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BREEDING PHENOLOGY AND HABITAT USE OF AMPHIBIANS IN THE DRAWDOWN ZONE OF A HYDROELECTRIC RESERVOIR

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***Abstract.*—Hydropower is the largest source of renewable energy in the world, yet relatively little is known about how dams and their operations influence terrestrial and semi-aquatic wildlife. We evaluated the impact of annual reservoir inundation on breeding Columbia Spotted Frogs (*Rana luteiventris*) and Western Toads (*Anaxyrus boreas*) in the drawdown zone of Kinbasket Reservoir in British Columbia, Canada. During spring and summer of 2010 and 2011, we conducted visual encounter surveys at 40 ponds in the drawdown zone to document the reproductive phenology of these species relative to the timing of reservoir inundation. We used a negative binomial regression to identify characteristics associated with *R. luteiventris* breeding activity (measured by number of egg masses located) in ponds in the drawdown zone. Pond elevation, mean temperature, mean pH, and presence of fish were all positively correlated with the number of *R. luteiventris* egg masses in a pond. These results point to a preference for breeding ponds that promote rapid larval development and/or those that are least frequently inundated by the reservoir. We emphasize that proposed hydroelectric developments and changes to existing reservoir operation regimes should recognize the importance of amphibian breeding habitat in drawdown zones.**

Key Words.—Anaxyrus boreas; breeding phenology; Columbia Spotted Frog; drawdown zones; habitat use; hydroelectric dam; *Rana luteiventris*; Western Toad

INTRODUCTION

Growing human populations and developing economies demand an increase in energy production, but our 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 turn to the production of renewable energy, such as hydroelectricity. Hydropower currently accounts for 15% of the electricity produced worldwide (World Energy Council 2013). At high latitudes, hydroelectric reservoirs 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; thus, the lowest water levels occur in the winter. Areas of hydroelectric reservoirs subject to frequent inundation and desiccation are commonly referred to as drawdown zones. Depending on the size of the reservoir, drawdown zones may encroach upon or completely encompass pre-existing riparian and terrestrial areas that are critical to the conservation of semiaquatic species such as many amphibians and reptiles (Semlitsch and Bodie 2003).

Increasing attention has been given to the plight of amphibians worldwide (e.g., Kiesecker 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 construction 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. More recently, Eskew et al. (2012) reported that reduced occupancy and abundance of several anuran species in South Carolina likely resulted from alterations in flow regimes associated with dams. However, the long-term effects of reservoir operations on amphibians remain unclear, particularly for populations persisting upstream of a dam.

One of the largest hydroelectric reservoirs in Canada, Kinbasket Reservoir, was formed in 1973 by the creation of the Mica Dam, the northernmost dam on the Columbia River. At 216 km long and with a licensed storage volume of 14.8 km^3 (12 million acre feet; BC Hydro. 2007), the reservoir has a maximum operating range of 707–754 m above sea level (ASL) with an annual average draught of 25.61 m (max: 39.03; min: 13.18; Virgil Hawkes and Krysia Tuttle, unpubl. report), which leaves a considerable mark on the landscape. Despite the large fluctuations in water level that accompany the operation of Kinbasket Reservoir, Columbia Spotted Frogs (*Rana luteiventris*), Western Toads (*Anaxyrus boreas*), and Long-toed Salamanders (*Ambystoma macrodactylum*) are known to breed in select areas of its drawdown zone (Virgil Hawkes and Krysia Tuttle unpubl. report).

These amphibians, like many others, do not provide parental care to their offspring. Hence, there is substantial selective pressure for breeding females to choose high-quality oviposition sites for their offspring (Resetarits and Wilbur 1989; Hopey and Petranka 1994). Previous research has identified a variety of biotic and abiotic factors that are important to amphibian breeding success, including water depth (Crump 1991; Pearl et al. 2007), water 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).

