm in snout-vent length.

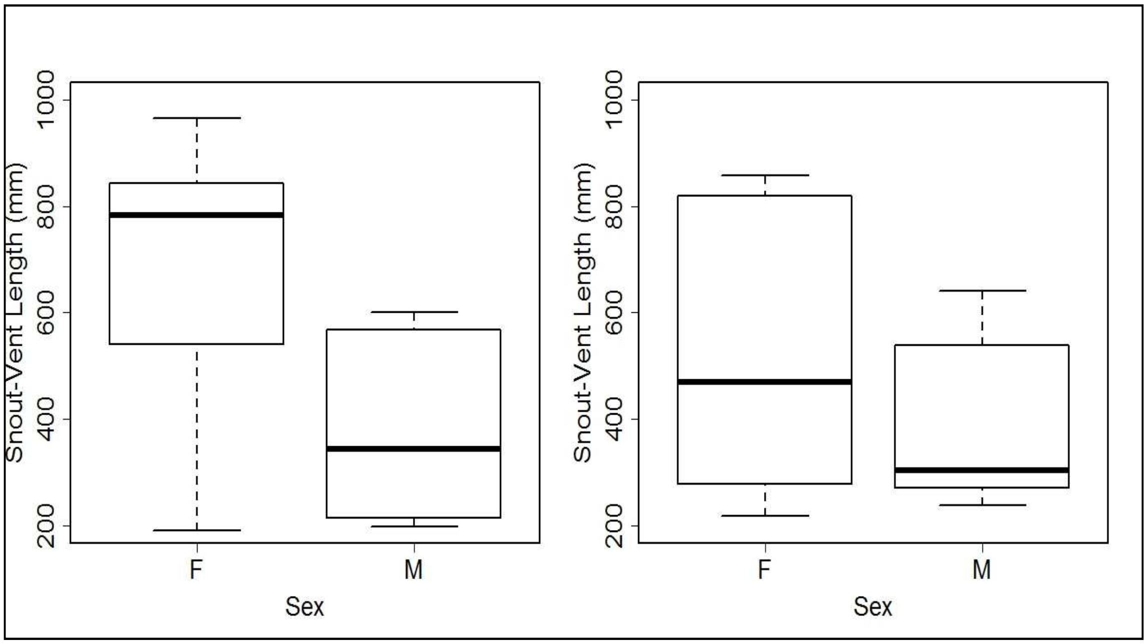

Figure 15. Snout-vent lengths of Common Garter Snakes (*Thamnophis sirtalis*) at the Valemount Peatland in 2010 (left) and 2011 (right). In 2010, n = 19 unique males and n= 20 unique females were captured and measured. In 2011, n = 16 unique males and n= 13 unique females were captured and measured. The upper and lower boundaries of the boxes represent the 25th and 75th percentiles. The horizontal line across each box is the median. Bars show the upper and lower limits of sampled snout-vent lengths.

Ptarmigan Creek

Very few Columbia Spotted Frogs were captured at Ptarmigan Creek (n = 12). Two juveniles were captured in 2010 (43 and 44 mm in SUL) and ten adults were captured in 2011 (57 to 78 mm SUL). In keeping with the trend observed at the Valemount Peatland, Western Toads were either adults (74 to 103 mm SUL) or young-of-the-year (12 to 22 mm SUL; Figures 16 and 17). No juvenile Western Toads were detected.

Male Common Garter Snakes at Ptarmigan Creek were similar in snout-vent length to those at the Peatland (197 to 632 mm), but the females at this site were generally smaller (217 to 612 mm) and captured less frequently (Figure 18). None of the captured females were gravid, and only one neonate garter snake was observed at this site in 2010. It measured 212 mm in snout-vent length.

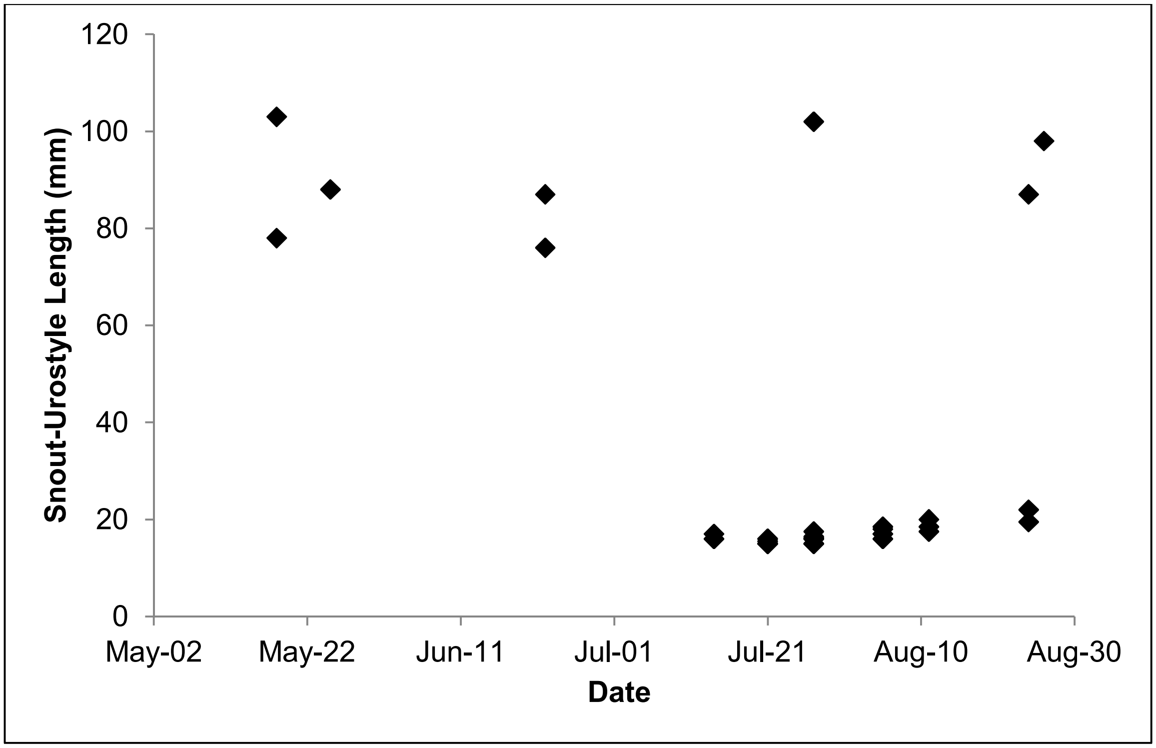

Figure 16. Snout-urostyle lengths for all captured Western Toads (*Anaxyrus boreas*) at Ptarmigan Creek in 2010.

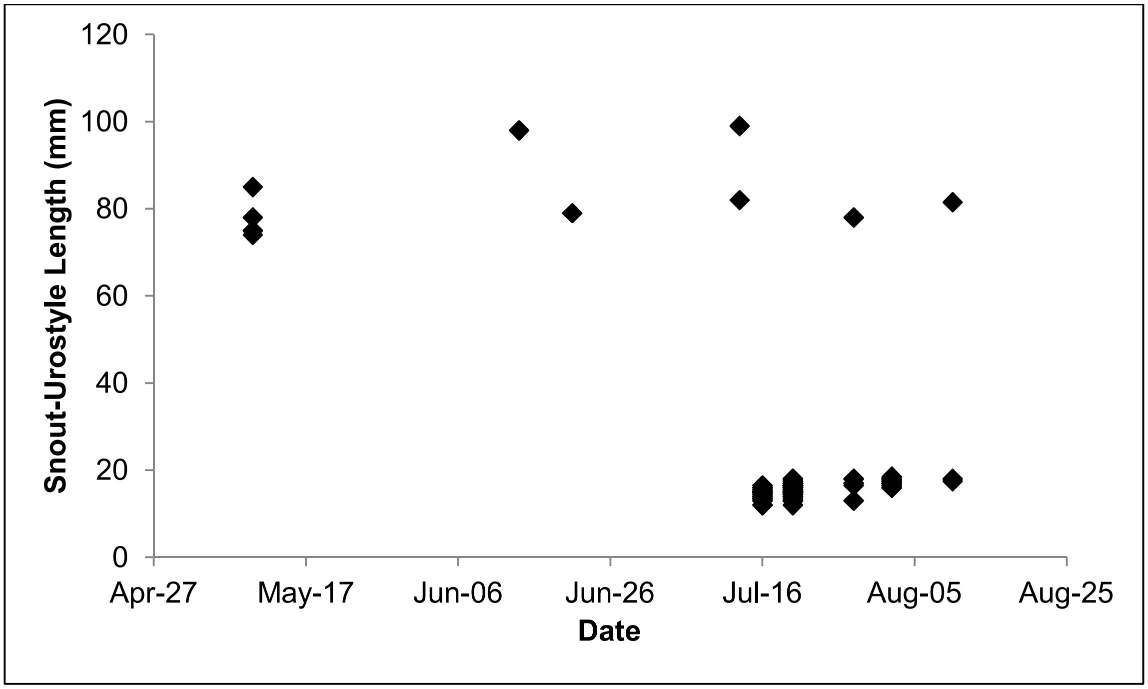

Figure 17. Snout-urostyle lengths for all captured Western Toads (*Anaxyrus boreas*) at Ptarmigan Creek in 2011.

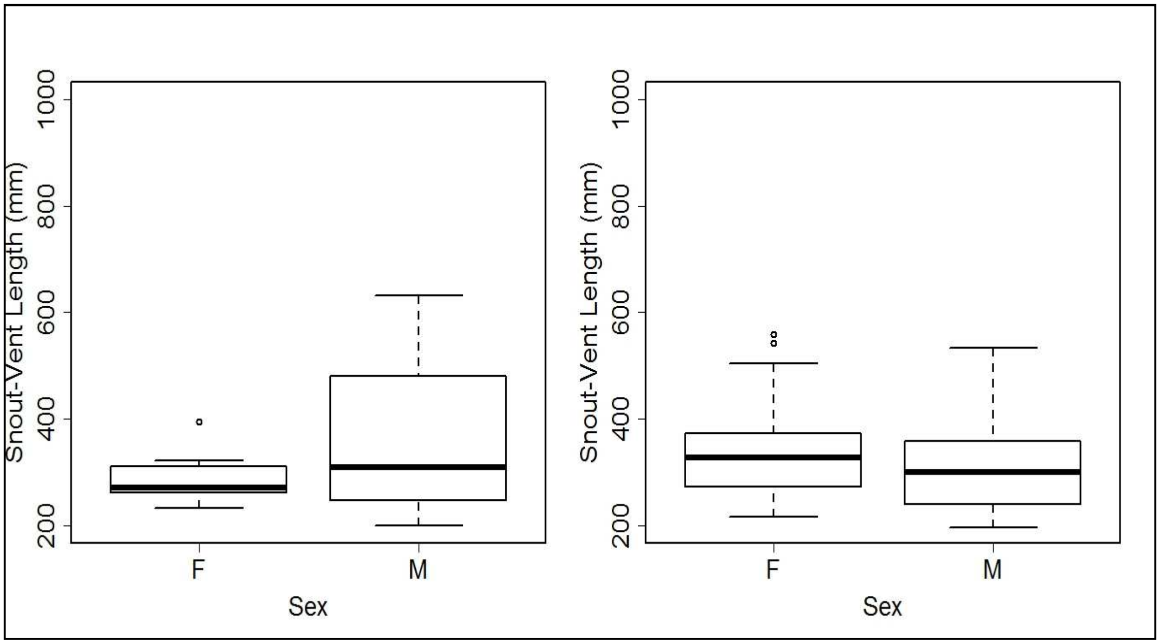

Figure 18. Snout-vent lengths of Common Garter Snakes (*Thamnophis sirtalis*) at Ptarmigan Creek in 2010 (left) and 2011 (right). In 2010, n = 23 unique males and n=9 unique females were captured and measured. In 2011, n = 62 unique males and n= 43 unique females were captured and measured. The upper and lower boundaries of the boxes represent the 25th and 75th percentiles. The horizontal line across each box is the median. Bars show the upper and lower limits of sampled snout-vent lengths.

Body Condition

An ANCOVA revealed a significant effect of year ($F_{1,130} = 477.93$, $p << 0.001$) on the relative mass of adult and juvenile Columbia Spotted Frogs at the Valemount Peatland. There was also significant heterogeneity of slopes between years in mass ($F_{1,130} = 9.91$, $p = 0.002$; Figure 19), compromising the test of the main effect. When I analysed large (> 58 mm SUL) and small frogs (< 58 mm SUL) separately, I found that small frogs had significantly lower relative mass in 2011 than in 2010 ($p = 0.015$). However, the relative mass of large frogs was still confounded by an interaction between mass and snout-urostyle length. Barrett et al. (2010) argue that when the coefficient of determination for the full model (i.e. the model that includes an interaction term) is only marginally higher than that of the reduced model, proceeding with the reduced model is justifiable. Without separating frogs by snout-urostyle length, the coefficient of determination for my full model (adjusted $R^2 = 0.9667$) was only slightly higher than when the interaction term was omitted (adjusted $R^2 = 0.9644$). Fitting parallel slopes appears justifiable in this case, because the model without an interaction term explains virtually as much of the total variation in mass as the full model does (Barrett et al., 2010). The simplified model indicates that all juvenile/adult Columbia Spotted Frogs had slightly lower body condition in 2011 than in 2010 ($p = 0.034$; Figure 20).

The mass of young-of-the-year Western Toads varied significantly with year ($F_{1,605} = 784.32$, $p << 0.001$), but there was also a significant interaction between year and snout-urostyle length ($F_{1,605} = 24.55$, $p << 0.001$; Figure 21). Separate analyses of large (>18 mm SUL) and small (<18.5 mm SUL) young-of-the-year toads revealed that small YOY toads had significantly lower relative mass in 2011 than in 2010 ($F_{1,350} = 249.69$, $p << 0.001$). However, there was no significant difference in relative mass of large YOY toads in 2010 and 2011 ($F_{1,251} = 1.26$, $p= 0.261$).

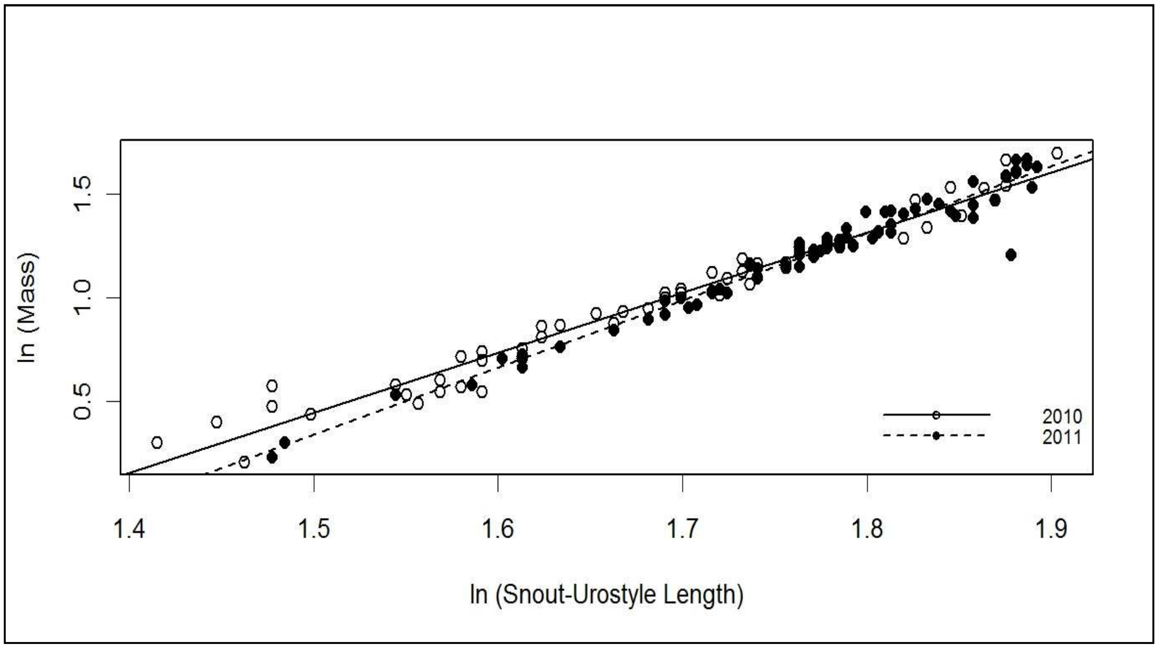

Figure 19. Mass (g) of adult and juvenile Columbia Spotted Frogs (*Rana luteiventris*) at the Valemount Peatland in 2010 (n = 53) and 2011 (n = 81), relative to snout-urostyle length (mm). Measurements have been natural log transformed. Adjusted $R^2 = 0.9667$.

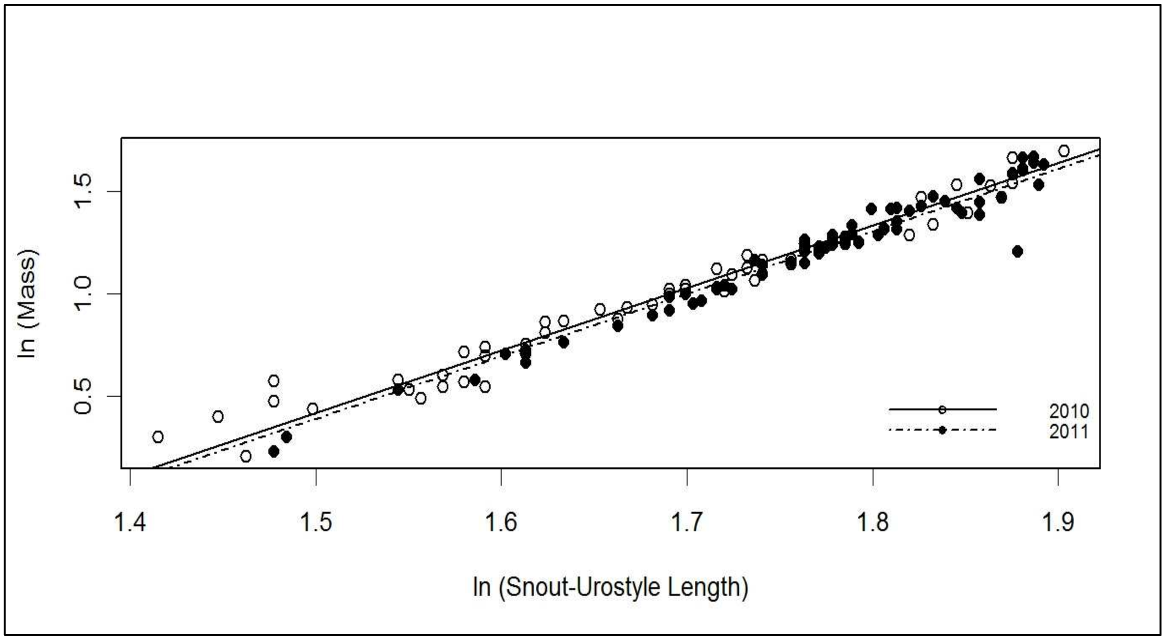

Figure 20. Mass (g) of adult and juvenile Columbia Spotted Frogs (*Rana luteiventris*) at the Valemount Peatland in 2010 (n = 53) and 2011 (n = 81), relative to snout-urostyle length (mm). Interaction effects have been dropped from the model. Measurements have been natural log transformed. Adjusted $R^2 = 0.9644$.

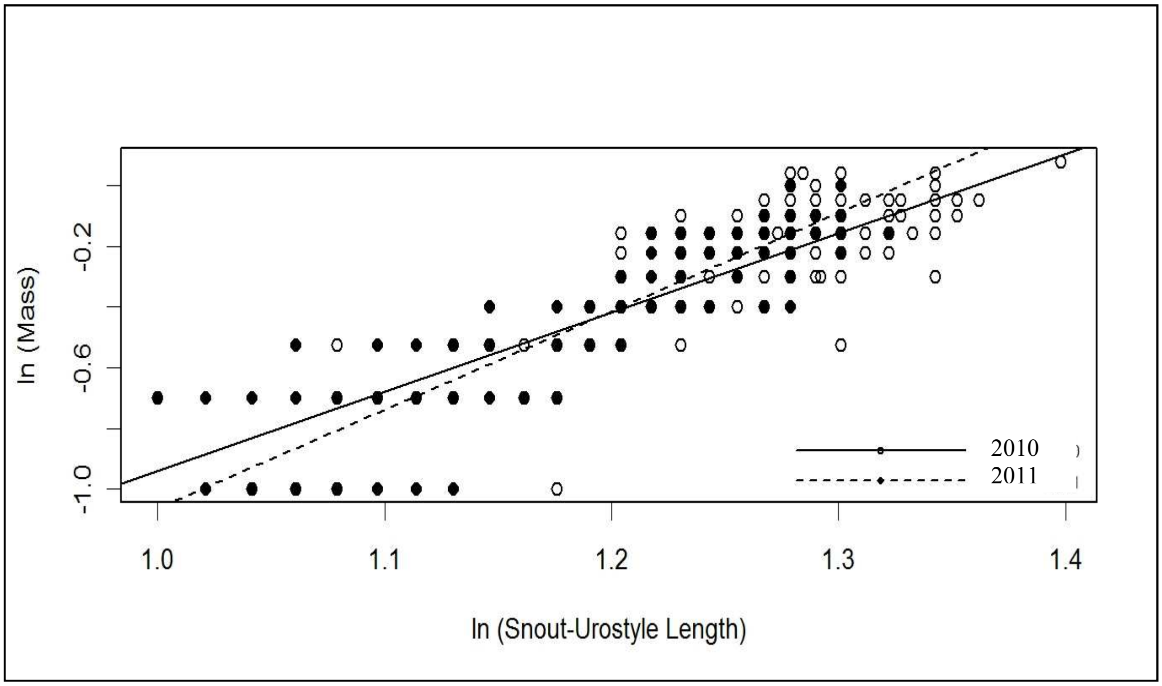

Figure 21. Mass (g) of young-of-the-year Western Toads (*Anaxyrus boreas*) at the Valemount Peatland in 2010 (n = 356) and 2011 (n = 253), relative to snout-urostyle length (mm). Measurements have been natural log transformed.

The relative mass of young-of-the-year Western Toads differed by site ($F_{2, 1063} = 252.38$, $p << 0.001$; Figure 22). Young-of-the-year toads at Ptarmigan Creek had significantly different relative masses from those at the Peatland or Cranberry Marsh ($p = 0.0007$). The relative masses of YOY toads at the latter two sites were not significantly different from each other ($p = 0.127$). However, there was heterogeneity of slopes between sites in mass ($F_{2, 1063} = 11.84$, $p << 0.001$) and this difference was attributed to toads at Ptarmigan Creek ($p = 0.0004$). Separate analyses of large (>16.5 mm SUL) and small (<16 mm SUL) YOY toads did not resolve this problem – the interaction between site and snout-urostyle length remained for small YOY toads ($F_{2, 567} = 10.64$, $p << 0.001$), but not large YOY toads ($F_{2, 538} = 1.5848$, $p = 0.206$). Large young-of-the-year toads at Cranberry Marsh had significantly lower relative mass than those at the Valemount Peatland and Ptarmigan Creek ($p = 0.0005$). Metamorphs at Cranberry Marsh were also visibly frail and emaciated in 2010 – many were observed being preyed upon by ants.

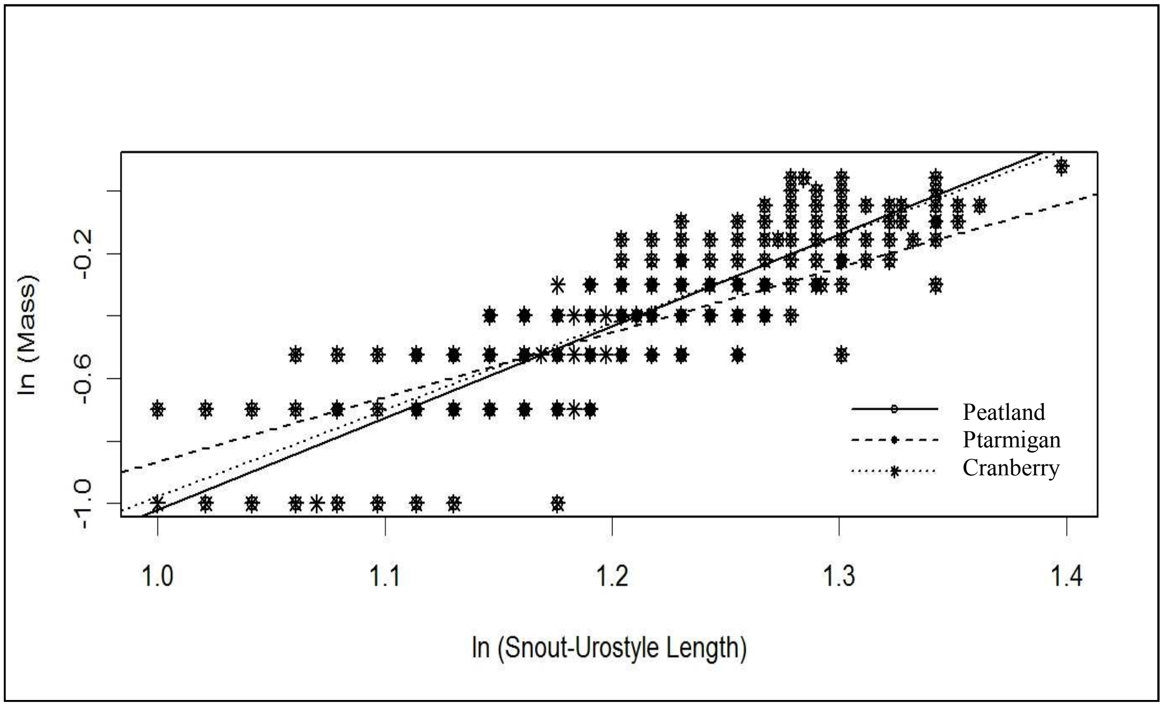

Figure 22. Mass (g) of young-of-the-year Western Toads (*Anaxyrus boreas*) relative to snout-urostyle length (mm) at three independent locations: Valemount Peatland (n = 609 toads), Ptarmigan Creek (n = 203 toads), and Cranberry Marsh (n = 257 toads). 2010 (n = 525) and 2011 (n = 544) data were pooled for this site comparison. Measurements have been natural log transformed.

