Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada

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ABSTRACT

We explored the use of beaver (*Castor canadensis*) as a surrogate species for amphibian conservation on small (1st–4th-order) streams in the Boreal Foothills of west-central Alberta. Anuran call surveys indicated that beaver create breeding habitat for the boreal chorus frog (*Pseudacris maculata*), wood frog (*Rana sylvatica*) and western toad (*Bufo boreas*). No calling males of any species were recorded on unobstructed streams. Wood frog, the most abundant species, exhibited high rates of juvenile recruitment on beaver ponds. Pit-fall traps captured more wood frogs on beaver ponds versus unobstructed streams, and most individuals (84%) were young-of-year. Abundance of young-of-year was strongly correlated with percent landscape occupied by beaver ponds indicating that anurans captured along streams originated in beaver ponds. Based on a novel combination of a digital elevation model and aerial photographs examined with GIS, statistical models showed that the probability of beaver pond occurrence on streams was positively associated with stream order and dependent on the interacting effects of distance to nearest forestry cutblock and availability of beaver foods (*Populus* spp.). We propose that the distribution and abundance of beaver ponds could be determined over large areas quickly and inexpensively by remote sensing and used to identify and monitor amphibian habitat, and possibly, populations. This work establishes the pre-eminence of beaver-created wetlands as amphibian habitat in the Boreal Foothills and that the incorporation of dam-building patterns into forest management strategies could aid amphibian conservation.

1. Introduction

Amphibian conservation has assumed a degree of urgency since discoveries in the 1980s indicating many species throughout the world were declining (Alford and Richards, 1999; Houlahan et al., 2000; Stuart et al., 2004; Beebee and Griffiths, 2005). Declines have been linked to many factors and the large number of studies concerning threats to amphibians indicates the complexity of causes behind declines (see recent reviews by Collins and Storfer, 2003; Blaustein et al., 2003; Carey and Alexander, 2003). Most specialists agree, however, that local habitat loss, degradation and alteration are major causes of declines (Blaustein et al., 1994; Wake, 1998; Alford and Richards, 1999; Semlitsch, 2002). Protection and restoration of ponds and wetlands are arguably critical steps for conserving pond-breeding amphibians (Pechmann et al., 2001; Stevens et al., 2002; Calhoun et al., 2003); low juvenile recruitment associated with a paucity of ponds or sub-optimal conditions

in remaining ponds on a landscape (i.e., reproductive sinks) can lead to the extirpation of populations (Marsh and Trenham, 2001). For example, Ducks Unlimited has been instrumental in the conservation of amphibians in many parts of North America through its waterfowl habitat programs (Stevens et al., 2002; Tori et al., 2002). Programs specifically designed for conserving amphibians usually include monitoring of population trends and examination of habitat-use patterns. Unfortunately, many amphibian species are cryptic and it is difficult to reliably estimate regional population sizes in the field, particularly in northern climates where breeding periods are brief and highly variable in response to very localized climatic conditions (Alford and Richards, 1999; Paszkowski et al., 2002; Stevens and Paszkowski, 2005). A valuable shortcut for assessing amphibian habitat and probable populations may be the use of surrogate species.

The concept of surrogate species in conservation biology has received growing attention because it offers simple, ecologically-based solutions for the management of communities and ecosystems (Simberloff, 1998; Caro and O'Doherty, 1999; Roberge and Angelstam, 2004). In boreal ecosystems of North American, the beaver (Castor canadensis) is a potential candidate for the conservation and management of anuran amphibians because of its profound influences on the physicochemical properties of streams through dam construction (Naiman et al., 1986, 1988; Snodgrass and Meffe, 1998; Schlosser and Kallemyn, 2000). Dams can exceed 16 per km on small streams in boreal landscapes (Naiman et al., 1988; Hillman, 1998), and in forested regions of the United States, beaver dam construction can influence the distribution and abundance of aquatic vertebrates such as fishes (Snodgrass and Meffe, 1998; Schlosser and Kallemyn, 2000), birds (Brown et al., 1996; McCall et al., 1996), and possibly amphibians. Abiotic and biotic changes to streams such as reductions in flow, higher water temperatures and increased rates of primary production may favour pond-breeding amphibians (Naiman et al., 1986, 1988; Snodgrass and Meffe, 1998). Russell et al. (1998) noted a higher abundance of anuran amphibians at beaver ponds versus unobstructed streams in South Carolina, USA. However, the generality of this trend in other ecoregions and whether beaver dams produce an environment that favours high juvenile recruitment to metamorphosis remains unclear. The beaver, whose presence and influence can be easily monitored through delineation of ponds with aerial photography (Slough and Sadleir, 1977; Howard and Larson, 1985; Johnston and Naiman, 1990), could serve as a surrogate for identifying amphibian habitat and locating populations, and be particularly useful in boreal landscapes and remote regions inaccessible by vehicle. If beaver create breeding sites for amphibians, a review and assessment of factors affecting the distribution of beaver ponds is a required step in developing beaver as a surrogate species.

As a potential contributor to landscape heterogeneity and biodiversity in the boreal forest, the beaver has been the subject of surprisingly few studies that examine where colonies are most abundant and where dams are most likely to be built on streams (but see Slough and Sadleir, 1977; Howard and Larson, 1985; Barnes and Mallik, 1997). Some patterns are evident, however. For example, beaver pond establishment is strongly influenced by stream hydrology and dependent on a reliable water source that can be effectively dammed (Howard and Larson, 1985; Barnes and Mallik, 1997). The structure and composition of vegetation in riparian zones may also influence beaver distributions on streams (Slough and Sadleir, 1977; Howard and Larson, 1985; Barnes and Mallik, 1997) because beaver employs a central-place foraging strategy harvesting trees and shrubs near open water (Schoener, 1979; Jenkins, 1980; McGinley and Whitham, 1985), and are very selective in choosing woody food stems showing strong preference for *Populus* spp. (Johnston and Naiman, 1990; Fryxell and Doucet, 1993; Basey and Jenkins, 1995; Gallant et al., 2004; Martell et al., 2006). Despite the apparent link between riparian zones and beaver, no published study has examined impacts of logging on beaver or the distribution of beaver and beaver ponds in landscapes dominated by forestry.