Breeding ponds in the drawdown zones of reservoirs are subject to unnatural fluctuations in water level, such that environmental conditions at an oviposition location may change considerably by the time eggs hatch or as tadpoles develop. At Kinbasket Reservoir, an oviposition site that is warm, calm, and predator-free in early May, could be inundated any time between June and August. Therefore, the environmental cues that influence female oviposition-site choices in the drawdown zone may not reflect the conditions experienced by their offspring. The characteristics associated with preferred breeding sites in a relatively undisturbed habitat may be absent or greatly modified in the drawdown zone of a hydroelectric reservoir. Our objectives were to describe the breeding phenology of Columbia Spotted Frogs and Western Toads in the drawdown zone of Kinbasket Reservoir, and identify factors that influence breeding pond use by Columbia Spotted Frogs in the drawdown zone. We predicted that amphibian embryos or tadpoles would be at risk of inundation by the reservoir each summer, and that most frogs would breed in ponds that promote rapid larval development (e.g., warmer ponds). We also hypothesized that breeding frogs would use ponds at a high elevation in the drawdown zone, because they are inundated later and for shorter periods of time than those at lower elevations (thus providing more time for metamorphosis before disturbance by the reservoir). Understanding how resident amphibians may persist under the disturbance regime of a hydroelectric reservoir is necessary to inform the operation of existing reservoirs and the development of future hydroelectric reservoirs.

MATERIALS AND METHODS

We conducted our research at the Valemount Peatland (hereafter the Peatland), a 550 ha wetland located in the northern reach of Kinbasket Reservoir (52°45’3”N; 119°9’6”W), British Columbia, Canada. The Peatland is a remnant of a large fen and is characterized by a series of ponds, springs, and marsh-like areas. It is located in the upper elevation of the drawdown zone (740−755 m ASL), and is typically not completely inundated by the reservoir until August. Most ponds are situated between 750 and 753 m ASL, and this area is usually available (i.e., not inundated) until mid- to late-September, but can be inundated as early as the middle of July. Only the lower elevations of the Peatland are regularly inundated; thus, the complexity of vegetation generally increases with elevation (Virgil Hawkes et al. unpubl. report). From late April to late August of 2010 and 2011, we conducted visual encounter surveys along the shorelines of all water bodies in the Peatland, in search of amphibian eggs or larvae.

The number of ponds in the Peatland varies by year, depending on precipitation levels, but ponds are typically smaller than 1,000 m^2 in area (ranging about 22−8,337 m^2). We surveyed each pond in the Peatland approximately once every 10 d in 2010 and once a week in 2011. In addition to conducting shoreline surveys, we also used a YSI Model 85 multi-parameter probe (YSI Incorporated, Yellow Springs, Ohio, USA) to record pH, temperature (° C), oxygen content (mg/L), and electrical conductivity (µS/cm) at various times of day (but at consistent locations in each pond). We received pond elevations and estimates of amphibian habitat availability in 2010 and 2011 from LGL Limited environmental resource associates (Sidney, British Columbia, Canada). We received annual reservoir elevations from BC Hydro (Vancouver, British Columbia, Canada). We noted any fish observations, but few were captured or identified to species. Juveniles of one species, Redside Shiners (*Richardsonius balteatus*), were present and abundant in many ponds sampled. We obtained precipitation records from the National Climate Data and Information Archive of Environment Canada (Environment Canada 2012).

We marked the location of each egg mass/string we observed using a hand-held Global Positioning System (GPSMap 60csx, Garmin International, Olathe, Kansas, USA) and kept careful records of egg mass counts/approximate ages and hatch dates. It was difficult to distinguish a single Western Toad egg string among several strings laid in one location; therefore, we estimated some numbers by visual inspection. We acknowledge this estimation introduces some subjectivity to our analyses. However, we wanted to avoid disturbing thousands of toad eggs to get a precise count and considered the level of potential error to be