Once females, recaptures, and fed individuals were removed from the data set, only 38 Common Garter Snakes remained for body condition analyses (18 at the Valemount Peatland and 20 at Ptarmigan Creek). An ANCOVA revealed no heterogeneity of slopes in mass ($F_{3, 34} = 1.129$, p = 0.295) and no significant difference in body condition for male garter snakes at the Peatland and Ptarmigan Creek ($F_{3, 34} = 1.097$, p = 0.302; Figure 23).

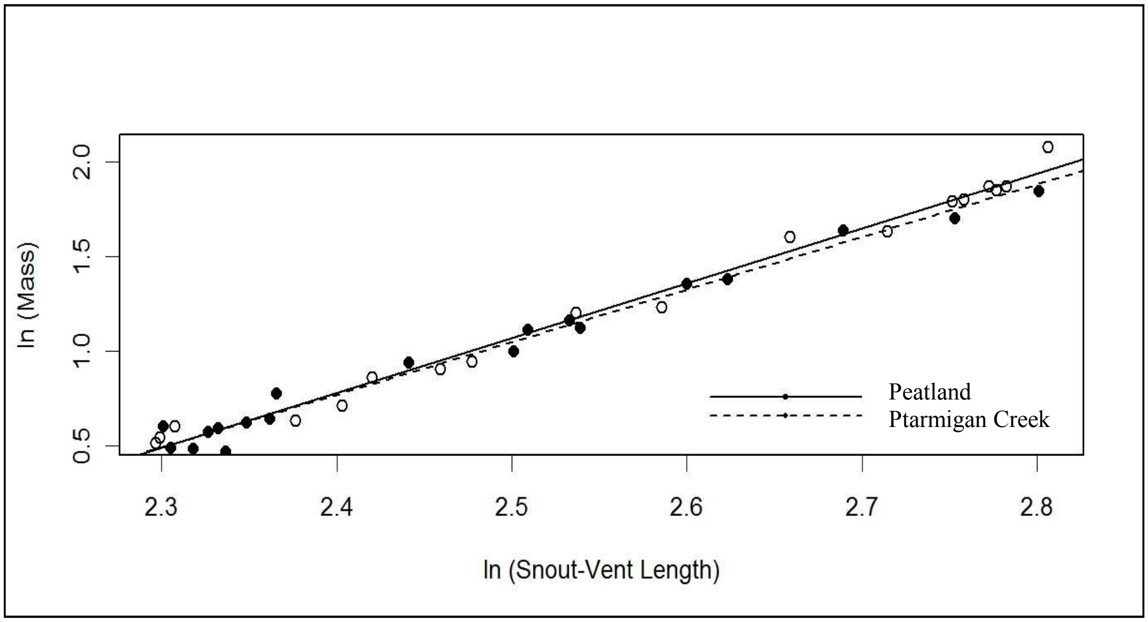

Figure 23. Mass (g) of male Common Garter Snakes (*Thamnophis sirtalis*), relative to snout-vent length (mm) at the Valemount Peatland (n = 18) and Ptarmigan Creek (n = 20). 2010 and 2011 data were pooled for this site comparison. Measurements have been natural log transformed.

Mark-recaptures and movement

Valemount Peatland

Of the 55 adult/juvenile Columbia Spotted Frogs captured in 2010, I was able to create unique “fingerprints” for 30 of them using the I^{3}SM2.1 program. I identified just 3 recaptured individuals from this sample of 30 (Figure 24). The mean (± SD) total distance travelled by these frogs was 20.75 m ± 25.07 m (range = 5.6 to 50.2 m). The mean movement rate for these individuals was 0.46 ± 0.43 m/day (range = 0.12 to 0.94 m/day). Improved photography procedures in 2011 made it possible to create fingerprints for all 71 captured adults/juveniles. Ten of these frogs were recaptured during the field season and three frogs were recaptures from 2010 (Figure 21). The mean (±SD) total distance travelled by recaptured frogs in 2011 was 24.2 ± 48.9 m (range = 0 to 134.6 m). The mean movement rate for these individuals was 0.87 ± 1.12 m/day (range = 0 to 2.7 m/day). Three frogs were captured in both 2010 and 2011 – all three were male and were found in the same ponds in both years. Frogs recaptured within the same year also demonstrated pond fidelity – ten of twelve were found at the same pond they were originally captured in. Only one Western Toad was recaptured over the course of this study (Figure 25), but this was not surprising, given how few were captured in the first place (7 adults in 2010 and 17 adults in 2011).

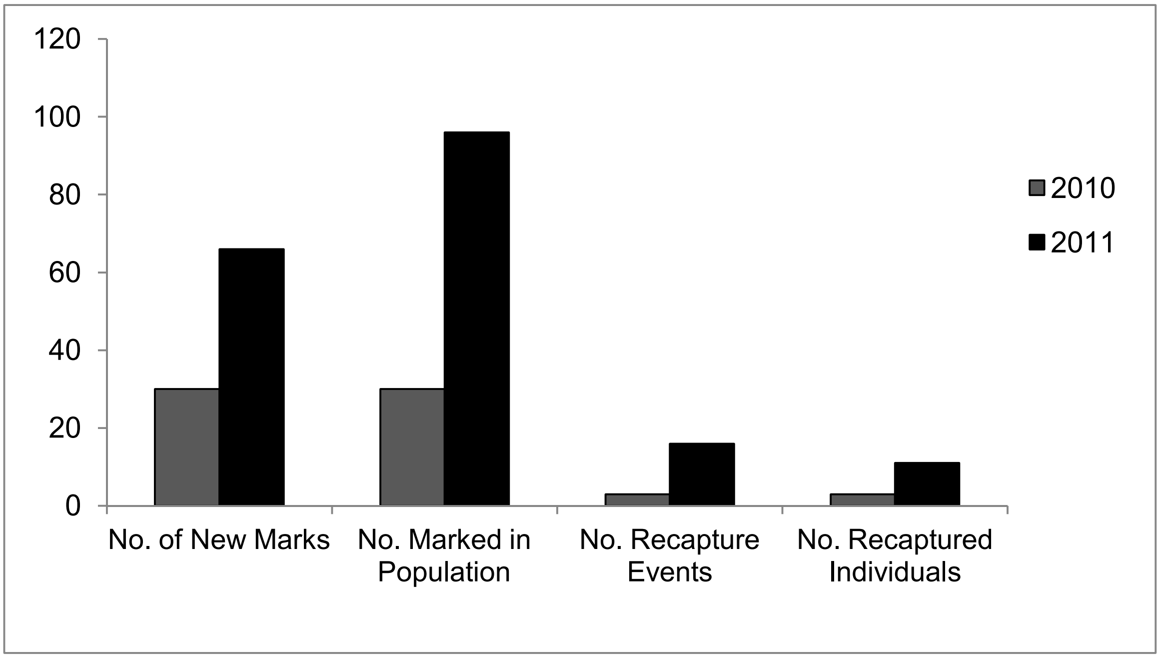

Figure 24. Columbia Spotted Frog (*Rana luteiventris*) mark-recapture history at the Valemount Peatland in 2010 and 2011. No. of New Marks = number of new individuals captured and marked in that year; No. Marked in Population = total number of marked individuals in the population (number marked in that year, plus all those marked in the previous years); No. Recapture Events = number of times a recapture was recorded in that year; No. Recaptured Individuals = number of unique individuals recaptured at least once in that year.

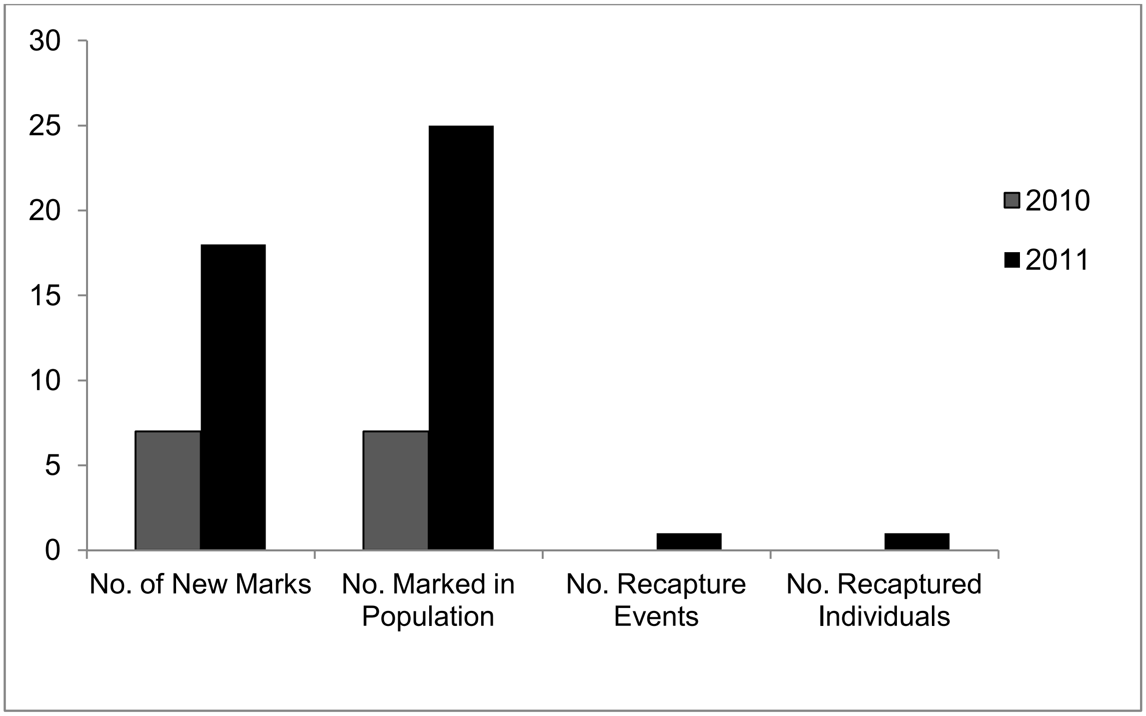

Figure 25. Western Toads (*Anaxyrus boreas*) mark-recapture history at the Valemount Peatland in 2010 and 2011. No. of New Marks = number of new individuals captured and marked in that year; No. Marked in Population = total number of marked individuals in the population (number marked in that year, plus all those marked in the previous years); No. Recapture Events = number of times a recapture was recorded in that year; No. Recaptured Individuals = number of unique individuals recaptured at least once in that year.

Of the 30 Common Garter Snakes captured at the Peatland in 2010, nine were recaptured over the course of the field season (Figure 26). The total movements of these snakes ranged from 1 to 174 m and minimum movement rates ranged from 0.05 to 9.15 m/day (Figure 27). The shortest movements (less than 2 m/day) were made by six gravid females. One gravid female was captured three times at the same location (9 m radius), over a period of 45 days. The fourth time she was captured after having given birth, at which point she had moved 80 metres from her former location to a pond shoreline, where thousands of metamorph Western Toads were located.

In 2011, four of 32 garter snakes were recaptures (Figure 26), including two that had been marked in the previous year. All were female. The two snakes recaptured within the 2011 season each moved less than a metre per day (0.17 and 0.72 m/day) and travelled 4.6 and 18 m between captures.

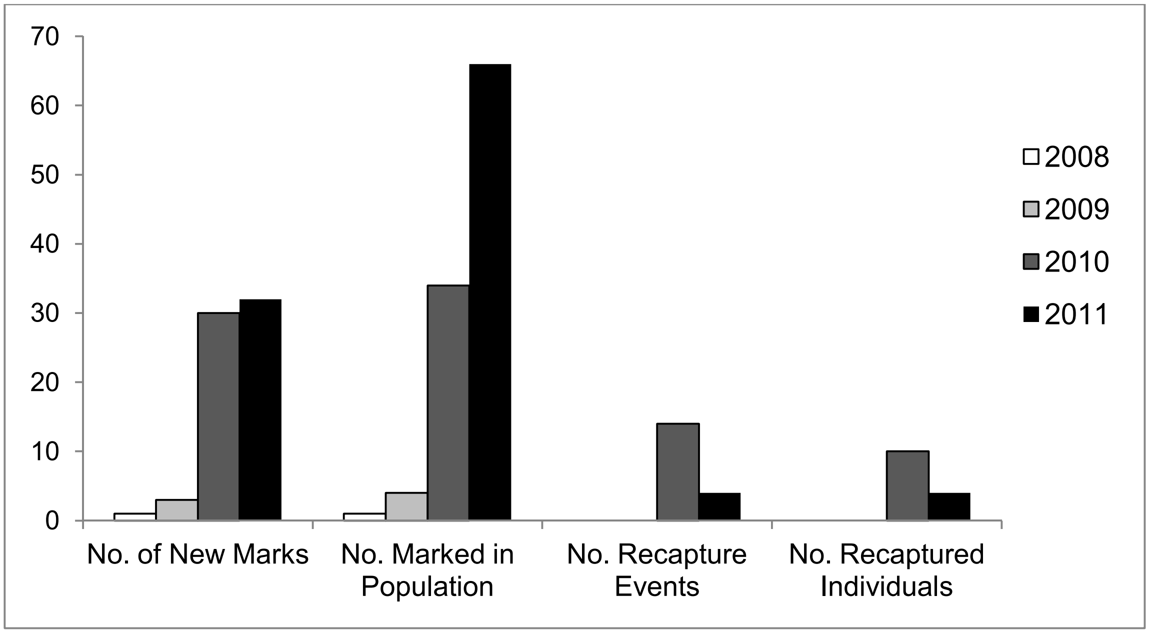

Figure 26. Common Garter Snake (*Thamnophis sirtalis*) mark-recapture history at the Valemount Peatland from 2008 to 2011. No. of New Marks = number of new individuals captured and marked in that year; No. Marked in Population = total number of marked individuals in the population (number marked in that year, plus all those marked in the previous years); No. Recapture Events = number of times a recapture was recorded in that year; No. Recaptured Individuals = number of unique individuals recaptured at least once in that year. Data from 2008 and 2009 were obtained by LGL environmental research associates.

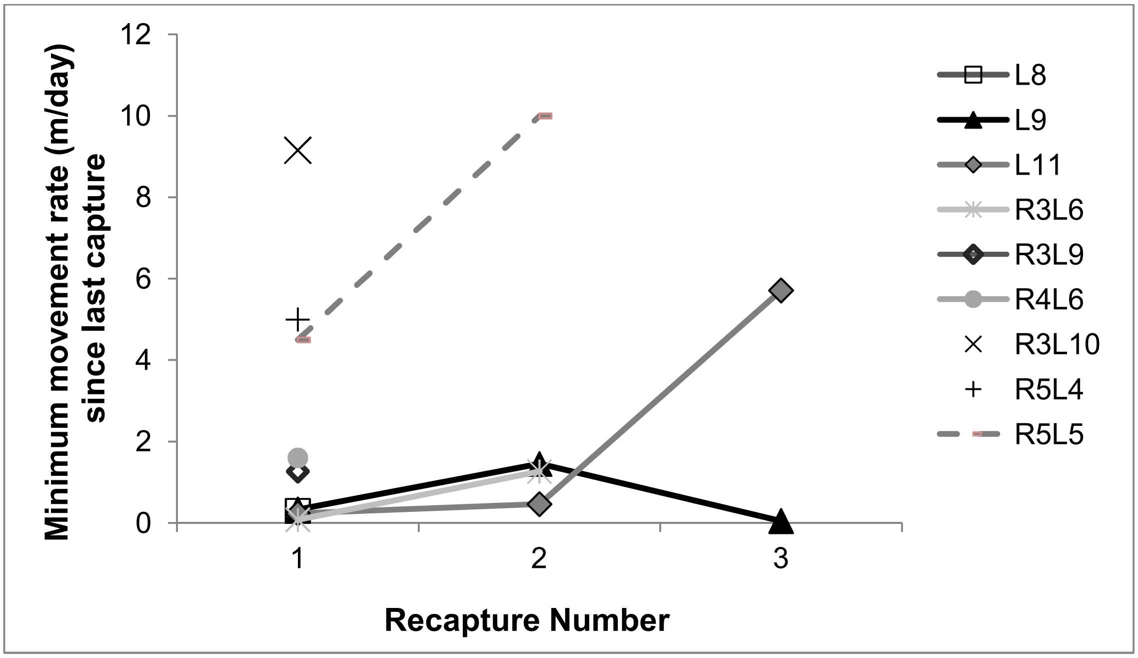

Figure 27. Minimum movement rate (m/day) recorded for recaptured Common Garter Snakes (*T. sirtalis*) at the Valemount Peatland in 2010. Solid lines (in the legend) represent gravid females, dashed lines represent adult males, and the single cross and x symbols each represent non-gravid females. L11 gave birth to her offspring between recaptures 2 and 3.

Ptarmigan Creek

There were no Western Toad recaptures at Ptarmigan Creek in either year and just one Columbia Spotted Frog recapture in 2011 (Figures 28 and 29). However, Common Garter Snakes were captured fairly frequently at this site. In 2010, 18% of all marked individuals were recaptured, and in 2011, 38% of all marked individuals were recaptured (Figure 30). Minimum movement rates in 2010 ranged from 0.2 to 8.7 m/day (Figure 31) and minimum distances travelled ranged from 6 to 100 m between captures. In the following year, a greater number of recaptures permitted a comparison of movement rates between the sexes. The minimum movement rates of non-gravid females ranged from 0 to 10.4 m/day (Figure 32), with the exception of one female that moved at least 43 m in one day. The distances travelled by females at this site ranged from 2.3 to 371.8 m between captures. Males made similar movements around the site. Their movements ranged from 0.5 to 138.4 m in minimum distance, at rates of 0.05 to 10.4 m/day (Figure 33), with the exception of one adult male that moved a minimum of 28 m/day. The two longest movements, made by one female and one male, were associated with travel into and out of the drawdown zone. Snakes within the drawdown zone appear to make quite short movements within a limited area around the main pond.

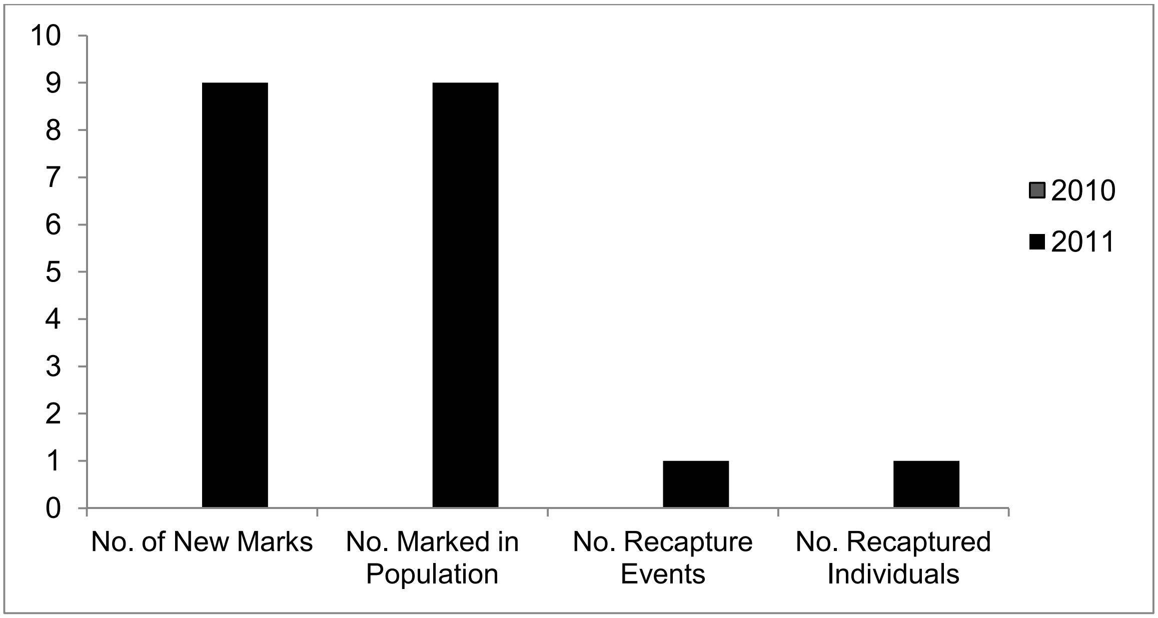

Figure 28. Columbia Spotted Frog (*Rana luteiventris*) mark recapture history at Ptarmigan Creek in 2010 and 2011. No frogs were successfully "marked" in 2010. No. of New Marks = number of new individuals captured and marked in that year; No. Marked in Population = total number of marked individuals in the population (number marked in that year, plus all those marked in the previous years); No. Recapture Events = number of times a recapture was recorded in that year; No. Recaptured Individuals = number of unique individuals recaptured at least once in that year.

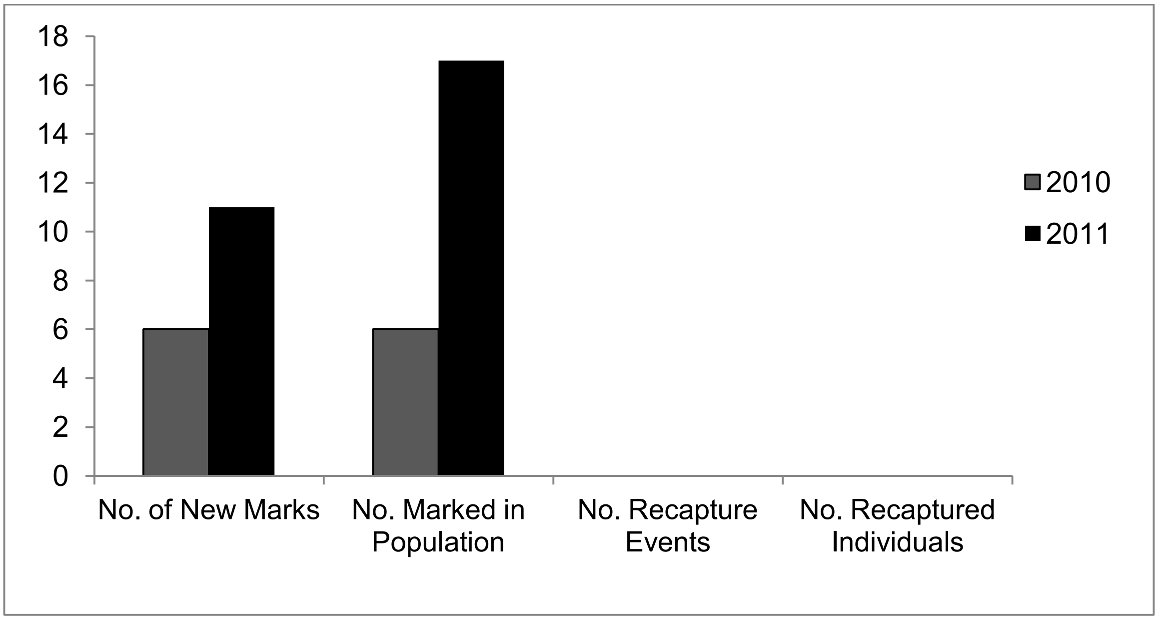

Figure 29. Western Toads (*Anaxyrus boreas*) mark-recapture history at Ptarmigan Creek in 2010 and 2011. No. of New Marks = number of new individuals captured and marked in that year; No. Marked in Population = total number of marked individuals in the population (number marked in that year, plus all those marked in the previous years); No. Recapture Events = number of times a

recapture was recorded in that year; No. Recaptured Individuals = number of unique individuals recaptured at least once in that year.

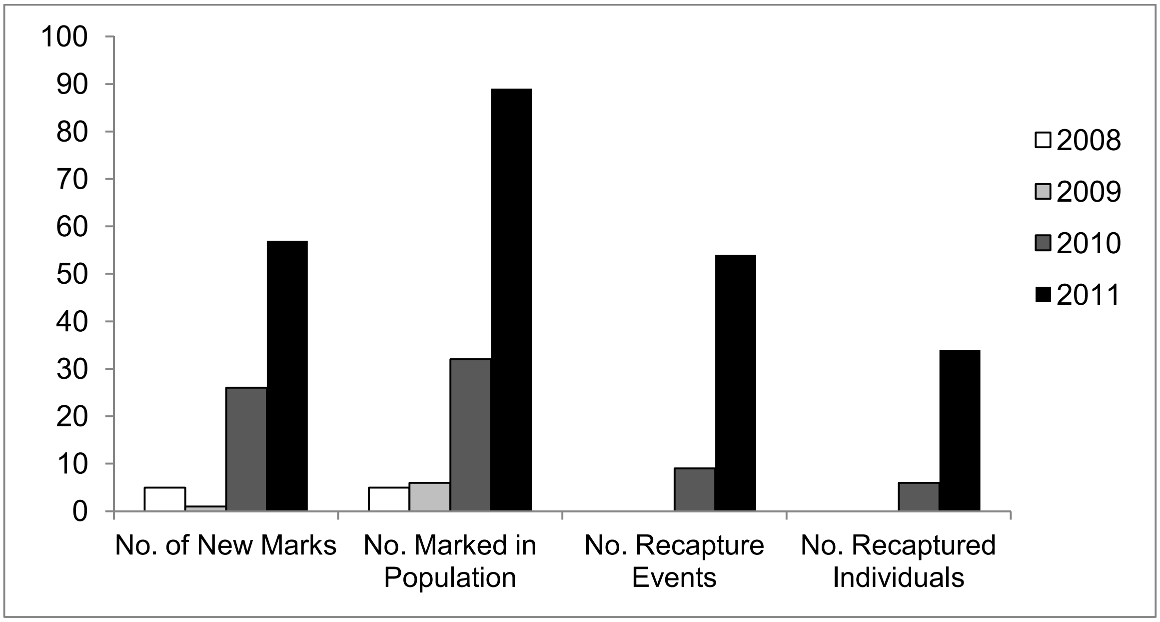

Figure 30. Common Garter Snake (*Thamnophis sirtalis*) mark-recapture history at Ptarmigan Creek from 2008 to 2011. No. of New Marks = number of new individuals captured and marked in that year; No. Marked in Population = total number of marked individuals in the population (number marked in that year, plus all those marked in the previous years); No. Recapture Events = number of times a recapture was recorded in that year; No. Recaptured Individuals = number of unique individuals recaptured at least once in that year. Data from 2008 and 2009 were obtained by LGL environmental research associate

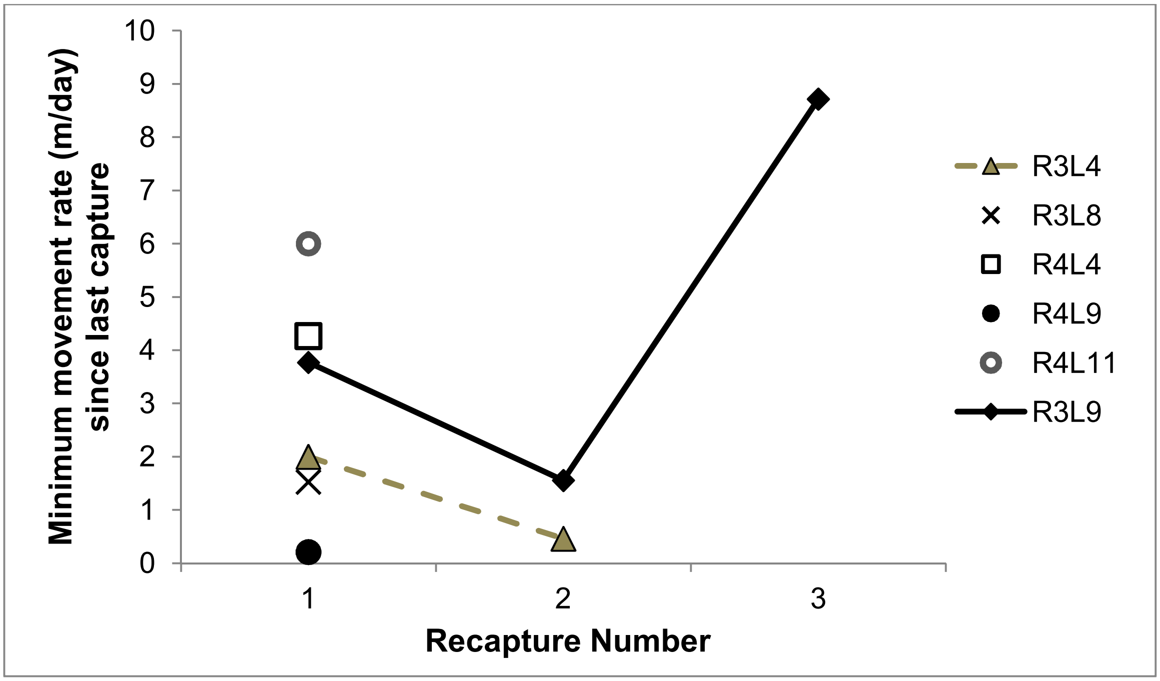

Figure 31. Minimum movement rate (m/day) recorded for recaptured Common Garter Snakes (*T. sirtalis*) at Ptarmigan Creek in 2010. R3L9 was a non-gravid female, R4L11 was a neonate, and the remainder were adult males.