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

2. Methods

2.1. Study area

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

2.2. Amphibian sampling

To assess the role of beaver in providing habitat for breeding amphibians, first we randomly selected 15 beaver-obstructed stream reaches (mean ± SE length = 190 ± 11.9 m; stream order = 2.2 ± 0.24). Most beaver-obstructed stream reaches (10 of 15) were located >1 km from each other to minimize potential non-independence of ponds; five reaches were separated by 0.5–1.0 km. These distances probably prevent the large number of migrants needed for immigration to play a meaningful role in local recruitment and population dynamics of anurans on ponds (Newman and Squire, 2001; Petranka et al., 2004). Each beaver-obstructed reach consisted of 1–6 consecutive beaver ponds that flooded areas ranging from 0.17–1.84 ha. On 15 beaver-obstructed reaches, we examined a total of 54 ponds in 2001 and 52 ponds in 2002. Two ponds combined during a heavy July rain in 2001, hence, the pond number changed between years. The same storm also resulted in the collapse of a dam on one pond (3rd-order beaver-obstructed reach) that remained partially damaged in spring 2002, creating a flooded area substantially smaller than the previous year (i.e., 0.05 ha in 2002 versus 0.35 ha in 2001).

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

To estimate the number of breeding wood frogs, boreal chorus frogs and western toads on beaver ponds and streams, we conducted 5 call surveys (Weir, 2001) from May 3–June 9 in 2001 and 6 call surveys from May 11-June 11 in 2002. Surveys began when ice cover receded from all ponds and surveys were completed when relatively few or no calling males were recorded. All surveys were conducted under optimal weather conditions (i.e., light or no rain, Beaufort Wind Scale <4, air temperature >5 °C) at night within a 3 h window starting 0.5 h after sunset. Each survey comprised a 180° point count for 5 min that covered pond and stream habitat extending <100 m from a survey station. Most ponds in our study were relatively small and had one survey station. We established two stations on three ponds because of their large area (>0.5 ha) and elongated shape. All unobstructed streams had two survey stations to provide complete coverage of the 200 m reach. To minimize disruption of reproductive activity, all surveys were conducted 7–10 m from the shoreline. Recording consisted of observers first identifying spatially distinct choruses of calling males for each species present and assigning ranks of aural intensity to choruses: Rank 1 = no overlap in calls and the number of males can be reliably estimated, Rank 2 = some overlap in calls and the number of males can be estimated (but less accurately than for Rank 1),

and Rank 3 = overlap in calls and the number of individuals cannot be estimated (Weir, 2001).

Next, we assigned a species-specific value for each Rank 3 chorus so that we could estimate population sizes of the wood frog and boreal chorus frog (no Rank 3 groups of western toads were recorded during our study). Stevens and Paszkowski (2004) calculated the mean value of Rank 3 choruses as 59 males for the wood frog using counts of egg masses, multiple call surveys, and a conservative 1:1 male to female sex-ratio. However, given the variability of this estimate (SD = 29) in their study we also use the Rank 3 chorus size ±1 standard deviation (20–98 males) to estimate population sizes of wood frog. To our knowledge, no study has quantitatively assessed the mean group size for Rank 3 choruses for the boreal chorus frog. We might expect, however, that their aggregations are smaller than those of wood frog choruses because (1) boreal chorus frog may be less abundant than the wood frog in the western boreal forest (Roberts and Lewin, 1979; Paszkowski et al., 2002); (2) calls emitted by the male boreal chorus frog are about twice as long in duration as calls of the wood frog, which may mean that a lower minimum number of individuals is needed to create a Rank 3 chorus; and (3) the boreal chorus frog is less likely than the wood frog to display temporally compressed explosive breeding (C.E. Stevens, personal observation). Thus, we proposed that 30 males represent a Rank 3 group of boreal chorus frogs but use additional values of 10 and 60 given the uncertainty in actual group size so that we could estimate total number of calling males on dammed stream reaches.

In summer 2001 we employed pitfall traps and drift fences on the nine paired stream reaches (unobstructed reach paired with one pond on a nearby beaver-obstructed reach) to measure abundance of post-metamorphic individuals and juvenile recruitment to metamorphosis. Pitfall traps were installed in pairs along drift fences; each fence had one trap placed at each end. The drift fence was a polyethylene sheet 5 or 10 m long, 30 cm high and partly buried in the soil. All fences were installed 3–7 m from water. Drift fences running parallel to the pond edge or unobstructed stream covered 20% of that shoreline. In addition, one 5-meter drift fence running perpendicular to each shoreline was installed to capture moving post-metamorphic anurans associated with that stream reach. The pitfall trap was a 7.6 L plastic bucket with a plastic funnel (Stevens and Paszkowski, 2005). Beaver ponds had 8–20 pitfall traps per site depending on size, whereas each unobstructed stream had 16 pitfall traps. Traps were opened from July 10–August 15, 2001 and checked every 3–5 days.

Captured anurans were marked (i.e., one toe clipped), weighed, measured for snout-vent length (SVL), and identified to age class. Individuals were identified as young-of-year (YOY) if they had remnants of a larval tail or SVL <27 mm for the wood frog, SVL <21 mm for the boreal chorus frog, and SVL <23 mm for the western toad. Classifications of YOY were based on maximum SVL lengths of captured newly metamorphosed juveniles with tail buds. Sub-adults (i.e., sexually immature individuals) and adults were lumped into one category (age-1 + or adult). All anurans were released 5–10 m from their point of capture. Trapping data was converted to catch per unit-effort [CPUE = (total captures × 100 days)/(trap

nights × number of pitfall traps)] for presentation of results. To infer patterns of juvenile recruitment for each species, we first examined statistical effects of stream type (unobstructed streams versus beaver ponds) on YOY captures and then compared differences in YOY and adult captures on pairs of sites (data from both site types within a pair were pooled) using ANOVA with error term = stream location.

