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The relationship of amphibian abundance to habitat features across spatial scales in the Boreal Plains[1]

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Abstract: We examined the relationship between amphibian abundance and habitat features at 8 spatial scales in boreal Alberta, Canada. Twenty-three local pond variables and 15 landscape variables at 7 scales (50, 100, 200, 500, 1000, 2000, and 5000 m) were incorporated into a Principal Component Analysis (PCA) for each scale. We analyzed amphibian relative abundance against the PC axis scores using regression for each species and each scale. We found that each species' abundance was best described at different spatial scales. Wood frog (*Lithobates sylvaticus*) abundance was best predicted by local, pond-linked variables, boreal chorus frog (*Pseudacris maculata*) abundance by 1000-m-scale landscape variables, and western toad (*Anaxyrus boreas*) by the 100-m scale. We found significant positive relationships with amphibian relative abundance and dissolved oxygen, deciduous forest cover, mixed forest cover, and urban cover. Pond depth, conductivity, total dissolved solids, aquatic plant density, low-shrub cover, and conifer cover showed negative relationships with abundance. We also investigated relationships between landform type and amphibian relative abundance. All 3 species were most abundant on wetlands in the moraine landform. Our research highlights the importance of developing conservation plans based on knowledge of individual species' biology because amphibians do not all respond to the same spatial scale.
Keywords: anuran, boreal, habitat, landscape, scale, wetland.

Résumé : Nous avons examiné les relations entre l'abondance des amphibiens et des caractéristiques de l'habitat selon 8 échelles spatiales en zone boréale en Alberta (Canada). Vingt-trois variables locales liées à l'étang et 15 variables associées au paysage à 7 échelles spatiales (50, 100, 200, 500, 1000, 2000 et 5000 m) ont été incorporées dans une analyse en composantes principales (ACP) pour chaque échelle. Nous avons analysé l'abondance relative des amphibiens en fonction des valeurs des axes CP par des régressions pour chaque espèce à chacune des échelles. Nous avons constaté que l'abondance était la mieux décrite à des échelles spatiales différentes selon l'espèce. L'abondance de la grenouille des bois (*Lithobates sylvaticus*) était la mieux prédite par des variables locales liées à l'étang, celle de la rainette faux-grillon boréale (*Pseudacris maculata*) par des variables du paysage à une échelle de 1000 m et celle du crapaud de l'Ouest (*Anaxyrus boreas*) à l'échelle de 100 m. Nous avons trouvé des relations positives significatives entre l'abondance relative des amphibiens et l'oxygène dissous, la couverture forestière feuillue, la couverture de forêt mélangée et celle du milieu urbain. La profondeur de l'étang, la conductivité, la quantité totale de solides dissous, la densité de plantes aquatiques, la couverture de petits arbustes et celle de conifères démontraient des relations négatives avec l'abondance. Nous avons aussi examiné la relation entre le type de paysage et l'abondance relative des amphibiens. L'abondance des 3 espèces était la plus élevée dans les milieux humides des paysages de moraine. Notre recherche met en évidence l'importance de développer des plans de conservation basés sur la connaissance de la biologie de chaque espèce puisque la réponse des amphibiens aux différentes échelles spatiales varie selon l'espèce.
Mots-clés : anoure, boréal, échelle, habitat, milieu humide, paysage.

Nomenclature: Crother *et al.*, 2000; Frost *et al.*, 2006.

Introduction

Global declines of amphibian populations have been well documented (Houlahan *et al.*, 2000), and habitat alteration is considered a major cause of decline (Stuart *et al.*, 2004). Most amphibians require both aquatic and terrestrial habitat to complete their life cycle (Trenham & Shaffer, 2005); therefore, loss of either habitat component could result in population declines. Susceptibility to habitat alteration has made amphibians a target for conservation efforts, and they also can serve as indicators of ecosystem health (Hopkins, 2007).

Understanding the relationship of a species to its habitat is a prerequisite for making realistic predictions about its response to large- and small-scale habitat change. A common problem with investigating patterns of habitat use is that patterns often change with different spatial scales of study (Turner, 1989). Several studies examining relationships between richness/abundance of temperate pond-breeding amphibian species and environmental variables at multiple spatial scales have suggested 200 m to 10 km to be appropriate scales for examining relationships between

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these species and habitat features (*e.g.*, Gibbs, Whiteleather & Schueler, 2005; Herrmann *et al.,* 2005). Suggested scales vary widely among studies, an outcome that is likely due to differences among species or geographical areas.

We examined the relationships between habitat features and amphibian abundance in boreal Alberta. The boreal plain ecozone covers 650 000 km^2 of western Canada; however, relatively little research has examined relationships between amphibians and their habitat here (but see Roberts & Lewin, 1979; Constible, Gregory & Anholt, 2001; Hannon *et al.,* 2002). This region is lightly disturbed, but it is poised for much greater industrial development over the next 20 y (Foote & Krogman, 2006). Alberta Sustainable Resource Development is currently creating industrial development setback distance guidelines so disturbances will be buffered from critical habitat for western toad (*Anaxyrus boreas*, formerly *Bufo boreas*) in the boreal region (Boreal/Foothills Sensitive Species Guidelines, unpubl. data). However, very little is known about western toad habitat use in the boreal, so identifying critical habitat is difficult. Knowledge of habitat factors that influence anuran abundance over multiple spatial scales may help steer habitat protection in the near future.

Our objectives were to 1) determine the relative abundance of 3 anuran species for 24 ponds in boreal Alberta, 2) identify the spatial scale most appropriate for predicting abundance patterns, and 3) examine relationships between anuran relative abundance and habitat features. To meet these objectives, we investigated relevant habitat scale for all 3 anuran species present at our sites in the boreal region of west-central Alberta, Canada: wood frog (*Lithobates silvaticus*, formerly *Rana sylvatica*), boreal chorus frog (*Pseudacris maculata*), and western toad. Knowledge of the life history of boreal amphibians is relatively scarce in comparison to amphibians from more southern regions (Elmberg, 1993). Our study of boreal populations is also novel because we synthesized information at various scales collected as part of a wider ecological and hydrological study of our study area: the Hydrology, Ecology, And Disturbance (HEAD) project.

Methods

STUDY SITES

The Hydrology, Ecology, And Disturbance (HEAD) is a multi-disciplinary research group that collected data at 125 wetlands in the Lake Utikuma region of Alberta, Canada. The goal of HEAD was to be able to predict the response of individual wetlands to disturbances. The wetland sites were approximately 20 km north of Utikuma Lake (56° 00' – 56° 20' N, 115° 20' – 115° 40' W) within the central mixed-wood subregion of the boreal forest region (Alberta Government, 2005). For extensive study of geomorphology, hydrology, limnology, submersed vegetation, and amphibian and waterfowl habitat quality, the HEAD group selected 24 focal wetlands in a 30- × 20-km study area. These 24 wetlands were selected from 125 candidate sites because they were deemed to be representative of waterbodies in this region; they varied in size (Table I) and occurred in approximately equal numbers in moraine, outwash, or glaciolacustrine landform types, representative of the region.

Grey luvisols and deep organic peat deposits were the dominant substrate types. All wetlands were relatively shallow, pan-shaped, and associated with established floating peat beds, and all had flocculent bottoms (substrate is loosely deposited at the bottom of the wetland and easily suspended; Hornung & Foote, 2006). Common tree species

TABLE I. Environmental variables selected for PCA analysis and their means and ranges over all 24 HEAD (Hydrology, Ecology, And Disturbance) group study wetlands near Lake Utikuma, Alberta, Canada in 2004.

