Herpetological Conservation and Biology 13(2):317–330.
Submitted: 5 September 2017; Accepted: 30 May 2018; Published 31 August 2018.

Microhabitat Selection by Western Toads (*Anaxyrus boreas*)

Constance L. Browne[1] *and Cynthia A. Paszkowski*

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada
[1]*Corresponding author, e-mail: cbrowne@unb.ca*

***Abstract.*—We examined microhabitat selection by adult Western Toads (*Anaxyrus boreas*) from May to October across 3 y at three areas (two forested, one agricultural) in north-central Alberta, Canada. We predicted that toads would selectively use microsites with warm temperatures in environments with cover and abundant prey, such as provided by woody debris and understory vegetation, with access to water/moisture, and in proximity to breeding and overwintering sites. We collected microhabitat data from sites used by toads, located with radio-telemetry, and from paired random locations. We constructed resource selection function (RSF) models using conditional logistic regression to examine shelter-type selection, and microhabitat selection using 16 environmental variables. We created separate RSF models for each area, year, season, and sex combination, yielding 23 microhabitat selection models and 12 shelter selection models. Microhabitat selection by Western Toads was complex and differed with season and sex. Contrary to expectations, toads did not select warmer microsites, which could indicate that experiencing relatively high temperatures was less important than other requirements, or that toads were shuttling between warm basking areas and cooler, sheltered microsites. Toads did select microsites that provided moist substrates and shelter, such as woody debris, tunnels, and shrub cover, and offered proximity to breeding ponds and overwintering sites. Woody debris and tunnels were the most consistently selected microhabitat features. Thus, land management practices (e.g., retention of downed wood, conservation of burrowing mammals) that preserve these key features could promote the persistence of Western Toad populations.**

Key Words.—amphibian; Boreal Toad; *Bufo boreas*; habitat; moisture; radio-telemetry; shelter; woody debris

Introduction

Resource Selection Functions (RSF) can be used to calculate the relative probabilities of selection of available habitats by an organism (Boyce and McDonald 1999; Manly et al. 2002; Johnson et al. 2006). Investigations of habitat selection are complicated because selection often differs among sex, age class, season, study areas, and even the scale of analysis (Turner 1989; Schooley 1994; Mysterud and Ims 1998; Muths 2003). For many amphibian and reptile species, every female has the opportunity to find at least one mate. Males may mate more frequently than females (Bull and Carey 2008) with some having multiple mating opportunities while other males may have none (Wilbur et al. 1978). For this reason, the habitat choices made by males and females could differ (Bartelt et al. 2004). Females might choose habitats with good foraging opportunities to maximize energy storage and gamete production. Males might make habitat choices to maximize mating opportunities. Both sexes must also balance the need to maximize current reproduction with survival to allow future opportunities for reproduction. Additionally, habitat selection could differ between sexes because of physical differences and limitations in sexually dimorphic species (Liang 2013).

Habitat needs may change seasonally, and this can result in changes in habitat use (Beck and Jennings 2003). The abiotic conditions of habitats selected can profoundly affect fitness of organisms, especially of ectotherms (Huey 1991). Freeze intolerant amphibian species living in northern environments must find shelter to survive cold winter weather (Storey and Storey 1986). Additionally, environmental moisture levels can strongly affect activity patterns of amphibians (Gibbons and Bennett 1974; Brattstrom 1979).

Selection occurs when essential habitat components are limited. Selection often differs among geographic locations because of differences in the proportions and configuration of habitat types (Mysterud and Ims 1998). Thus, it is important to consider context when interpreting patterns of habitat selection. Amphibians and reptiles in temperate climates require habitat suitable for overwintering, breeding, and foraging within an area accessible based on their movement capabilities. They may also require movement corridors if essential habitat components are separated by inhospitable habitat (Rothermel and Semlitsch 2002).

Habitat selection can also change depending on the scale of analysis (Turner 1989; Wiens 1989; Boyce 2006). Johnson (1980) described four orders of selection processes: (1) First-order selection: Geographic range of a species, (2) Second-order selection: Home range (or components within the range of the local population), (3) Third-order selection: Habitat components within the home range, and (4) Fourth-order selection: Food items (or microhabitat elements). A critical decision in designing an RSF is what to include as available habitat

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(Manly et al. 2002; Northrup et al. 2013). As selection occurs at multiple scales, the area from which available points are drawn must fit the research question to yield valid conclusions (Johnson 1980; Boyce et al. 2003; Boyce 2006). Alternatively, multigrain models can be used and may provide higher predictive accuracy under some circumstances (e.g., fragmented landscapes, highly vagile species; Meyer and Thuiller 2006). A variety of statistical approaches are appropriate for RSF analyses (Manly et al. 2002; Pearce and Boyce 2006; Lele 2009), but logistic regression models are most commonly used for finer-grain RSFs (i.e., 90% of 341 studies; Meyer and Thuiller 2006).

Our goal was to examine habitat use and selection by Western Toads (*Anaxyrus boreas*) to assess which features are essential and limited. Previously, we described overwintering sites used by Western Toads (Browne and Paszkowski 2010a) and examined land-class selection during the active season within the range of the local population (second-order selection of Johnson 1980; Browne 2010), and land-class selection during the active season within the home range of individuals (third-order selection of Johnson 1980; Browne 2010; Browne and Paszkowski 2014) at three study areas. In the current study, we examine microhabitat selection (fourth-order selection of Johnson 1980) by Western Toads during the active season, in the same areas investigated in the previous studies, to assess whether similar essential habitat components are limited across different landscapes in north-central Alberta, Canada. We chose a matched case, used-available design because to examine fourth-order selection, used points must be paired with available points dictated by the movement abilities of the study animal at this fine spatial scale.