We also correlated both (Euclidean) distance to nearest beaver pond and density of nearby beaver ponds with CPUE of juvenile wood frog along unobstructed streams using univariate linear regressions to determine whether terrestrial populations were dependent on the density and distribution of nearby beaver ponds through dispersal of individuals from breeding habitats (e.g., Marsh and Trenham, 2001). Density of nearby ponds was measured as % area of landscape within 500 m and 1000 m of an unobstructed reach that was occupied with beaver ponds. We chose these scales because Newman and Squire (2001) reported for wood frogs in North Dakota that genetic differences between frogs from neighbouring ponds began to be detectable at a distance around 1000 m. We did not choose smaller distances (e.g., 250 m) because this resulted in most of the study sites being assigned a zero value for having no ponds in the surrounding landscape. Goodness-of-fit of linear regression models were evaluated with R^2 statistics. All analyses were on log10 transformed CPUE values to satisfy assumptions of parametric analyses and executed in SPLUS (Insightful Corporation; Crawley, 2002). Significance levels were set at a 0.10 probability to reduce the chance of committing a Type I error in analysis of low sample sizes for the amphibian component of our study (e.g., n = 9 pairs).

2.3. GIS analysis

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

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

To examine the influence of stream hydrology, forest structure and composition, and industrial activity on beaver occupancy of streams we used the binomial family of generalized linear mixed models (GLME), with a random effect, to predict beaver pond occurrence with a suite of habitat variables in SPLUS (Chao, 2003). Random effects can accommodate non-independence within groups, such as individuals within populations, when quantifying habitat selection, and were added to our models because of potential autocorrelation in the measured response among stream locations within a watershed that would otherwise produce incorrect variance estimates (Gillies et al., 2006). We expected observations within a watershed to be non-independent and representative of an independent population unit compared to observations from other watersheds given that dispersal by beaver generally follow stream channels and for distances up to 5 km (Van Deelen and Pletscher, 1996; Sun et al., 2000). Prior to the GLME, potential multicollinearity among the habitat variables was assessed with Pearson correlation tests and one of the two highly correlated variables was eliminated (r > |0.8|) (Table 1). We excluded % deciduous forest because it was highly correlated with both mean height and % *Populus* (r = 0.91), the latter variable reflecting abundance of a well-documented preferred food plant of beaver.

Our model consisted of correlates of beaver food plants (mean forest height and % *Populus*; see Fryxell and Doucet, 1993; Gallant et al., 2004), hydrological parameters (stream order and slope; see Howard and Larson, 1985; Barnes and Mallik, 1997), distance to nearest cutblock and road because of their influence on forest composition and structure, and stream hydrology (Jones, 2000; Swank et al., 2001). We also added elevation to the model as a correlate of watershed position because preliminary observations suggested that beaver ponds were clustered at higher locations within watersheds (Fig. 1). Two 2-way interactions were added as cor-
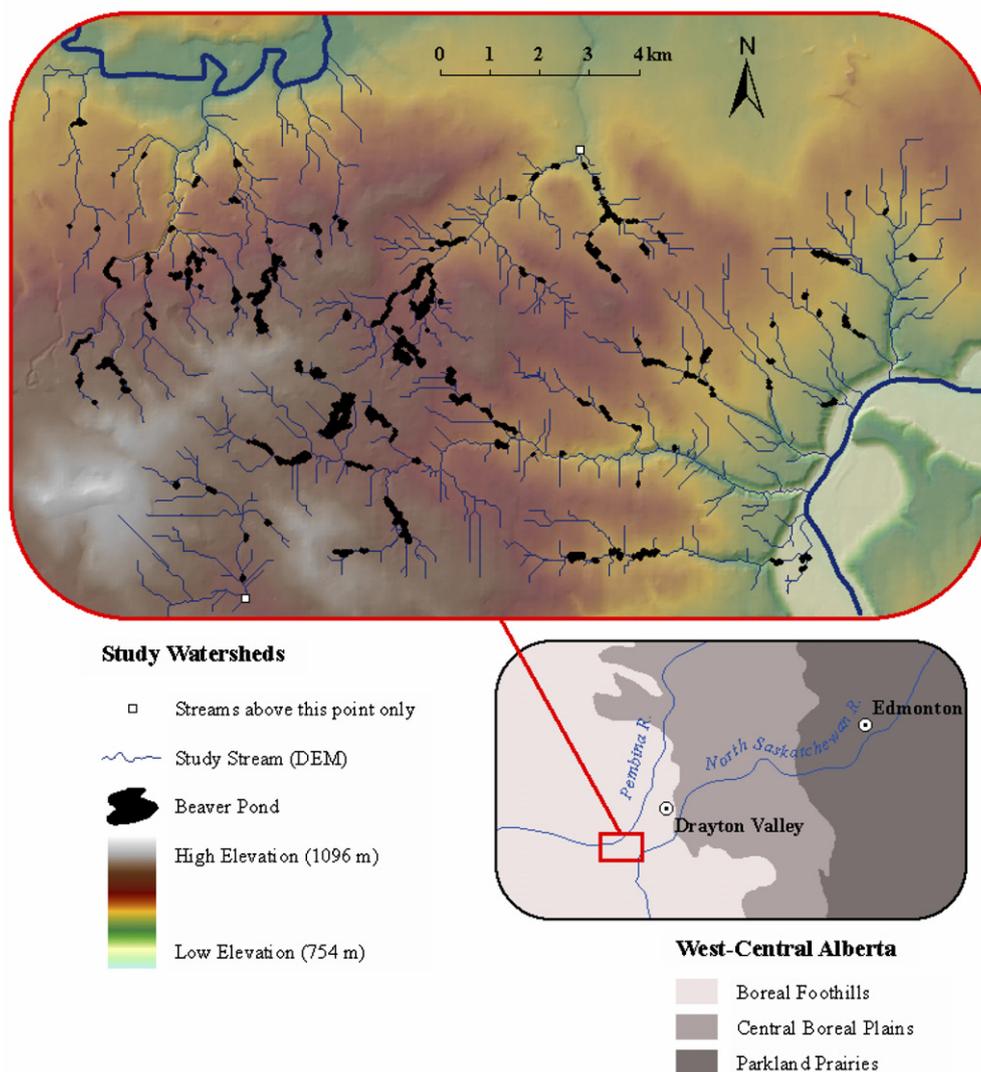
Fig. 1 – Study streams and watersheds examined for the presence of beaver ponds in west-central Alberta. Streams were delineated with a digital elevation model (DEM) in ArcGIS whereas beaver ponds were identified from aerial photography taken in 1997.