Local variables	Mean (range)
Turbidity	6.2 (2.95–9.11) NTU (Nephelometric Turbidity Units)
Chlorophyll-a	12.91 (2.93–39.05) μg·L^{-1}
Conductivity	0.138 (0.039–0.318) mS·cm^{-1}
Dissolved oxygen	9.26 (1.36–15.48) mg·L^{-1}
PH	8.94 (7.27–9.43)
Water temperature	21 (18–25) °C
Submersed aquatic vegetation (SAV)	2.55 (1.0–3.8)
Wetland depth	67.5 (29.0–128.4) cm
Secchi depth	66.8 (29.0–128.4) cm
Secchi depth:wetland depth	1.0 (0.9–1.0)
Total nitrogen	1993 (923–4137) μg·L^{-1}
Total dissolved solids (TDS)	0.1 (0–0.2) g·L^{-1}
Total phosphorus	72 (29–371) μg·L^{-1}
Invertebrate biomass/volume	8.8 (1.6–26.1) mg·L^{-1}
Predatory invertebrate biomass/volume	2.6 (0.24–9.6) mg·L^{-1}
Aquatic plant density	0.54 (0.20–1.07) proportion of plant volume
Woody debris	7.44×10^{-4} (0–0.01) proportion cover
Dominant vegetation type	A = aquatic, C = conifer, D = deciduous, G = grass/wildflower, S = shrub
Beaver structures	0.83 (0 = absent, 1 = present)
Percent vegetation cover	91.5 (80–100) %
Median vegetation height	162.8 (30–800) cm
Wetland area	91 403 (6 312–367 774) m^2
Wetland perimeter	1423 (315–3070) m
Landscape variables (land-cover types)	**Mean (range) % cover within a 5000-m radius of each wetland**
Closed conifer	8 (4–14)
Open conifer	26 (12–41)
Pine	0.1 (0–0.8)
Closed deciduous	26 (10–46)
Open deciduous	3.9×10^{-4} ($0–5.0 \times 10^{-3}$)
Mixed forest	9 (7–10)
Low shrub	5 (2–9)
Tall shrub	8 (4–12)
Moss	0.3 (0.1–0.6)
Mesic herbaceous	5 (2–9)
Wet herbaceous	0.2 (0.05–0.3)
Urban (roads and well pads)	0.5 (0.1–1.2)
Agricultural areas	9.8×10^{-3} (0–0.03)
Young stands (burnt)	0.22 (0.04–0.44)
Wetlands	12 (2–24)
Landform (number of sites)	glaciolacustrine (7), moraine (10), or outwash plain (7)

around the 24 wetlands were trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), and paper birch (*Betula papyrifera*).

Study species

Wood frog and boreal chorus frog are widespread and abundant throughout most of Alberta and are considered to be "secure" (Alberta Government, 2000). The western toad is much less abundant and has a patchy distribution in western and central Alberta (Russell & Bauer, 2000); provincially the species has the general status of "sensitive" (Alberta Government, 2000). These 3 species are widely distributed in western and northern North America (Stebbins, 1985) and are the only amphibians that occur in northwestern Alberta (Russell & Bauer, 2000).

Amphibian sampling

We conducted 7 sets (~every 2 weeks) of visual surveys for amphibians at each of the 24 HEAD research wetlands from May to August 2004. This time period encompassed the peak breeding seasons and periods of metamorph emergence for all 3 species. Visual surveys were conducted by walking slowly along the wetland perimeter and searching for amphibians within 1 m of each side of the observer. Surveys were conducted for a 2-h period or until the entire perimeter was surveyed. We attempted to capture every amphibian seen. At a few ponds we did not see any chorus frogs or western toads, but we heard them calling. To account for their presence, we added 1 animal to the count for each wetland during each of the first 3 surveys if one or more individuals were heard calling at that site. We standardized our relative abundance data to numbers of individuals caught per 10 h for each of the 3 species over the course of the summer (rounded to whole numbers). Each wetland was surveyed regularly throughout the summer, and each was surveyed equally during the breeding and young-of-the-year (YOY) emergence periods.

For all species, we found that the number of captures during a visit to a wetland depended on air temperature (which ranged from 2 to 29 ºC and is also associated with weather and time of day; general linear mixed model [GLMM]; R Development Core Team, 2007; $P < 0.05$ for each temperature coefficient). We checked whether mean temperature over all visits varied significantly among wetlands. We found that mean temperatures (range of means = 13–19 ºC) did not vary significantly among wetlands, indicating that each wetland was sampled equally over the range of temperatures we experienced that summer (one-way ANOVA; SPSS Inc., 1989–2007; $F_{23, 144} = 0.616$, $P = 0.912$). Thus, we did not include air temperature in any further analyses. We did not compare relative abundance among species because of potential differences in our ability to detect and capture the 3 species of anurans.

Environmental variables collection

Local environmental variables

We collected and acquired data for 24 local environmental variables for each wetland (Table I). First, we calculated area and perimeter for each wetland using aerial photographs and Sigma Scan Pro (Systat Software Inc., 1999). Photos from 2000 were used for 21 of the wetlands; when photos from 2000 were not available or did not clearly show wetland edges, we defaulted to 1986 photos. The wetland edge was considered to be where thick vegetation met open water; this edge was clearly visible from photos and was comparable across years.

We acquired local water chemistry and aquatic flora and fauna data from the HEAD project. The University of Alberta Biogeochemical Analytical Laboratory analyzed water samples (collected 9 June and 30 June 2004) for total nitrogen (TN) and total phosphorus (TP). The average reading from the 2 sample dates was used for estimates of TN and TP for each wetland. Turbidity, chlorophyll-a (CHL-a), conductivity, water temperature (°C), dissolved oxygen (DO), pH, total dissolved solids (TDS), submersed aquatic vegetation (SAV), secchi depth, and wetland depth were randomly sampled at 5 locations within the open water of each wetland in June 2004. One measurement was taken from each of the 5 random locations for each variable except for turbidity, which had multiple readings (1–4) for each location; the average of these multiple readings was used as the value for that location. In turn, we used the average of the 5 random points to achieve 1 value for each variable per wetland for our analyses. SAV was recorded as a categorical count from 1 to 5, 1 being scant vegetation and 5 being dense vegetation (see Bayley & Prather, 2003 for details). SAV was collected visually from a small boat.

Aquatic plant density is the proportion of plant volume in an aquatic quadrat sampled. Aquatic plant density could sometimes be > 1 because the full height of emergent vegetation was recorded but quadrat volume was calculated using only water volume. This measure of aquatic vegetation was more detailed than the SAV variable and was collected within 2 m of the wetland edge (where tadpoles are more likely to be), but it was collected in 2001 (rather than 2004). Even though this variable was not collected in the same year we sampled amphibians, we felt that previous pond characteristics were relevant (*e.g.*, Piha, Luoto & Merila, 2007). Please see Hornung and Foote (2006) for a detailed description of the methods of sampling aquatic plant density.

Invertebrates can be competitors or predators for amphibian larvae (Chivers *et al.,* 1999; Mokany, 2007), so we included 2 estimates of aquatic invertebrate biomass for each wetland: total invertebrates and predatory invertebrates. Invertebrate biomass was estimated for all 24 wetlands during 4 systematic surveys conducted between 10 May and 5 September 2001. Three sub-sampling locations were established at each wetland using a stratified random design that was randomly selected along a transect that ran parallel to the wetland shore and was one-third the entire shoreline length. The transect at each wetland was set away from confounding factors such as roads, seismic lines, or oil-well locations. The aquatic/terrestrial interface zone, emergent vegetation zone, and submergent vegetation zone were swept vertically (bottom-up) with 2 sweeps from each aquatic zone (total of 6 sweeps) using a standard D-shaped invertebrate dip net (net opening 640 cm^2). Water depth was measured at each sweep location to calculate the volume of water sampled. Invertebrates were identified to an informative taxonomic resolution, which was usually genus but was sometimes family or species. Biomass was estimated by assigning each individual to a size class and then averaging over the 3 sampling locations to give an estimate of invertebrate biomass·volume^{-1}·wetland^{-1}·sampling round^{-1} (see Hornung & Foote, 2006).

We collected data on terrestrial vegetation using a quadrat every 5 m along a 100-m transect parallel to each wetland's edge. Each quadrat was a 1- × 10-m rectangle oriented perpendicular to the shoreline and abutting the wetlands edge. We visually estimated percent total vegetation cover and percent cover and height for the 3 most dominant plants for each quadrat, and then calculated an average percent vegetation cover and median height for each wetland. Dominant vegetation type was categorized into 5 groups: aquatic plants (*e.g.*, *Carex*, *Typha*), grasses and wildflowers (*e.g.*, *Poa*, *Gypsophila*), shrubs (*e.g.*, *Rhododendron*, *Salix*), conifers (*e.g.*, *Picea*), and deciduous trees (*e.g.*, *Populus*). We calculated the percent cover of each of these vegetation types for each quadrat and then calculated an average percent cover for each category from the 20 samples for each wetland. The vegetation type that had the highest percent cover average was designated as the dominant vegetation type for the wetland.

The length and width of all terrestrial woody debris within 10 m of the wetland edge was recorded and proportion cover calculated. However, we had to estimate the total woody debris for 2 wetlands. Only one-quarter of the wetland's edge was surveyed for one wetland; we assumed that the proportion of woody debris was similar around the remainder. The other wetland had too much woody debris to measure. We conservatively assigned this wetland a woody debris proportion cover of 0.01 (twice the amount of the next greatest value).