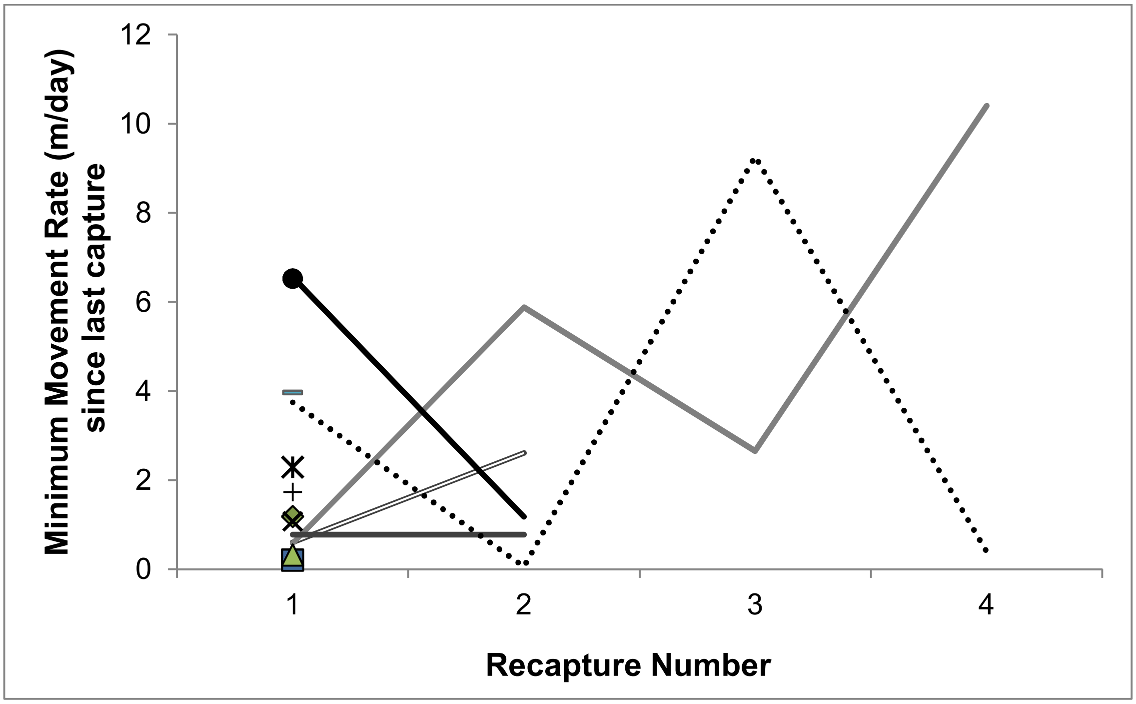

Figure 32. Minimum movement rates (m/day) recorded for recaptured female Common Garter Snakes (*T. sirtalis*) at Ptarmigan Creek in 2011. All females were non-gravid. One female, not included in this figure, moved 43 m in one day. Dashed lines and symbols represent juveniles – the rest are adult females.

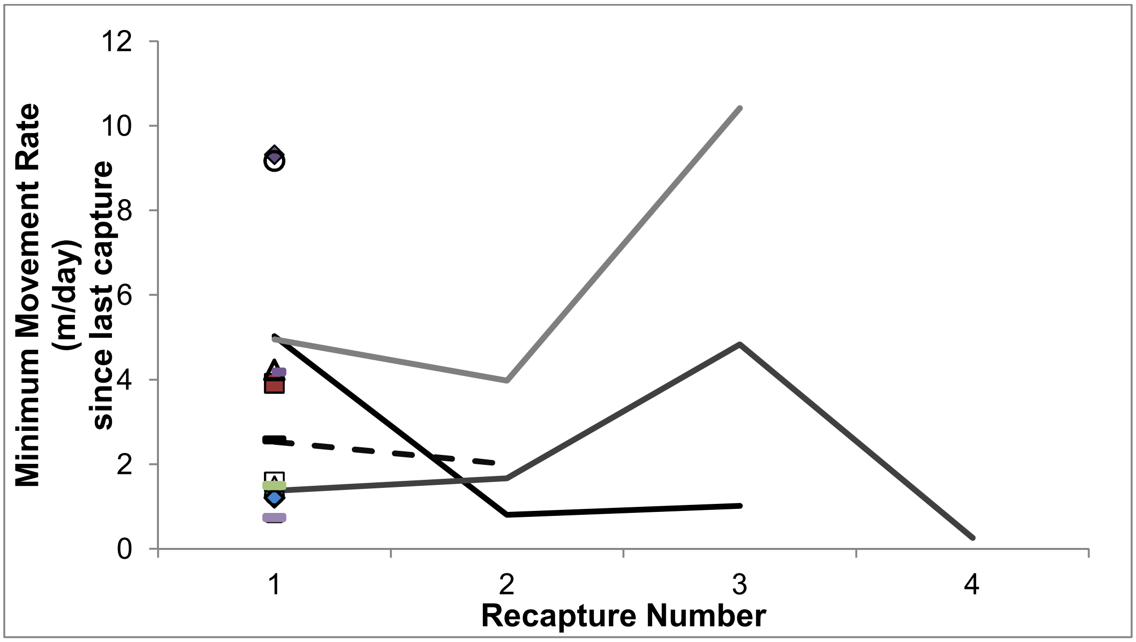

Figure 33. Minimum movement rates (m/day) recorded for recaptured male Common Garter Snakes (*T. sirtalis*) at Ptarmigan Creek in 2011. Dashed lines represent juveniles.

Growth of *Thamnophis sirtalis*

Growth rates for Common Garter Snakes generally decreased with increasing snout-vent length (Figure 34) but this trend was not quite significant (Pearson's r = -0.279; p = 0.09). My non-parametric analysis of male and female growth rates indicated there is no significant difference in growth between the sexes (two sample t = 1.5985; df = 19.878; p = 0.125). This was not surprising, given that the mean daily growth of males (0.58 mm/day) was not much different than that of females (0.53 mm/day; Figure 35). Too few recaptures were made at the Valemount Peatland to compare growth rates of garter snakes at this site and at Ptarmigan Creek.

The mean daily growth of gravid females (0.311 ± 0.278), was less than that of non-gravid females (0.690 ± 0.890), but the large standard errors of these estimates preclude meaningful interpretation of this trend. When gravid females were removed from the data set, the weak relationship between growth rate and snout-vent length disappeared completely (Pearson`s r = - 0.18; p = 0.326).

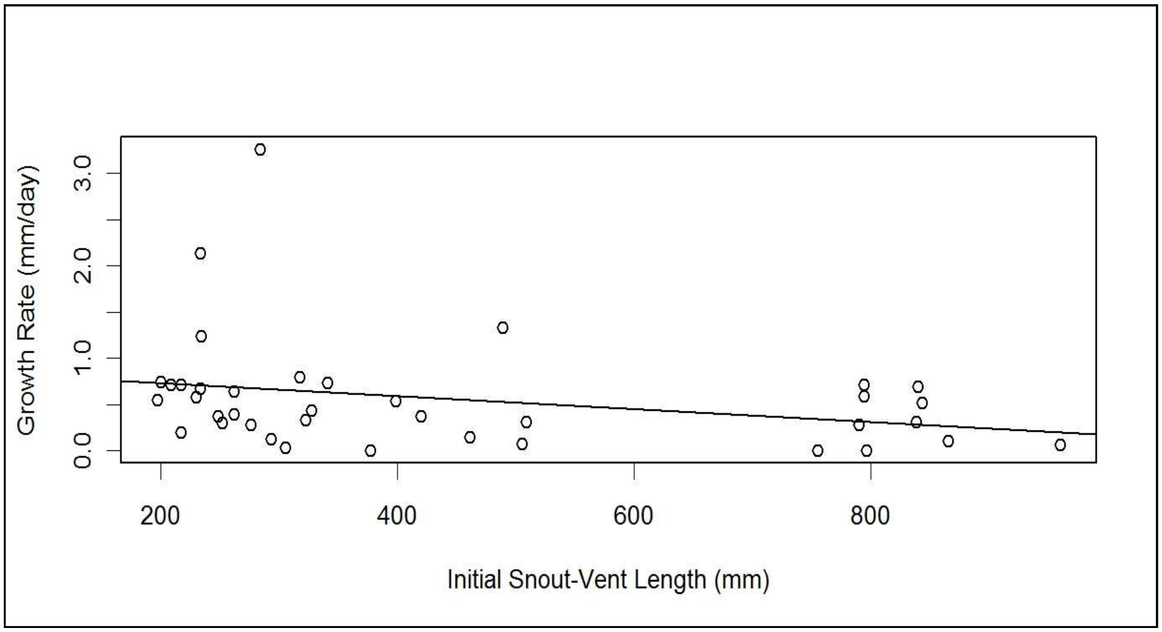

Figure 34. Individual Common Garter Snake (*T. sirtalis*) growth rates (mm/day) relative to their snout-vent length (mm) at initial time of capture. Snakes from Ptarmigan Creek and the Valemount Peatland were included in this analysis.

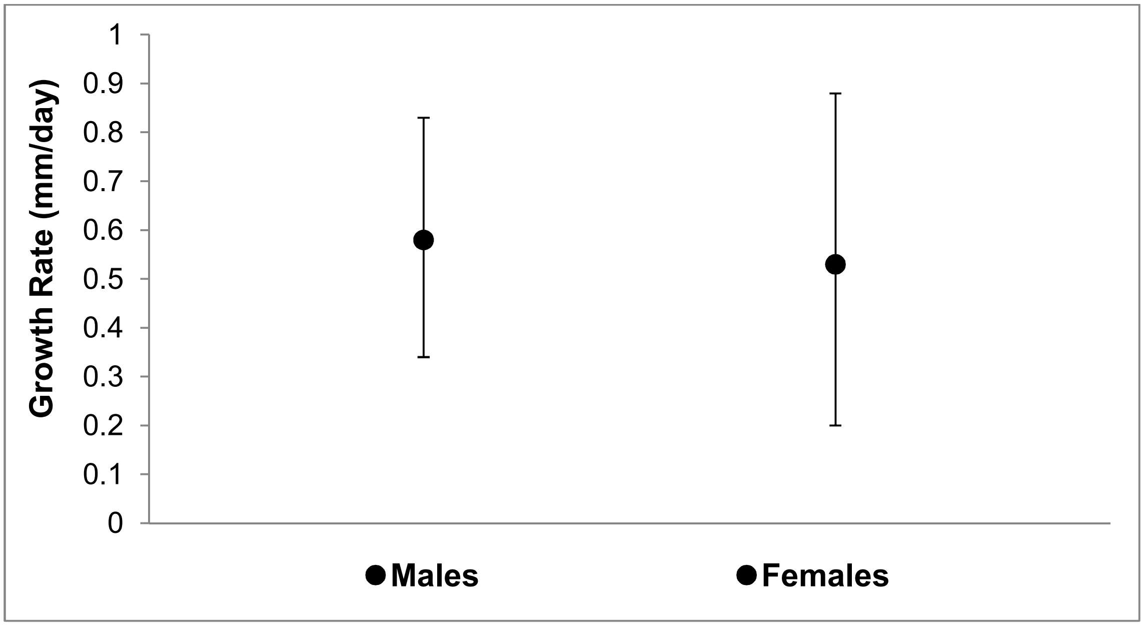

Figure 35. Mean growth rates (mm/day) of male and female Common Garter Snakes in the drawdown zone of Kinbasket Reservoir. Data from two sites, the Valemount Peatland and Ptarmigan Creek, were collected during the active seasons of 2010 and 2011 and pooled. Bars represent the 95% confidence intervals of the mean.

Food Habits of *Thamnophis sirtalis*

The predominant prey of Common Garter Snakes at both Ptarmigan Creek and the Valemount Peatland was the Western Toad. At the Peatland, approximately 50% of all snakes captured (in 2010 and 2011) had food in their stomach (Figure 36). Half of these snakes had consumed Western Toad tadpoles, metamorphs, or adults. The other half had unidentifiable or irremovable stomach contents. At Ptarmigan Creek, two thirds of all snakes had recently fed, and nearly 90% of those snakes had consumed Western Toads (Figure 37). However, not all stomach contents were removed and confirmed by visual inspection. Snakes were often captured while in the act of foraging for tadpoles and metamorph toads. The familiar shape and size of these toads made them easy to identify and count by gentle palpation of the snake`s stomach. As many as 10 metamorph toads were found in the stomach of one Common Garter Snake at Ptarmigan Creek – force feeding each toad back to the snake added an additional 25 minutes to the capture period for that snake. I therefore decided to limit this stress wherever possible and trusted the palpation technique to identify Western Toads in the stomachs of snakes, particularly when they were observed foraging along the shoreline of ponds. The results presented here must be interpreted this caveat in mind. Although I cannot rule out alternative prey types, it is apparent that Western Toads are important prey for Common Garter Snakes in the drawdown zone.

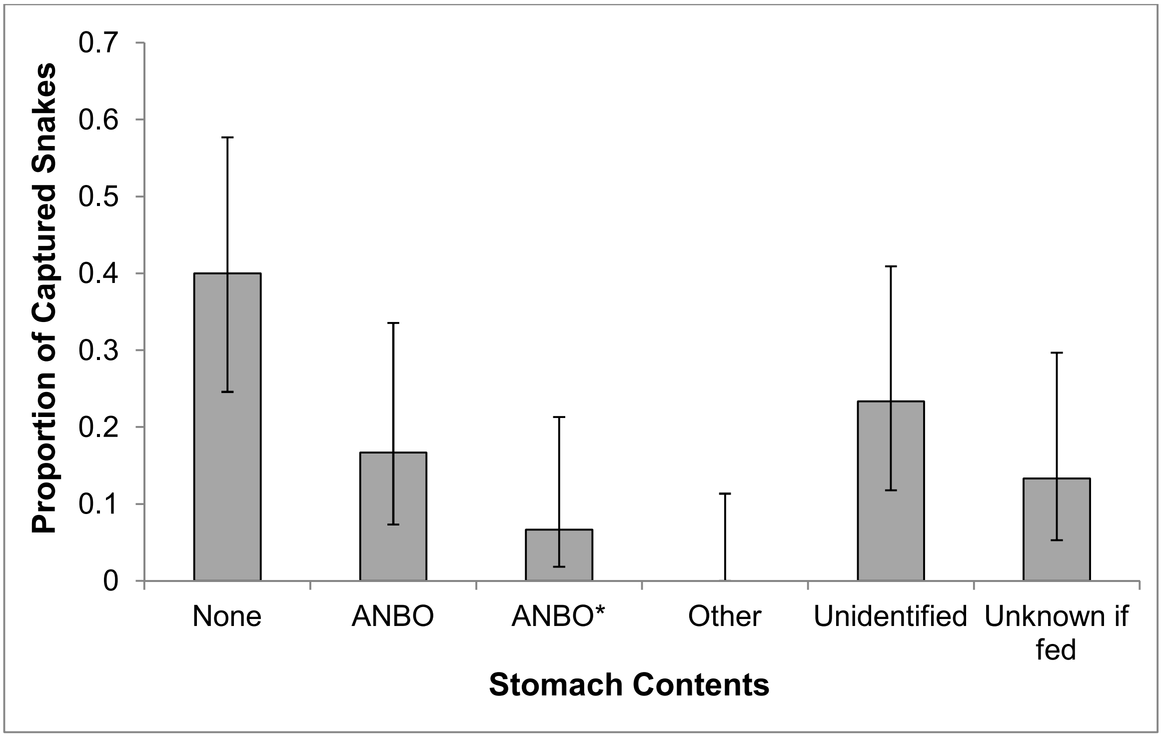

Figure 36. Stomach contents of Common Garter Snakes (*T. sirtalis*) at the Valemount Peatland. None = Empty stomach; ANBO = Western Toad (*Anaxyrus boreas*) of any age (i.e. tadpoles, young-of-the-year, or adult); ANBO* = Western Toads were determined to be the prey type, but this was not visually confirmed by removal of stomach contents; Other = prey type other than Western Toad; Unidentified = stomach contents could not be removed, or were too digested to identify upon removal; Unknown if Fed = unable to determine if stomach was completely empty.

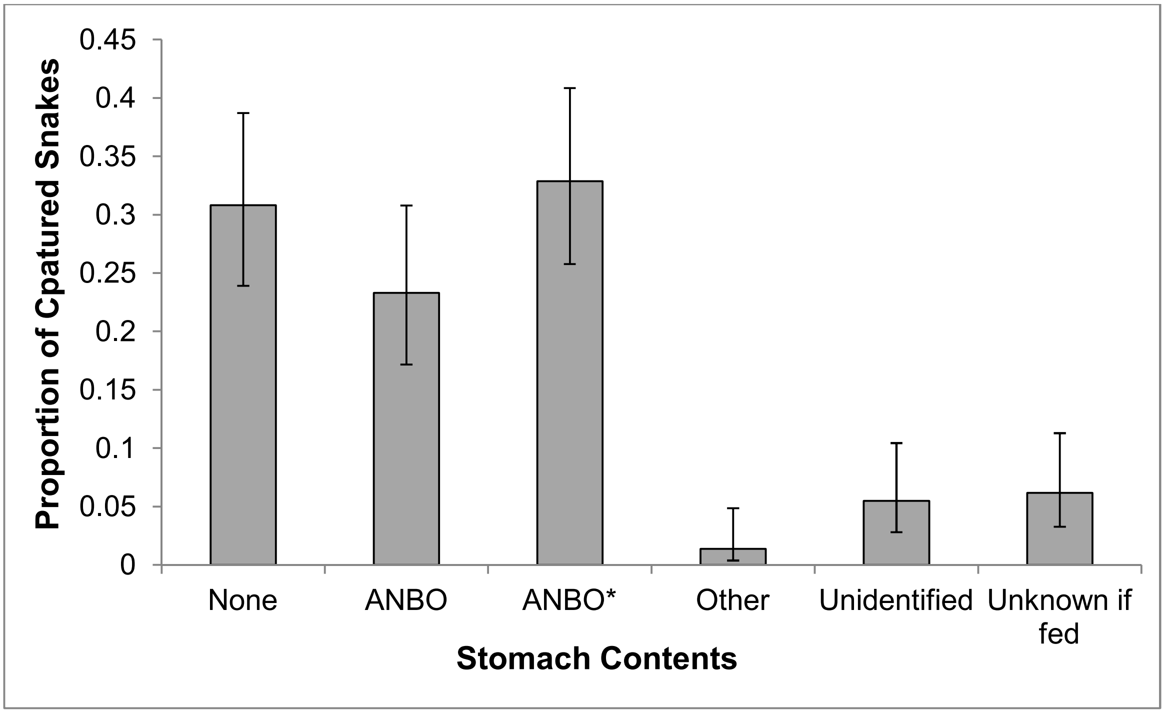

Figure 37. Stomach contents of Common Garter Snakes (*T. sirtalis*) at Ptarmigan Creek: None = Empty stomach; ANBO = Western Toad (*Anaxyrus boreas*) of any age (i.e. tadpoles, young-of-the-year, or adult); ANBO* = Western Toads were determined to be the prey type, but this was not visually confirmed by removal of stomach contents; Other = prey type other than Western Toad; Unidentified = stomach contents could not be removed, or were too digested to identify upon removal; Unknown if Fed = unable to determine if stomach was completely empty.

DISCUSSION

Common Garter Snakes, Columbia Spotted Frogs, and Western Toads were observed in the drawdown zone of Kinbasket Reservoir throughout the active season. These species make frequent use of the habitat available in the drawdown zone, despite the flooding that occurs every summer. Long-toed Salamanders were rarely detected, but they did use ponds in the Valemount Peatland for breeding, alongside Columbia Spotted Frogs and Western Toads. The drawdown zone clearly plays an important role in the life cycles of local amphibian populations. Continued efforts to document amphibians in the drawdown zone should incorporate pitfall trapping (Beneski et al., 1986; Fukumoto and Herrero, 1998; Crosswhite et al., 1999) to increase the probability of detecting Long-toed Salamanders, which are secretive by nature.

The absence of Columbia Spotted Frog breeding activity in the drawdown zone at Ptarmigan Creek is notable - there may be particular biotic or abiotic characteristics that make this pond less suitable for breeding in, relative to the ditch pond, which is located outside the drawdown zone. Alternatively, the low elevation of this site may mean that there is insufficient time for Columbia Spotted Frog tadpoles to metamorphose prior to inundation by the reservoir (see Chapter 3 for further discussion of this subject). Female Columbia Spotted Frogs lay just one egg mass per season; therefore the number of egg masses observed at a site can provide a good indication of the number of breeding females present in the area (Crouch and Paton, 2000). Given that only one Columbia Spotted Frog egg mass was located at Ptarmigan Creek (upland of the drawdown zone), the effective size of this population is probably very low.

Western Terrestrial Garter Snakes (*Thamnophis elegans*) were not detected at either site, despite being present in the general area. These snakes were often found ~ 30 km south of Ptarmigan Creek, but were far upland of the drawdown zone at that site. In British Columbia, Western Terrestrial Garter Snakes are most commonly found adjacent to aquatic habitat (Matsuda et al., 2006); their absence at two of the most productive riparian areas in the drawdown zone is unexpected. Both *T. elegans* and *T. sirtalis* may prey heavily on anuran tadpoles and metamorphs when they are available (Arnold and Wassersug, 1978; Kephart and Arnold, 1982; Jennings et al., 1992), yet not a single Western Terrestrial Garter Snake was observed foraging at known amphibian breeding ponds. A lesser reliance on amphibian prey may be characteristic of Western Terrestrial Garter Snakes in British Columbia – both Gregory (1984) and Farr (1988) reported that *T. elegans* consumed far more slugs and small mammals than amphibians on Vancouver Island and in Creston, respectively. Kephart and Arnold (1982) also found that *T. elegans* readily switched to alternative prey during periods of low prey availability. Perhaps the benefits of foraging for alternative prey, upland of the drawdown zone, are greater than those gained by competing with Common Garter Snakes for anuran prey.

The non-detection of juvenile Western Toads in the drawdown zone suggests that this species uses the drawdown zone primarily for breeding. Newly metamorphosed and juvenile Western Toads generally migrate away from breeding sites (Bull, 2009) and their behaviour and habitat preferences at this stage are not well documented. Therefore, the absence (or non-detection) of juveniles in the drawdown zone is probably not related to reservoir disturbance. Although adult Western Toads were found most frequently during the breeding season, they were also observed in the months of June, July and August. This suggests that the drawdown zone also provides summer foraging habitat for some adult toads. Only one Western Toad was recaptured over the course of this study; therefore it is uncertain whether adult toads remain in the habitat after breeding, or if they move into and out of the drawdown zone over the course of the active season. These questions would be best answered by a telemetry study.

Roughly ten per cent of all marked Columbia Spotted Frogs at the Valemount Peatland were recaptured at some point. These frogs made short movements within the drawdown zone and tended to be recaptured in the same ponds in which they were first observed. The high pond fidelity demonstrated by these frogs suggests that there are sufficient food resources within reach of certain ponds to allow frogs to forage in a small area for a prolonged period of time. It also indicates that these frogs may be especially vulnerable to sudden habitat changes. Pond-breeding amphibians typically have strong site fidelity, because returning to high quality breeding, foraging and overwintering habitats has energetic and survival benefits (Matthews and Priesler, 2010). However, site fidelity can be problematic if habitat quality decreases from one year to the next. Increased reservoir height and frequency of inundation at the Valemount Peatland (see Chapter 4) could have consequences for Columbia Spotted Frogs, which appear to have strong associations with specific ponds and breeding locations in the drawdown zone.