Table 1 – Mean ± SE values (and range) of habitat parameters on unoccupied versus beaver-occupied sites, including coefficients and P values from univariate GLMEs predicting beaver pond occupancy on a network of streams in 15 watersheds of west-central Alberta					
	Unoccupied stream sites ($n = 459$)	Beaver sites on streams ($n = 114$)	Coefficient	t_{557}	P^A
Mean elevation (m)	919 ± 2.4 (785–1047)	933 ± 3.5 (800–1012)	0.608 ± 0.27[B]	2.3	0.025
Stream order (1–4)	1.65 ± 0.04 (1–4)	2.25 ± 0.09 (1–4)	0.561 ± 0.101	5.5	<0.001
Stream slope	3.5 ± 0.17 (0.18–19.2)	2.87 ± 0.21 (0.47–14.1)	−0.0647 ± 0.0373	−1.7	0.084
Forest within 100 m					
Mean height (m)[a]	16.9 ± 0.29 (0–33.5)	15.9 ± 0.62 (1.2–34.9)	−0.0302 ± 0.0173	−1.7	0.083
% deciduous[a,b]	55.4 ± 1.5 (0–100)	49.1 ± 2.6 (0.3–100)	−0.725 ± 0.35[B]	−2.1	0.039
% *Populus*[b]	48.7 ± 1.5 (0–100)	43.4 ± 2.7 (0–100)	−0.669 ± 0.342[B]	−2.0	0.051
Nearest disturbance					
Cutblock (m)	627 ± 30.8 (0–3416)	866 ± 63.2 (0–2394)	0.0335 ± 0.0176[B]	1.9	0.058
Road (m)	241 ± 9.9 (0–1751)	224 ± 21.3 (10–1424)	0.000231 ± 0.058[B]	0.0	0.997

a,b = a pair of parameters with high correlation (>0.8) has the same letter.
A Statistical significance accepted at alpha = 0.05.
B Change per 100 units.

relates of complex hydrological scenarios: (1) stream order × stream slope; and (2) stream order × distance to nearest road. The first interaction was based on the prediction that a reliable but manageable source or volume of water was essential to the establishment and maintenance of beaver ponds (e.g., fast-moving, narrow streams or slow-moving, wide streams). The second interaction reflected the possibility that road crossings serve as useful 'pinch-points' for intercepting stream flow for beaver damming, particularly on high-order streams that move large volumes of water. Two 'forage' interactions of (1) % nearby *Populus* × mean forest height, and (2) % nearby *Populus* × distance to nearest cutblock, were also included to determine whether beaver modified their surroundings or selected stream locations for a particular height class of *Populus*.

Our final GLME model excluded non-significant interactions ($P > 0.10$) but retained all individual correlates. This procedure helped control 'confounding' as a source of biased estimation of effects for cases where their influences of multiple correlates on a response were inseparable (Greenland et al., 1999). We also present habitat coefficients and their significance from univariate models predicting beaver pond occurrence on streams. Hypothesis testing through use of Akaike's Information Criterion (Burnham and Anderson, 2002) was not explored because the algorithm in the GLME was a penalized quasi-likelihood (PQL), which may be unreliable in accurately estimating likelihoods (Engel, 1998). However, PQL is an effective method for estimating parameters from clustered binary data (Heo and Leon, 2005). It is also considerably less computationally demanding than other methods (Gillies et al., 2006). The fit of the full GLME model was first assessed through a visual examination of the standardized residuals plotted against the fitted values. We also used receiver operator characteristics (ROC) on withheld subsets of our model data (20%) to assess fit and predictive performance as model verification. ROC-area under the curve estimates $\geqslant 0.7$ was considered a model with good accuracy (Swets, 1998). As an additional assessment of the predictive capacity of our GLME model, we used coefficients to estimate the probability of occurrence of beaver ponds for each study site, and obtained a probability cut-off point that maximized both specificity and sensitivity curves simultaneously with a model-training dataset (80% of data) only (Swets, 1998). That cut-off point was used to determine whether or not a beaver pond was predicted for each site in a subset of data (20%) that had been withheld specifically for testing. Using observed and predicted occurrences of beaver ponds and unobstructed streams in this dataset we then estimated the % of sites correctly classified (PCC). Models with a PCC score $\geqslant 70\%$ are considered to have reasonable predictive power (Nielsen et al., 2004).

3. Results

3.1. Amphibian populations

No calling anurans were recorded on unobstructed streams during repeated call surveys. In contrast, call surveys in 2001 and 2002 on beaver ponds produced total estimates of 1184 boreal chorus frogs (potential range 524–3164), 3809 wood frogs (potential range = 1430–6188), and 69 western toads. Note that values for boreal chorus frog and wood frog reflect, in part, conservative estimates of numbers of calling males in Rank 3 choruses and the inherent variability of these estimates based on methods described earlier. Using the estimated low and high estimates of Rank 3 chorus sizes, the number of breeding anurans per km of dammed stream for the boreal chorus frog were, on average, between 59–179 males/km in 2001 and 116–531 males/km in 2002, and comparable estimates for the wood frog were 221–925 males/km in 2001 and 303–1359 males/km in 2002. Population estimates for the western toad were 14 males/km in 2001 and 10 males/km in 2002 (Fig. 2).