Finally, we recorded the presence or absence of beaver dams and beaver lodges (usually abandoned) on land within 10 m of the entire wetland perimeter. We included this variable because beaver structures are used as hibernation sites by western toad (C. Browne, unpubl. data), and the channels cut by beavers into pond edges provide wet access to forested edges and are used by tadpoles.

Presence of fish was not included as a variable because fish (brook stickleback, *Culaea inconstans*) were only present in 2 wetlands. Preliminary analysis of our data indicated that the inclusion of fish presence/absence did not increase the explanatory power of our models. Although the abundance of small-bodied fish has previously been found to influence the abundance of anuran amphibians in small boreal lakes in Alberta (Eaton *et al*., 2005), fish presence did not lead to the exclusion of any amphibian species from these systems or from our wetlands.

LANDSCAPE ENVIRONMENTAL VARIABLES

We used a land-cover classification geographical information system (GIS) layer to determine the proportion of cover in various land-class categories within 50-, 100-, 200-, 500-, 1000-, 2000-, and 5000-m buffers from the perimeter of each wetland (Environmental Systems Research Institute, 1999–2004). We chose the 7 landscape buffer sizes based on preliminary results from radio-tracking western toads in the aspen parkland and boreal regions of Alberta (C. Browne, unpubl. data) and estimates from the literature of dispersal distances for anurans (*e.g.*, Muths, 2003).

The initial land-cover classification was a raster layer (cell size 25 × 25 m) of 26 land classes created from a Landsat 7 Thematic Mapper (TM) satellite scene taken September 9, 1999 (Ducks Unlimited, 2003). We created buffers around each of the wetlands and used the thematic raster summary to calculate the number of cells of each land class within each buffer area (Beyer, 2004). Because some of our sites were less than 1 km apart, we had overlapping buffers for some sites at the larger landscape scales. To assess the potential effect of compromised independence or spatial autocorrelation, we included our UTM northings and eastings as factors in a curve-fitting regression analysis against the relative abundance data for each species (SPSS Inc., 1989–2007; $P > 0.5$ for all). We found these variables were not significant and excluded them from further analysis.

We identified 15 land classes (consolidated from 20 original classes) within the 5000-m wetland buffers (see Table I) based on those delineated by Ducks Unlimited (2003). We were not able to detect wetlands or other landscape features smaller than the raster layer cell size of 25 × 25 m.

LANDFORM

We identified the landform type of each site using surficial geology maps created by the Alberta Geological Survey (*e.g.*, Paulen, Pawlowicz & Fenton, 2004). Three geological landform types were represented at our 24 wetlands: outwash plains ($n = 7$), moraines ($n = 10$), and glaciolacustrine sites ($n = 7$). Outwash plains are relatively flat and consist of sands and other fine sediments. Moraines are piles of rocks, silts, and sands left behind during glacial retreat. They contain more depressions than the other 2 landforms. Glaciolacustrine sites are flat areas with clay and extensive peatlands.

DATA ANALYSES

Our data analysis included 2 steps for both the local scale and each of the 7 landscape scales. Firstly, we incorporated the environmental variables into a Principal Components Analysis (PCA; McCune & Mefford, 1999). Our PCAs accomplished multiple tasks. The analyses simultaneously ran 999 PCAs using randomized data and determined whether the amount of variance explained by the real data for each PC explained significantly more variation than the randomized data (to determine how well the PCs explained the variation in the environmental variable data set). To help interpret relationships between amphibians and landform type, we also performed a Multi-Response Permutation Procedure (MRPP) on the variables used for each of the 8 PCAs with pairwise comparisons to determine whether environmental variables distinguished among the 3 landform types at each landscape scale. Finally, we noted environmental variables showing high correlations ($R^2 \geq 0.5$) with the PC axes so that we could relate them back to amphibian occurrence data during our second step.

Secondly, for each amphibian species and at each scale, we used the first 3 PC axis scores as independent variables in a generalized linear model regression analysis (GLM testing main effects only; R Development Core Team, 2007) against relative abundance data for each wetland. There are 2 main reasons why we chose our PCA approach rather than directly entering the raw variables in a GLM. First, many of our variables were correlated and could not be included together in a GLM (Appendix I), and we did not want to make subjective decisions about which variables were more "important" than others. Second, there were many independent variables that we wanted to test, but only 24 ponds were sampled; therefore, we were limited in how many variables we could include in our GLM. By using PCA we reduced the variables into 3 main axes and, therefore, were able to examine all of the variables simultaneously in one GLM. Wood frog captures were normally distributed over wetlands, so the regressions assumed a Gaussian distribution and used an identity link function. However, the boreal chorus frog and western toad data included more zeros and small capture values than larger values; data for these species approximated negative binomial distributions. Thus, our regressions for these 2 species assumed this distribution and used a log-link function. We then compared delta Akaike's Information Criteria (ΔAIC; Burnham & Anderson, 2002) values among scales within each species to determine which set of environmental factors best explained amphibian relative abundance.

To help us interpret our results, we used Pearson's correlations between abundance data and each of the raw environmental variables. We also created partial plots for each significant variable to visually assess our statistical models. We used Cook's distance to determine if any outlier points exhibited a large degree of influence on the parameters for each of our models. We used ANOVA with an LSD *post hoc* test (SPSS Inc., 1989–2007) to determine if differences in amphibian abundances occurred among landform types. Kruskall–Wallis tests were used instead of ANOVA when abundance distributions were not normally distributed (SPSS Inc., 1989–2007).

Results

Relative abundance

We caught wood frogs at all 24 wetlands, boreal chorus frogs at 22 sites, and western toads at 20 sites. Mean captures per 10 h of searching were 26.79 (range: 4–60) for wood frog, 9.29 (0–70) for boreal chorus frog, and 8.38 (0–66) for western toad.

Environmental variables and PCAs

At the local scale, the first PC axis (PC1) was positively correlated with wetland depth and secchi depth and negatively correlated with DO. PC2 was positively correlated with conductivity, aquatic plant density, and TDS. PC3 was not significant at the local scale (Table II). For the landscape environmental variables, both closed deciduous vegetation and low shrub cover were important environmental variables explaining landscape variation in the PC1s of each scale (except the 5000 m scale), proportions of mesic herbaceous cover were prominent in PC2s, and the amount of urban habitat was important in either PC2s or PC3s (see Table II for the breakdown of influential environmental variables for the PCs at each scale).

Land cover occurring on the 3 landform types became more distinct as the scale of measurement increased (Table II). At 50–100 m scales, the moraine sites could be differentiated from the glaciolacustrine sites. At 200–500 m scales, moraine sites were also differentiated from outwash sites. At the 1000-m scale and larger, all the sites could be grouped by landform (see MRPP results in Table II).

Relationships between amphbians and environmental variables

We used ΔAICs to compare among the regression models: if ΔAIC of a model is less than 2, then there is substantial evidence supporting the validity of this model compared to others (Burnham & Anderson, 2002). For wood frog, the best model was decidedly the local one (ΔAIC = 0; Table III). The first 2 factors (PC1 and PC2) had significantly negative coefficients, meaning that wood frogs were more abundant in shallower wetlands with higher DO and lower conductivity, TDS, and aquatic plant density (Tables II and III). However, if we compare only among the nested landscape-scale models, the model that best explains the relative abundance of wood frog is the 500-m-scale model (only PC1 was significant; ΔAICs = 7.15; Table III). This result indicates that wood frogs are associated with closed deciduous and mixed forest and are negatively associated with open conifer or low shrub habitat (Tables II and III). The 1000-m-scale model produced similar results but had a slightly higher AIC value (Figure 1), suggesting that noise rather than new information was added at this larger spatial scale.

For boreal chorus frog, the best models described the 1000- and 2000-m scales (PC1 and PC3 were significant; ΔAICs = 0 and 1.15 respectively; Table III; Figure 1). High relative abundances of boreal chorus frog are therefore associated with closed deciduous forest, mixed forest, and urban habitat. Relative abundances were lower at sites that had higher proportions of open conifer and low shrub habitat (Tables II and III).