The body condition of an animal is linked, among other things, to its probability of survival (Reading, 2007) and is also assumed to reflect its quality of habitat (Reading and Clarke, 1995; Pope and Matthews, 2002). Without data from undisturbed areas outside the reservoir, it is not possible to infer the relative quality of habitat in the drawdown zone using estimates of body condition. However, comparisons of Columbia Spotted Frog body conditions from one year to the next may help to identify the variables that influence the survivorship of this species in the drawdown zone. The results of my ANCOVA indicate that adult/juvenile Columbia Spotted Frogs had higher body condition in 2010 than in 2011. This inter-annual difference could be due to variation in prey availability, breeding pond characteristics (Seale, 1982; Crump, 1991; Egan and Paton, 2004; Pearl et al., 2007), or density of predators (Laurila and Aho, 1997), among other things. Without data on each of these variables, it is difficult to identify one or more as the potential cause for reduced Columbia Spotted Frog body condition in 2011. However, weather conditions can have a strong influence on all of these variables and have been linked to the body condition of many anurans. Reading and Clarke (1995) hypothesized that hot, dry summer conditions decreased food availability and increased the metabolic rate of adult Common Toads (*Bufo bufo*), leading to reduced body condition upon entering hibernation. The influence of mild winter temperatures and warm pre-spawning conditions on the body condition of hibernating anurans is less clear. Reading and Clarke (1995), Tomašević et al. (2007), and Reading (2007) found that warm winters have a negative influence on female *Bufo bufo* body condition, which they ascribe to the high metabolic rates experienced by hibernating toads at higher temperatures. Pope and Matthews (2002) and MacCaffrey and Maxell (2010) documented a negative correlation between winter severity and body condition and survivorship of Mountain Yellow-legged Frogs (*Rana muscosa*) and Columbia Spotted Frogs, respectively. These authors argued that longer winters and increased snowpack reduced the condition of hibernating frogs. Upon closer inspection, these seemingly opposing points of view are not mutually exclusive. Pope and Matthews (2002) and MacCaffery and Maxell (2010) studied two frog species at high altitudes (1370 to 3700 m ASL) whereas the Common Toad studies were conducted in southern England and Belgrade, at presumably much lower elevations (< 300 m ASL). A “severe winter” is likely relative in this case. The results of my analysis of body condition of Columbia Spotted Frogs do not fully support or contradict either of these hypotheses. The summer of 2010 was much drier than average (Figure 4). Numerous ponds desiccated over the course of the summer and temperatures hovered near the mean 30-year maximum for several weeks. The frogs that I captured in 2010 may have experienced lower prey availability than average (i.e. in wetter years). They also endured similar conditions in the previous summer (Figure 4). The winter that followed was longer and characterised by much higher snowfall than average. This may account for the lower body condition detected for Columbia Spotted Frogs in 2011, relative to the previous year. I suspect that the hot dry summer in 2010 and long winter are also responsible for the decrease in number of juvenile frogs captured in 2011. Although the summer of 2009 was also quite hot and dry, the much deeper snowpack likely reduced the extent of desiccation in the Peatland that year.

Too few adults were captured in the drawdown zone to conduct a similar analysis using Western Toads. Instead, I compared the body condition of young-of-the-year toads at the Valemount Peatland in 2010 and 2011. Small YOY toads (<18.5 mm SUL) weighed significantly less in 2011 than in 2010, while large YOY toads (>18mm SUL) had similar body condition in both years. Further research is required to tease out the influence of maternal effects (Mousseau and Fox, 1998; Loman, 2002; Räsänen et al., 2005) and environmental conditions experienced by larvae (Smith-Gill and Berven, 1979; Semlitch and Caldwell, 1982; Denver et al., 1998) on the body condition of these toads. Metamorph toads were sampled opportunistically and from different ponds in each year. Differences in mass may be biased by variation in natal pond quality and have little to do with inter-year variation in weather conditions or habitat quality in the drawdown zone.

Comparisons of metamorph body condition at each study site were more informative. Although my analysis of body condition of YOY Western Toads was confounded by an interaction between snout-urostyle length and study site, I found that large metamorph Western Toads (>16 mm SUL) in the drawdown zone had significantly higher body condition than those at Cranberry Marsh. This trend may reflect differences in habitat quality or may be related to density-dependent effects. The body mass of anuran metamorphs has been negatively correlated with larval and post- metamorphic density, when all other factors are held constant (Berven and Chadra, 1988; Goater, 1994). Reduced body mass at high densities is presumed to result from greater competition for food resources; lower food availability at the larval stage (i.e. in the pond) often leads to lighter metamorphs at emergence. Although I could not quantify larval densities in the field, the number of Western Toad eggs and larvae found at

Cranberry Marsh in 2010 was at least four-times that of the Valemount Peatland (Boyle, unpublished data). As the marsh steadily desiccated in 2010, tens of thousands of toad larvae were observed in very small pools of water. Desiccation was also an issue at the Valemount Peatland, but the majority of metamorphs captured there had emerged from spring-fed ponds. The lower body condition of metamorphs at Cranberry Marsh is expected, given the extreme desiccation and density-related stress experienced by larvae at this site in 2010. However, a clear relationship between site and body condition was only detected for large metamorph toads. Semlitsch and Caldwell (1982) hypothesized that *Scaphiopus holbrooki* tadpoles with an early growth advantage (i.e. those that are bigger to start with) would metamorphose quickly to escape the negative effects of density stress. This would alleviate density-dependent effects experienced by the remaining, smaller tadpoles, which would benefit from increased food availability per capita. However, at Cranberry Marsh, the pressure to metamorphose early would remain for small tadpoles, as the water level continually dropped. Perhaps the reduced body masses detected for large YOY toads at Cranberry Marsh resulted from large tadpoles metamorphosing early under conditions of low food availability. Small YOY may not have exhibited this trend because surviving individuals would have metamorphosed early under conditions of sufficient food availability. Having not surveyed Cranberry Marsh in the following year, I cannot comment on the environmental conditions experienced by tadpoles in 2011, except to note that water levels were much more stable.

Alternatively, metamorph toads with longer SULs may simply have been those that were on land for a slightly longer period. Differences in body mass could then be related to food availability in the terrestrial environment. Ultimately, Western Toad metamorphs at Cranberry Marsh were of significantly lower body condition than those at the Peatland or Ptarmigan Creek, suggesting that the habitat in the drawdown zone is not of particularly low quality, as far as young-of-the-year toads are concerned.

The relative masses of male Common Garter Snakes at the Valemount Peatland were virtually equal to those at Ptarmigan Creek. Whether or not the mean body condition of snakes in the drawdown zone is greater or lesser than elsewhere in the region remains unclear. The proportion of snakes that had recently eaten was fairly high in the drawdown zone (47% and 63%), relative to those at wetlands elsewhere in their range (36% in northern California: Kephart, 1982; 37% on Vancouver Island: Gregory, 1984). Although I could not track each snake to obtain an estimate of individual feeding rates, these data hint that Common Garter Snakes at these sites in Kinbasket Reservoir may have more abundant prey, relative to other populations. It is also possible there is less competition for prey in the drawdown zone. Indeed, the Western Terrestrial Garter Snake was absent from both sites. Regardless, the high probability of capturing a snake with food in its stomach indicates that the local population makes heavy use of the drawdown zone as foraging habitat.

Anurans are the most common prey of Common Garter Snakes at Kinbasket Reservoir. The vast majority of recently fed snakes had consumed Western Toad larvae, metamorphs or adults. I suspect the non-detection of Columbia Spotted Frogs in the stomachs of captured snakes is due to the greater ease in which Western Toads are captured, not to an aversion to Columbia Spotted Frogs as potential prey. As larvae and metamorphs, Western Toads tend to aggregate in large numbers. Although this conspicuous behaviour decreases the effort required by predators to capture one or more toads, it also provides ‘safety in numbers’ for the prey, particularly for the faster individuals (Arnold and Wassersug, 1978).

The daily movements of Common Garter Snakes at the Peatland and Ptarmigan Creek were short (0 to 10 m/day). Common Garter Snakes are capable of moving quite large distances, particularly in northern regions (Gregory and Stewart, 1975; Larsen, 1987), as they must travel to and from suitable overwintering sites and foraging areas. Such large movements would not be captured at my study sites, where the regularly surveyed areas are small and consist of marsh and pond areas (i.e. primarily foraging habitat). However, my estimates of mean minimum distance travelled are in keeping with those reported by Fitch and Shirer (1971), who used radio-telemetry to track female *T. sirtalis* movements in a natural history reservation adjacent to a river (an area likely to have suitable garter snake foraging habitat).

At the Peatland, the majority of recaptured snakes were gravid females. These females made shorter movements between captures than non-gravid females or males, presumably due to their reduced vagility (Seigel et al., 1987; Charland and Gregory, 1995). One female in particular remained in a small area while gravid and then moved a relatively large distance after having given birth. Her proximity to thousands of metamorphosing Western Toads suggested this movement was associated with increased foraging effort after a long period of aphagia (Gignac and Gregory, 2005; Gregory et al., 1999). Recapture rates were much higher at Ptarmigan Creek, although no gravid females were observed there. The repeated capture of individuals making short movements around the site (including many with full stomachs) indicates it is a profitable foraging area for Common Garter Snakes.

Growth estimates for individual Common Garter Snakes varied considerably, but averaged 0.5 to 0.6 mm/day, regardless of sex. Much of the literature on growth in *Thamnophis spp.* does not report mean daily growth, but my estimates are in keeping with those reported for two populations of *T. sirtalis* in Kansas (Fitch, 1965) and higher than those observed by Carpenter (1952) in Michigan. I suspect small samples sizes played a role in the lack of sex-differences in growth rates in this study. There were clear size differences between adult males and females — differences in growth rate should play a large role in this (Shine, 1990). Sex and size-related differences in growth rate are well documented in this species (e.g. Carpenter, 1952; Fitch, 1965; Peterson et al., 1998).

Long-term growth data for snakes in the drawdown zone would enhance our understanding of the life history strategies of these populations. Bronikowski and Arnold (1999) found that Western Terrestrial Garter Snakes had slower growth, lower fecundity, higher adult survival, and matured later at sites with inconsistent prey availability, relative to sites with continuous access to prey. Given that snakes in the drawdown zone appear to rely on Western Toads as a major food source, it would be interesting to see if and how growth, survivorship, and fecundity of Common Garter Snakes vary with toad availability. Western Toads are known for their explosive breeding habits – the response of local garter snake populations to periods of reduced toad breeding activity would provide further information about their vulnerability to reservoir disturbances.

CHAPTER 3 –REPRODUCTIVE PHENOLOGY AND BREEDING POND USE BY AMPHIBIANS IN THE DRAWDOWN ZONE

INTRODUCTION

In oviparous species that lack parental care, there is substantial selective pressure for females to choose high-quality oviposition sites for their offspring. Choosing a poor-quality oviposition site can limit female reproductive fitness via reduced embryo survival, poor juvenile performance, or altered offspring phenotype (Refsnider & Janzen, 2010). Because of the wide variety of aquatic habitats in which they breed, amphibians are model organisms for studies of oviposition-site choice (Resetarits, 1996). Efforts to identify the variables associated with oviposition-site decisions by amphibians point to a variety of biotic and abiotic factors, including: water depth (Crump, 1991; Pearl et al., 2007), temperature (Seale, 1982; Sjögren et al., 1988), vegetation structure (Wells, 1977; Pearl et al. 2007), acidity (Gascon and Planas, 1986), hydroperiod (Egan and Paton, 2004), and presence of predators (Resetarits, 1996) or conspecifics (Howard, 1980; Resetarits and Wilbur, 1989). These factors may ultimately influence larval development, timing of metamorphosis (e.g. Atlas, 1935; Newman, 1989; Berven, 1990), and survival (e.g. Freda, 1986; Cortwright and Nelson, 1990). Aquatically breeding amphibians should select environments that maximize the survivorship of their offspring (Resetarits and Wilbur, 1989; Hopey and Petranka, 1994). However, breeding ponds in the drawdown zones of reservoirs are subject to unnatural levels of inundation and desiccation, such that environmental conditions at an oviposition location may change considerably by the time eggs hatch or as tadpoles develop. An oviposition site that was warm, calm and predator-free in early May could be much colder and accessible to large fish by August. Therefore, the environmental cues that influence female oviposition-site choices in the drawdown zone may not reflect the conditions experienced by their offspring.

Unpredictable environmental conditions are not unique to the drawdown zones of reservoirs. Many amphibians breed in temporary pools, which are subject to temperature extremes and increased desiccation risk (Bonner et al., 1997). The larvae of these species may plastically adapt to conditions that affect habitat quality, such as food availability, desiccation risk, and presence of predators (Newman, 1992). For instance, McCollum and Leimburger (1997) found that *Hyla chrysoscelis* tadpoles had altered tail morphology and color in response to the presence of predatory dragonflies — likely to improve swimming speed and reduce the risk of predation via camouflage. Tadpoles may also delay metamorphosis at low temperatures (Smith-Gill and Berven, 1979; Marian and Pandian, 1985) or high larval density (Smith-Gill and Berven, 1979; Semlitch and Caldwell, 1982), and accelerate metamorphosis in response to food restriction (Berven and Chadra, 1988; Denver et al., 1998) or reduction of water level (Denver et al., 1998). Tadpoles that develop rapidly may escape aquatic predators or desiccation, but they are often smaller at metamorphosis than more slowly developing conspecifics (e.g. Newman, 1985; Morey and Reznik, 2004), and may suffer fitness consequences (Berven and Gill, 1983; Smith, 1987). Thus, the timing of metamorphosis has been a major focus of amphibian ecology and conservation research. This stage is important to the overall life history of a species (Smith-Gill and Berven, 1979) and should be carefully monitored in disturbed areas such as drawdown zones.

Kinbasket Reservoir has been in operation since the Mica Dam was constructed in 1973. The presence of amphibians in the drawdown zone of this reservoir indicates these species have persisted despite the habitat destruction and dramatic water-level fluctuations associated with reservoir operation. What is not clear is how these species persist in spite of this frequent disturbance. I monitored larval development of Western Toads (*Anaxyrus boreas*) and Columbia Spotted Frogs (*Rana luteiventris*) in the Valemount Peatland to establish the timing of reservoir inundation relative to tadpole development and metamorphosis. To determine if yearly inundation of the breeding habitat poses a threat to amphibian reproduction and survival, it is important to identify when and where these species breed within the drawdown zone, and to record how quickly they develop to metamorphosis.

Davis and Verrell (2005) suggest that the tendency of Columbia Spotted Frogs to breed communally renders them particularly vulnerable to anthropogenic disturbances. In light of the great extent of disturbance caused by reservoir drawdown, it is important to identify relevant habitat characteristics associated with favoured Columbia Spotted Frog breeding ponds in the Peatland. I therefore investigated pond characteristics associated with breeding activity of Columbia Spotted Frogs in the drawdown zone. If survival of embryos or tadpoles is threatened by reservoir inundation each summer, it is likely that frogs lay their eggs in ponds that promote rapid larval development (e.g. warmer ponds). They may also prefer ponds that are at a high elevation in the drawdown zone, in order to "buy time" for offspring to metamorphose. I tested these hypotheses by collecting detailed information about the water physicochemistry, size and location of all ponds at the Valemount Peatland. I used generalized linear models to identify correlations between these pond characteristics and use of ponds by breeding Columbia Spotted Frogs. I also sampled a subset of ponds for aquatic invertebrates, to determine if these potential tadpole predators or competitors play a role in use of breeding ponds by this species.

METHODS

All ponds were regularly surveyed for amphibian eggs and larvae. In 2010, each pond was surveyed approximately every 10 days, and in 2011, ponds were surveyed approximately once a week. In addition to conducting shoreline surveys, I also recorded pH, temperature, oxygen content (mg/L) and conductivity (uS/cm) at various times of day, but at consistent locations in each pond. The latter three variables were measured using a YSI 85 Dissolved Oxygen/ Conductivity Instrument. Pond areas were determined by GPS tracking of each shoreline. I considered a "pond" to be any body of water with an identifiable shoreline. Reservoir elevation data were provided by BC Hydro and LGL Limited environmental research associates (LGL), who also shared ortho-photos and 1-m contour data for use in ArcGIS. Pond elevations were recorded to the nearest 1 metre. Fish were noted, but not captured or identified to species.

The location of each egg mass/string observed was marked by GPS. Careful records of egg counts, approximate ages and hatch dates were kept. It was difficult to distinguish a single Western Toad egg string among several strings laid in one location; therefore some numbers were estimated. Larval amphibians were captured in dip nets and staged according to Gosner's (1960) table for anuran embryos and larvae. Although individual tadpoles could not be distinguished and observed over time, Gosner stages provided a general indication of the development rate of amphibians in the drawdown zone.

Because several aquatic invertebrates will prey on larval amphibians (Caldwell et al., 1980; Lardner, 2000) and may influence female oviposition decisions (Resetarits, 1996), I also sampled 19 ponds for macroinvertebrates in 2011 (12 ponds with breeding activity of Columbia Spotted Frogs and 7 without). A D-frame dip net was used to sweep the surface of the substrate at three separate locations in each pond. Sample locations within each pond were chosen with a bias to avoid large woody debris, which could become tangled in the dip net. Samples were thoroughly searched for invertebrates, which were identified to the family level, and immediately returned to the water. This was a time-consuming process, so not all ponds were sampled for aquatic invertebrates. However, all nineteen ponds were sampled within a period of 18 days (May 17th to June 4th, 2011), to reduce any effect of temporal variation in insect community assemblages.

Statistical Analyses

I performed two negative binomial regression analyses to test the influence of selected variables on use of breeding ponds by Columbia Spotted Frogs. Negative binomial regression is a form of generalized linear regression that is recommended for overdispersed count data (White and Bennetts, 1996; Richards, 2008; Lindén and Mäntyniemi, 2011). "Overdispersed" is a term used for data sets in which the variance is greater than the mean (Ver Hoef and Boveng, 2007). Overdispersion is fairly common in ecological data sets, which often include counts of organisms that are clustered together in space or time and contain many zeroes (O'Hara and Kotze, 2010). Negative binomial regression assumes that the “extra” variance in these data is a quadratic function of the mean (as opposed to being equal to the mean, which is characteristic of Poisson regression; Lindén and Mäntyniemi, 2011).

My first analysis elucidated the relationship between abundance of Columbia Spotted Frog eggs and the abundance of invertebrates. After identifying the aquatic invertebrate groups present in the Peatland, I included the abundance of six invertebrates as potential factors: chironomid larvae (midge larvae), anisopteran nymphs (dragonfly nymphs), planoribids (freshwater snails), ephemopteran nymphs (mayfly nymphs), hirudineans (leeches), and corixids (water boatmen). Of these species, only leeches (Schalk et al., 2002) and dragonfly nymphs (Caldwell et al., 1980; McCollum and Leimberger, 1997; Peacor and Werner, 1997) are likely predators of larval amphibians. However, Morin et al. (1988) documented strong competition between aquatic insects (mosquitoes, midges, mayflies, and water boatmen) and the larvae of two anuran species; tadpoles of both species had reduced mean body mass when reared with the herbivorous aquatic insects. Freshwater snails also compete with tadpoles for access to periphytic algae and can positively influence tadpole growth (Brönmark et al., 1991). Therefore, my global model included both potential invertebrate predators and potential invertebrate competitors. I had no reason to believe that earthworms, freshwater clams, or freshwater amphipods influence breeding decisions of Columbia Spotted Frogs; therefore I did not include them in my analysis. Due to time and logistical constraints, detailed invertebrate data could be collected only in 2011, from a subset of ponds (n = 19). Because of these limitations, the abundance of invertebrate predators and competitors could not be included in a single analysis with other pond characteristics as explanatory variables. Ideally, a single negative binomial regression analysis would be performed to evaluate the relative importance of these variables to use of breeding ponds by Columbia Spotted Frogs.

My second regression analysis tested the influence of water physicochemistry, pond area, pond elevation, presence of fish, and abundance of Western Toad eggs on abundance of Columbia Spotted Frog eggs. Each pond in the drawdown zone was treated as one datum ($n = 40$ ponds). I limited the number of variables included in these analyses to prevent overfitting the model (see Babyak (2004) for further discussion on this topic). Pond elevation was included because ponds at higher elevations in the drawdown zone are available for a longer period of time (see below; Hawkes et al., 2011). Pond area was included because large ponds may simply have more space available for breeding amphibians and their eggs, or may have a longer hydroperiod than smaller ponds (Van Buskirk, 2005). Water conductivity has been negatively correlated with abundance of amphibians (Browne et al., 2009) and survival of amphibian embryos and larvae (Karraker et al., 2008); thus it was also included as an explanatory variable in my analysis. Mean pH of ponds was included because acidic conditions can decrease sperm motility (Schlichter, 1981) and reduce larval growth and survivorship (Beattie and Tyler-Jones, 1992). Consequently, there may be selective pressure against breeding in ponds with low pH levels. Many anurans preferentially breed in warm water (Seale, 1982; Sjögren et al., 1988) and avoid breeding in ponds where fish are present (Monello and Wright, 1999; Egan and Paton, 2004); thus mean pond temperature and presence of fish were included as explanatory variables. Finally, the total number of Western Toad eggs observed in each pond was included in my global model to incorporate the possibility that Columbia Spotted Frogs are deterred by Western Toad breeding activity and/or eggs (e.g. Petranka et al., 1994). Dissolved oxygen level co-varied with pH ($r = 0.68$, $n = 40$, p □ 0.001) and was left out of the analyses to reduce redundancy in the model (Burnham and Anderson, 2010). I chose to use pH as a proxy for dissolved oxygen content (and not vice-versa) because pH stayed relatively constant during sampling, whereas dissolved oxygen content fluctuated continuously (i.e. dissolved oxygen measurements were less precise).

Due to some spatial autocorrelation in the location of Columbia Spotted Frog eggs in 2011 (Moran's I: $p = 0.046$), that was not detected in 2010 (Moran's I: $p = 0.151$), I pooled data from both years (Moran's I: $p = 0.077$). Although the pooled data were nearly significant for spatial autocorrelation, the lack thereof in 2010 supports my assumption that proximity of ponds is not the most important factor in breeding pond use by Columbia Spotted Frogs.

Water quality variables were averaged across both years, and frog and egg counts were totalled. Ponds that desiccated early in either year were not included in this analysis, due to a lack of water physiochemistry data (N = 4 ponds omitted). Only one of the ponds that dried up completely was used for breeding by Columbia Spotted Frogs.

I also repeated the above analysis using the presence or absence (as opposed to abundance) of Columbia Spotted Frog eggs as a response variable. Because presence of eggs is a binary variable, a different form of GLM was required for this analysis (family = binomial). I ran a separate binomial regression analysis for each year of this study, because some ponds were used for breeding in one year and not the other. Abundances of frog and toad eggs were converted to presence or absence records, and water quality variables were averaged within each year. Elevation data were not included in this analysis because of the small number of ponds in certain elevation bands (Figure 1). For example, no Columbia Spotted Frog eggs were found at 749 m ASL, but there are only two ponds at this elevation in the Peatland.

To evaluate the explanatory power of all candidate models, I used Akaike's Information Criterion (AIC). The precision of a model will decrease as the number of explanatory variables increases. However, including too few explanatory variables in a model will increase the bias of the model (i.e. the difference between the estimated value of a variable and its true, unknown value; Mazerolle, 2006; Burnham and Anderson, 2010). AIC values account for this trade-off and measure the loss of information associated with a particular model. Therefore, a lower AIC value indicates a better fit. I also generated AICc (Akaike's Information Criterion corrected) values, which are adjusted for a small sample size, and Akaike weights (*w*), which represent the weight of evidence in favour of a particular model, relative to the other models being considered (Burnham and Anderson, 2010). All statistical tests were performed with R V2. 13.1 (© 2011).

RESULTS

Reproductive Phenology

The majority of ponds in the Valemount Peatland are located at 751 and 752 m ASL (Figure 38). The reservoir flooded these ponds in both years, but did so at very different rates in 2010 and 2011. In 2010, the water levels in Kinbasket Reservoir were close to average (Figure 39) and increased relatively slowly due to low precipitation in that year. In 2011, the reservoir was flooded much more rapidly, due to a deep snowpack and higher levels of rainfall (see Chapter 2 for precipitation data). The water levels peaked well above average in this year (Figure 39). Consequently, amphibian habitat in the drawdown zone was available for a shorter period than usual in 2011 (Figure 40).

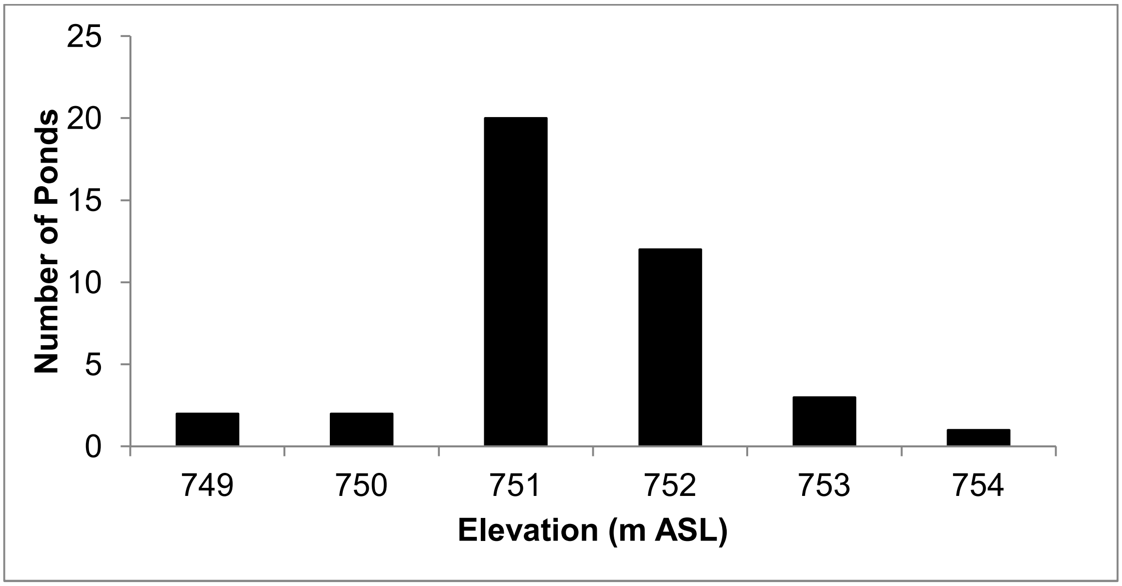

Figure 38. Elevational distribution of ponds in the Peatland. This figure includes only those ponds that were incorporated in regression analyses.