The combined total number of anurans captured using pitfall traps and drift fences was 3264 individuals on both beaver ponds and unobstructed streams, the majority of which were wood frog (3064 individuals) followed by western toad (120 individuals) and boreal chorus frog (80 individuals) (Fig. 3).
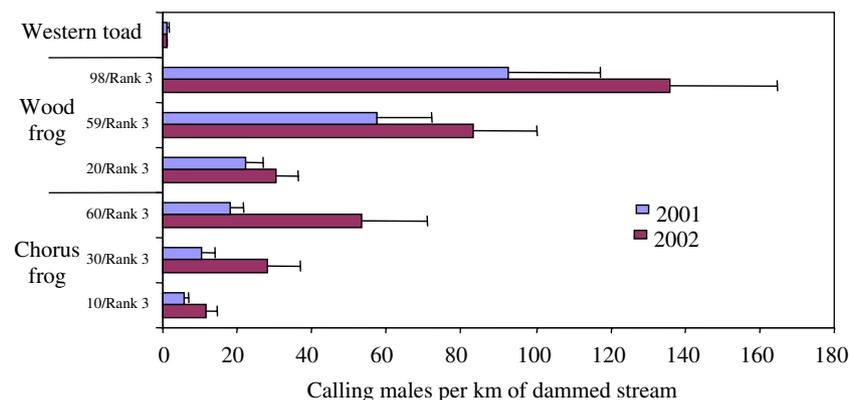
Fig. 2 – Mean (±SE) number of calling male western toad, wood frog, and boreal chorus frog per km of 15 beaver-obstructed stream reaches in west-central Alberta surveyed during spring 2001 and 2002. Abundance estimates were derived by counting males in each Rank 1 and 2 chorus, and assigning estimated males to each recorded Rank 3 chorus for the wood frog and boreal chorus frog (see Stevens and Paszkowski, 2005). Note that estimates vary according to the proposed range of number of males calling in a Rank 3 chorus. No Rank 3 choruses were encountered for western toad.
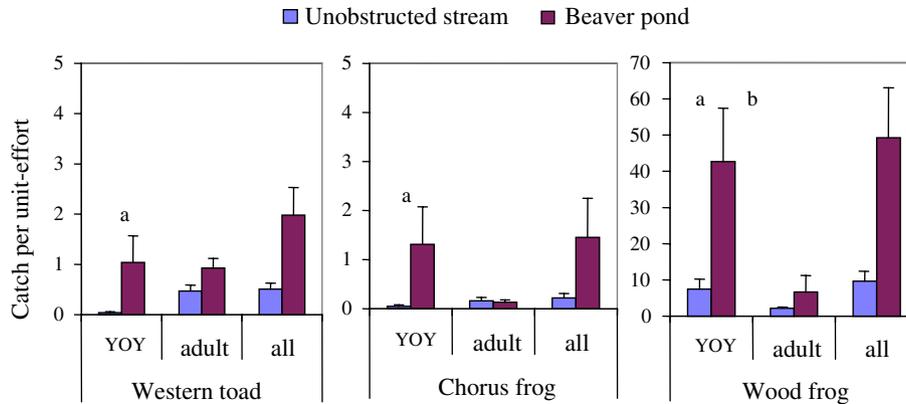
Fig. 3 – Pitfall trap data for three anuran species as mean (±SE) catch per-unit effort [CPUE = (total captures × 100 days)/(trap nights × number of pitfall traps)] of post-metamorphic young-of-year (YOY) and adults (age-1+) on nine pairs of unobstructed streams and beaver ponds. Trapping was conducted from July 10 to August 15, 2001 in the Boreal Foothills of Alberta. At P < 0.01, ANOVAs (with site location as a random effect) indicated that CPUE of YOY western toad, chorus frog and wood frog were higher on beaver ponds versus unobstructed stream (a), and that the wood frog was the only species with catches comprised of significantly more YOY than adults (b).

Most wood frogs captured were YOY (i.e., 2648 individuals) representing 81% of total anuran captures. Less than 1% of YOY wood frogs were recaptured within a sampling year. In addition, the majority of YOY captures were adjacent to beaver ponds. For example, beaver ponds had 5.7-times more YOY wood frog than nearby unobstructed streams, and 29- and 24-times more YOY western toad and YOY boreal chorus frog, respectively. Using ANOVA, we found that log-transformed YOY captures were significantly higher on beaver ponds versus unobstructed streams for all 3 species (wood frog $F_{1,8} = 5.1$, $P = 0.054$; western toad $F_{1,8} = 5.1$, $P = 0.055$; boreal chorus frog $F_{1,8} = 4.6$, $P = 0.064$) (Fig. 3). However, only wood frog captures were characterized by significantly more YOY than adults ($F_{1,8} = 8.6$, $P = 0.019$). YOY outnumbered adults approximately 5.7:1. YOY boreal chorus frog similarly outnumbered adult boreal chorus frogs (4.6:1), however, log-transformed CPUE did not differ significantly ($F_{1,8} = 2.1$, $P = 0.182$), possibly because of low power to detect differences if they existed. For example, our statistical power (at an alpha = 0.10) to detect 2-times more YOY than adults was only 0.28 for boreal chorus frog compared to 0.95 for wood frog. In contrast to both the wood frog and boreal chorus frog, we recorded fewer YOY western toad than adult western toad. The difference in log-transformed CPUE between age classes was statistically similar ($F_{1,8} = 1.8$, $P = 0.134$).

On unobstructed stream reaches ($n = 9$) we observed a total of 412 YOY wood frogs. Capture rates were highly variable among sites: 0.2–24.4 CPUE. Varying CPUE among stream reaches may be due to the fact that some sites were far (e.g., 636 m) from a potential source of anurans whereas others were close (e.g., 90 m) to a beaver pond (overall mean ± SE = 253 ± 57.8 m). Unobstructed streams also varied in % area of surrounding landscape occupied by beaver ponds: 0–5% at 500-m scale (mean ± SE = 2.0 ± 0.67%) and 0.04–5.76% at a 1000-m scale (mean ± SE = 2.1 ± 0.64%). Based on univariate linear regression, Euclidean distance to nearest beaver pond ($t_7 = -1.4$, $P = 0.21$) was negatively related to CPUE of juvenile wood; however this relationship was not significant. In con-

trast, % landscape occupied by beaver ponds at both the 500-m scale ($t_7 = 4.3$, $P = 0.004$; Fig. 4) and 1000-m scale ($t_7 = 2.73$, $P = 0.029$) significantly predicted CPUE of juvenile wood frogs on unobstructed streams. More juveniles were captured in landscapes with higher densities of beaver ponds (Fig. 4). The slope coefficient in the 500-m scale model ($b = 0.203$) was slightly (14%) higher than that in the 1000-m scale model ($b = 0.178$), and the goodness-of-fit was considerably better for the smaller spatial scale model: $R^2 = 0.72$ versus 0.52.