The relative abundance of western toad was best explained by using habitat data representing the 100-m scale (PC1 significant), followed by the 50-m (PC1 significant) and 5000-m scales (PC1 and PC2 significant; ΔAICs = 0, 0.85, and 1.01, respectively; Table III; Figure 1). At the smaller landscape scales, western toads were associated with closed deciduous and mixed forest. Relative abundance was positively associated with tall shrub habitat but showed a negative relationship with low shrub habitat (Tables II and III). At the 5000-m scale, relative abundance was again associated with closed deciduous forest, tall shrub habitat, mesic herbaceous vegetation, and moss. Toads were less abundant at wetlands with higher proportions of surrounding closed or open conifer stands, recently burned sites, pine, low shrubs, and, surprisingly, higher coverage by wetlands on the landscape (Tables II and III).

Based on Pearson correlations, wood frog and western toad abundance and DO were very weakly correlated compared to wetland depth or secchi depth (Table IV); therefore, depth was likely driving the relationship between abundance

TABLE II. Principal Components Analysis using local and landscape scale environmental variables. The variables surround 24 study wetlands at 8 increasing scales (radii, excluding the local scale). The variables listed have a high correlation ($R^2 \geq 0.5$) with each principal component (PC) and have positive correlations unless marked with a negative sign (–). We also present the amount of variation explained by that PC (% var) and a *P*-value describing whether the PC explains significantly more variation than 999 PCs using randomized data. Finally, our Multi Response Permutation Procedure (MRPP) shows that when the wetlands are labelled with their landform type, the ability to detect separate landform groups in the PCA scatter-plot is positively correlated with increasing scale of measurement (T-value). The MRPP pairwise comparison results demonstrate which groups can be detected at which scale. * denotes statistical significance at the α = 0.05 level.

	Variables listed have $R^2 \geq 0.5$ with each PC axis									
Scale (m)	PC1 variables	% var	*P*	PC2 variables	% var	*P*	PC3 variables	% var	*P*	Landform MRPP T (*P*)
Local	Wetland depth Secchi depth – DO	20	0.001*	Conductivity Aquatic plant density TDS	14	0.008*	NA	11	0.146	–0.384 (0.288) landform label does not create groups
50	– Low shrub Closed deciduous Mixed forest Tall shrub	32	0.001*	– Open conifer	21	0.002*	NA	11	0.994	–1.681 (0.065) moraine *versus* glacio-lacustrine
100	– Closed deciduous Low shrub	28	0.001*	Mesic herbaceous	24	0.001*	NA	12	0.863	–4.658 (0.002*) moraine *versus* glacio-lacustrine
200	–Closed deciduous Open conifer Low shrub – Mixed forest	27	0.002*	Mesic herbaceous	23	0.001*	NA	14	0.238	–5.829 (< 0.001*) moraine *versus* glacio-lacustrine and moraine *versus* outwash
500	Closed deciduous – Low shrub – Open conifer Mixed forest	33	0.001*	– Urban	16	0.163	NA	14	0.113	–6.384 (< 0.001*) moraine *versus* glacio-lacustrine and moraine *versus* outwash
1000	Closed deciduous – Low shrub – Open conifer Mixed forest	33	0.001*	– Wetlands	19	0.005*	Urban	14	0.038*	–6.321 (< 0.001*) all pairwise comparisons
2000	Closed deciduous – Low shrub	32	0.001*	Mesic herbaceous	28	0.001*	Urban	13	0.375	–6.339 (< 0.001*) all pairwise comparisons
5000	– Wetlands Moss Mesic herbaceous – Burnt Tall shrub – Pine	43	0.001*	– Closed deciduous Closed coniferous Open coniferous Low shrub	28	0.001*	Open deciduous	10	0.987	–5.806 (< 0.001*) all pairwise comparisons

and PC1. Of the local PC2 variables, wood frog abundance showed the strongest correlation with conductivity, while chorus frog abundance was more correlated with total dissolved solids; both species were least correlated with aquatic plant density (Table IV). At the landscape level, closed deciduous forest showed the strongest correlation with abundance of the PC1 variables for all 3 species (at the significant spatial scales; Table IV).

Partial plots for each of the wood frog models show a relatively even spread of data points (Figure 2), suggesting that our regressions did not violate any analytical assumptions. Outliers appear to exist in the chorus frog and western toad partial plots (Figure 2), but Cook's distance values for the data points were all less than 1, indicating that none of these points exhibits a large degree of influence on the parameters, and therefore they should be retained in the analysis. The only models with Cook's distance values greater than 1 were the 200 m wood frog, 200 m western toad, and 1000 m western toad models; we did not change our methodology to adjust these models because we wanted our models to be comparable and consistently analyzed.

RELATIONSHIPS BETWEEN AMPHIBIANS AND LANDFORM

We caught all species at wetlands within each landform from May through August. However, all species displayed higher relative abundances at moraine sites. Wood frogs were marginally more abundant in moraine than in glaciolacustrine sites but not outwash wetlands ($F_{2, 21} = 2.614$, $P = 0.097$, LSD *post hoc* test $P = 0.047$). Boreal chorus frogs were significantly more abundant in moraine sites than in either of the other landforms ($\chi^2_2 = 7.55$, $P = 0.023$), and western toads had significantly higher relative abundances in moraine than in outwash sites but not glaciolacustrine wetlands ($\chi^2_2 = 6.24$, $P = 0.044$; pairwise differences confirmed with a parametric ANOVA using LSD *post hoc*

TABLE III. Generalized Linear Model regression coefficients using the first 3 principal components (PCs) of a Principal Components Analysis (PCA; environmental variables at 24 study wetlands at 8 increasing scales) as independent variables against relative abundance of the 3 amphibian species. If the coefficient was significant at the $\alpha = 0.05$ level (denoted by a * next to the PC coefficient *P*-value), then we note the direction of the coefficient's correlation with the relative abundance data, otherwise "NA". We used this information to relate the important environmental variables that describe the PCs to the amphibian relative abundance data. We compared AIC and ΔAIC values to determine the scale at which the environmental data describes the relative abundance for each species. The models for which there is substantial evidence have their ΔAIC marked with "§". A "¤" indicates the best models of the landscape models for the wood frog.

Species	Scale (m)	PC1 coef. *P*	Coef. direction	PC2 coef. *P*	Coef. direction	PC3 coef. *P*	Coef. direction	AIC	ΔAIC
Wood frog	Local	0.033*	–	0.004*	–	0.222	NA	194.48	0 §
	50	0.853	NA	0.088	NA	0.341	NA	204.85	10.36
	100	0.216	NA	0.288	NA	0.109	NA	203.45	8.97
	200	0.072	NA	0.862	NA	0.473	NA	204.87	10.39
	500	0.015*	+	0.521	NA	0.701	NA	201.63	7.15 ¤
	1000	0.043*	+	0.876	NA	0.135	NA	202.12	7.64 ¤
	2000	0.089	NA	0.716	NA	0.353	NA	204.81	10.33
	5000	0.998	NA	0.205	NA	0.390	NA	206.60	12.12
Chorus frog	Local	0.223	NA	0.002*	–	0.019	NA	151.67	6.86
	50	0.987	NA	0.001*	+	0.499	NA	159.25	14.44
	100	0.005*	–	0.003*	+	0.357	NA	155.92	11.11
	200	0.002*	–	0.082	NA	<0.001*	+	150.84	6.03
	500	< 0.001*	+	0.004*	–	0.575	NA	148.42	3.61
	1000	< 0.001*	+	0.296	NA	<0.001*	+	144.81	0 §
	2000	< 0.001*	+	0.649	NA	0.002*	+	145.96	1.15 §
	5000	0.049*	+	0.027*	–	0.010*	+	154.83	10.02
Western toad	Local	0.029*	–	0.166	NA	0.319	NA	153.84	5.48
	50	< 0.001*	+	0.343	NA	0.235	NA	149.21	0.85 §
	100	< 0.001*	–	0.052	NA	0.105	NA	148.36	0 §
	200	0.040*	–	0.032*	–	0.996	NA	154.00	5.64
	500	0.023*	+	0.001*	+	0.496	NA	150.71	2.35
	1000	0.095	NA	0.138	NA	0.333	NA	157.88	9.52
	2000	0.003*	+	0.026*	+	0.634	NA	153.31	4.95
	5000	0.009*	+	0.001*	–	0.343	NA	149.37	1.01 §