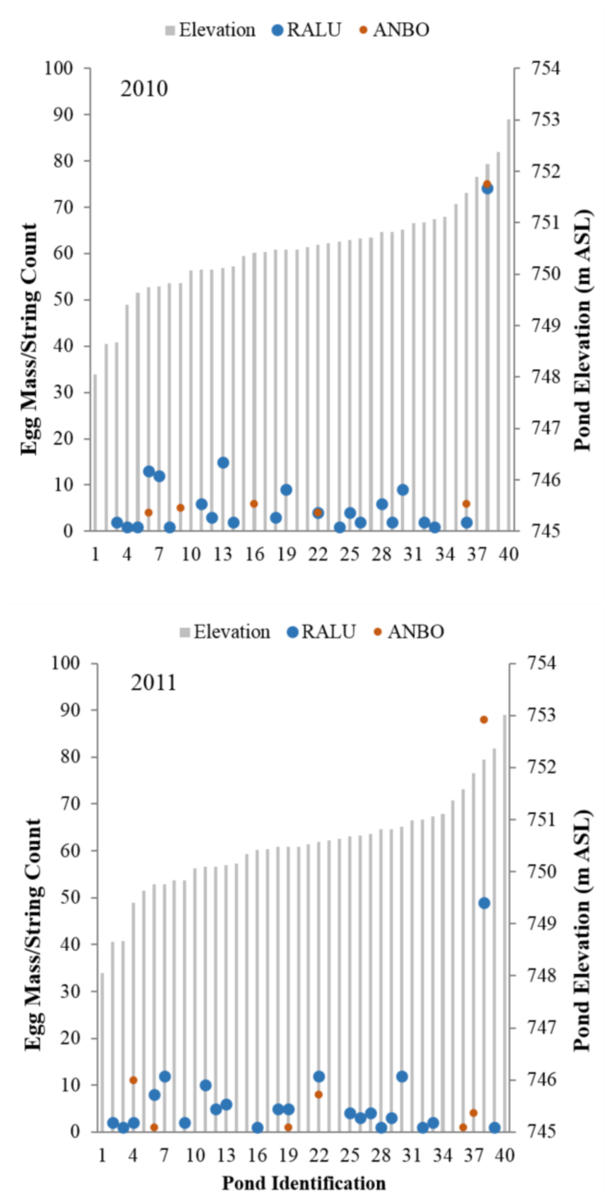

FIGURE 1. Counts of egg masses/egg strings of Columbia Spotted Frogs (RALU = *Rana luteiventris*) and Western Toads (ANBO = *Anaxyrus boreas*) detected in ponds (n = 40) in the Valemount Peatland, Kinbasket Reservoir, British Columbia, Canada, in 2010 and 2011. Grey bars depict the elevation (m ASL) of each pond in Peatland. All ponds fall within the drawdown zone of the reservoir. Ponds that desiccated completely in early spring of either year (n = 4) could not be included in analyses and therefore are not shown here.

acceptable for our purposes. We also considered our detection probability for frog and toad egg strings/masses to be high, given that we conducted repeated shoreline surveys (every 7–10 d) with two observers. We used Gosner's (1960) table to stage anuran embryos and larvae. Although we could not distinguish individual tadpoles observed over time, Gosner stages provided a general indication of the development rate of amphibians in the drawdown zone. We used GPS tracking to map the shorelines of each pond and calculate pond areas in ArcGIS 9.2 (Esri Inc., Redlands, California, USA).

***Statistical analyses.*—**We performed a negative binomial regression analysis in R (R Core Team 2012) to test the influence of seven potential correlates on the abundance of egg masses of Columbia Spotted Frogs in a pond: temperature, pH, conductivity, pond area, pond elevation, presence of fish, and abundance of Western Toad egg strings. Each pond in the drawdown zone was treated as one datum (n = 40 ponds); we therefore limited the number of variables included in these analyses to prevent overfitting the model (Babyak 2004). Due to significant correlation between inter-annual measurements of the predictor variables (see Results), we excluded survey year as a potential correlate, and chose to average the physicochemical variables across both years and to pool anuran egg mass/string counts. 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). We chose to use pH as a proxy for dissolved oxygen content (and not vice-versa) because measurements of pH were more precise than those for dissolved oxygen content, which fluctuated continuously during measurement. We surveyed all ponds in the Peatland but excluded those that dried out early in the field season from our analyses due to a lack of water physicochemistry data and some uncertainty about the number of egg masses/strings present prior to desiccation (n = 4 ponds omitted).