3.2. Beaver pond distributions

The total length of study-stream habitat (estimated with a digital elevation model) that was available for occupation by
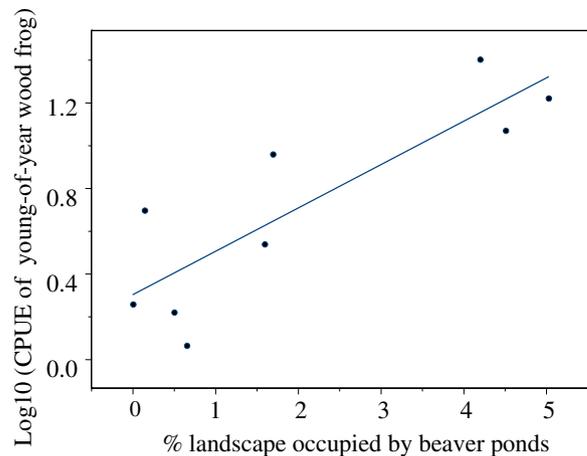
Fig. 4 – Scatterplot with a linear least square smoother of % landscape occupied by beaver ponds (within 500 m) versus log10 transformed catch per unit-effort [CPUE = (total captures)/(trap nights × number of pitfall traps)] of young-of-year wood frog on nine unobstructed streams in west-central Alberta (y = 0.304 + 0.203x).

beaver in our study landscape (145 480 500 m²) was 325 596 m (1st-order = 167 148 m, 2nd-order = 87 552 m, 3rd-order = 45 383 m, and 4th-order = 25 513 m). Aerial photographs (1:15 000) from 1997 indicated that of the total length of stream habitat estimated with a digital elevation model, approximately 10% was flooded by beaver dams creating 590 beaver ponds (total area = 1 233 792 m²). Only 24 basin (non-beaver) ponds or wetlands (total area = 78 934 m²) were detected in the study watersheds. Fifty-eight percent of beaver ponds were on 1st and 2nd-order streams, whereas the remaining 42% were on 3rd- and 4th-order streams. On average (mean ± SE), the area of beaver ponds was 2091 ± 148 m² (range 50–46 269 m²). Based on Weyerhaeuser Canada, Ltd. vegetation inventory data, forestry and petroleum sectors were active in the region and had built over 240 km of roads to drill 446 oil and gas wells, and to harvest trees from approximately 10% of the study area. Cutblocks were of varying age since logging

(1–60 years); however most had been cut within 20 years (75% of total area harvested) and were occupied by trees under 5 m in height (72% of total area harvested). Some of the logging in our study area was immediately adjacent to stream reaches: 12 648 m along 1st-order streams, 3580 m along 2nd-order streams, 443 m along 3rd-order streams, and 156 m along 4th-order streams.

Of the 573 stream locations randomly chosen in the 15 study watersheds, 114 points were on beaver-obstructed stream reaches (Table 1). Of the eight habitat features examined with univariate GLMEs, stream order, elevation and % deciduous were correlated with beaver pond occurrence (P < 0.05; Table 1). There were also non-significant correlations involving stream slope, mean forest height, % *Populus*, and distance to nearest cutblock (P < 0.10). Based on univariate models, beaver ponds were more likely to occur on larger but lower-gradient streams, and in regions with lower levels

Table 2 – Coefficients (±SE) associated with habitat correlates in the full GLME model predicting beaver pond occupancy on low-order (1–4) streams grouped on 15 adjoining watershed in west-central Alberta

	Coefficient ± SE	t_{549}	P[a]
Intercept	−15.46 ± 3.34	−4.63	<0.0001
Mean elevation (m)	1.29 ± 0.348[b]	3.73	0.0002
Stream order (1–4)	1.482 ± 0.209	7.09	<0.0001
Stream slope	0.228 ± 0.129	1.77	0.0770
% *Populus* (within 100 m)	−0.93 ± 0.632[b]	−1.47	0.1421
Mean forest height (m; within 100 m)	−0.0152 ± 0.0242	−0.63	0.5303
Distance to nearest cutblock (m)	−0.045 ± 0.035[b]	−1.29	0.1965
Distance to nearest road (m)	−0.095 ± 0.063[b]	−1.52	0.1292
Stream order × mean slope	−0.143 ± 0.0468	−3.05	0.0024
% *Populus* × nearest cutblock	0.016 ± 0.0058[b]	2.7	0.0072

Note: ROC = 0.78 and PCC = 70% for GLME model testing data.
a Statistical significance accepted at alpha = 0.05.
b Change per 100 units.
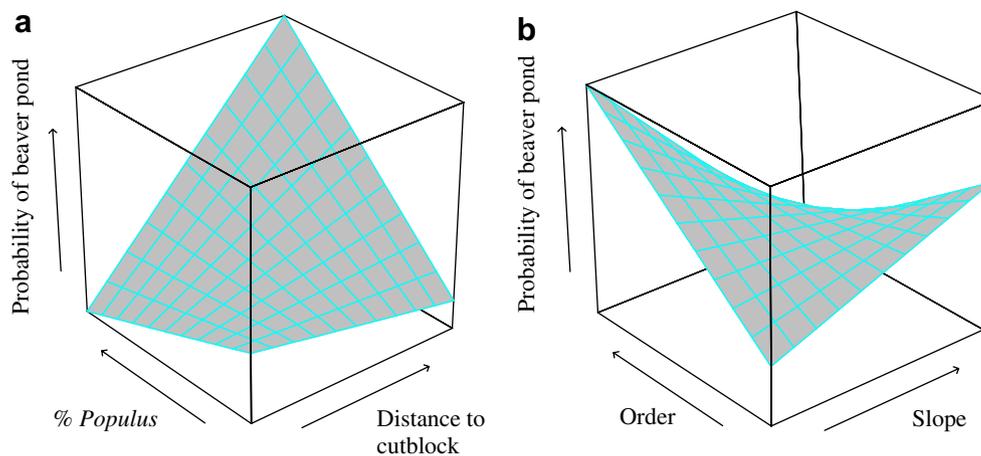
Fig. 5 – The interacting effects of % nearby *Populus* × distance to nearest cutblock (a), and stream order × slope (b) on the presence of beaver ponds on small streams in the Boreal Foothills that were assessed in a generalized linear model. % *Populus* was determined from a 100 m radius of stream location and for non-flooded area only. Cutblocks were of varying age since logging (1–60 years post-harvest); however most were cut within 20 years (75% of total area harvested) and comprised of *Populus* trees <5 m in height (72% of total area harvested). Stream order and slope were calculated using a digital elevation model.

of beaver food resources. Interestingly, beaver ponds were more likely to occur further from cutblocks, and the effect of cutblocks may extend over long distances and beyond the riparian zone given that, on average, occupied streams were 627 m from a cutblock (Table 1).