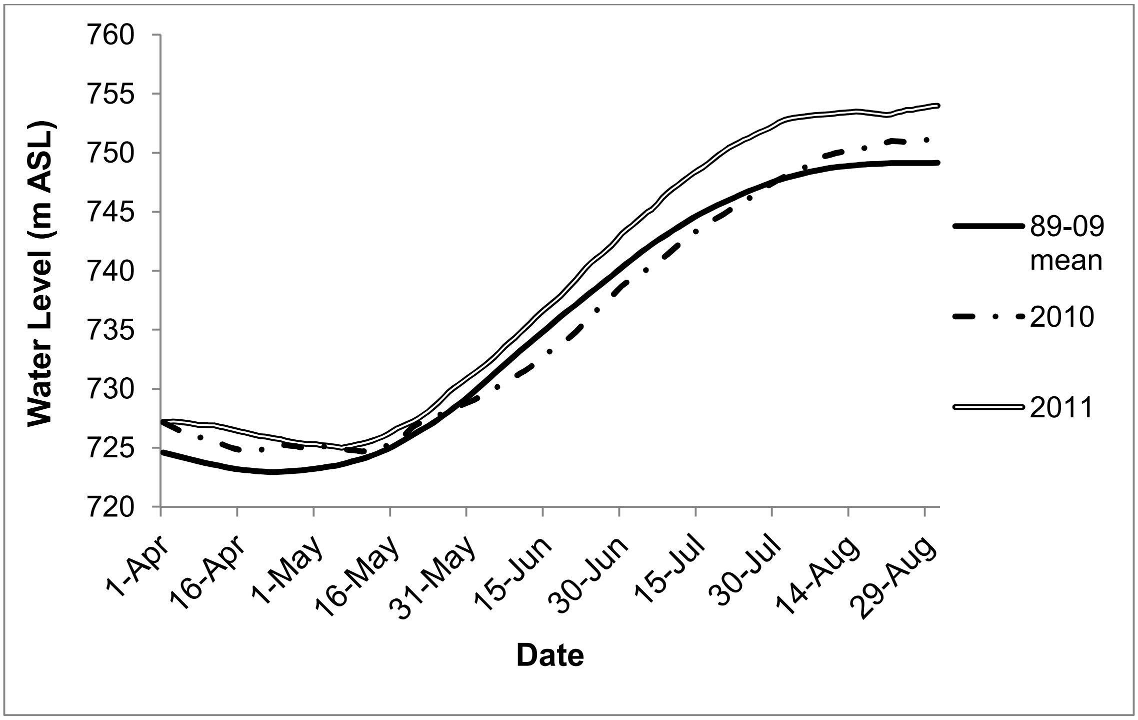

Figure 39. Kinbasket Reservoir water levels (m ASL) in 2010 and 2011. The 20 year mean (1989 to 2009) is provided for reference (data provided by BC Hydro).

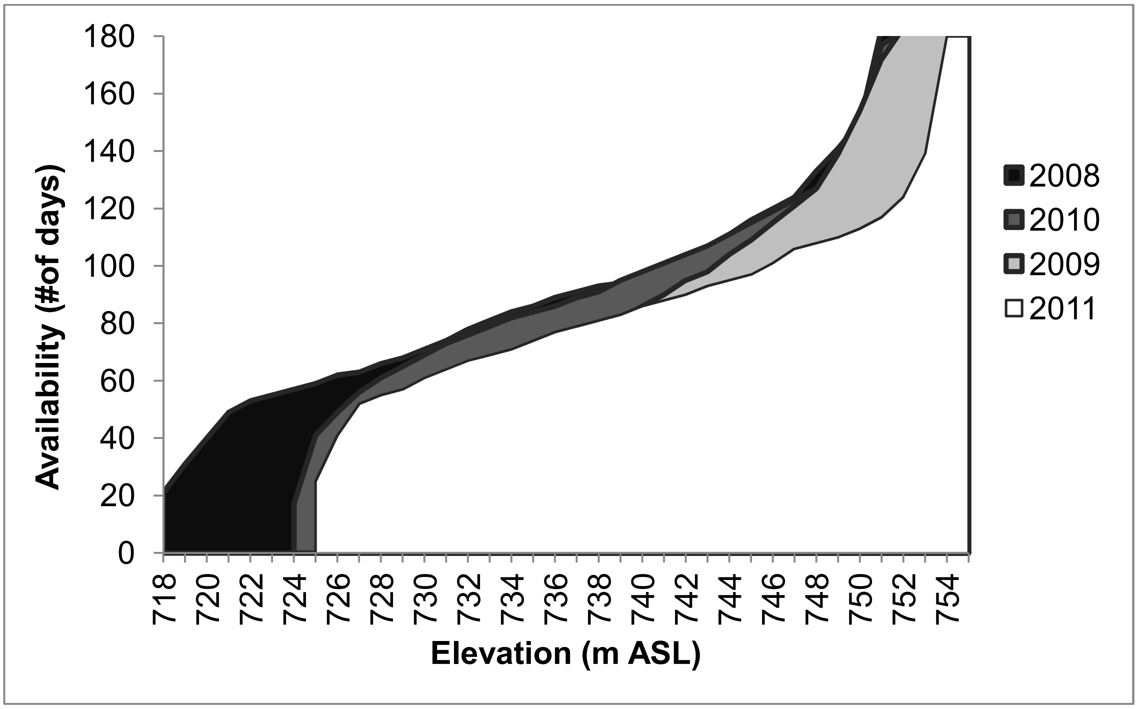

Figure 40. Number of days in the active season (April 1 to September 30 ≃ 180 days) in which habitat was available, by elevation. Modelled after Hawkes et al. (2011).

2010

In 2010, the majority of amphibian breeding activity took place prior to my arrival at the Peatland on April 27th, but freshly laid Columbia Spotted Frog egg masses were found as late as May 5th in one pond. All Western Toad egg strings were found at relatively late stages of development, making their oviposition dates difficult to estimate. Many eggs hatched prior to the first visual encounter survey of the year. Breeding activity of Long-toed Salamanders was not detected in 2010, but a single adult salamander was found adjacent to a previously identified breeding pond.

Columbia Spotted Frogs utilized roughly half of the available ponds in the Peatland for breeding (24 of 45), whereas Western Toads bred in just 7 of a possible 45 ponds (Figure 41). One large, spring-fed pond ("Pond 12") had a very high number of eggs of both species relative to all other ponds. This pond is within the drawdown zone but is not consistently inundated due to its relatively high elevation (753 m ASL). Little rain and a light snowpack (see Chapter 2) contributed to the desiccation of 19 Columbia Spotted Frog eggs masses and at least 6 Western Toad egg strings in 2010. It can be especially difficult to see desiccated toad egg strings; therefore it is possible I did not locate all failed egg strings. Five breeding ponds dried up completely and the water in many other ponds decreased substantially over the course of the summer.

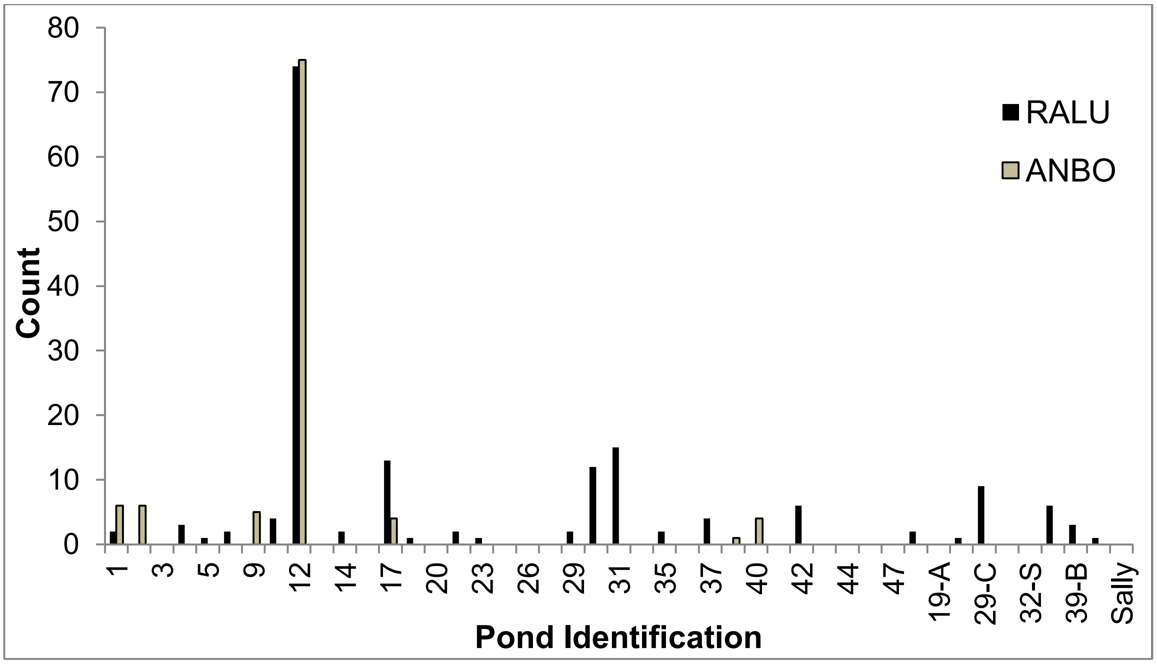

Figure 41. Total Columbia Spotted Frog (*Rana luteiventris* = RALU) and Western Toad (*Anaxyrus boreas* = ANBO) egg counts in the Valemount Peatland in 2010. Pond identification numbers/names are arbitrary.

Columbia Spotted Frog tadpoles were particularly difficult to locate and capture because of their brownish green coloration and tendency to forage and hide in the benthic zone of the ponds. However, Western Toads exhibit schooling behaviour and have jet black coloration, and thus were seen and captured fairly easily. Therefore, I followed larval development of Western Toads larval development more closely than larval development of Columbia Spotted Frogs, but it was clear that both species had sufficient time to metamorphose prior to reservoir inundation. The first observations of young-of-the-year (for both species) were made on July 22, 2010. At this time, the reservoir was still several metres below the elevation of the Peatland, at 745 m ASL. The last larval observations were made on July 24th (Columbia Spotted Frog) and August 6th (Western Toad). Figures 42 and 43 depict the developmental stages of Columbia Spotted Frog and Western Toad tadpoles, relative to the reservoir water level in 2010. By the final day of the field season (August 23), only 9 ponds had been inundated by the reservoir.

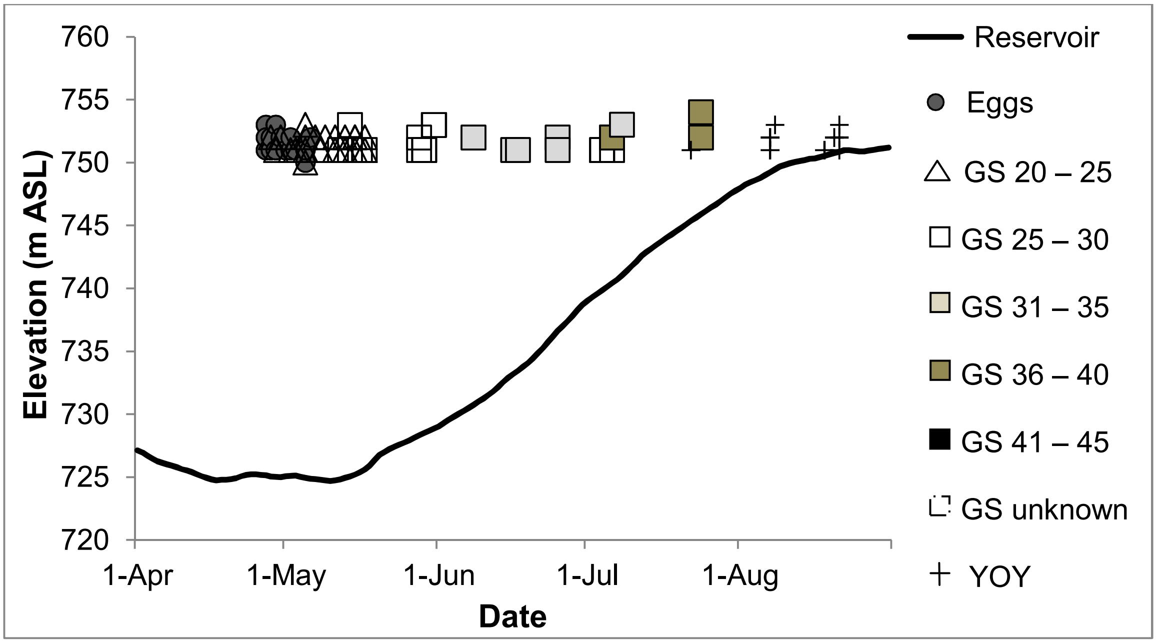

Figure 42. Observed Columbia Spotted Frog (*R. luteiventris*) larval developmental stages relative to Kinbasket Reservoir water levels in 2010. GS = Gosner Stage (Gosner, 1960). Each point represents a single observation at a given date and elevation in the drawdown zone. Shape and shade of symbols indicate the developmental stage of these observations, from embryo to young-of-the-year (YOY).

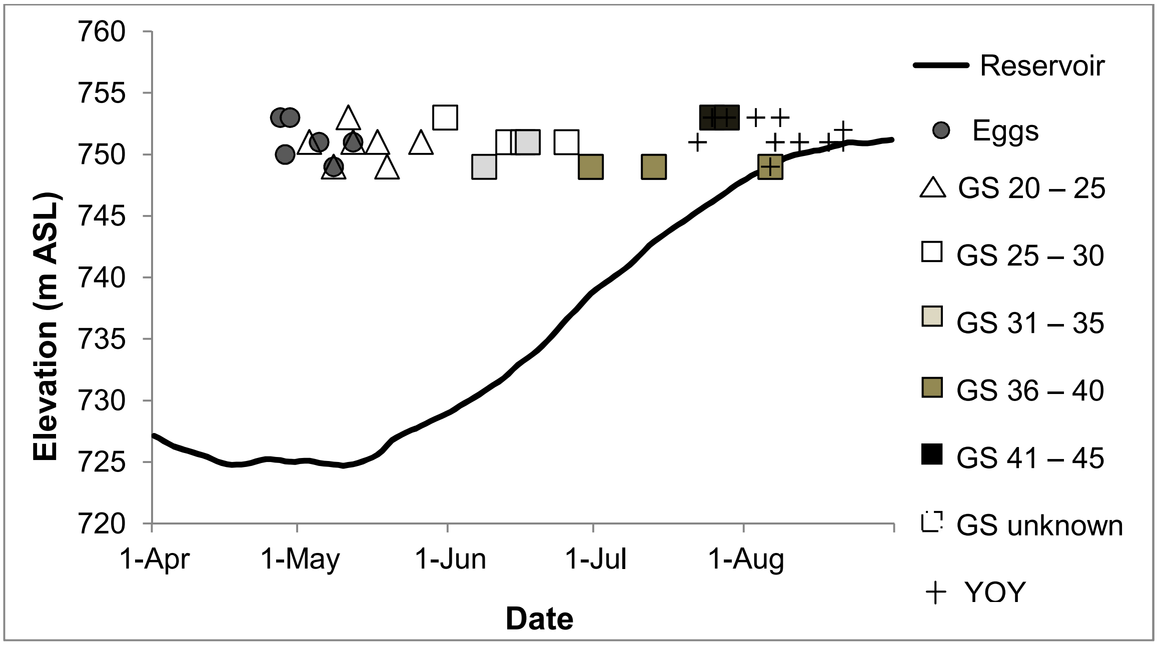

Figure 43. Observed Western Toad (*Anaxyrus boreas*) larval developmental stages relative to Kinbasket Reservoir operational levels in 2010. GS = Gosner Stage (Gosner, 1960). Each point represents a single observation at a given date and elevation in the

drawdown zone. Shape and shade of symbols indicate the developmental stage of these observations, from embryo to young-of-the-year (YOY).

2011

Amphibian breeding activity commenced an estimated 1- 2 weeks later in 2011 than in the previous year. Visual encounter surveys began on April 27th. On this date, male Columbia Spotted Frogs performed advertisement calls from several different ponds. Egg masses were located shortly thereafter. Twenty-five of 50 available ponds were used for breeding by Columbia Spotted Frogs (Figure 44). A breeding aggregation of Western Toads was observed on May 1, 2011, when an estimated 35 to 40 male toads were recorded calling and jostling for space at the southwest corner of Pond 12. Prior to this date, no toad eggs strings had been found. A total of 9 ponds and one ephemeral pool ("slough") were utilized by breeding Western Toads in 2011 (Figure 44). Long-toed salamander eggs and/or larvae were also observed in the slough, as well as in 5 ponds in the Peatland. However, the slough slowly desiccated over the course of the summer, and all tadpoles were presumed dead by the end of July. It was not possible to track the development of Long-toed Salamander larvae due to an extremely low capture rate for this species.

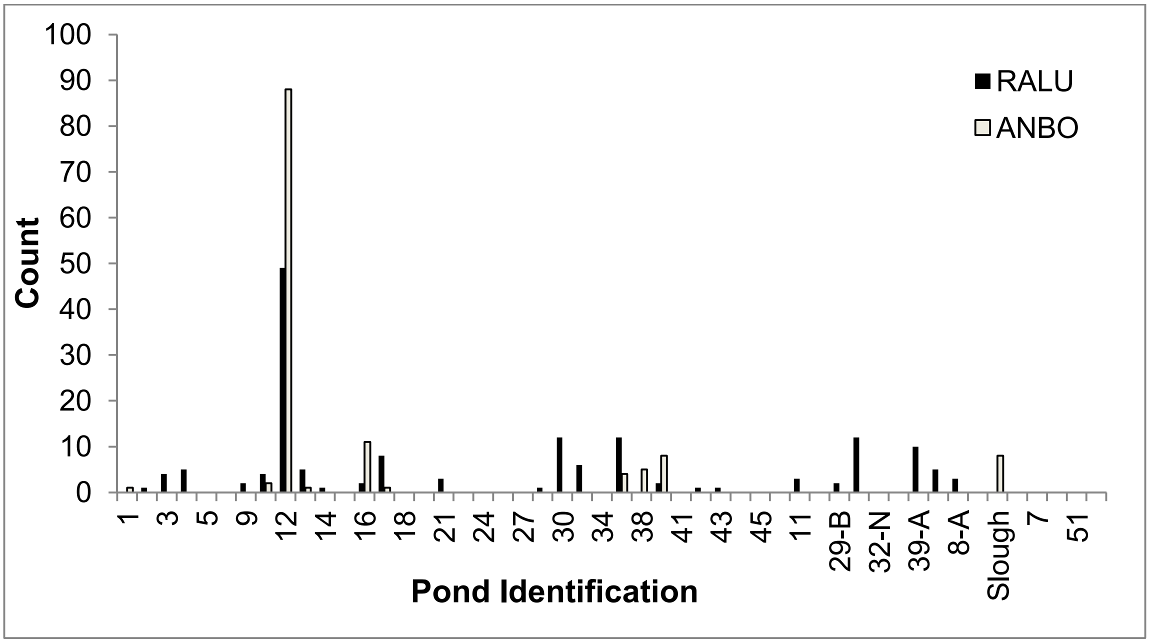

Figure 44. Total Columbia Spotted Frog (RALU = *Rana luteiventris*) and Western Toad (ANBO = *Anaxyrus boreas*) egg counts in the Valemount Peatland in 2011. Pond identification numbers/names are arbitrary.

Despite an apparently later start to the breeding season, the first observations of young-of-the-year in 2011 closely coincided with those in 2010. Although many larvae had yet to metamorphose, the first young-of-the-year Columbia Spotted Frog was observed on July 26, 2011 (vs. July 22 in 2010). The first Western Toad metamorph was observed on July 14, 2011 (vs. July 22 in 2010). However, the reservoir's water level was substantially higher at this point in 2011. While many tadpoles were still developing in their natal ponds, the reservoir had reached 750 m ASL and was flooding the Peatland. Once the reservoir breached a pond, its shoreline was no longer surveyable, and the fate of resident tadpoles was indeterminable. The last observed Gosner stages for these tadpoles (within 1 week of inundation) ranged from 32-43 for Western Toads and 37-41 for Columbia Spotted Frogs. At Gosner stage 32, hind limbs are present but toes have not yet differentiated. Forelimbs are not visible until Gosner stage 41 and metamorphosis is not complete until Gosner stage 46, when the tail is resorbed and the mouth is fully formed (Gosner, 1960). However, individuals may begin the transition to land as early as Gosner stage 43 (pers. obs.). Figures 45 and 46 depict the developmental stages of Columbia Spotted Frog and Western Toad tadpoles, relative to the reservoir water level in 2011. All ponds were inundated by August 1st.

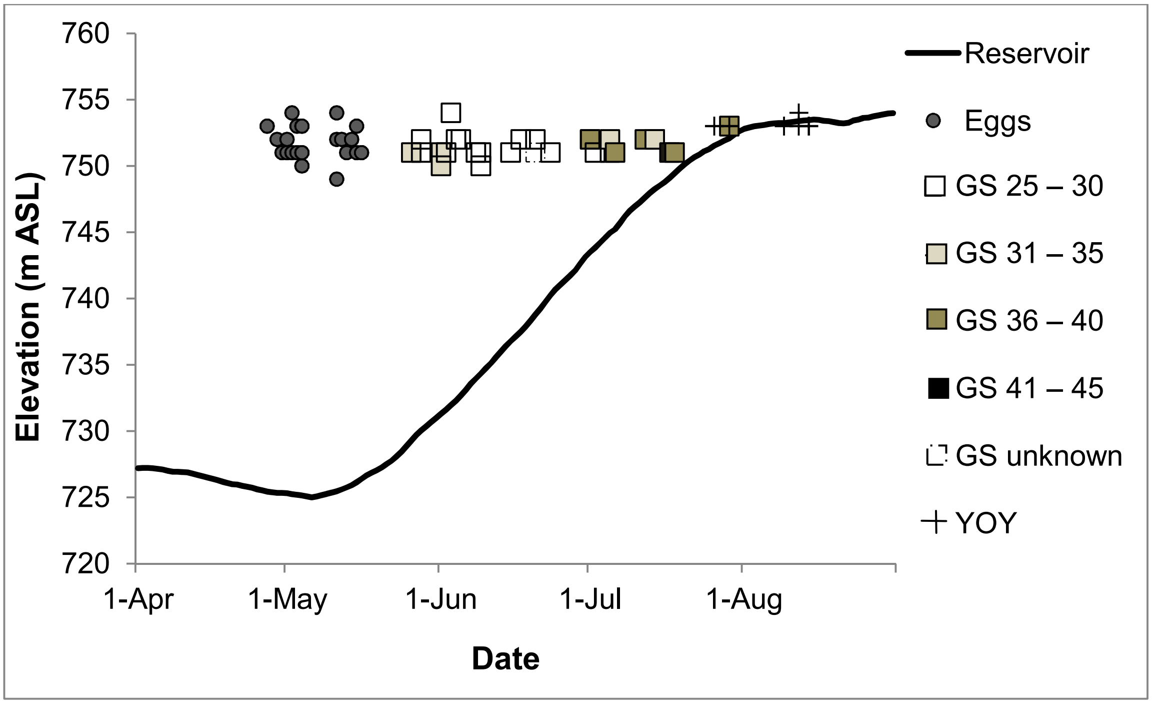

Figure 45. Observed Columbia Spotted Frog (*R. luteiventris*) larval stages relative to reservoir operation levels in 2011. GS = Gosner Stage (Gosner, 1960). Each point represents a single observation at a given date and elevation in the drawdown zone. Shape and shade of symbols indicate the developmental stage of these observations, from embryo to young-of-the-year (YOY).

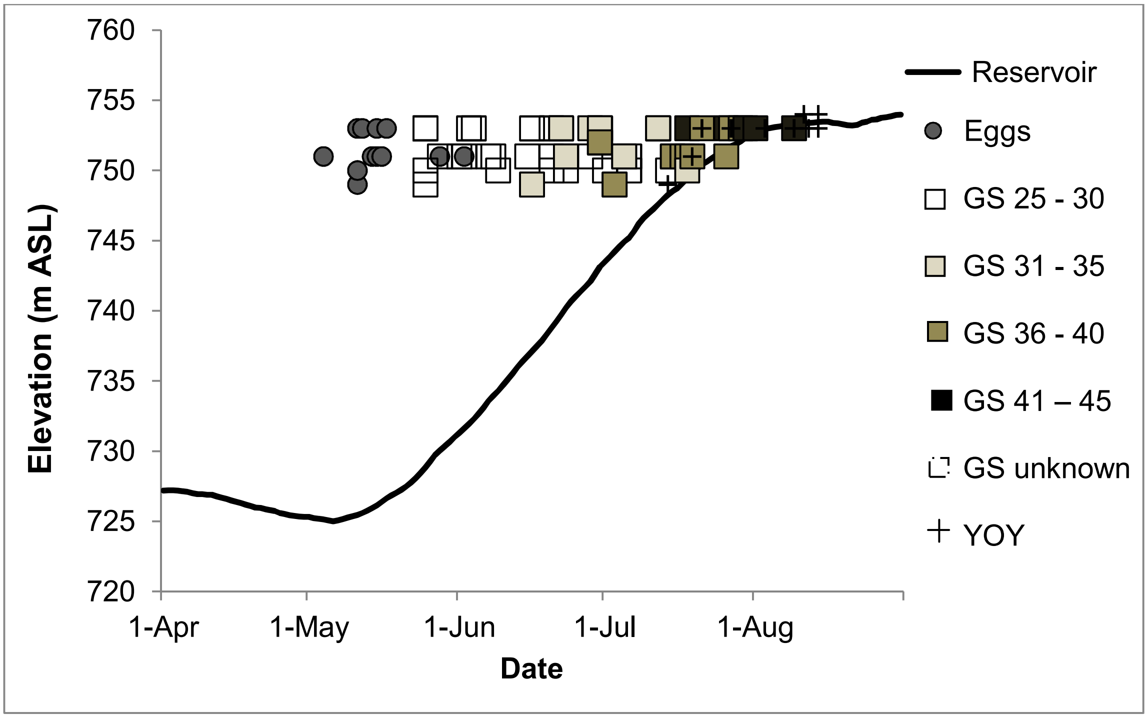

Figure 46. Observed Western toad (*Anaxyrus boreas*) larval development stages relative to reservoir operation levels in 2011. GS = Gosner Stage (Gosner, 1960). Each point represents a single observation at a given date and elevation in the drawdown zone. Shape and shade of symbols indicate the developmental stage of these observations, from embryo to young-of-the-year (YOY).