We used Moran's autocorrelation coefficient (Moran's *I*) to test the possibility that proximity of breeding ponds (to one another) is the most important factor in breeding pond use by Columbia Spotted Frogs. To evaluate the explanatory power of all candidate models, we used AICc (Akaike's Information Criterion corrected) values and generated Akaike weights (*w*) to assess the weight of evidence in favor of each model relative to the others being considered (Burnham and Anderson 2010). A significance level of $\alpha = 0.05$ was used for all hypothesis tests. We used R packages 'ape' (Version 3.3) to calculate Moran's *I* (Paradis et al. 2004), 'MASS' (Version 7.3-44) to run generalized linear models (Venables and Ripley 2002), and 'AICcmodavg' (Version 2.0-3) to calculate AICc values (Mazerolle 2015).

RESULTS

The majority of ponds in the Valemount Peatland were located between 750 and 753 m ASL, inclusive (Fig. 1). The reservoir flooded these ponds in both years, but did

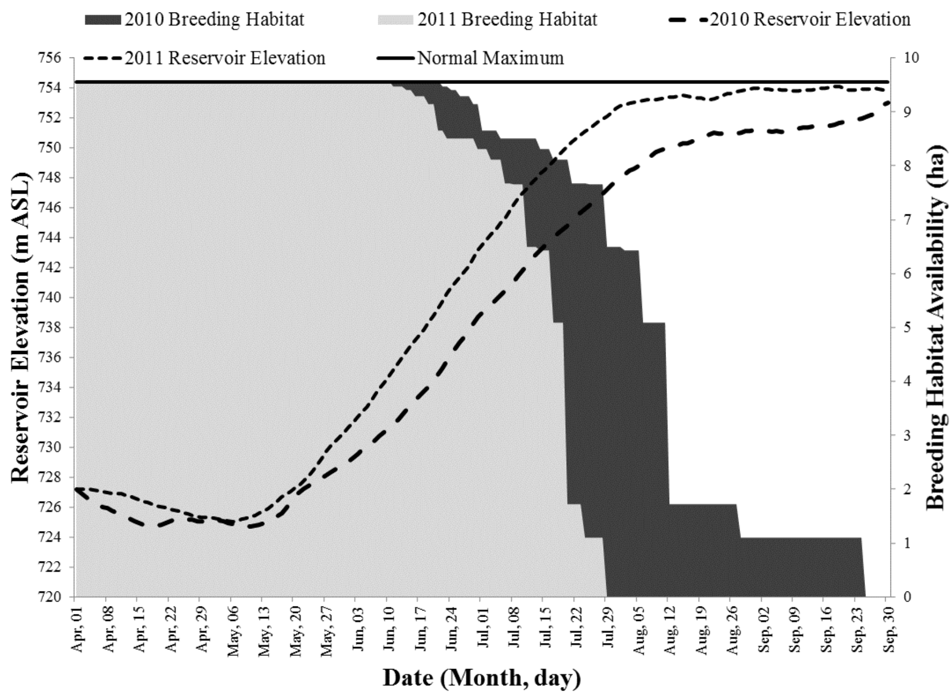

FIGURE 2. Area of amphibian breeding habitat (hectares) available in Kinbasket Reservoir, British Columbia, Canada, in 2010 (dark grey area) and 2011 (light grey) from 1 April to 30 September of each year. The rate of reservoir inundation (reservoir elevation over time) in 2010 and 2011 is depicted by the slope of the dashed lines. The Valemount Peatland is located at high elevation in the drawdown zone of Kinbasket Reservoir (747–754 m ASL).

so at very different rates in 2010 and 2011 (Fig. 2). In 2010 the water levels in Kinbasket Reservoir were close to average and increased slowly relative to the following year (Fig. 2). In 2011 the reservoir was flooded more rapidly due to a deep snowpack and higher levels of rainfall (Fig. 3). Thus, amphibian habitat in the drawdown zone was available for a shorter period than usual in 2011 (Fig. 2).

In 2010, Columbia Spotted Frogs used 24 ponds in the Peatland for breeding, whereas Western Toads bred in just six. One large, spring-fed pond had a very high number of egg strings/masses of both species relative to all other ponds (Pond #38; Fig. 1). This pond was not inundated every year due to its relatively high elevation (752 m ASL) in the drawdown zone.