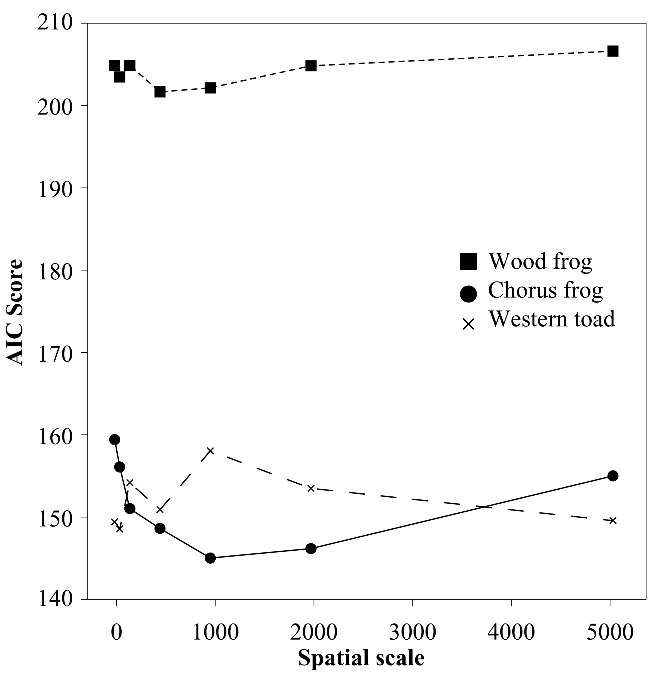

FIGURE 1. Model fit as described by Akaike's Information Criterion (AIC) score for each landscape spatial scale examined.

tests). The 2 frog species were caught more often in outwash sites than in glaciolacustrine plains, but the reverse was true for western toad (Figure 3).

Discussion

RELATIVE ABUNDANCE

Capture rates of amphibians (27 wood frogs, 9 boreal chorus frogs, and 8 western toads captured per 10 h of searching) were comparable to other sites in our region. Stevens, Paszkowski, and Stringer (2006) observed amphibians at the comparable rates of 30 wood frogs, 1 chorus frog, and 3 western toads per 10 h of searching in the boreal foothills region of Alberta. Surveys at 239 wetlands in the Aspen Parkland ecoregion in/near Elk Island National Park, Alberta from May to August 2003 captured amphibians at rates of 25 wood frogs, 17 boreal chorus frogs, and 8 western toads per 10 h of searching (C. Browne, unpubl. data). Paszkowski *et al.* (2002) captured wood frogs at rates of 40 frogs per 10 h of searching along streams in the boreal region of Alberta north of Wandering River; chorus frogs were not observed, and western toads were only heard calling at these sites.

SPATIAL SCALE

Our findings support the view that factors at multiple spatial scales influence patterns of anuran abundance. The abundance of wood frogs was more strongly related to local variables than landscape variables, but the reverse was true for boreal chorus frogs and western toads. This suggests that wood frog abundance is more strongly determined by the habitat features of breeding ponds than the terrestrial habitat used by juveniles and adults for most of the year. Other

TABLE IV. Pearson correlations between amphibian species abundance and raw environmental variables. Landscape variables were measured at 500 m for the wood frog, 1000 m for the chorus frog, and 100 m for the western toad, the scales at which our anuran abundance data is best described by the environmental variables.

Variables	Wood frog	Chorus frog	Western toad
Local variables			
Turbidity	–0.047	0.077	0.149
Chlorophyll-a	0.370	0.085	0.456
Conductivity	–0.548	–0.393	0.200
Dissolved oxygen	0.083	–0.204	0.067
PH	–0.225	–0.421	0.102
Water temperature	0.070	0.091	0.299
Submersed aquatic vegetation (SAV)	0.216	–0.300	0.068
Wetland depth	–0.408	0.011	–0.317
Secchi depth	–0.442	–0.062	–0.316
Secchi depth:wetland depth	–0.146	–0.618	0.116
Total nitrogen	0.087	–0.067	0.584
Total dissolved solids (TDS)	–0.450	–0.559	0.038
Total phosphorus	0.103	0.120	–0.151
Invertebrate biomass/volume	0.047	–0.015	0.016
Predatory invertebrate biomass/volume	0.484	0.381	0.295
Aquatic plant density	–0.465	–0.282	0.245
Woody debris	–0.254	–0.078	–0.063
Beaver structures	–0.506	–0.116	0.071
Percent vegetation cover	0.016	0.349	0.236
Median vegetation height	–0.343	–0.265	–0.033
Wetland area	–0.298	–0.168	–0.092
Wetland perimeter	–0.231	–0.185	–0.175
Landscape variables			
Closed conifer	–0.505	–0.366	–0.112
Open conifer	–0.385	–0.344	–0.095
Closed deciduous	0.492	0.417	0.517
Mixed forest	0.422	0.148	0.105
Low shrub	–0.481	–0.304	–0.441
Tall shrub	0.055	0.202	0.044
Moss	0.100	–0.008	–0.241
Mesic herbaceous	–0.189	–0.009	–0.309
Wet herbaceous	0.128	0.315	–0.103
Urban (roads and well pads)	0.137	0.405	–0.077
Agricultural areas	–0.130	–0.163	N/A
Young stands (burnt)	–0.001	0.017	–0.216
Wetlands	–0.275	–0.269	–0.015

studies have also found that the quality of breeding habitat is more influential than landscape variables for the wood frog (*e.g.*, Herrmann *et al.*, 2005). The reverse is likely true for chorus frogs and western toads. All 3 species showed stronger relationships (smaller *P*-values) with both local and landscape scale PC-axis variables than with landform. The relationship between anuran abundance and landform is interesting because it suggests we may be able to predict patterns of abundance to some extent based on a very coarse and easy-to-measure environmental variable. Relationships with landform likely reflect correlations between landform type and habitat variables at smaller scales (*e.g.*, deciduous forest cover, conductivity of wetlands) to which amphibians respond directly.

Each of the anuran species in our study responded to environmental variables at different spatial scales among the 7 landscape scales that we examined. The wood frog responded most strongly to variables at the 500-m scale, boreal chorus frog at the 1000-m scale, and western toad at the 100-m scale. This result is consistent with the fact that patterns of terrestrial habitat use differ among species (Rittenhouse & Semlitsch, 2007).

The pattern among AIC values and scales for the western toad was different from that of the 2 frog species. For the most part, frogs responded most strongly to a particular scale (lowest AIC value), and then each larger/smaller scale from that focal scale showed a weaker relationship (higher AIC value). Western toad, on the other hand, showed strong relationships to both very small (50 and 100 m) and very large scales (5000 m). We believe this pattern reflects the fact that western toads move between patches of essential habitat for breeding, foraging, and hibernation in their annual cycle, rather than using terrestrial habitat equally radiating from the breeding pond. The area within 100 m of a breeding site is likely important for adult amphibians during the breeding season, for YOY when they emerge, and for tadpoles because the immediate landscape influences local conditions (*e.g.*, shade from canopy, runoff, etc.) in nursery wetlands. However, after breeding, adult western toads may move long distances to reach preferred habitat patches (*e.g.*, Muths, 2003: 2324 m). Rittenhouse and Semlitsch (2007) examined the distribution of amphibians during the non-breeding season using kernel density estimation and found that kernel estimates for western toad did not peak near the breeding site, a pattern that also suggests

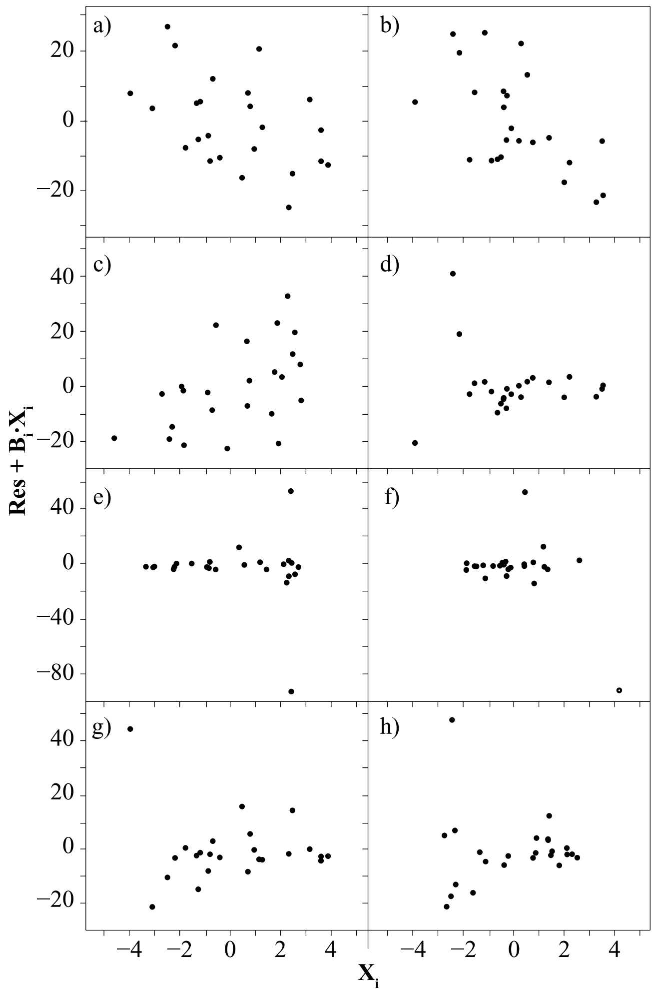

FIGURE 2. Partial plots for significant variables from our GLM analyses. The variable of interest is on the x-axis. The y-axis is ($Res + B_i*X_i$), where Res = the model residuals, B_i = the coefficient value for the variable of interest, and X_i = is the variable of interest. Partial plots are of a) wood frog local PC1, b) wood frog local PC2, c) wood frog 500 m landscape PC1, d) chorus frog local PC2, e) chorus frog 1000 m landscape PC1, f) chorus frog 1000 m landscape PC3, g) western toad local PC1, and h) western toad 100 m landscape PC1.