Breeding Pond Characteristics

Aquatic Invertebrates

Although not all sampled invertebrates could be identified to the Family level, it was evident that the ponds were dominated by 3 taxa: segmented worms (Oligochaeta), Freshwater shrimp (Gaamaridae), and tiny freshwater clams (Sphaeriidae). Sampled Oligochaetes belonged to either the Family Lubricidae (earthworms) or Family Tubificidae (sludge worms). However, they were not carefully distinguished while in the field, so they are simply referred to as Oligochaetes here. Invertebrates belonging to 13 other families were also observed. Figure 47 summarizes the identification and relative abundances of the aquatic invertebrates in the Peatland. There was some inter-pond variation in invertebrate composition and richness; the number of aquatic invertebrate 'families' in a single pond varied from 3 to 10. The invertebrate family richness of a pond did not appear to increase with elevation in the drawdown zone (Figure 48).

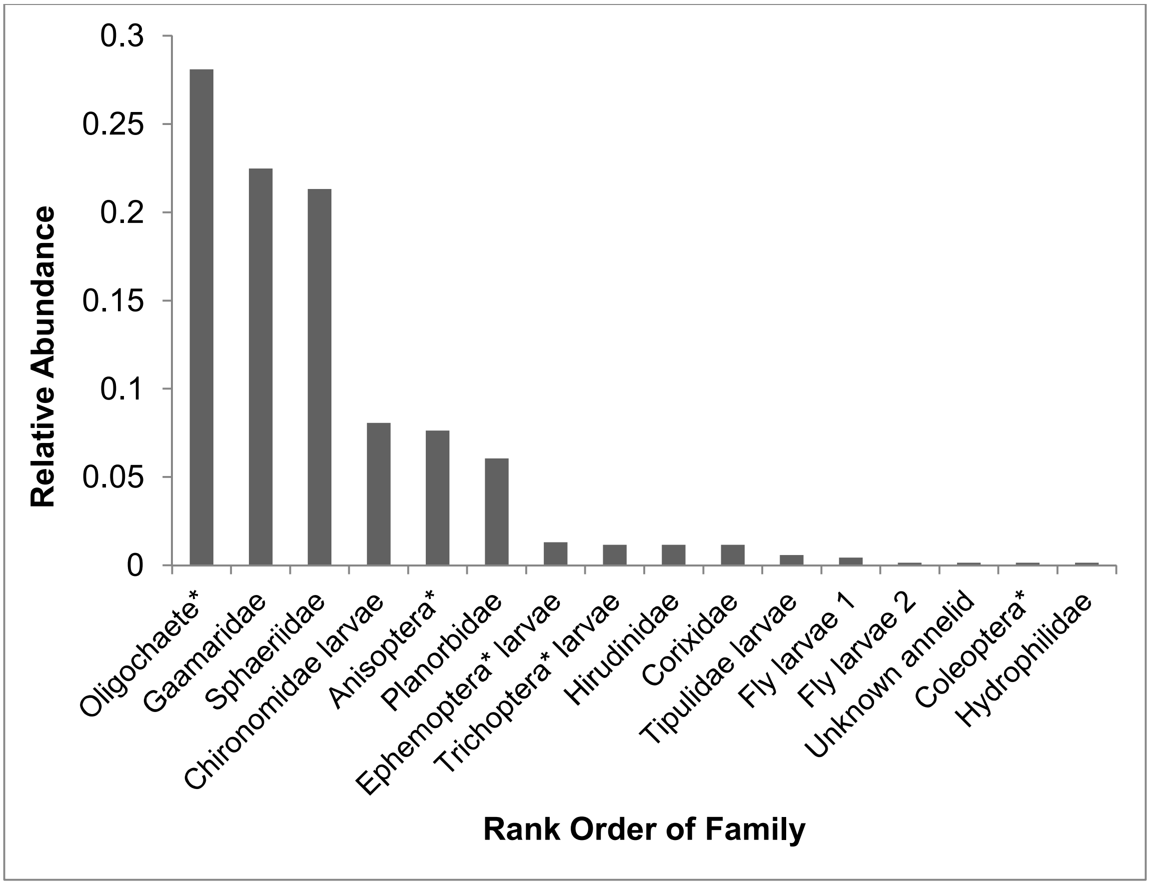

Figure 47. Relative abundances of aquatic invertebrates sampled in the Valemount Peatland in 2011 (N = 20 ponds). Invertebrates were classified to the level of Family, unless indicated by an asterisk. Oligochaete = segmented worm, Subclass of Phylum Annelida; Gaamaridae = freshwater shrimp, Family of Order Amphipoda; Sphaeriidae = freshwater clam, Family of Order Pelecypoda; Chironomidae = midge larvae, Family of Order Diptera; Anisoptera= dragonfly nymphs, sub-order of Order Odonata; Planorbatidae= freshwater snails, Family of Order Bassomatophora; Ephemoptera = mayfly, Order of Class Insecta; Trichoptera = caddisfly, Order of Class Insecta; Hirudinidae= freshwater leech, Family of Order Arhynchobdellida; Corixidae= water boatman, Family of Order Hemiptera; Tipulidae= cranefly, Family of Order Diptera; Coleoptera = unidentified aquatic beetle, Order of Class Insecta; Hydrophilidae= Scavenger beetle, Family of Order Coleoptera.

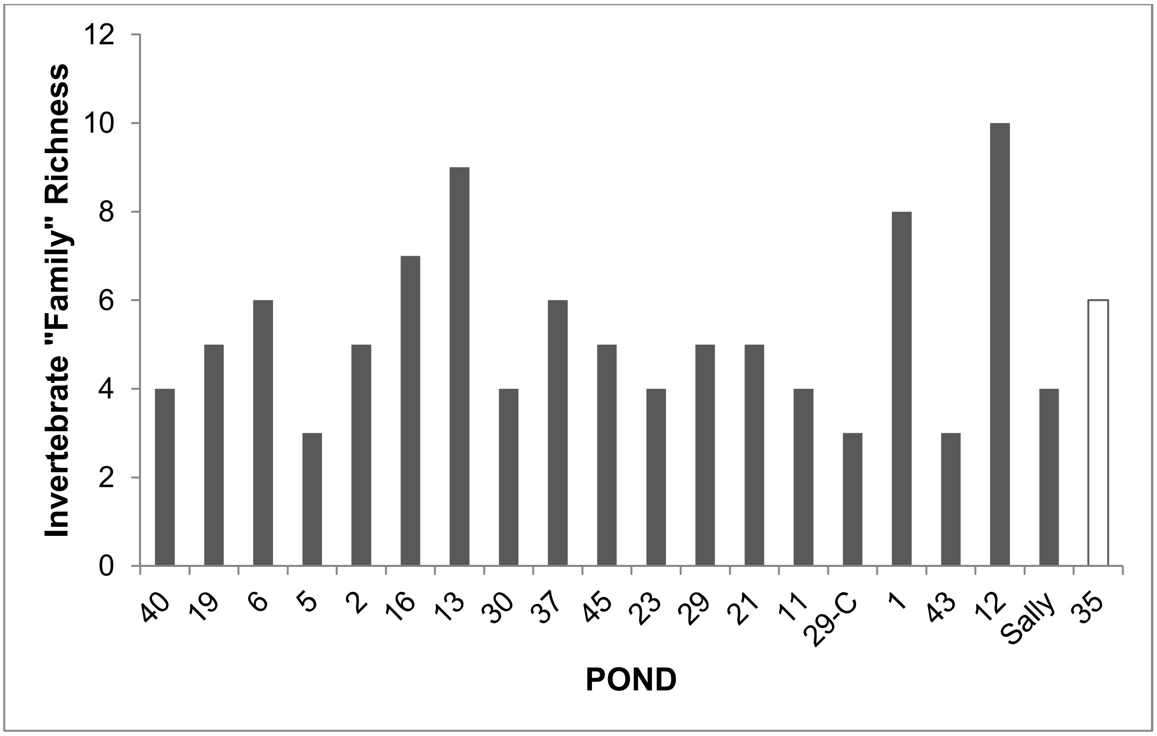

Figure 48. Number of different macroinvertebrate “Families” identified in 20 ponds in the Valemount Peatland. Ponds are ordered from lowest to highest elevation, from left to right. Pond 35 is located just outside the drawdown zone and wasn’t included in invertebrate abundance analyses. It is shown here for comparative purposes.

Negative binomial regression analysis revealed that the number of Columbia Spotted Frog eggs in a pond is negatively related to the abundance of midge larvae and positively related to the abundance of freshwater snails (Akaike weight = 0.81; Table 3). However, the explanatory power of this best-fit model was quite low ; the AICc value of a model with no predictor variables (i.e. just an intercept) was quite close to that of the best-fit model (ΔAICc = 2.5).

Table 3. Candidate negative binomial regression models predicting Columbia Spotted Frog (*Rana luteiventris*) egg abundances in ponds, relative to macroinvertebrate abundances.

MODEL	Parameters	AIC	AICc	ΔAICc	AICw
Midge.larvae + Snail	2	92.10	94.96	0	0.81
Midge.larvae + Snail + Mayfly.nymph	3	93.50	98.12	3.16	0.17
Midge.larvae + Snail + Mayfly.nymph + Dragonfly.nymph	4	95.21	102.21	7.25	0.02
Midge.larvae + Snail + Mayfly.nymph + Dragonfly.nymph + Leech	5	96.94	107.12	12.16	0.002
Midge.larvae + Snail + Mayfly.nymph + Dragonfly.nymph + Leech + Boatman	6	98.93	113.32	18.36	8.3e-05

Best Fit Equation : log (FrogEggs) = 1.51 - 0.33(Midge.larvae) + 0.18(Snail)

Pond Physicochemistry

Water physicochemistry characteristics (pH, temperature, conductivity and dissolved oxygen) were obtained for 40 ponds in both field seasons. Although these variables fluctuate over time, their mean values in 2010 were strongly correlated with those in 2011 (*temperature*: Pearson's r = 0.682, p □ 0.001; *pH*: r = 0.779, p □ 0.001; *dissolved oxygen*: r = 0.642, p □ 0.001; *conductivity*: r = 0.589, p □ 0.001; Figures 49 - 52). In other words, a pond with a low mean temperature in 2010 also had a low mean temperature in the following year, relative to other ponds. Therefore, it is unlikely that any physicochemical differences detected between ponds would be due to chance or to variation in sampling periods.

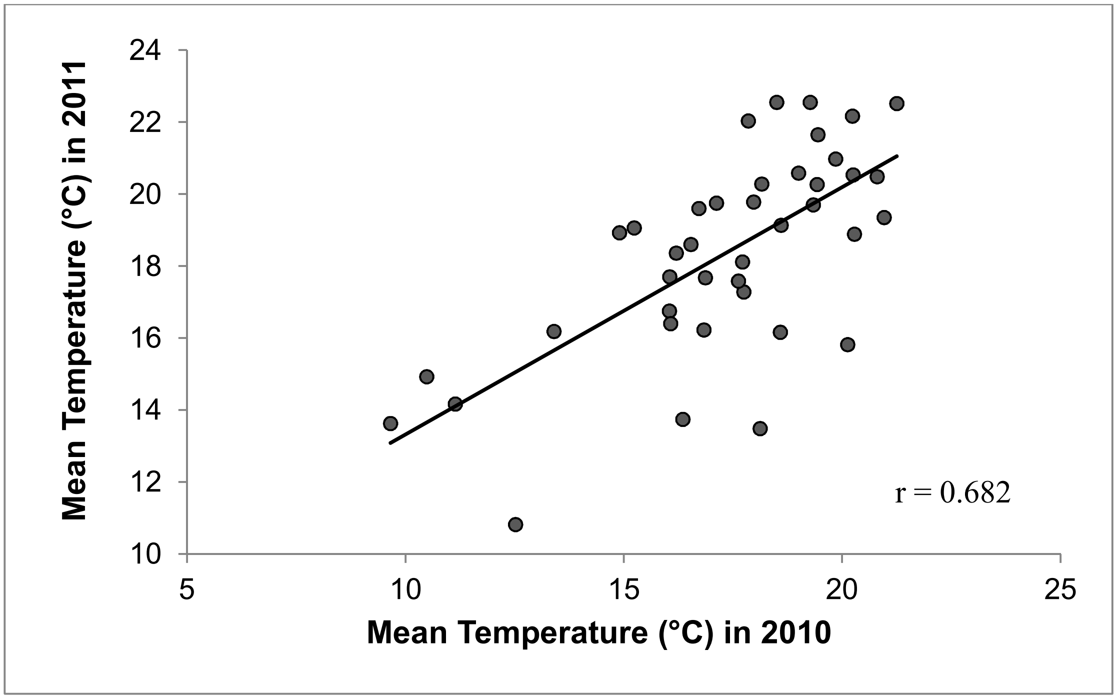

Figure 49. Mean temperatures (°C) of ponds in the Valemount Peatland in 2010 and 2011. Pearson's r = 0.682 (p >0.001).

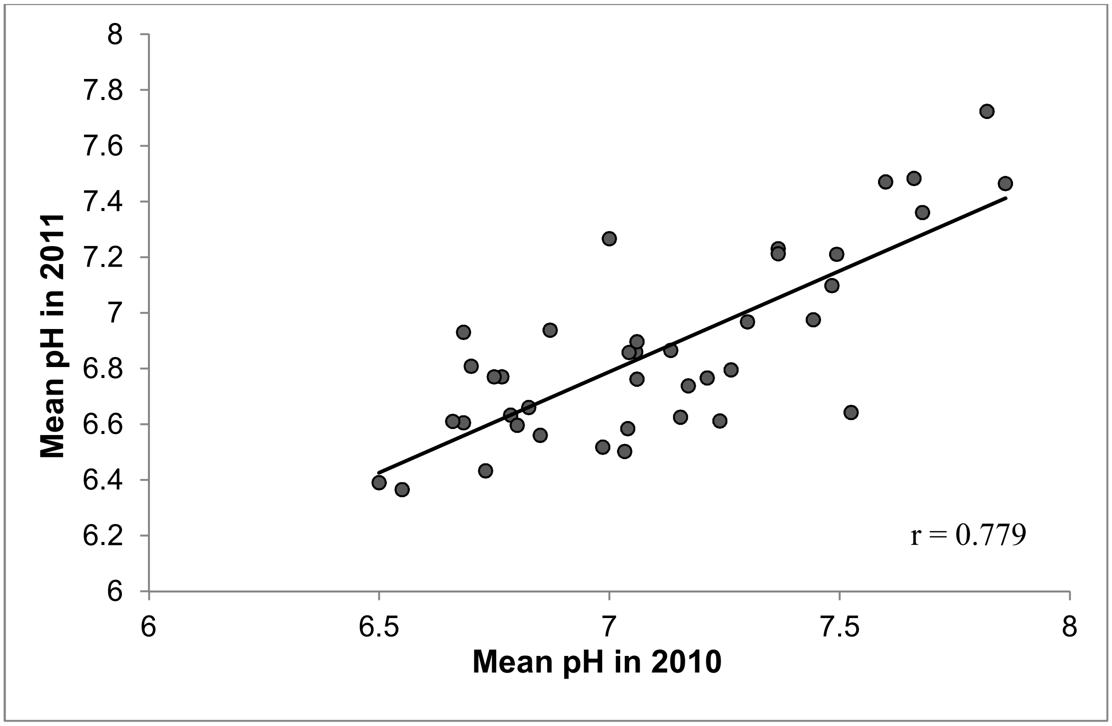

Figure 50. Mean pH of ponds in the Valemount Peatland in 2010 and 2011. Pearson's r = 0.779 (p >0.001).

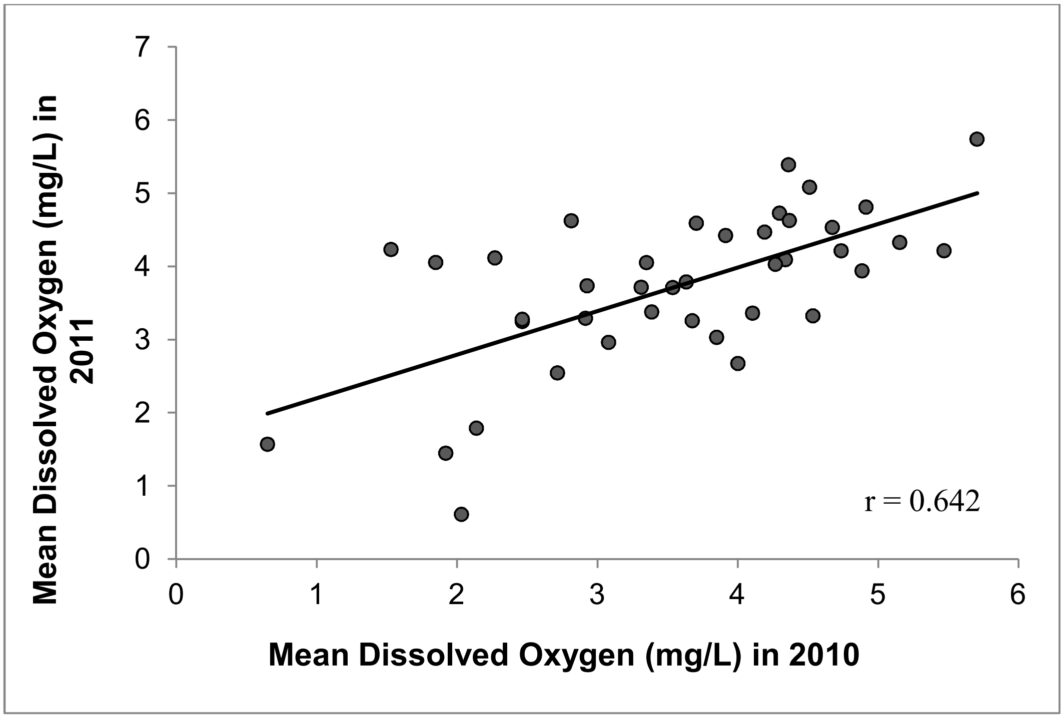

Figure 51. Mean dissolved oxygen content (mg/L) of ponds in the Valemount Peatland in 2010 and 2011. Pearson’s r = 0.642 (p > 0.001).

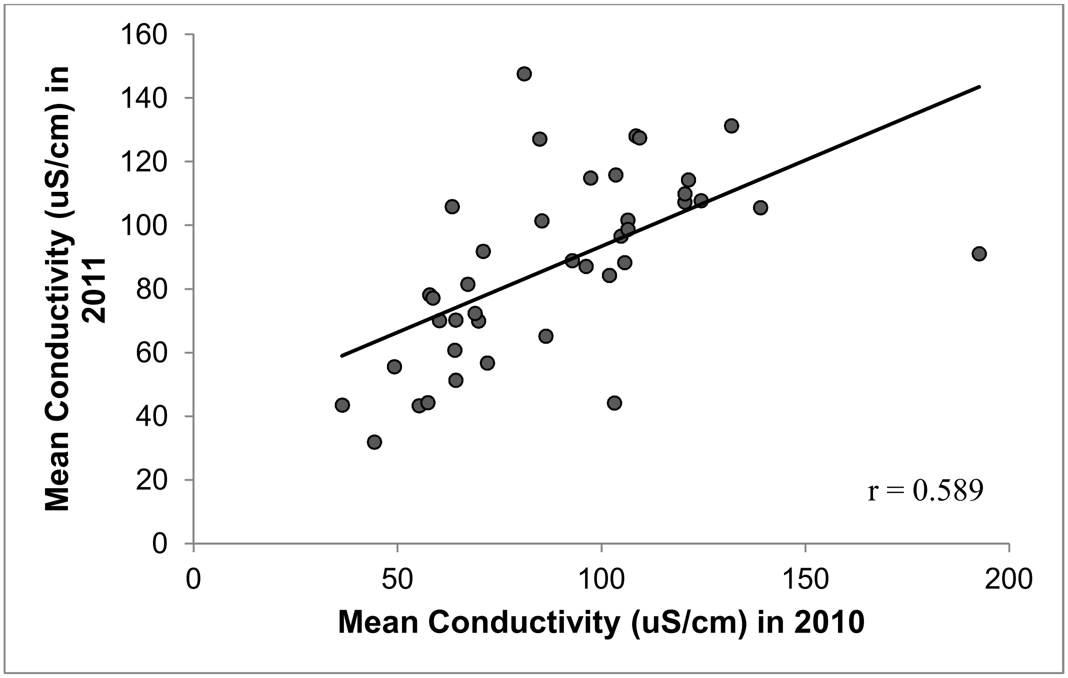

Figure 52. Mean conductivity (uS/cm) of ponds in the Valemount Peatland in 2010 and 2011. Pearson’s r = 0.589 (p >0.001).

Pond Area and Presence of Fish

The ponds in the Peatland ranged from 25.9 to 8336.9 m^2 in area, but the majority (28 of 40) were smaller than 1000 m^2 (Figure 53). The largest pond ("Pond 12") was considerably larger than all others, contributing to a skewed distribution of pond sizes (Figure 53). Fish were observed in 14 of 40 ponds in the Peatland. I did not attempt to capture fish for identification, but the small schools of fish commonly observed were likely Redside Shiners (*Richardsonius balteatus*).

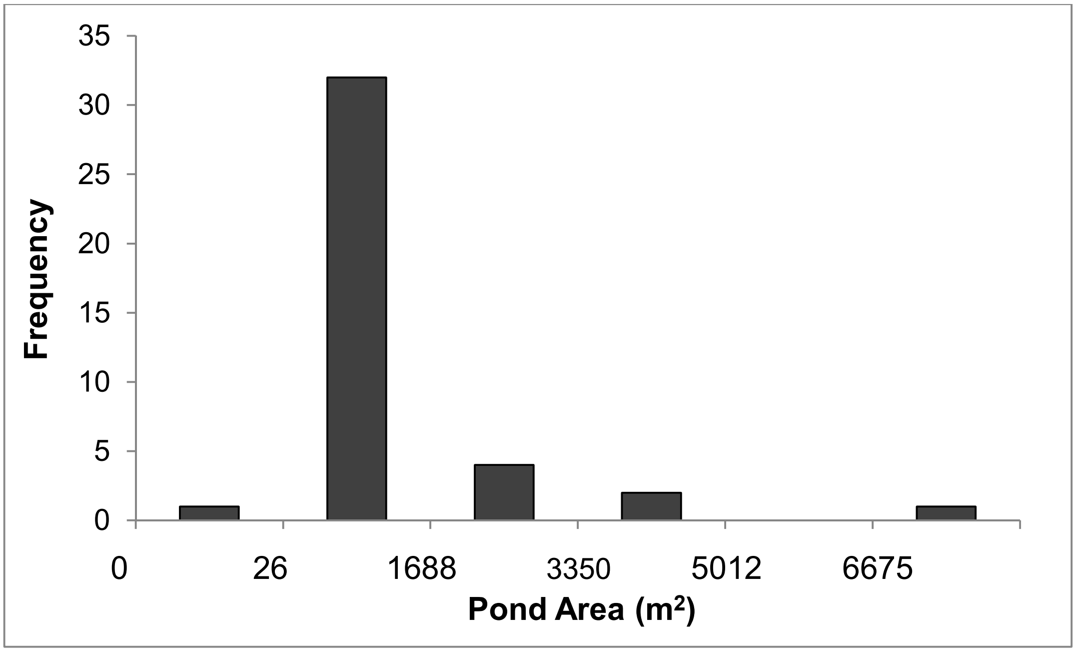

Figure 53. Frequency distribution of ponds in the Valemount Peatland by area (m^2).

Abundance of Columbia Spotted Frog eggs

The negative binomial regression model that best fit the data indicated that the number of Columbia Spotted Frog eggs in a pond increases with temperature, pH, the number of Western Toad eggs in the pond, and the presence of fish (Akaike weight = 0.74; Table 4). However, the influence of Western Toad egg abundance may have been skewed by the very high number of toad and frog eggs in one pond ("Pond 12"; Figures 41 and 44). When counts from 2010 and 2011 were pooled, 37% of all Columbia Spotted

Frog eggs were located in Pond 12, as were 75% percent of all Western Toad eggs. I removed Pond 12 and repeated the analysis to see if/how the best candidate model would differ. The (new) best fit model for the data, Pond 12 excluded, identified temperature, pH, and the presence of fish as explanatory variables (Akaike weight = 0.72, Table 5). The coefficients for these variables were virtually unchanged from the best fit model that included Pond 12.

Table 4. Candidate negative binomial regression models predicting Columbia Spotted Frog (*Rana luteiventris*) egg counts per pond in the Valemount Peatland. Data from 2010 and 2011 were pooled. Abbreviations: Temp = Temperature; ToadEggs = Number of Western Toad (*Anaxyrus boreas*) eggs; Fish = Presence of fish; Cond = Conductivity; Elev = Elevation.

MODEL	Parameters	AIC	AICc	ΔAICc	AICw
pH + Temp + ToadEggs + Fish	4	212.33	216.87	0	0.74
pH + Temp + ToadEggs + Fish + Cond	5	213.88	219.37	2.5	0.21
pH + Temp + ToadEggs + Fish + Cond + Area	6	215.72	222.36	5.49	0.05
pH + Temp + ToadEggs + Fish + Cond + Area + Elev	7	217.17	233.16	16.29	0.0002
Best Fit Equation: log (FrogEggs)	= -11.55 + 1.12(pH) + 0.25(Temp) + 1.18(Fish) + 0.019(ToadEggs)				

Table 5. Candidate negative binomial regression models predicting Columbia Spotted Frog (*Rana luteiventris*) egg counts per pond in the Valemount Peatland. Data from 2010 and 2011 were pooled, but counts from Pond 12 were excluded (see text for explanation). Abbreviations: Temp = Temperature; ToadEggs = Number of Western Toad (*Anaxyrus boreas*) eggs; Fish = Presence of fish; Cond = Conductivity; Elev = Elevation.

MODEL	Parameters	AIC	AICc	ΔAICc	AICw
pH + Temp + Fish	3	198.18	201.99	0	0.72
pH + Temp + ToadEggs + Fish	4	199.88	204.50	2.51	0.20
pH + Temp + ToadEggs + Fish + Cond	5	201.54	207.15	5.16	0.05
pH + Temp + ToadEggs + Fish + Cond + Area	6	203.43	210.23	8.24	0.011
pH + Temp + ToadEggs + Fish + Cond + Area + Elev	7	205.61	222.17	20.18	0.00003

Best Fit Equation: log(FrogEggs) = -11.73 + 1.15(pH) + 0.25(Temp) + 1.18(Fish)

Presence of Columbia Spotted Frog eggs

The binomial regression model that best predicted the presence of Columbia Spotted Frog eggs in 2010 included three variables: pH, presence of fish, and presence of Western Toad eggs (Akaike weight = 0.62; Table 6). The former two variables were positively correlated with presence of breeding Columbia Spotted Frogs, whereas the presence of Western Toad eggs was negatively correlated with the presence of Columbia Spotted Frog eggs.