In 2010, at least 19 egg masses of Columbia Spotted Frogs and six egg strings of Western Toads failed due to desiccation. This year was also characterized by little rain and a light snowpack (Fig. 3). Four breeding ponds dried up completely and the water in many other ponds decreased substantially over the course of the summer. We observed the first Columbia Spotted Frog and Western Toad metamorphs 22 July 2010. On this date the reservoir water level was at about 745 m ASL. This was still quite far from reaching the lowest breeding pond at 748.5 m ASL.

In 2011, Columbia Spotted Frogs used 25 ponds for breeding. Western Toads used nine ponds and one ephemeral water body (not among the 40 ponds analysed) for breeding. Amphibian breeding activity commenced an estimated two weeks later than in the previous year; however, the first observations of metamorphs closely coincided with those in 2010. We made the first observation of Columbia Spotted Frog metamorphs 26 July, while we observed the first Western Toad metamorph 14 July 2011. However, the water level of the reservoir was substantially higher in July 2011 than July of the previous year. While many tadpoles were still developing in their natal ponds, the reservoir had reached 750 m ASL and was beginning to inundate many of the ponds at this elevation (Fig. 1). Once the reservoir breached a pond, the shoreline could no longer be surveyed and the fate of resident tadpoles was indeterminable. The last observed Gosner stages for tadpoles (in all ponds), within one week of inundation, ranged from 32 to 43 for Western Toads and from 37 to 41 for Columbia Spotted Frogs (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). All ponds were inundated by 1 August 2011.

We measured physicochemical characteristics (pH, temperature, conductivity, and dissolved oxygen) for 40 ponds in both years (Table 1). Although these variables fluctuate over time, their mean values (for each pond) in

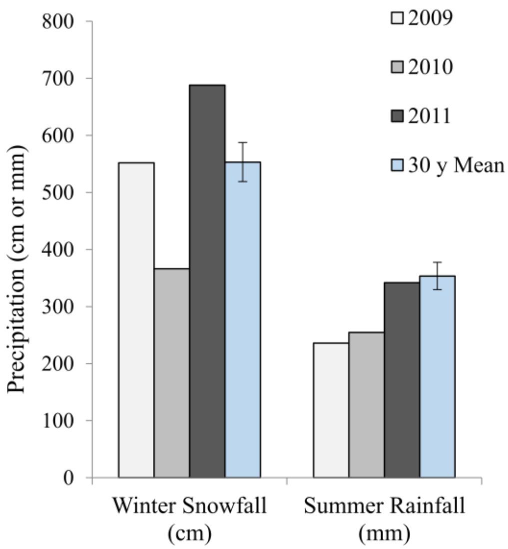

FIGURE 3. Total precipitation recorded at the Mica Dam in 2009, 2010, and 2011. The 30-y mean (1971–2000) is included for comparative purposes. Winter Snowfall was recorded in centimeters from 1 September of the previous year to 31 March of the plotted year. Summer Rainfall was recorded in millimeters from 1 April to 31 August 31 of the plotted year. Bars represent the standard error of the mean. Data were obtained from the National Climate Data and Information Archive of Environment Canada.

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: $r = 0.589$, $P < 0.001$; n = 40 for all). In other words, a pond with a low mean temperature in 2010 tended to have a low mean temperature in the following year, relative to other ponds. Fish were observed in 14 of 40 ponds in the Peatland. We found no evidence of spatial autocorrelation in our egg mass counts (Moran's I: $P = 0.08$). The negative binomial regression model that best fit the data indicated that the number of Columbia Spotted Frog egg masses in a pond increases with temperature, pH, elevation, and the presence of fish (Akaike weight = 0.64; Table 2).

DISCUSSION

In the Valemount Peatland, two seemingly opposing environmental stressors (desiccation and inundation) may have pressured breeding amphibians into choosing oviposition locations that maximized the developmental rate of their offspring. A dry spring and/or summer may have reduced the threat of early inundation, but consequently increased the likelihood of pond desiccation. On the other hand, a wet spring and summer, which might otherwise be ideal for amphibian breeding success, could have signaled early flooding in a reservoir drawdown zone.