that western toads travel to specific resources that are not evenly distributed on the landscape and not necessarily located near the breeding site.

Wood frog relative abundance was best described by the local scale variables in our study, but of the landscape scales, the model for the 500-m scale was the most parsimonious. Wood frog abundance was likely most strongly related to this landscape scale because wood frogs tend to use terrestrial habitat within 500 m of their breeding site (*e.g.*, Rittenhouse & Semlitsch, 2007: 394 m). Boreal chorus frogs in this study responded most strongly to the 1000-m scale. Little is known about the movement abilities/patterns of boreal chorus frogs, but Spencer (1964) examined boreal chorus frog movements in montane Colorado and found they moved up to 750 m from breeding ponds. Our results suggest that the most explanatory spatial scales identified by models of anuran abundance may be related to the amount of habitat surrounding breeding ponds used during the annual cycle of particular species.

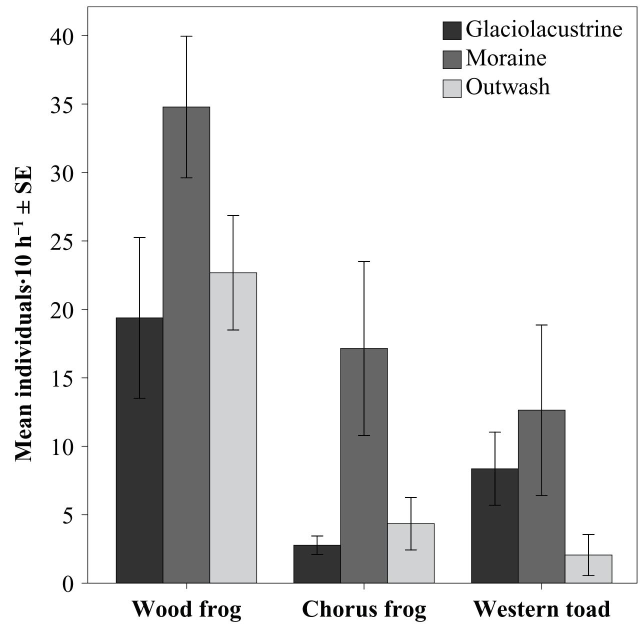

FIGURE 3. Differences among landforms in mean relative abundance of each species.

Our results are comparable to other multi-scale studies that have studied ecologically similar species. Price *et al.* (2004) found results for the American toad (*A. americanus*) similar to our findings for western toad: American toad occurrences were best predicted by variables at the 100- and 3000-m spatial scales (*versus* 500 or 1000 m) along the US shores of Lake Michigan and Lake Huron. Price *et al.* (2004) found that the 500-m scale was best for predicting patterns of abundance for western chorus frogs (*Pseudacris triseriata*). This spatial scale was smaller than those identified by our models for boreal chorus frog; however, the greatest recorded distance from a breeding pond is smaller for the western chorus frog (Kramer, 1973: 213 m) than for boreal chorus frog (Spencer, 1964: 750 m), so this disagreement may reflect differences in movement patterns between these 2 species. Gibbs, Whiteleather, and Schueler (2005) found surprisingly large spatial scales (5–10 km) to be most significant for amphibians in New York. Their methodology differed from ours in that they examined changes in presence/absence of amphibians at wetlands within a 21–29-y period. Therefore, extinction–recolonization dynamics would have influenced their dependent variables, whereas our relative abundance values reflected contemporary population dynamics and habitat conditions.

HABITAT RELATIONSHIPS

LOCAL ENVIRONMENTAL VARIABLES

All 3 species showed significant relationships with local wetland variables (Table III). Wood frog and western toad abundances were negatively related to wetland depth and positively related to dissolved oxygen (Tables II, III). Shallower wetlands tend to be warmer during the day (Barandun & Reyer, 1997), and both warm temperatures and high oxygen levels facilitate tadpole growth (Collins, 1979; Feder & Moran, 1985). For the western toad, Holland (2002) investigated breeding site preference in Colorado and found that water temperature and depth were key variables in site selection, with toads preferring warmer temperatures and waters ≤ 10 cm deep for egg deposition. Conversely, Petranka, Kennedy, and Murrey (2003) and Skidds *et al.*(2007) found wood frogs to be positively associated with pond depth in North Carolina and Rhode Island, respectively; however, the majority of their ponds were temporary, whereas our ponds were permanent. Our results suggest that wood frogs prefer shallower wetlands provided that the wetland hydroperiod is sufficient for larval development. Previous studies have also found positive relationships between dissolved oxygen and presence/abundance (adult or tadpole) or tadpole growth for wood frogs (*e.g.*, Stevens, Paszkowski & Scrimgeour, 2006) and toads of the genus *Anaxyrus* (*e.g.*, Noland & Ultsch, 1981), but others have found no relationship (*e.g.*, Schiesari, 2006).

The relative abundances of wood frog and boreal chorus frog were negatively correlated with conductivity, total dissolved solids, and aquatic plant density (Tables II, III). Conductivity is often correlated with total dissolved solids, dissolved organic particles, mineral particles, or eutrophication (Pellet, Hochn & Perrin, 2004). High conductivity could be the result of local soil qualities (*e.g.*, alkaline soils), disturbance, runoff, or increasing concentrations of solutes as water seasonally evaporates and is not replaced (Welch & MacMahon, 2005). Significant negative relationships between conductivity and anuran species richness have also been reported in other studies (*e.g.*, Hecnar & M'Closkey, 1996). Western toads may be more tolerant to water with high ion concentrations than wood frogs and boreal chorus frogs (toads have been observed to swim across brackish water; Taylor, 1983), which may explain why this species did not show the same negative relationships with local PCA axis 2. We found a negative relationship between frog abundance and aquatic plant density, but others have found positive relationships for the wood frog (*e.g.*, Stevens, Paszkowski & Scrimgeour, 2006). This unexplained result may be an artifact if conductivity is actually driving the relationship between frog abundance and PCA axis 2 (correlations between frog abundance and conductivity are higher than correlations between abundance and aquatic plant density).

LANDSCAPE ENVIRONMENTAL VARIABLES

For the spatial scales that most successfully predicted abundance for each species, wood frog, boreal chorus frog, and western toad were positively associated with closed deciduous forest cover and negatively associated with low shrub cover (Tables II, III). Wood frog and chorus frog also showed a positive relationship with mixed forest and a negative relationship with open conifer cover. Constible, Gregory, and Anholt (2001) also found wood frog, but not boreal chorus frog, to be associated with deciduous forest in the boreal region of northeastern Alberta. Other positive relationships with deciduous and mixed forest cover have been reported for the wood frog, American toad, and spring peeper (*P. crucifer*) in New York State (Gibbs, Whiteleather & Schueler, 2005) and New Brunswick (Waldick, Freedman & Wassersug, 1999).

Terrestrial invertebrate density is positively related with density of understory vegetation, and understory is greater in deciduous than coniferous stands (Willson & Comet, 1996; Ferguson & Berube, 2004). Ferguson and Berube (2004) found that shrub habitat had lower invertebrate abundance than deciduous forest (but still higher than coniferous forest) in the boreal region of northwestern Ontario. Invertebrates are food for frogs and toads; therefore, density of understory vegetation and invertebrates can explain the patterns we observed. If invertebrate abundance in shrub stands is intermediate between deciduous and coniferous stands, then shrub stands may offer a habitat of intermediate quality for foraging by amphibians. Furthermore, habitat types with a greater density of understory vegetation could provide more cover to protect amphibians from predation and desiccation.