The binomial regression model that best predicted presence of Columbia Spotted Frog eggs in 2011 included just two variables: temperature and presence of fish (Akaike weight = 0.51; Table 7). Each of these variables was positively associated with breeding activity of Columbia Spotted Frogs in the Peatland. The next "best" candidate model included pond conductivity as an explanatory variable (Akaike weight = 0.35).

Table 6. Candidate binomial regression models predicting Columbia Spotted Frog (*Rana luteiventris*) egg presence in ponds in the Valemount Peatland in 2010. Abbreviations: Temp = Temperature; TEggPresence = Presence of Western Toad (*Anaxyrus boreas*) eggs; Fish = Presence of fish; Cond = Conductivity; Elev = Elevation.

MODEL	**Parameters**	**AIC**	**AICc**	**ΔAICc**	**AICw**
pH + Fish +TEggPresence	3	45.05	46.19	0	0.62
pH + Fish + TEggPresence + Temp	4	45.96	47.72	1.53	0.29
pH + Fish + TEggPresence + Temp + Cond	5	47.80	50.34	4.15	0.08
pH + Fish + TEggPresence + Temp + Cond + Area	6	49.72	53.22	7.03	0.018

Best Fit Equation: log(FrogEggPresence) = -24.65 +3.50(pH)+3.22(Fish) – 2.08(TEggPresence)

Table 7. Candidate binomial regression models predicting Columbia Spotted Frog (*Rana luteiventris*) egg presence in ponds in the Valemount Peatland in 2011. Abbreviations: Temp = Temperature; TEggPresence = Presence of Western Toad (*Anaxyrus boreas*) eggs; Fish = Presence of fish; Cond = Conductivity; Elev = Elevation.

MODEL	**Parameters**	**AIC**	**AICc**	**ΔAICc**	**AICw**
Temp + Fish	2	39.96	40.63	0	0.51
Temp + Fish + Cond	3	40.24	41.39	0.76	0.35
Temp + Fish + Cond + TEggPresence	4	41.99	43.76	3.13	0.11
Temp + Fish + Cond + TEggPresence + pH	5	43.99	46.53	5.90	0.02
Temp + Fish + Cond + TEggPresence + pH + Area	6	45.98	49.48	8.85	0.006
Best Fit Equation: log(FrogEggPresence) = -11.79 + 0.62(Temp) + 3.29(Fish)					

DISCUSSION

Given the long-term persistence of anurans in the Peatland, it is not surprising that there is generally sufficient time for amphibian breeding and metamorphosis to occur before the area is inundated by Kinbasket Reservoir. However, this window of time can be very narrow, particularly in years with high levels of precipitation. In 2011, heavy rainfall and substantial snowmelt contributed to the rapidly increasing water level in Kinbasket Reservoir. Tadpoles that had not metamorphosed by mid-July were at risk of being swept into the reservoir. Although it was not possible to quantify tadpole survivorship, it seems safe to assume that the cold, turbulent, and fish-stocked waters of Kinbasket Reservoir are not conducive to larval survivorship. In 2010, however, the reservoir did not reach the Peatland until later in the summer, at a much slower rate than in the following year. In fact, desiccation was a greater threat to amphibian eggs and tadpoles than was inundation by the reservoir. Amphibians commonly breed in ephemeral ponds, which tend to be warmer and free of predatory fish, but such ponds also are associated with a greater risk of desiccation. It is possible that the erosion processes associated with reservoir drawdown increase the desiccation risk of ponds in the drawdown zone via reduction of vegetative cover (Ham, 2010) and/or altered shorelines.

Further research would be required to test this hypothesis, however. In the Peatland, two seemingly opposing environmental stressors (desiccation and inundation) may pressure breeding amphibians to choose oviposition locations that maximize the developmental rate of their offspring. A dry spring and/or summer may reduce the threat of early inundation, but consequently increase the likelihood of pond desiccation. On the other hand, a wet spring and summer, which might otherwise be ideal for amphibian breeding success, could signal early flooding in a reservoir drawdown zone. My observation of tadpoles at early stages of development when Kinbasket Reservoir inundated the Peatland highlights the importance of early breeding and rapid larval development in these populations.

The role of aquatic invertebrate abundances in use of breeding ponds by Columbia Spotted Frogs was not clearly revealed by my negative binomial regression analysis. The predictive ability of my best fit model was not much greater than that of a model containing only an intercept. In other words, there are other, more relevant pond characteristics that influence the abundance of Columbia Spotted Frog eggs that have not been considered by this analysis. That said, of all the macroinvertebrates included in my global model, midge larvae and snails had the closest relationship to abundance of Columbia Spotted Frog eggs in ponds. This result coincides with previous research by Brönmark et al. (1991), who documented a positive relationship between snail presence and tadpole growth, and by Morin et al. (1988), who reported a negative influence of midge larvae (among other invertebrates) on size at metamorphosis in two anurans. Thus, there is some evidence for selective pressure associated with these macroinvertebrate species. Nonetheless, the results of this analysis have limited value until tested in conjunction with other relevant variables.

Abundance of Columbia Spotted Frog eggs (pooled from 2010 and 2011) was positively correlated with mean pond pH, mean temperature (°C), abundance of Western Toad eggs, and presence of fish. A positive relationship between water temperature and embryo/larval development rate is well documented in this species (e.g. Johnson, 1965; Bull and Shepherd, 2003) and in many other anurans (e.g. Marian and Pandian, 1985;

Álvarez and Nicieza, 2002; Reading, 2010). Several species of frogs preferentially oviposit in warm locations (e.g. Seale, 1982; Sjögren et al., 1988) to capitalize on this relationship; it is no surprise to have documented the same trend for Columbia Spotted Frogs in the drawdown zone. The role of pH in amphibian breeding pond use is less straightforward. The mean pH levels of ponds in the Peatland ranged from 6.43 to 7.77. These conditions are less acidic than the extremes tolerated by most amphibians (Pierce, 1985) and also less alkaline than those known to hinder larval development in some species (Fominykh, 2008). It seems unlikely that breeding Columbia Spotted Frogs are attracted or deterred by such slight inter-pond variations in pH in the Peatland. However, mean pH also serves as a proxy for dissolved oxygen content (mg/L) due to the significant correlation between these two variables ($r = 0.68$, $n = 40$, $p < 0.001$). A positive relationship between pH and dissolved oxygen content is expected in ponds with aquatic vegetation. Carbonic acid, formed when carbon dioxide is dissolved in water, is a natural source of acidity in fresh water (Wurts, 2003). As aquatic plants photosynthesize, they remove carbon dioxide from the water, thereby increasing the pH (Verduin, 1951; Wurts, 2003) while also releasing oxygen. In the Peatland, all physicochemical measurements of water were taken during daylight hours, when oxygen concentrations are likely at their highest and carbon dioxide concentrations are at their lowest (i.e. pH is at its highest). The increasing abundance of Columbia Spotted Frog eggs in ponds with a higher pH may in fact be the result of a preference for ponds with slightly more oxygen/aquatic vegetation.

Aquatic vegetation cover is a potentially important explanatory factor that I did not quantify for this study. Aquatic vegetation in amphibian breeding ponds can provide shelter from predators (Babbitt and Tanner, 1997; Baber and Babbitt, 2004; Kopp et al., 2006), protection from UV-B rays (Palen et al., 2005) and material for attachment of egg masses (Egan and Paton, 2004). A positive relationship between density of vegetative cover and oviposition site use has been documented in several ranid species, including *Rana luteiventris* (Pearl et al. 2007), *Rana aurora* (Cary, 2010), *Rana nigromaculata* (Wang et al., 2008), and *Lithobates sylvaticus* (formerly *Rana sylvatica*; Egan and Paton, 2004). I did not attempt to estimate total pond vegetative cover because it varies temporally and can be difficult to measure accurately and objectively (particularly for large ponds). Columbia Spotted Frog egg masses were frequently attached to aquatic vegetation, such as sedge (*Carex* spp.) and horsetail (*Equisetum* spp.), and this vegetation could be either emergent or submergent (pers. obs.). Visually estimating the percentage of submergent vegetation was difficult even within 1-m^2 quadrat samples.

The relationship between presence of fish and use of habitat by amphibians often varies with the species being studied. Brown et al. (2012) found that amphibian occupancy and abundance are generally negatively correlated with fish presence, but anurans in the families Ranidae and Bufonidae do not follow this trend. The authors hypothesized that a positive relationship between fish and *Rana* spp. is the result of a shared preference for permanent wetlands. Welch and MacMahon (2005) studied habitat associations of Columbia Spotted Frogs in Utah and determined that constant seasonal water temperature, stable minimum water levels, and high emergent vegetation cover best predicted the presence of frog eggs in randomly selected ponds. These qualities are consistent with those of permanent wetlands. This is likely the reason my best fit model identified a positive relationship between fish presence and abundance of Columbia Spotted Frog eggs.

The positive influence of abundance of Western Toad eggs on the abundance of Columbia Spotted Frog eggs was detected only when Pond 12 was included in the model. This pond was clearly the primary location for anuran breeding activity in the Peatland. Generally, Western Toads and Columbia Spotted Frogs prefer different microhabitats for oviposition. A typical Western Toad breeding location is quite shallow, with lots of sun exposure and a sandy bottom (McGee and Keinath, 2004; Matsuda et al., 2006; Bartelt et al., 2010). Indeed, 9 of the 10 ponds with Western Toad eggs in the Peatland possess one or more of these qualities. Pond 12, however, possesses none of them, suggesting that there are alternative benefits to breeding in this location. Although Pond 12 is one of the biggest ponds in the Peatland, pond area was not included in the candidate model that best fit the data. Pond temperature, pH, and fish presence were better predictors of egg abundance than pond area. This pond was also one of just two locations where Columbia

Spotted Frogs and Western Toads laid eggs in the same microhabitat (i.e. at the same location within the pond and within ~ 1 m of each other). In both years, all eggs of both species were deposited at the far west end of Pond 12, at the highest elevation possible, close to upland habitat. Contrary to my expectations, pond elevation was not included in the best fit model. This may be due to the scale at which elevation was recorded. The majority of ponds were found between 750 and 753 m ASL and elevation was recorded to the nearest 1 metre. Although habitat at higher elevations in the drawdown zone is available for a greater number of days each active season, perhaps the difference between 750 and 751 m ASL (for example) is negligible. Future studies could use distance to upland habitat to represent the length of time each oviposition site is available relative to other sites in the immediate area.

Binomial regression of presence of Columbia Spotted Frog eggs in the Peatland yielded different results for each year of this study. Using data from 2010, I identified a positive relationship between breeding activity of Columbia Spotted Frogs, pH, and presence of fish. Presence of Western Toad eggs decreased the probability of breeding activity of Columbia Spotted Frogs in ponds. This negative association between breeding locations of Western Toads and Columbia Spotted Frogs is in keeping with what I observed in the field and with the different oviposition-site preferences typically exhibited by these species. Temperature was not included among the best fit model's predictor variables, despite its influence on abundance of frog eggs in the pooled data set. Although more frogs will breed in ponds with a higher mean temperature, it seems that Columbia Spotted Frogs were not completely averse to breeding in ponds with lower mean temperatures in 2010. However, the presence of Columbia Spotted Frog eggs was positively correlated with mean pond temperature in 2011. This difference may be related to the earlier start to the breeding season in 2010 – air temperatures were significantly warmer and the snowpack was considerably lighter in the early spring of 2010 than in 2011 (see Chapter 2; Corn, 2003).

Whether or not Columbia Spotted Frogs can adjust their oviposition decisions according to these inter-year and inter-pond differences is not clear. My results can only point to pond characteristics that are potentially important to breeding Columbia Spotted Frogs. One of the major limitations of this study, as well as others, is a lack of congruity with similar research in terms of the variables recorded. Cary (2010) assessed the habitat characteristics associated with oviposition sites of Northern Red-Legged Frogs (*Rana aurora*), and included water depth, fish presence, amphibian presence, canopy cover, woody debris, and vegetation cover among her potential explanatory variables. Pearl et al (2007) examined the pond depth, substrate slope, vegetation density, and horizontal shading of Columbia Spotted Frog oviposition sites, relative to random locations. Welch and MacMahon (2005) included relative changes in pond size and temperature, water depth, conductivity, and mean vegetative cover in their analysis of occurrence of Columbia Spotted Frog in ponds. Financial, logistical, geographical and temporal limitations often dictate the variables that are measured for a field study, as do the varied motivations and hypotheses of the researchers. However, these differences can make direct comparisons of species or populations more difficult. Results of these studies (including mine) must be interpreted in light of the reality that explanatory variables are not equally relevant in all environments, nor can they always be accounted for.

Site fidelity is one such variable that is frequently overlooked in habitat use and selection studies (Piper, 2011). Site fidelity may be defined as the tendency of an animal to return to a location it previously occupied (Switzer, 1993). Within the context of amphibian ecology, a common form of site fidelity is the tendency of adult amphibians to return to their natal ponds to breed (i.e. pond philopatry). Searching unfamiliar territory for suitable breeding habitat can be associated with increased mortality risk, whereas returning to the same pond to breed each year may have survival and reproductive benefits (see Johnson and Gaines, 1990; Semlitsch, 2008; Matthews and Priesler, 2010; Piper, 2011). Adult Columbia Spotted Frogs exhibit a high degree of site fidelity (Funk et al., 2005); therefore, the repeated presence of Columbia Spotted Frog eggs in a pond may not reflect habitat quality, but rather a preference for familiar habitat. Indeed, at the Valemount Peatland, many Columbia Spotted Frog eggs were found in precisely the same locations in 2011 as in 2010. However, the proximity of ponds and connectivity of the habitat in the Peatland would facilitate dispersal if the quality of a particular breeding pond declined. In other words, the consequences associated with dispersal to new breeding ponds (e.g. increased predation risk, Yoder et al., 2004) should be minimal at this site. Apparent preferences for particular breeding ponds should therefore reflect true differences in pond characteristics across the Peatland.

Generally, Columbia Spotted Frogs in the Peatland are more likely to breed in ponds with higher mean temperatures, higher mean pH, and the presence of fish. These characteristics point to a preference for both warmer ponds and more permanent breeding ponds. In the Valemount Peatland, pond desiccation and reservoir inundation are two major threats to the survival of larval amphibians. Given that tadpole development rate increases with temperature (Smith-Gill and Berven, 1979; Marian and Pandian, 1985), a preference for warmer breeding ponds in the drawdown zone could increase the likelihood of metamorphosis prior to desiccation or reservoir inundation. As well, ponds that support fish are presumably the most resistant to desiccation. Frogs that breed in these ponds would benefit from a reduced risk of offspring death in dry years. Future research on amphibian habitat use in drawdown zones should incorporate vegetation density and pond hydroperiod to evaluate the relative importance of these variables.

CHAPTER 4 – MANAGEMENT IMPLICATIONS

By October of 2014, BC Hydro will have installed the first of two new generating units at Mica Dam. The addition of these new turbines will increase the generating capacity of Kinbasket Reservoir by roughly 1000 megawatts (BC Hydro, 2008), to meet the increasing energy demands of British Columbians. As a result, the maximum operational level of the reservoir will be raised by approximately 60-70 cm (BC Hydro, 2008; V. Hawkes, pers.comm.). The repercussions for amphibian and reptile habitat in the drawdown zone could be great. Not only will previously undisturbed areas around the reservoir become part of the drawdown zone, but the depth and duration of flooding may increase in all existing areas of the drawdown zone. Given that the current inundation regime has reduced vegetation complexity and accelerated erosion at the Valemount Peatland (Ham, 2010), increasing the extent or duration of flooding will likely aggravate the situation further. In 2010, many of the amphibian breeding ponds at the Peatland desiccated before eggs could hatch and larvae could metamorphose. The already high desiccation risk at this site could be amplified by increased rates of erosion and reduction in vegetative cover.

Higher maximum water levels alone may not directly impact amphibians and reptiles, because the amount of water in the reservoir is largely dictated by precipitation levels. The elevation of the reservoir typically peaks in September, as the active season draws to an end. At this time, reptiles and amphibians at northern latitudes transition from foraging to overwintering habitats. The results of my research suggest that the *timing* of reservoir inundation is the major limiting factor for amphibian and reptile populations in the drawdown zone. In 2011, the water level in the reservoir increased rapidly, due to high precipitation and snowmelt runoff. This reduced the amount of time available for amphibian metamorphosis to occur before breeding ponds were flooded by the reservoir. I was unable to quantify the population level impacts of early inundation in the drawdown zone, but I observed the flooding of many Western Toad and Columbia Spotted Frog breeding ponds in 2011 — before all tadpoles had metamorphosed. Factors affecting Western Toad reproductive success could have serious consequences for Common Garter Snakes as well, because they prey heavily on Western Toad larvae and metamorphs. To protect the amphibian and garter snake populations at Kinbasket Reservoir, it is important that no drastic, lasting changes are made to the current inundation regime. Repeated, early inundation of the Valemount Peatland and Ptarmigan Creek could reduce anuran offspring survivorship and negatively impact amphibian and garter snake populations.

Efforts to protect amphibian populations located upstream of hydroelectric dams should include an investigation of their reproductive phenology. Paton and Crouch (2001) found that the length of time required for 95% of metamorphs to emigrate from breeding ponds differed by species. Reservoir inundation will likely affect each species of amphibian differently, depending on when flooding occurs. At Kinbasket Reservoir, there is a narrow window of time for Western Toads and Columbia Spotted Frogs to reproduce prior to inundation of the drawdown zone. Their persistence in the area suggests that successful reproduction occurs more often than not — likely due to plasticity in the onset of breeding and age at metamorphosis (Díaz Paniagua, 1992; Jakob et al., 2003). However, it should not be inferred that these species are equally resilient to other hydroelectric reservoirs with similar inundation regimes. Energy demands, precipitation levels, and topography influence the timing and extent of reservoir inundation, while local weather patterns influence the timing of amphibian breeding activity. The construction of a fifth generating unit is already underway at Mica Dam. Whether or not the amphibian and reptile populations in the drawdown zone of Kinbasket Reservoir can tolerate this latest anthropogenic disturbance remains to be seen.

LITERATURE CITED

Aleksiuk, M., & Gregory, P. T. (1974). Regulation of seasonal mating behavior in *Thamnophis sirtalis parietalis*. *Copeia*, *1974*(3), 681–689.

Álvarez, D., & Nicieza, A. G. (2002). Effects of temperature and food quality on anuran larval growth and metamorphosis. *Functional Ecology*, *16*(5), 640–648.

Angilletta, M. J., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, *44*(6), 498 –509.

Arnold, S.J., & Wassersug, R.J. (1978). Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): Social behavior as a possible defense. *Ecology,* 59(5), 1014- 1022.

Arnold, S.J. (2003). Too much natural history, or too little? *Animal Behavior*, *65*, 1065–1068.

Atlas, M. (1935). The effect of temperature on the development of *Rana pipiens*. *Physiological Zoology*, 8(3), 290-310.

Babbitt, K. J., & Tanner, G. W. (1998). Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia*, *114*(2), 258–262.

Baber, M. J., & Babbitt, K. J. (2004). Influence of habitat complexity on predator-prey interactions between the fish (*Gambusia holbrooki*) and tadpoles of *Hyla squirella* and *Gastrophryne carolinensis*. *Copeia*, *2004*(1), 173–177.

Babyak, M. (2004). What you see may not be what you get: A brief, nontechnical introduction to overfitting in regression-type models. *Psychosomatic Medicine*, *66*(3), 411–421.

Bain, M.B, Finn, J.T, & Booke, H.E. (1988). Streamflow regulation and fish community structure. *Ecology, 69*(2), 382–392.

Barclay, J. S. (1976). Waterfowl use of Oklahoma reservoirs. *Proceedings of the Oklahoma Academy of Science*, *1976*(5), 141-51.

Barrett, T. J., Tingley, M. A., Munkittrick, K. R., & Lowell, R. B. (2010). Dealing with heterogeneous regression slopes in analysis of covariance: new methodology applied to environmental effects monitoring fish survey data. *Environmental monitoring and assessment*, *166*(1), 279–291.

Bartelt, P. E., Gallant, A. L., Klaver, R. W., Wright, C. K., Patla, D. A., & Peterson, C. R. (2011). Predicting breeding habitat for amphibians: a spatiotemporal analysis across Yellowstone National Park. *Ecological Applications*, *21*(7), 2530–2547.

Baxter, R. M. (1977). Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics*, *8*, 255–283.

B.C. Conservation Data Centre. (2012). BC Species and Ecosystems Explorer. B.C. Ministry of Environment. Victoria, B.C. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed Apr 9, 2012).

BC Hydro. (2008). Mica unit 5 project description. Submitted to BC Environmental Assessment Office and Canadian Environmental Assessment Agency. 40 pp + Appendices.

Beattie, R. C., & Tyler-Jones, R. (1992). The effects of low pH and aluminum on breeding success in the frog *Rana temporaria*. *Journal of Herpetology*, *26*(4), 353–360.

Beneski, J. T., Zalisko, E. J., & Larsen, J. H. (1986). Demography and migratory patterns of the Eastern Long-Toed Salamander, *Ambystoma macrodactylum columbianum*. *Copeia*, *1986*(2), 398–408.

Berger, L., Speare, R., Daszak, P., Green, D., Cunningham, A., Goggin, C., Slocombe, R., et al. (1998). Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(15), 9031–9036.

Bernal, M. H., & Clavijo, J. A. (2009). An essay on precision in morphometric measurements in anurans: inter-individual, intra-individual and temporal comparisons. *Zootaxa*, *2246*, 32–44.

Berven, K. A., & Chadra, B. G. (1988). The relationship among egg size, density and food level on larval development in the wood frog (*Rana sylvatica*). *Oecologia*, *75*(1), 67–72.

Berven, K. A., & Gill, D. E. (1983). Interpreting geographic variation in life-history traits. *American Zoologist*, *23*(1), 85–97.

Blanchard, F. N., & Finster, E. B. (1933). A method of marking living snakes for future recognition, with a discussion of some problems and results. *Ecology*, *14*(4), 334–347.

Bonner, L. A., Diehl, W. J., & Altig, R. (1997). Physical, chemical and biological dynamics of five temporary dystrophic forest pools in Central Mississippi. *Hydrobiologia*, *353*(1), 77–89.

Booth, D. (1998). The environmental consequences of growth: Steady state economics as an alternative to ecological decline. Routledge, London. 238 pp.

Brandao, R. A. & Araujo, A. F. B. (2008). Changes in anuran species richness and abundance resulting from hydroelectric dam flooding in central Brazil. *Biotropica*, *40*(2), 263-266.

Brönmark, C., Rundle, S. D., & Erlandsson, A. (1991). Interactions between freshwater snails and tadpoles: competition and facilitation. *Oecologia*, *87*(1), 8–18.

Bronikowski, A. M., & Arnold, S. J. (1999). The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. *Ecology*, *80*(7), 2314–2325.

Brown, D. J., Street, G. M., Nairn, R. W., & Forstner, M. R. J. (2012). A place to call home: Amphibian use of created and restored wetlands. *International Journal of Ecology*, *2012*, 1–11.

Browne, C. L., Paszkowski, C. A., Lee Foote, A., Moenting, A., & Boss, S. M. (2009). The relationship of amphibian abundance to habitat features across spatial scales in the boreal plains. *Ecoscience*, *16*(2), 209–223.

Bull, E.L., & Shepherd, J.F. (2003). Water temperature at oviposition sites of *Rana luteiventris* in northeastern Oregon. *Western North American Naturalist*, 63(1), 108-113.

Burnham, K. P., and D. R. Anderson. (2010). Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, Berlin, Germany.

Caldwell, J. P., Thorp, J. H., & Jervey, T. O. (1980). Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia*, *46*(3), 285–289.

Carfagno, G. L. F., & Weatherhead, P. J. (2008). Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. *Journal of Animal Ecology*, *77*(2), 416–424.

Carpenter, C. C. (1952). Growth and maturity of the three species of *Thamnophis* in Michigan. *Copeia*, *1952*(4), 237–243.

Cary, J. A. (2010). Determining habitat characteristics that predict oviposition site selection for pond-breeding northern red-legged frogs (*Rana aurora*) in Humboldt County, California. M.Sc. Thesis. Humboldt State University. 40 pp + Appendices.

Charland, M.B., and Gregory, P.T. (1995). Movements and habitat use in gravid and nongravid female garter snakes (Colubridae*: Thamnophis*). *Journal of Zoology*, *236*, 543-561.

Corn, P. S. (2003). Amphibian breeding and climate change: Importance of snow in the mountains. *Conservation Biology*, *17*(2), 622–625.

Cortwright, S. A. & Nelson, C. E. (1990). An examination of multiple factors affecting community structure in an aquatic amphibian community. *Oecologia*, *83*(1), 123-131.

Crivelli, A.J., Grillas, P., & Lacaze, B. (1995) Effects on fisheries and waterbirds of raising water levels at Kerkini Reservoir, a Ramsar site in northern Greece. *Environmental Management*, 19(3), 417-430.

Crosswhite, D.L., Fox,. S.F., & Thill, R.E. (1999) Comparison of methods for monitoring reptiles and amphibians in upland forests of the Ouachita Mountains. *Proceedings of the Oklahoma Academy of Science¸ 79*, 45-50.

Crouch, W. B., & Paton, P. W. C. (2000). Using egg-mass counts to monitor wood frog populations. *Wildlife Society Bulletin*, *28*(4), 895–901.

Crump, M. L. (1991). Choice of oviposition site and egg load assessment by a treefrog. *Herpetologica*, *47*(3), 308–315.

Cushman, R.M. (1985). Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management,* 1985(5), 330–339.

Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, 128(2), 231-240.

Davis, A. B., & Verrell, P. A. (2005). Demography and reproductive ecology of the Columbia Spotted Frog (*Rana luteiventris*) across the Palouse. *Can. J. Zool.*, *83*(5), 702–711.

Denver, R. J., Mirhadi, N., & Phillips, M. (1998). Adaptive plasticity in amphibian metamorphosis: Response of *Scaphiopus hammondii* tadpoles to habitat desiccation. *Ecology*, *79*(6), 1859–1872.