Our full GLME model, which had adequate predictive power and accuracy (ROC = 0.78 and PCC = 70% for model testing data), suggested that beaver pond occurrence was positively related to elevation and stream order, as was noted for the univariate models (Table 2). We also noted significant interaction between stream slope and stream order (Table 2; Fig. 5). Beaver ponds were more likely to occur either on high gradient streams of low-order (1–2) or on low gradient streams of high-order (3–4) (Fig. 5). The relation between distance to cutblock and beaver pond occurrence in the full GLME was significantly dependent on available levels of *Populus* within 100 m of the stream location (Table 2; Fig. 5). Stream locations in close proximity to a cutblock were less likely to be occupied by a beaver pond regardless of the level of nearby *Populus* (Fig. 5).

4. Discussion

The present study supports the use of beaver as a surrogate species indicative of the occurrence of amphibian habitat and populations on boreal streams. In our study area, calling wood frog, boreal chorus frog and western toad were recorded only in association with beaver dams. Thus, we infer that beaver create breeding habitat for anuran amphibians as suggested in a similar study by Russell et al. (1998) that found more post-metamorphic anurans in riparian zones on beaver ponds versus unobstructed streams in North Carolina, USA. Beaver may have a particularly large role in maintaining amphibian populations in the Boreal Foothills of Alberta also because the majority of standing water on the landscape (94%) was created by beaver impoundment of small streams. However, distribution of beaver ponds was not random, with stream order and proximity to cutblocks being important environmental factors influencing their occurrence. These relationships are discussed in detail below and may have implications for industry in the boreal forest if the conservation of amphibians is a goal of resource managers.

4.1. Amphibians in beaver ponds

Critical to understanding the value of beaver ponds as amphibian habitat is an assessment of whether beaver ponds are potential population sources (Gill, 1978) characterized by relatively high rates of juvenile recruitment to metamorphosis. Based on our pitfall trapping results it appears that the wood frog, and possibly the boreal chorus frog, experienced high rates of juvenile recruitment in beaver ponds. For both species, the number of juveniles, as reflected by CPUE, was statistically higher on beaver ponds than on unobstructed streams, and approximately 2-times higher than the number of adults captured on both habitat types combined. However, patterns of juvenile recruitment and age distributions observed for boreal chorus frog were possibly affected by the ability of adult boreal chorus frogs to escape from pitfall traps (Stevens and Paszkowski, 2005). In addition, although more

western toads were trapped more frequently adjacent to beaver ponds than near unobstructed streams, the number of juveniles and adults were similar. This pattern may reflect the fact that beaver ponds are poor larval environments for toads (e.g., too cold, inadequate food) leading to low juvenile recruitment, or it could be an artefact of sampling biases (Stevens and Paszkowski, 2005). For example, partial fencing of riparian zones around ponds could have missed either in-stream movements of juvenile toads (Adams et al., 2005) or emerging aggregations of juvenile toads from particular shoreline locations where the water was warmer or the overhead canopy was open (Black and Black, 1969; Noland and Ultsch, 1981). During 3 years of pitfall trapping in our study area, however, no visual observations of western toads in ponds or streams were made outside of the breeding season, and only one observation of a large group of newly metamorphosed toads was made adjacent to a pond (by C.E. Stevens). With respect to our assessment of beaver ponds as breeding habitat, we acknowledge that amphibian abundance fluctuates widely from year to year, and that our inferences concerning recruitment are limited, as they are based on a single year of pitfall trapping. Some species, such as the western toad, may undergo "boom years" of high reproductive output that maintain the long-term persistence of populations (Eaton et al., 2005; Green, 2003; Stevens et al., 2006b).

Despite lack of strong evidence provided by our pitfall trapping for high recruitment of western toads from beaver ponds, the strong correlation between % landscape occupied with beaver ponds and abundance of juvenile wood frogs on unobstructed streams suggests that the anurans recorded on these sites originated from beaver ponds. Natal ponds were likely within distances of 500 m or slightly further given that there was a stronger relationship between CPUE of juvenile wood frogs on unobstructed streams in relationship to the density of beaver ponds at the smaller (500-m) than the larger (1000-m) spatial scale (also see Newman and Squire, 2001). The fact that numerous anurans were recorded in an eco-region where beaver ponds are the primary source of breeding habitat indicates that some ponds in the region must act as sources within a larger metapopulation. For example, older beaver ponds provide suitable breeding habitats because these sites offer warm and well-oxygenated environments to anuran larvae thereby enhancing development and growth rates (Stevens et al., 2006a). The seasonal hydroperiod of beaver ponds is also relatively stable (Gill, 1978; Schlosser and Kallemyn, 2000). Only one pond (of 54) surveyed for calling anurans disappeared due to dam collapse during the 2 years of our study. In addition, beaver ponds in boreal regions may support lower abundance and diversity of predatory fishes because of winterkill triggered by anoxic conditions (Tonn and Magnuson, 1982) and the restriction of fish movements by dams (Schlosser and Kallemyn, 2000). Beaver ponds on 1st–3rd-order streams in the Boreal Foothills seldom contained fish (i.e., 15 of 54 ponds surveyed), and the only fish present was the small-bodied brook stickleback (*Culaea inconstans*; Stevens et al., 2006a) even though cyprinids (e.g., *Pimephales promelas*) and larger fishes such as bull trout (*Salvelinus confluentus*) and northern pike (*Esox lucious*) occur in local watersheds (Nelson and Paetz, 1992).