Chorus frogs showed a positive relationship with urban cover (roads and well pads) at the 1000-m landscape scale (Tables II, III). We expected either a negative relationship or no relationship with urban habitat for all 3 amphibian species since traffic volumes can be a serious threat to amphibian populations (Fahrig *et al.,* 1995). However, traffic volumes are relatively low in our study region. The positive relationship between chorus frogs and roads and wells could simply reflect the species' preference for open habitat, or ditching around construction may provide breeding habitat. Eigenbrod, Hecnar, and Fahrig (2008) found a similar unexplained positive relationship between traffic density and abundance for wood frog in Ontario and speculated that features associated with roads, such as ditches, attracted frogs. Alternatively, urban cover may have been related to other variables that influence chorus frog abundance; for example, urban cover was absent from all glaciolacustrine sites, and this landform appears to offer poor habitat for the species (*i.e.*, pond conductivity is high and deciduous forest cover is low; Appendix II).

We were surprised that the amount of wetland cover surrounding our ponds was not a significant factor boosting abundance and in fact was negatively associated with western toad relative abundance at the 5000-m scale, since wetland connectivity is important for amphibian dispersal (*e.g.*, Elmberg, 1993). We suspect that amphibian abundance in the Utikuma landscape is limited not by the simple number of wetlands but by local pond conditions and the amount of suitable terrestrial habitat for foraging and hibernation.

LANDFORM

Johnson (1980) suggested that habitat selection is a hierarchical process in which observation of relationships can change along a continuum of spatial scales. One of the basic principles of hierarchy theory is that habitat selection is constrained by the level above and clarified by the level below (Allen & Starr, 1982). Based on the hierarchy concept, we believe that the relationships we observed between anuran abundance and landform are the result of correlations with landform and environmental variables at smaller spatial scales (*e.g.*, our local or landscape-scale variables) that directly influence anuran abundance. The most parsimonious explanation of why wood frogs and chorus frogs are most abundant at moraine sites and least abundant at glaciolacustrine sites is that deciduous forest cover is significantly more abundant at moraine sites and least abundant at glaciolacustrine sites (Appendix II), and this variable is positively related with frog abundance (Tables II, III, and IV). In contrast, viewing western toad abundance in light of associations between our environmental variables and landform types (Appendix II) does not offer a similar clear explanation for why this species should be least abundant at outwash sites.

Conclusion

We found that environmental variables measured at different spatial scales differ in their ability to predict anuran abundance on the Boreal Plain and that each of 3 species of anurans responded differently in terms of which spatial scale best predicted abundance. Many researchers assume that most anuran activity occurs within 1 km of wetlands and set their spatial scale of study at this distance (*e.g.*, Knutson *et al.,* 1999). A spatial scale of 1 km would have produced significant models for 2 of the species in our study, but variables measured at a 1-km scale were not significant for the western toad. Researchers and managers must have knowledge of the biology of species of concern in order to study or conserve populations and communities of these ecologically sensitive animals (Hopkins, 2007). Even in a simple amphibian community characterized by wide-spread, generalist species, we documented very different responses among species regarding the spatial scales that affected abundances; presumably, in a richer community with habitat specialists these patterns would be even more obvious.

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Appendix I. Correlation matrix of local pond variables and landscape variables (measured at the 500-m scale).

	Turb	Chl-a	Cond	DO	pH	Temp	SAV	Depth	Secchi	S:D	TN	TDS
Turb	1											
Chl-a	0.098	1										
Cond	–0.143	0.095	1									
DO	0.232	0.350	0.116	1								
PH	0.014	0.266	0.351	0.517	1							
Temp	0.122	0.114	0.210	–0.295	–0.041	1						
SAV	–0.073	0.403	–0.280	0.302	0.201	–0.119	1					
Depth	–0.065	–0.527	0.215	–0.585	–0.147	0.223	–0.438	1				
Secchi	–0.074	–0.531	0.250	–0.560	–0.114	0.215	–0.416	0.995	1			
S:D	–0.128	0.123	0.264	0.412	0.309	–0.173	0.319	–0.366	–0.278	1		
TN	0.036	0.657	0.458	0.116	0.269	0.219	0.218	–0.295	–0.291	0.13	1	
TDS	–0.126	–0.033	0.648	0.091	0.609	0.011	–0.130	0.125	0.175	0.401	0.287	1
TP	0.292	–0.116	–0.018	0.214	0.148	0.120	0.000	–0.128	–0.125	0.076	0.078	0.024
Invert	0.002	0.225	0.554	0.399	0.299	0.254	–0.192	–0.217	–0.211	0.134	0.381	0.213
PredInvert	0.388	0.280	–0.189	0.427	0.115	0.298	0.072	–0.449	–0.460	0.081	0.170	–0.224
APD	–0.113	0.023	0.640	–0.032	0.227	0.243	–0.170	0.105	0.137	0.298	0.274	0.417
Wood	–0.197	–0.134	–0.015	–0.240	0.093	0.147	0.071	0.339	0.359	0.102	–0.136	–0.034
Beaver	0.354	–0.352	0.172	–0.188	–0.130	0.073	0.054	0.427	0.427	–0.134	0.042	0.000
VegCov	0.130	–0.120	–0.071	0.068	–0.282	0.057	–0.489	–0.129	–0.132	0.080	–0.233	–0.339
VegHeight	–0.111	–0.141	0.006	0.128	0.123	–0.082	–0.078	–0.112	–0.098	0.173	–0.227	0.070
Area	0.040	–0.174	0.070	0.078	0.282	–0.109	–0.199	0.216	0.210	–0.236	–0.224	0.136
Perimeter	–0.022	–0.291	0.041	0.091	0.171	–0.175	–0.170	0.238	0.251	–0.030	–0.410	0.150
Cconifer	0.102	–0.098	0.505	0.259	0.108	–0.127	–0.097	0.123	0.148	0.181	–0.014	0.116
Oconifer	–0.061	–0.163	0.362	–0.439	–0.006	0.111	–0.111	0.338	0.357	0.024	0.011	0.365
Cdecid	0.034	0.220	–0.420	0.233	–0.186	0.141	0.082	–0.398	–0.420	–0.017	0.081	–0.455
Mixed	0.003	0.106	–0.351	0.382	–0.034	–0.160	0.114	–0.518	–0.501	0.368	–0.025	–0.125
Lshrub	0.055	–0.137	0.435	–0.301	0.176	–0.062	–0.213	0.446	0.448	–0.205	0.004	0.519
Tshrub	–0.350	–0.297	–0.039	0.030	0.136	–0.471	–0.135	0.086	0.099	0.169	–0.142	0.152
Moss	–0.067	0.203	0.339	0.319	0.363	–0.051	–0.105	–0.042	–0.034	0.113	0.220	0.308
MesicHerb	–0.136	–0.210	0.329	0.093	0.199	–0.296	–0.010	0.312	0.324	0.014	–0.149	0.278
WetHerb	0.224	–0.153	–0.114	–0.040	0.030	0.283	–0.362	0.221	0.191	–0.328	–0.048	–0.234
Urban	0.429	–0.247	–0.157	0.215	0.129	0.237	–0.071	0.132	0.141	0.018	–0.340	0.000
Agri	0.316	–0.233	–0.029	–0.178	–0.106	0.216	–0.155	0.453	0.435	–0.429	–0.200	0.000
Burnt	0.143	–0.262	–0.284	–0.041	0.129	–0.097	0.004	0.382	0.371	–0.268	–0.543	–0.047
Wetlands	0.192	0.172	–0.044	0.029	0.241	–0.094	0.324	0.136	0.113	–0.348	–0.019	–0.022