Contrary to our predictions, the eggs and tadpoles of amphibians in the Peatland were not at risk of reservoir inundation every summer. Given the long-term persistence of anurans in the Peatland, it may not be 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 narrow, particularly in years with high levels of precipitation. In 2011 higher than average 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, we assume 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 in 2010 than was inundation by the reservoir. The possibility that reservoir inundation could keep some tadpoles from death by desiccation is likely slim, given that pond desiccation risk is presumably greatest in dry years (i.e., years with lower than average snowpack and/or rainfall). In these years reservoir water levels would also be lower than average, and inundation of the Peatland would occur later in the summer zone, with some areas/ponds not being inundated at all in that year.

Our prediction that breeding frogs would use warmer ponds more frequently was supported by our regression

TABLE 1. Physicochemical characteristics of 40 ponds in the drawdown zone of Kinbasket Reservoir, Valemount, British Columbia, Canada. Egg masses of Columbia Spotted Frogs (*Rana luteiventris*) were detected in 23 ponds in both 2010 and 2011, although the ponds with breeding activity differed between years. Values reflect Mean ± Standard Deviation (Range).

Egg Masses	Year	Temperature (°C)	Dissolved Oxygen (mg/L)	pH	Conductivity (µS/cm)
Present	2010	18.0 ± 2.6 (12.5−21.0)	4.1 ± 1.1 (1.8−5.7)	7.2 ± 0.4 (6.7−7.9)	90.2 ± 30.6 (44.3−192.6)
	2011	19.6 ± 2.8 (13.6−22.6)	4.0 ± 1.1 (1.4−5.7)	6.9 ± 0.3 (6.4−7.7)	87.6 ± 28.2 (43.3−128.1)
Absent	2010	16.4 ± 2.8 (9.7−21.3)	2.8 ± 1.2 (0.7−4.5)	6.9 ± 0.4 (6.5−7.5)	86.7 ± 31.0 (36.4−131.9)
	2011	16.7 ± 2.8 (10.8−22.5)	3.3 ± 1.1 (0.6−5.1)	6.8 ± 0.3 (6.4−7.5)	86.6 ± 28.2 (31.9−147.6)

TABLE 2. Candidate negative binomial regression models predicting counts per pond of egg masses of Columbia Spotted Frogs (*Rana luteiventris*) in the Valemount Peatland, British Columbia, Canada. Data from 2010 and 2011 were pooled. Abbreviations: Temp = Temperature (°C); ToadEggs = Number of Western Toad (*Anaxyrus boreas*) egg strings; Fish = Presence of fish; Cond = Electrical Conductivity (µS/cm); Elev = Elevation (m).

MODEL	Parameters	AIC	AICc	ΔAICc	AICw
pH + Temp + Fish + Elev	4	210.21	214.75	0	0.64
pH + Temp + ToadEggs + Fish + Elev	5	210.86	216.36	1.6	0.28
pH + Temp + ToadEggs + Fish + Area +Elev	6	212.62	219.27	4.52	0.07
pH + Temp + ToadEggs + Fish + Cond + Area + Elev	7	214.57	222.57	7.82	0.001

Best Fit Equation: log (FrogEggs) = -855.9 + 1.54 (pH) + 0.34 (Temp) + 2.37 (Fish) + 1.12 (Elev)

Null deviance: 165.3 Residual deviance: 78.54 Degrees of Freedom: 79 (Total), 74 (Residual)

model, which showed that the abundance of Columbia Spotted Frog egg masses in a pond was positively correlated with mean temperature, mean pond pH, elevation, 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). Several species of frogs preferentially oviposit in warm locations (e.g., Seale 1982; Sjögren et al. 1988) to capitalize on this relationship.

As expected, ponds at higher elevation in the Peatland tend to contain greater numbers of egg masses of Columbia Spotted Frogs. These ponds are the last to be inundated by the reservoir every summer (if at all) and also the first to be exposed as water levels decrease in the winter. Relatively low frequency and duration of reservoir disturbance likely increase the appeal of ponds at high elevation to breeding Columbia Spotted Frogs.