4.2. Beaver pond distributions: implications for amphibians

Although there has been extensive research on beaver food habits (e.g., Schoener, 1979; Jenkins, 1980; McGinley and Whitham, 1985; Johnston and Naiman, 1990; Fryxell and Doucet, 1993; Basey and Jenkins, 1995; Gallant et al., 2004; Martell et al., 2006), relatively few studies have examined factors associated with colony distributions at a landscape scale (but see Slough and Sadleir, 1977; Howard and Larson, 1985; Barnes and Mallik, 1997). Our model identified important variables correlated with the occurrence of beaver ponds and associated amphibian populations in the Boreal Foothills. The clustering of beaver ponds at higher elevations in a watershed may reflect both selection for particular streams and a tendency of beaver to disperse to nearby stream locations (Sun et al., 2000). Preferred locations for dam-building beaver in our study included higher-order streams. These streams may provide increased reliability of the water necessary for creating and maintaining deep ponds throughout the year, particularly during drought years (Howard and Larson, 1985; Barnes and Mallik, 1997). Deep ponds provide escape from terrestrial predators, safe under-ice travel during winter, and a medium for transporting construction materials and food stores (Hill, 1982). However, too much flow on a stream can result in the blow-out of dams, particularly during spring run-off (Stock and Schlosser, 1991; Hillman, 1998). Consistent with our findings that beaver select streams with an intermediate level of flow, a New England study identified wide, slow-moving streams as beaver habitat (Howard and Larson, 1985), whereas a study on the boreal shield characterized beaver habitat as small, fast-moving streams (Barnes and Mallik, 1997). Implications of beaver site selection for amphibian populations depend on whether abundance and diversity of predatory fishes occur on beaver ponds associated with higher-order streams (Snodgrass and Meffe, 1998). For example, fish can have a significant impact on larval survival, and can even slow growth and development of anuran larvae through behavioural changes and reduction in feeding (Werner and McPeek, 1994; Baber and Babbitt, 2003).

4.3. Forest management, beaver ponds and amphibians

Much to the annoyance of road maintenance personnel, beaver often build dams in culverts and occupy streams near roads (Payne and Peterson, 1986; McKinstry and Anderson, 1999). Thus, we were surprised that beaver pond occurrence was unrelated to distance to nearest road in our study and propose that trapping and shooting of beaver in roadside ponds (Loker et al., 1999) or the lack of woody vegetation adjacent to roads offset hydrological benefits of pond creation (Curtis and Jensen, 2004). The negative but moderate-to-weak relationships of deciduous trees and forest height with beaver pond occurrence on streams suggested that beaver had affected the overstory and overall structure of riparian zones and had depleted stands of deciduous trees by the time aerial photographs were taken (also see Johnston and Naiman, 1990; Donkor and Fryxell, 1999; Barnes and Mallik, 2001). We did find that stream reaches

nearer to cutblocks were less likely to be occupied by a beaver pond regardless of the level of nearby *Populus*. Cutblocks, which were typically new (<20 years) and regenerating with *Populus* in our study landscape, may be avoided because of the paucity of large, standing trees that are generally preferred by foraging beaver (McGinley and Whitham, 1985; Fryxell and Doucet, 1993; Gallant et al., 2004). However, other mechanisms may underlie beaver pond distributions given that their mean distance to the nearest cutblock was substantial at 627 m. Thus, cutblocks did not affect food availability of beaver, as they employ a central-place foraging strategy focused on areas within 20–30 m of ponds (Johnston and Naiman, 1990; Donkor and Fryxell, 1999; Barnes and Mallik, 2001). Increased competition for food with elevated populations of ungulates (e.g., *Odocoileus hemionus*) from nearby cutblocks may have resulted in beaver avoiding habitat in regions that were recently harvested (Hebblewhite et al., 2005).

To further amphibian conservation, forestry planning and energy development in boreal ecosystems could incorporate landscape-use patterns of dam-building beaver such as described by our study. Beneficial models specific to an eco-region can also be generated through interpretation of aerial photography and application of a digital elevation model in GIS. We found that likelihood of beaver pond occurrence decreased with the presence of nearby cutblocks, and propose that forestry activities that alter stand composition and age may impact beaver foraging and habitat-use, and ultimately, the associated amphibian populations on boreal streams. The protection of older growth deciduous forest near high-gradient streams of low-order, for example, may promote the creation and longevity of ponds for beaver colonies and high-quality larval habitat for breeding amphibians. Such stands are the least protected on the landscape at present (Lee et al., 2004). Further research identifying underlying mechanisms and scale of effects of forestry activities on beaver populations and ponds are needed to aid the persistence of boreal amphibian populations. Maintaining summer foraging habitat and the connectivity of ponds for amphibians along stream networks should also be a part of management plans, particularly on unobstructed streams in regions of high densities of beaver ponds (i.e., >5% of landscape occupied by ponds; this study).

Our documentation that almost all beaver ponds supported breeding anurans whereas unobstructed streams had essentially none validates the application of a surrogate species approach and supports its use at broader scales by linking it to remote sensing. Anuran habitat could be evaluated and monitored over large areas very efficiently. Local inferences on the occurrence and size of amphibian populations may also be possible, particularly in landscapes where beaver ponds are the most commonly available breeding habitat. We recommend that local "on-the-ground" sampling of amphibians, such as egg censuses or call surveys, be used to validate the approach and rule out unforeseen factors limiting amphibian distribution or depressing abundance, such as pathogens, introduced predators, or poor water quality. In summary, we have established that beaver activities can dictate the extent and distribution of anuran aquatic habitat in a forested landscape. In the Boreal Foothills of Alberta, the sur-

rogate species concept is supported and promises a means of efficient habitat evaluation and for establishing amphibian conservation strategies. The beaver may prove a useful surrogate species for conserving pond-breeding amphibians in other parts of the boreal forest of Canada and in other montane regions in western North America.

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