	TP	Invert	PredInvert	APD	Wood	Beaver	VegCov	VegHeight	Area	Perimeter	CConifer
TP	1										
Invert	0.403	1									
PredInvert	0.596	0.332	1								
APD	0.156	0.454	0.064	1							
Wood	–0.047	–0.133	0.013	0.156	1						
Beaver	0.176	–0.158	–0.068	0.202	0.145	1					
VegCov	0.053	0.178	0.288	–0.074	0.152	–0.192	1				
VegHeight	–0.169	–0.129	–0.174	0.033	0.269	–0.017	0.191	1			
Area	–0.140	–0.285	–0.309	–0.356	–0.163	–0.127	–0.022	0.172	1		
Perimeter	–0.124	–0.323	–0.211	–0.388	–0.072	–0.065	0.080	–0.032	0.830	1	
Cconifer	–0.160	0.306	–0.378	0.353	–0.161	0.194	–0.021	0.310	0.210	0.052	1
Oconifer	–0.039	–0.057	–0.531	0.358	–0.290	0.130	–0.369	–0.035	0.214	0.120	0.377
Cdecid	0.062	0.017	0.583	–0.309	0.231	–0.200	0.399	0.000	–0.341	–0.310	–0.501
Mixed	–0.031	–0.049	0.283	–0.430	–0.002	–0.491	0.359	0.217	–0.067	–0.065	–0.195
Lshrub	–0.094	–0.071	–0.528	0.142	–0.178	0.207	–0.383	–0.131	0.427	0.423	0.231
Tshrub	0.062	0.048	0.010	–0.020	0.253	–0.025	0.177	–0.139	–0.140	0.130	–0.241
Moss	0.336	0.520	0.160	0.292	–0.168	–0.222	–0.173	–0.277	–0.078	–0.132	0.105
MesicHerb	–0.093	–0.030	–0.202	–0.026	–0.022	0.213	–0.150	–0.108	0.313	0.564	0.173
WetHerb	0.645	0.204	0.606	0.041	0.274	0.149	0.400	–0.136	0.001	–0.014	–0.362
Urban	0.580	0.122	0.547	–0.088	0.126	0.044	0.088	–0.279	0.020	0.219	–0.311
Agri	–0.007	–0.197	–0.208	–0.313	–0.122	0.162	–0.266	–0.204	0.437	0.364	–0.013
Burnt	–0.169	–0.452	–0.160	–0.484	0.056	0.005	–0.041	0.010	0.589	0.713	–0.039
Wetlands	0.274	–0.441	–0.655	0.443	–0.272	–0.462	–0.462	0.082	0.131	–0.012	0.211

APPENDIX I. Continued.

	Oconifer	Cdecid	Mixed	LShrub	Tshrub	Moss	MesicHerb	WetHerb	Urban	Agri	Burnt
Oconifer	1										
Cdecid	–0.884	1									
Mixed	–0.618	0.656	1								
Lshrub	0.752	–0.858	–0.969	1							
Tshrub	–0.344	0.076	0.161	–0.141	1						
Moss	–0.059	–0.075	0.102	–0.045	0.323	1					
MesicHerb	0.174	–0.515	–0.316	0.491	0.479	0.205	1				
WetHerb	–0.308	0.321	–0.107	–0.196	0.160	0.064	–0.081	1			
Urban	–0.197	0.139	0.067	–0.050	0.051	0.217	0.120	0.509	1		
Agri	0.185	–0.199	–0.247	0.403	–0.384	–0.091	0.030	0.026	0.409	1	
Burnt	0.082	–0.306	–0.119	0.365	0.078	–0.211	0.543	0.073	0.301	0.326	1
Wetlands	0.274	–0.441	–0.655	0.443	–0.272	–0.138	0.108	–0.092	–0.114	0.280	0.252

Note: Turb = turbidity, Chl-a = chlorophyll-a, Cond = conductivity, DO = dissolved oxygen, Temp = water temperature, SAV = submersed aquatic vegetation, Depth = wetland depth, Secchi = secchi depth, S:D = secchi depth:wetland depth, TN = total nitrogen, TDS = total dissolved solids, TP = total phosphorus, Invert = invertebrate biomass/volume, PredInvert = predatory invertebrate biomass/volume, APD = aquatic plant density, Wood = woody debris, Beaver = beaver structures, VegCov = percent vegetation cover, VegHeight = median vegetation height, Area = wetland area, Perimeter = wetland perimeter, Cconifer = closed conifer, Oconifer = open conifer, Cdecid = closed deciduous, Mixed = mixed forest, Lshrub = low shrub, Tshrub = tall shrub, MesicHerb = mesic herbaceous, WetHerb = wet herbaceous, Agri = agricultural areas, Burnt = young stands.

APPENDIX II. Mean ± SE of local and landscape (measured at the 500-m scale) environmental variables and dependent variables (anuran abundance) among the landform types glaciolacustrine (n = 7), moraine (n = 10), and outwash (n = 7). Units for each variable are listed in Table I. Kruskal–Wallis tests were conducted to determine if significant differences existed among landform types for each variable. Significant differences were not found unless indicated by a * (P < 0.05), ** (P < 0.01), or *** (P < 0.001).

Variables	Glaciolacustrine	Moraine	Outwash
Local variables			
Turbidity	5.23 ± 0.55	6.15 ± 0.62	7.24 ± 0.30
Chlorophyll-a	11.35 ± 3.52	16.48 ± 3.80	9.37 ± 2.79
Conductivity*	0.20 ± 0.03	0.12 ± 0.02	0.11 ± 0.02
Dissolved oxygen	7.37 ± 2.06	10.00 ± 1.47	10.09 ± 1.45
pH	9.01 ± 0.16	9.02 ± 0.16	8.77 ± 0.31
Water temperature	20.78 ± 0.86	21.52 ± 0.43	20.08 ± 0.55
Submersed aquatic vegetation (SAV)	2.33 ± 0.39	2.50 ± 0.26	2.86 ± 0.33
Wetland depth	72.19 ± 5.97	59.40 ± 9.72	74.43 ± 11.7
Secchi depth	72.19 ± 5.97	58.24 ± 9.25	73.49 ± 11.4
Secchi depth:wetland depth	1.00 ± 0.00	0.99 ± 0.01	0.99 ± 0.01
Total nitrogen	2272 ± 157	2032 ± 187	1656 ± 169
Total dissolved solids (TDS)	0.13 ± 0.02	0.09 ± 0.01	0.09 ± 0.01
Total phosphorus	73.01 ± 10.7	81.72 ± 32.29	58.01 ± 11.5
Invertebrate biomass/volume*	11.22 ± 2.67	9.80 ± 1.91	4.81 ± 0.83
Predatory invertebrate biomass/volume**	1.43 ± 0.18	4.16 ± 0.78	1.72 ± 0.53
Aquatic plant density**	0.74 ± 0.09	0.52 ± 0.05	0.36 ± 0.05
Woody debris	0.75 ± 0.21	155.7 ± 106	32.10 ± 14.35
Beaver structures	0.86 ± 0.14	0.70 ± 0.15	1.00 ± 0.00
Percent vegetation cover	88.61 ± 2.73	94.55 ± 1.76	90.14 ± 3.06
Median vegetation height	150.0 ± 39.0	175.5 ± 74.9	157.5 ± 82.9
Wetland area	88 177 ± 18 044	63 083 ± 20 084	135 086 ± 59 563
Wetland perimeter	1282 ± 101	1228 ± 201	1841 ± 394
Landscape variables			
Closed conifer*	0.081 ± 0.022	0.035 ± 0.007	0.062 ± 0.012
Open conifer**	0.443 ± 0.050	0.142 ± 0.017	0.279 ± 0.055
Closed deciduous**	0.099 ± 0.031	0.484 ± 0.035	0.256 ± 0.085
Mixed forest	0.061 ± 0.010	0.102 ± 0.009	0.079 ± 0.020
Low shrub*	0.090 ± 0.013	0.031 ± 0.005	0.077 ± 0.022
Tall shrub	0.113 ± 0.021	0.113 ± 0.013	0.092 ± 0.020
Moss	0.006 ± 0.002	0.005 ± 0.001	0.003 ± 0.001
Mesic herbaceous	0.062 ± 0.012	0.033 ± 0.005	0.058 ± 0.018
Wet herbaceous	0.001 ± 0.000	0.004 ± 0.002	0.001± < 0.001
Urban (roads and well pads)	0	0.008 ± 0.004	0.011 ± 0.004
Agricultural areas	0	< 0.001±< 0.001	0.001± < 0.001
Young stands (burnt)	0.002 ± 0.001	0.003 ± 0.001	0.005 ± 0.001
Wetlands	0.043 ± 0.018	0.040 ± 0.012	0.076 ± 0.033
Dependent variables			
Wood frog	19.43 ± 5.86	34.80 ± 5.16	22.71 ± 4.17
Chorus frog*	2.86 ± 0.67	17.20 ± 6.34	4.43 ± 1.91
Western toad*	8.43 ± 2.66	12.70 ± 6.21	2.14 ± 1.50

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