Díaz-Paniagua, C. (1992). Variability in timing of larval season in an amphibian community in SW Spain. *Ecography*, *15*(3), 267–272.

Egan, R. S., & Paton, P. W. C. (2004). Within-pond parameters affecting oviposition by wood frogs and spotted salamanders. *Wetlands*, *24*(1), 1–13.

Environment Canada (2012) National Climate Data and Information Archive. Available: www.climate.weatheroffice.gc.ca. (Accessed January 20, 2012).

Faccio, S. D. (2003). Postbreeding emigration and habitat use by Jefferson and Spotted Salamanders in Vermont. *Journal of Herpetology*, *37*(3), 479–489.

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society, 14*(1), 21.

Falke, J. A., & Gido, K. B. (2006). Spatial effects of reservoirs on fish assemblages in Great Plains streams in Kansas, USA. *River Research and Applications*, *22*(1), 55–68.

Farr, D. R. (1988). The ecology of garter snakes, *Thamnophis sirtalis* and *T. elegans*, in southeastern British Columbia. M.Sc. Thesis, Univ. Victoria, Victoria, B.C. 141 pp.

Farr, D. R., & Gregory, P. T. (1991). Sources of variation in estimating litter characteristics of the garter snake, *Thamnophis elegans*. *Journal of Herpetology*, *25*(3), 261-268.

Fitch, H. S. (1965). An ecological study of the garter snake, *Thamnophis sirtalis*. University of Kansas Publications, Museum of Natural History. 15(10), 493-564.

Fitch, H. S., & Shirer, H.W. (1971). A radiotelemetric study of spatial relationships in some common Snakes. *Copeia*, *1971*(1), 118–128.

Fort, K. T., & Otter, K. A. (2004). Effects of habitat disturbance on reproduction in Black-Capped Chickadees (*Poecile atricapillus*) in northern British Columbia. *The Auk*, *121*(4), 1070–1080.

Fominykh, A. S. (2008). An experimental study on the effect of alkaline water pH on the dynamics of amphibian larval development. *Russian Journal of Ecology*, *39*(2), 145–147.

Freda, J. (1986). The influence of acidic pond water on amphibians: A review. *Water, Air, & Soil Pollution*, 30(1-2), 439-350.

Friggens, M.M. & Beier, P. (2010). Anthropogenic disturbance and the risk of Xea-borne disease transmission. *Oecologia, 164*, 809-820.

Fukumoto, J. & Herrero, S. (1998). Observations of the long-toed salamander, *Ambystoma macrodactylum*, in Waterton Lakes National Park, Alberta. *Canadian Field Naturalist*, *112*(4), 579-585.

Funk, W., Greene, A., Corn, P., & Allendorf, F. (2005). High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biology Letters*, *1*(1), 13–16.

Gascon, C., & Planas, D. (1986). Spring pond water chemistry and the reproduction of the wood frog, *Rana sylvatica*. *Canadian Journal of Zoology*, *64*(2), 543–550.

Gardner, T. (2001). Declining amphibian populations: a global phenomenon in conservation biology. *Animal Biodiversity and Conservation*, *24*(2), 25-44.

Gibbons, J.W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., et al. (2000). The global decline of reptiles, déjà vu amphibians. *BioScience*, 50(8), 653-666.

Gignac, A., & Gregory, P. T. (2005). The effects of body size, age, and food intake during pregnancy on reproductive traits of a viviparous snake, Thamnophis ordinoides. *Ecoscience*, *12*(2), 236–243.

Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (1996). A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology*, *33*(4), 786-792.

Goater, C.P. (1994). Growth and survival of postmetamorphic toads: Interactions among larval history, density, and parasitism. *Ecology*, *75*(8), 2264–2274.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, *16*(3), 183–190.

Green, A. (2001). Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology*, *82*(5), 1473–1483.

Greene, H. W. **(**1994). Systematics and natural history, foundations for understanding and conserving biodiversity. *American Zoologist*, 34**,** 48–56.

Gregory, P. T. (1984). Habitat, diet, and composition of assemblages of garter snakes (*Thamnophis*) at eight sites on Vancouver Island. *Canadian Journal of Zoology*, *62*(10), 2013–2022.

Gregory, P. T. (2006). Influence of income and capital on reproduction in a viviparous snake: direct and indirect effects. *Journal of Zoology*, *270*(3), 414–419.

Gregory, P.T. (2011).Temporal dynamics of relative-mass variation of red-sided garter snakes (*Thamnophis sirtalis parietalis*) at a communal hibernaculum in Manitoba. *Ecoscience, 18*(1), 1-8.

Gregory, P. T., Crampton, L. H., & Skebo, K. M. (1999). Conflicts and interactions among reproduction, thermoregulation and feeding in viviparous reptiles: are gravid snakes anorexic? *Journal of Zoology*, *248*(2), 231–241.

Gregory, P. T., & Larsen, K. W. (1993). Geographic variation in reproductive characteristics among Canadian populations of the common garter snake (*Thamnophis sirtalis*). *Copeia*, 946–958.

Gregory, P. T., & Stewart, K. W. (1975). Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. *Canadian Journal of Zoology*, *53*(3), 238–245.

Tuttle, K. N., & Gregory, P. T. (2012). Growth and maturity of a terrestrial ectotherm near its northern distributional limit: does latitude matter? *Canadian Journal of Zoology*, *90*(6), 758–765.

Hannah, L., Lohse, D., Hutchinson, C., Carr, J.L. & Lankerani, A. (1994). A preliminary inventory of human disturbance of world ecosystems. *Ambio*, 23, 246-50.

Hannah, L., Carr, J.L., & Lankerani, A. (1995). Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation*, *4*, 128-155.

Ham, D.G. (2010). CLBMON-8. Kinbasket Reservoir monitoring of the Valemount Peatland. Year 2 report prepared by Northwest Hydraulic Consultants for BC Hydro. 30 pp. + Appendices.

Hawkes, V.C., Houwers, C., Fenneman, J.D., & Muir, J.E. (2007). Kinbasket and Arrow Lakes reservoir revegetation management plan: Kinbasket Reservoir inventory of vegetation resources. Annual Report – 2007. LGL Report EA1986. Unpublished report by LGL Limited environmental research associates, Sidney, B.C., for BC Hydro Generations, Water Licence Requirements, Burnaby, BC. 82 pp. + Appendices.

Hawkes, V.C. & Tuttle, K.N. (2010). CLBMON-37. Kinbasket and Arrow Lakes Reservoirs: Amphibian and reptile life history and habitat use assessment. Annual Report – 2009. LGL Report EA3075. Unpublished report by LGL Limited environmental research associates, Sidney, B.C., for BC Hydro Generations, Water License Requirements, Burnaby, BC. 70 pp. + Appendices.

Hawkes, V.C., & Tuttle, K.N. (2012). CLBMON-58. Kinbasket Reservoir: Monitoring of Impacts on Amphibians and Reptiles from Mica Units 5 and 6 in Kinbasket Reservoir. Year 1 Annual Report – 2012. LGL Report EA3303. Unpublished report by LGL Limited environmental research associates, Sidney, B.C., for BC Hydro Generations, Water License Requirements, Burnaby, BC. 75 pp. + Appendices.

Hawkes, V.C., Tuttle, K.N., & Gibeau P. (2011). CLBMON-37. Kinbasket and Arrow Lakes Reservoirs: and reptile life history and habitat use assessment. Year 3 Annual Report – 2010. LGL Report EA3075A. Unpublished report by LGL Limited environmental research associates, Sidney, B.C., for BC Hydro Generations, Water License Requirements, Burnaby, BC. 90 pp. + Appendices.

Hayek, L. A., Heyer, W. R., & Gascon, C. (2001). Frog morphometrics: a cautionary tale. *Alytes*, *18*(3-4), 153–177.

Hoef, J. M., & Boveng, P. L. (2007). Quasi-poisson vs. negative binomial regression: How should we model overdispersed count data? *Ecology*, *88*(11), 2766–2772.

Holden P.B., & Stalnaker, C.B. (1975). Distribution and abundance of mainstream fishes of the Middle and Upper Colorado River Basins, 1967–1973.*Transactions of the American Fisheries Society*, *1975*(100), 217–231.

Hopey, M. E., & Petranka, J. W. (1994). Restriction of wood frogs to fish-free habitats: How important is adult choice? *Copeia*, *1994*(4), 1023-1025.

Houghton, J. (2005). Global warming. *Reports on Progress in Physics*, *68*(6), 1343-1403.

Howard, R.D. (1980). Mating behaviour and mating success in wood frogs, *Rana sylvatica*. *Animal Behaviour*, *28*(3), 705–716.

Jakob, C., Poizat, G., Veith, M., Seitz, A., & Crivelli, A. J. (2003). Breeding phenology and larval distribution of amphibians in a Mediterranean pond network with unpredictable hydrology. *Hydrobiologia*, *499*(1), 51–61.

Jennings, W. B., Bradford, D. F., & Johnson, D. F. (1992). Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. *Journal of Herpetology*, *26*(4), 503-505.

Johnson, O.W. (1965). Early development, embryonic temperature tolerance and rate of development in *Rana pretiosa luteiventris* Thompson. Doctoral dissertation, Oregon State University, Corvallis.

Johnson, M. L., & Gaines, M. S. (1990). Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, *21*(1), 449–480.

Jones, K. B. (1988). Comparison of herpetofaunas of a natural and altered riparian ecosystem. Management of amphibians, reptiles, and small mammals in North America*. USDA Forest Service General Technical Report, RM-166*, 222–227.

Karraker, N. E., Gibbs, J. P., & Vonesh, J. R. (2008). Impacts of road de-icing salt on the demography of vernal pool-breeding amphibians. *Ecological Applications: A Publication of the Ecological Society of America*, *18*(3), 724–734.

Kephart, D. G., & Arnold, S. J. (1982). Garter snake diets in a fluctuating environment: A seven-year study. *Ecology*, *63*(5), 1232–1236.

Kiesecker J.M, Blaustein A.R, & Belden, L.K (2001). Complex causes of amphibian population declines. *Nature*, (410) 681–684.

Kopp, K., Wachlevski, M., & Eterovick, P. C. (2006). Environmental complexity reduces tadpole predation by water bugs. *Canadian Journal of Zoology*, *84*(1), 136–140.

Lardner, B. (2000). Morphological and life history responses to predators in larvae of seven anurans. *Oikos*, *88*(1), 169–180.

Larsen, K. W. (1987). Movements and behavior of migratory garter snakes, *Thamnophis sirtalis*. *Canadian Journal of Zoology*, *65*(9), 2241–2247.

Laurila, A., & Aho, T. (1997). Do female common frogs choose their breeding habitat to avoid predation on tadpoles? *Oikos*, *78*(3), 585–591.

Lind, A. J., Welsh, H.H.J., & Wilson, R.A. (1996). The effects of a dam on breeding habitat and egg survival of the Foothills Yellow-legged frog (*Rana boylii*) in Northwestern California. *Herpetological Review*, *1996*(27), 62-67.

Lindén, A., & Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, *92*(7), 1414–1421.

Lindström, T. (1973). Life in a lake reservoir: Fewer options, decreased production. *Ambio*, *2*(5), 145-153.

Loman, J. (2002). Microevolution and maternal effects on tadpole *Rana temporaria* growth and development rate. *Journal of Zoology*, *257*, 93–99.

Marian, M. P., & Pandian, T. J. (1985). Effect of temperature on development, growth and bioenergetics of the bullfrog tadpole *Rana tigrina*. *Journal of Thermal Biology*, *10*(3), 157–161.

Martin-Smith, K. M. (2011). Photo-identification of individual weedy seadragons *Phyllopteryx taeniolatus* and its application in estimating population dynamics. *Journal of Fish Biology*, *78*(6), 1757–1768.

Matthews, K. R., Knapp, R.A., & Pope, K. L. (2002). Garter snake distributions in high-elevation aquatic ecosystems: Is there a link with declining amphibian populations and nonnative trout introductions? *Journal of Herpetology*, *36*(1), 16-22.

Matthews, K. R., & Preisler, H. K. (2010). Site fidelity of the declining amphibian *Rana sierra* (Sierra Nevada yellow-legged frog). *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(2), 243–255.

Matsuda, B. M., Green, D. M., & Gregory, P.T. (2006). Amphibians and reptiles of British Columbia. Royal BC Museum, Victoria, BC. 288 pp.

Maxell, B.A., Werner, J.K., Hendricks, P., and Flath, D.L. (2003). Herpetology in Montana; a history, status summary, checklists, dichotomous keys, accounts for native, potentially native, and exotic species, and indexed bibliography. *Northwest Fauna,* 5, 1-138.

Mazerolle, M. J. (2001). Amphibian activity, movement patterns, and body size in fragmented peat bogs. *Journal of Herpetology*, *35*(1), 13–20.

Mazerolle, M. J. (2006). Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia*, *27*(2), 169–180.

McAfee, M.E. (1980).Effects of water drawdown on the fauna in small cold water reservoirs. *Water Resources Bulletin, 16*(4), 690-696.

McCaffery, R. M., & Maxell, B. A. (2010). Decreased winter severity increases viability of a montane frog population. *Proceedings of the National Academy of Sciences*, *107*(19), 8644.

McCollum, S., & Leimberger, J. (1997). Predator-induced morphological changes in an amphibian: Predation by dragonflies affects tadpole shape and color. *Oecologia*, *109*(4), 615–621.

McEwen, D. C., & Butler, M. G. (2010). The effects of water-level manipulation on the benthic invertebrates of a managed reservoir. *Freshwater Biology*, *55*(5), 1086–1101.

McGee, M., & Keinath, D. (2004). Species assessment for boreal toad (*Bufo boreas boreas*) in Wyoming. Unpublished report. Prepared for United States Department of the Interior, Bureau of Land Management, Wyoming State Office, Cheyenne, Wyoming. 86 pp.

Moldowan, P.D. & Tattersall, G.J. (2011). Use of non-invasive sport recognition software in a mark-recapture study of spotted salamanders (*Ambystoma maculatum*). Poster session presented at the joint 21st Annual Meeting of the Canadian Amphibian and Reptile Conservation Network and 25th Annual Meeting of the Canadian Association of Herpetologists, Thunder Bay, Ontario.

Monello, R. J., & Wright, R. G. (1999). Amphibian habitat preferences among artificial ponds in the Palouse region of northern Idaho. *Journal of Herpetology*, *33*(2), 298–303.

Morey, S. R., & Reznick, D. N. (2004). The relationship between habitat permanence and larval development in California spadefoot toads: field and laboratory comparisons of developmental plasticity. *Oikos*, *104*(1), 172–190.

Morin, P. J., Lawler, S.P., & Johnson, E. A. (1988). Competition between aquatic insects and vertebrates: Interaction strength and higher order interactions. *Ecology*, *69*(5), 1401–1409.

Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, *13*(10), 403–407.

Naiman, R. J., Decamps, H., & Pollock, M. (1993). The role of riparian corridors in maintaining regional biodiversity. *Ecological applications*, *3*(2), 209–212.

Newman, R. A. (1989). Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. *Ecology*, *70*(6), 1775–1787.

Newman, R. A. (1992). Adaptive plasticity in amphibian metamorphosis. *BioScience*, *42*(9), 671–678.

Nilsson, C., Ekblad, A., Gardfjell, M., & Carlberg, B. (1991). Long-term effects of river regulation on river margin vegetation. *Journal of Applied Ecology*, *28*(3), 963–987.

Nilsson, C., & Berggren, K. (2000). Alterations of riparian ecosystems caused by river regulation. *BioScience*, *50*(9), 783–792.

Nussbaum, R.A., Brodie, E.D., & Storm, R.M. (1983). Amphibians and reptiles of the Pacific Northwest. University Press of Idaho, Moscow, ID. 332 pp.

Palen, W. J., Williamson, C. E., Clauser, A. A., & Schindler, D. E. (2005). Impact of UV-B exposure on amphibian embryos: Linking species physiology and oviposition behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1569), 1227–1234.

Patla, D.A. & Keinath, D. (2005). Columbia Spotted Frog (*Rana luteiventris* formerly *R. pretiosa*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/columbiaspottedfrog.pdf

Paton, P. W., & Crouch III, W. B. (2002). Using the phenology of pond-breeding amphibians to develop conservation strategies. *Conservation Biology*, *16*(1), 194–204.

Peacor, S. D., & Werner, E. E. (1997). Trait-mediated indirect interactions in a simple aquatic food web. *Ecology*, *78*(4), 1146-1156.

Pearl, C. A., Adams, M. J., & Wente, W. H. (2007). Characteristics of Columbia Spotted Frog (*Rana luteiventris*) oviposition sites in northeastern Oregon, USA. *Western North American Naturalist*, *67*(1), 86–91.

Peterson, C. C., Walton, B. M., & Bennett, A. F. (1998). Intrapopulation variation in ecological energetics of the garter snake *Thamnophis sirtalis*, with analysis of the precision of doubly labeled water measurements. *Physiological and Biochemical Zoology*, *71*(4), 333–349.

Petranka, J. W., Hopey, M. E., Jennings, B.T., Baird, S.D., & Boone, S. J. (1994). Breeding habitat segregation of Wood Frogs and American Toads: The role of interspecific tadpole predation and adult choice. *Copeia*, *1994*(3), 691–697.

Pierce, B. A. (1985). Acid tolerance in amphibians. *BioScience*, *35*(4), 239–243.

Piper, W. (2011). Making habitat selection more ‘familiar’: A review. *Behavioral Ecology and Sociobiology*, *65*(7), 1329–1351.

Pope, K.L & Matthews, K.R. (2002). Influence of anuran prey on the condition and distribution of *Rana muscosa* in the Sierra Nevada. *Herpetologica*, 58(3), 354-363.

Pounds, J.A. (2001). Climate and amphibian declines. *Nature*, (410) 639–640.

Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., Marca, E. L., et al. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, *439*(7073), 161–167.

Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, *22*(3), 521–533.

Räsänen, K., Laurila, A., & Merilä, J. (2005). Maternal investment in egg size: environment- and population-specific effects on offspring performance. *Oecologia*, *142*(4), 546–553.

Reading, C.J. (2007). Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia*, 151(1), 125-131.

Reading, C. J., & Clarke, R. T. (1995). The Effects of density, rainfall and environmental temperature on body condition and fecundity in the Common Toad, *Bufo bufo*. *Oecologia*, *102*(4), 453–459.

Refsnider, J. M., & Janzen, F. J. (2010). Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-Site choice. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 39-57.

Resetarits, W.J. (1996). Oviposition site choice and life history evolution. *American Zoologist*, *36*, 205–215.

Resetarits, W. J., & Wilbur, H. M. (1989). Choice of Oviposition Site by *Hyla chrysoscelis*: Role of predators and competitors. *Ecology*, *70*(1), 220-228.

Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, *45*(1), 218–227.

Rossman, D. A., Ford, N.B., & Seigel, R.A. (1996). The garter snakes: evolution and ecology. University of Oklahoma Press, Norman.

Rouse, J. D., Bishop, C. A., & Struger, J. (1999). Nitrogen pollution: An assessment of its threat to amphibian survival. *Environmental Health Perspectives*, *107*(10), 799-803.

Sacchi, R., Scali, S., Pellitteri-Rosa, D., Pupin, F., Gentilli, A., Tettamanti, S., Cavigioli, L., et al. (2010). Photographic identification in reptiles: a matter of scales. *Amphibia-Reptilia*, *31*(4), 489–502.

Sanzo, D., & Hecnar, S. J. (2006). Effects of road de-icing salt (NaCl) on larval wood frogs (*Rana sylvatica*). *Environmental Pollution*, *140*(2), 247-256.

Schalk, G., Forbes, M. R., & Weatherhead, P. J. (2002). Developmental plasticity and growth rates of green frog (*Rana clamitans*) embryos and tadpoles in relation to a leech (*Macrobdella decora*) predator. *Copeia*, *2002*(2), 445-449.

Schlichter, L. C. (1981). Low pH affects the fertilization and development of *Rana pipiens* eggs. *Canadian Journal of Zoology*, *59*(9), 1693–1699.

Seale, D. B. (1982). Physical factors influencing oviposition by the woodfrog, *Rana sylvatica*, in Pennsylvania. *Copeia*, 627–635.

Seigel, R. A., Huggins, M. M., & Ford, N. B. (1987). Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia*, *73*(4), 481–485.

Semlitsch, R. D., & Caldwell, J. P. (1982). Effects of density of growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. *Ecology*, *63*(4), 905–911.

Semlitsch, R. D. (2008). Differentiating migration and dispersal processes for pond-breeding amphibians. *The Journal of Wildlife Management*, *72*(1), 260–267.

Sewell, W. R. D. (1966). The Columbia River Treaty: Some lessons and implications. *Canadian Geographer*, *10*(3), 145–156.

Shine, R. (1990). Proximate determinants of sexual differences in adult body size. *The American Naturalist*, *135*(2), 278–283.

Sjögren, P., Elmberg, J., & Berglind, S.-Å. (1988). Thermal preference in the pool frog *Rana lessonae*: Impact on the reproductive behaviour of a northern fringe population. *Holarctic Ecology*, *11*(3), 178–184.

Slough, B. G., & Mennell R.L. (2006). Diversity and range of amphibians of the Yukon Territory. *Canadian Field-Naturalist*, *120*(1): 87-92.

Smith, D. C. (1987). Adult recruitment in chorus frogs: Effects of size and date at metamorphosis. *Ecology*, *68*(2), 344–350.

Smith, D., & Peterson, R. (1991). Behavior of beaver in lakes with varying water levels in northern Minnesota. *Environmental Management*, *15*(3), 395–401.

Smith-Gill, S. J., & Berven, K. A. (1979). Predicting amphibian metamorphosis. *The American Naturalist*, *113*(4), 563–585.

Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H., & Bradshaw, C.J.A. (2008). Measuring the meltdown: Drivers of global amphibian extinction and decline. *PLoS ONE*, 3(2), 1-8.

Stanford, K. M., & King, R. B. (2004). Growth, survival, and reproduction in a northern Illinois Population of the Plains Gartersnake, *Thamnophis radix*. *Copeia*, *2004*(3), 465–478.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L., et al. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, *306*(5702), 1783-1786.

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, *7*(6), 533–555.

Sztatecsny, M., & Schabetsberger, R. (2005). Into thin air: vertical migration, body condition, and quality of terrestrial habitats of alpine common toads, Bufo bufo. *Canadian Journal of Zoology*, *83*(6), 788–796.

Tabacchi, E., Planty-Tabacchi, A.M., & Decamps, O. (1990). Continuity and discontinuity of the riparian vegetation along a fluvial corridor. *Landscape Ecology*, 5, 9-20.

Tabacchi, E., Correll, D. L., Hauer, R., Pinay, G., Planty-Tabacchi, A.M., & Wissmar, R. C. (1998), Development, maintenance and role of riparian vegetation in the river landscape. *Freshwater Biology*, *40*, 497–516.

Taylor, C.A, Knouft, J.H., & Hiland, T.M. (2001). Consequences of stream impoundment on fish assemblages in a small North American drainage. *Regulated Rivers: Research & Management*, *17*, 687–698.

Tomašević, N., Cvetković, D., Aleksić, I., & Crnobrnja-Isailović, J. (2007). Effect of climatic conditions on post-hibernation body condition and reproductive traits of Bufo bufo females. *Archives of Biological Sciences*, *59*(3), 51–52.

Tuttle, K.N. & Gregory, P.T. (in press). Growth and maturity of a terrestrial ectotherm near its northern distributional limit: Does latitude matter? *Canadian Journal of Zoology.*

Tuttle, K. N., & Gregory, P. T. (2009). Food habits of the Plains Garter Snake (*Thamnophis radix*) at the northern limit of its range. *Journal of Herpetology*, *43*(1), 65-73.

Van Buskirk, J. (2005). Local and landscape influence on amphibian occurrence and abundance. *Ecology*, *86*(7), 1936–1947.

Van Tienhoven, A. M., Den Hartog, J. E., Reijns, R. A., & Peddemors, V. M. (2007). A computer-aided program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. *Journal of Applied Ecology*, *44*(2), 273–280.

Verduin, J. (1951). Photosynthesis in naturally reared aquatic communities. *Plant Physiology*, *26*(1), 45–49.

Vitousek, P. (1994). Beyond global warming – ecology and global change. *Ecology*, *75*(7), 1861–1876.

Wang, Y., Wu, Z., Lu, P., Zhang, F., & Li, Y. (2008). Breeding ecology and oviposition site selection of black-spotted pond frogs (*Rana nigromaculata*) in Ningbo, China. *Frontiers of Biology in China*, *3*(4), 530–535.

Wassersug, R. J., & Sperry, D. G. (1977). The Relationships of locomotion to differential predation on *Pseudacris Triseriata* (Anura: Hylidae). *Ecology*, *58*(4), 830–839.

Webb, J. K., Brook, B. W., & Shine, R. (2003). Does foraging mode influence life history traits? A comparative study of growth, maturation and survival of two species of sympatric snakes from south-eastern Australia. *Austral Ecology*, *28*(6), 601–610.

Welch, N. E., & MacMahon, J. A. (2005). Identifying habitat variables important to the rare Columbia Spotted Frog in Utah (USA): An information-theoretic approach. *Conservation Biology*, *19*(2), 473–481.

Wells, K. D. (1977). Territoriality and male mating success in the Green Frog (*Rana clamitans*). *Ecology*, *58*(4), 750–762.

White, G. C., & Bennetts, R. E. (1996). Analysis of frequency count data using the negative binomial distribution. *Ecology*, *77*(8), 2549–2557.

Whittier, J. M., & Crews, D. (1990). Body mass and reproduction in female Red-Sided Garter Snakes (*Thamnophis sirtalis parietalis*). *Herpetologica*, *46*(2), 219–226.

Wilbur, H. M., & Collins, J. P. (1973). Ecological aspects of amphibian metamorphosis: Nonnormal distributions of competitive ability reflect selection for facultative metamorphosis. *Science*, *182*(4119), 1305–1314.

World Energy Council. (2007). Survey of energy resources, 2007. London, UK. 593 pp. + Appendices.

Wurts, W.A. (2003). Pond pH and ammonia toxicity. *World Aquaculture, 34*(2), 20-21.

Yoder, J. M., Marschall, E. A., & Swanson, D. A. (2004). The cost of dispersal: Predation as a function of movement and site familiarity in Ruffed Grouse. *Behavioral Ecology*, *15*(3), 469–476.