The influence of pond pH on abundance of egg masses of Columbia Spotted Frogs 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). Thus, it seems unlikely that breeding Columbia Spotted Frogs are either 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. 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 were likely at their highest and carbon dioxide concentrations were at their lowest (i.e., pH is at its highest). The increasing abundance of Columbia Spotted Frog egg masses in ponds with a higher pH may in fact be the result of a preference for ponds with slightly more oxygen or aquatic vegetation.

Aquatic vegetation cover is a potentially important explanatory factor that we did not quantify for this study. Aquatic vegetation in amphibian breeding ponds can provide shelter from predators (Babbitt and Tanner 1998; Baber and Babbitt 2004; Kopp et al. 2006), protection from UV-B radiation (Palen et al. 2005), and material for attachment of egg masses (Egan and Paton 2004). A positive relationship between density of vegetative cover and use of oviposition sites 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). We 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). Future research in the drawdown zone of Kinbasket could use aerial photos to estimate the vegetative cover for each pond.

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 ranids and bufonids did not follow this trend. Brown et al. (2012) 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 egg masses in randomly selected ponds. These qualities are consistent with those of permanent wetlands, which may explain the positive relationship between presence of fish and abundance of Columbia Spotted Frog egg masses in our best fit model. The co-occurrence of amphibians and predatory fish in breeding ponds may also be influenced by the body and/or clutch size of the focal amphibian species, as well as the availability of refugia for developing tadpoles (Hecnar and M'Closky 1997). Further research, incorporating fish detection probability, is required to elucidate the relationship between Columbia Spotted Frog breeding activity and fish presence in the Peatland.

Whether Columbia Spotted Frogs adjust their oviposition decisions according to inter-year and inter-pond differences is not clear. Our results can only point to pond characteristics that are potentially important to breeding Columbia Spotted Frogs and the survival of their offspring. 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, presence of fish, presence of amphibians, 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 oviposition sites of Columbia Spotted Frogs 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 Frogs 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 ours) must be interpreted in light of the reality that explanatory variables cannot always be accounted for, nor may they be equally relevant in all environments.

***Management implications.*—**To meet the increasing energy demands of British Columbians, two new generating units are being installed at Mica Dam; they became operational in late 2014 and 2015. The addition of these new turbines increases the generating capacity of Kinbasket Reservoir by roughly 1,000 megawatts (BC Hydro, unpubl. report). One of the predicted outcomes associated with the installation of the new turbines is an increase in the elevation of Kinbasket Reservoir by 60 to 70 cm during the summer months (BC Hydro, unpubl. report; Virgil Hawkes and Charlene Wood, unpubl. report). This increase in elevation coupled with seasonal and annual fluctuations in reservoir elevations could have implications for pond-breeding amphibians using the drawdown zone. Recent studies suggest that Columbia Spotted Frog and Western Toad populations will be affected indirectly through changes to and availability of important breeding habitats (Virgil Hawkes and Charlene Wood, unpubl. report). Our research highlights the relationship between the availability of wetland and pond habitats occurring in the drawdown zone of Kinbasket Reservoir and the persistence of pond-breeding amphibian populations. The results of our study further suggest that both Columbia Spotted Frog and Western Toad populations can persist in the drawdown zones of large hydroelectric reservoirs, potentially by selecting for breeding habitats that promote rapid larval development or those that occur at the highest elevation in the drawdown zone and are associated with the shortest inundation periods. The continued availability of these important breeding habitats is required to ensure these species persist. Mitigating for the potential impacts of two new turbines at Mica Dam on pond-breeding amphibians and their habitats may require operational changes to the timing, frequency, and duration of reservoir inundation in the drawdown zone. Recognizing that these proposed changes could result in substantive financial implications to power providers, the construction of physical works (i.e., habitat enhancements) to protect important habitats, in lieu of operational changes, has been suggested (Virgil Hawkes et al., unpubl. report). Regardless of the management action taken, the recognition of the presence of important pond-breeding amphibian habitat in the drawdown zones of large hydroelectric reservoirs is paramount when considering the conservation of sensitive species in managed landscapes.

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