We hypothesize that Western Toads select microsites that provide opportunities for growth (including appropriate thermal and moisture conditions) and protection from predators in proximity (based on movement capabilities of the toad) to breeding and overwintering locations. We predict that toads will selectively use microsites with warm temperatures in environments with cover and abundant prey, such as provided by woody debris and understory vegetation. However, we expected these patterns to change during the breeding and pre-hibernation seasons when toads may be less selective as they are required to move to/from locations, such as breeding ponds and overwintering sites, that fulfill other specialized, biological needs. We also predict that during dry periods, toads will focus more strongly on microsites that minimize water loss.

Materials and Methods

Study areas.—We tracked toads in three areas of north-central Alberta, Canada, that differed in land use. The Parkland study area was within the Aspen Parkland natural region and within Elk Island National Park (EINP; http://www.albertaparks.ca/media/442827/nsr2005_final_letter.pdf). This study area was centered on two shallow lakes (10–20 ha) and primarily surrounded by upland forest (Quaking Aspen, *Populus tremuloides*, Balsam Poplar, *P. balsamifera*, White Spruce, *Picea glauca*, Hazelnut, *Corylus cornuta*) and marsh. At EINP, the mean daily average temperature was -12° C for January and 17° C for July, and mean yearly precipitation was 482 mm from 1981–2010 (http://climate.weather.gc.ca/climate_normals/index_e.html).

The Pasture study area was 10 km west of our Parkland area in an agricultural landscape with patches of forest and peatland. Agricultural uses included cattle grazing, cultivation of hay and crops (wheat, barley, oats, canola, timothy, alfalfa), and rural housing. Forest patches included *Populus tremuloides*, *P. balsamifera*, *Picea glauca*, Black Spruce (*P. mariana*), Paper Birch (*Betula papyrifera*), Tamarack (*Larix laricina*), and Jack Pine (*Pinus banksiana*). This study area was centered on four man-made ponds (0.09–0.4 ha) in an inactive sand quarry that was sparsely vegetated and used for Cattle (*Bos taurus*) grazing later in the season.

The Boreal Forest study area was located north of Lac La Biche, approximately 150 km north of our Parkland area, and within the Boreal Forest natural region (http://www.albertaparks.ca/media/442827/nsr2005_final_letter.pdf). This region is influenced by the forestry and oil/gas industries (e.g., forest cut-lines made during seismic exploration, pipelines) and comprised mostly shrub swamps, peatland, upland boreal mixed-wood forest, and forestry cut-blocks. Common tree/shrub species included *Populus tremuloides*, *P. balsamifera*, *Picea glauca*, *P. mariana*, *B. papyrifera*, *L. laricina*, *Pinus banksiana*, Willow (*Salix* spp.), and Dwarf Birch (*B. nana*). This study area was centered on a 0.07-ha, shallow stream-fed pond located within a major utility corridor and next to a gravel road. At the St. Lina weather station (86 km from our Boreal Forest area), the mean daily average temperature was -14° C for January and 16° C for July, and mean yearly precipitation was 355 mm from 1981–2010 (http://climate.weather.gc.ca/climate_normals/index_e.html). Our Boreal Forest area was typically cooler than our Parkland and Pasture areas during the active season (Appendix 1). For more details, see Browne and Paszkowski (2010a, 2014).

Active period seasons.—We divided the active period into three seasons based on our observations of toad behavior: breeding (May-June), foraging (July-August), and pre-hibernation (September-October). Breeding season was the period when most toads congregated around breeding ponds. The pre-hibernation season

began when most toads moved to the vicinity of their hibernation sites (Browne and Paszkowski 2010b) and increased their use of underground retreats. Toads arrived at hibernacula gradually from 27 August to 10 October; arrival dates did not differ significantly among study areas or years (Browne and Paszkowski 2010b).

Radio-telemetry.—We captured adult toads during their active periods (May to October) either at breeding ponds (78%) or opportunistically while tracking other individuals. We worked at the Parkland and Pasture areas in 2004, the Boreal Forest area in 2005, and the Pasture area in 2006. We measured snout-urostyle length (SUL) using a ruler (to nearest mm), mass using a spring scale (to nearest gram; Pesola, Schindellegi, Switzerland), and recorded sex of each toad at the time of capture. We gave toads we captured between May and August unique toe clips (one or two toes; thumbs never clipped) for identification and age determination via skeletochronology (Chris Garrett, unpubl. data; Michelle Mark, unpubl. data).

We followed methods described by Bartelt and Peterson (2000) for attaching radio transmitters. We used transmitter models BD-2, BD-2T, and PD-2 (1.0–2.3 g; Holohil Systems Ltd., Carp, Ontario, Canada), which had minimum battery lives of 28 d to 3 mo. We attached transmitters to waist belts made of soft surgical-grade polyethylene tubing (outside diameter = 0.965 mm; CA-63018-667, VWR International, Edmonton, Alberta, Canada) and a large flyline eyelet (size 9; The Fishin' Hole, Edmonton, Alberta, Canada). Transmitters plus belts were always < 10% of toad weight, and usually < 5%. We located toads 2–4 times per week and recorded UTM coordinates using a Garmin eTrex handheld GPS (Garmin, Olathe, Kansas, USA). We radio-tracked 116 toads; 102 had sufficient data to be included in analyses. We analyzed data from eight females and eight males in Parkland 2004; four/four in Pasture 2004; 13/13 in Boreal Forest 2005; and 30/22 in Pasture 2006.

Microhabitat data.—We recorded microhabitat features within a 0.25 m^2 square grid around a toad for each telemetry location and also at a paired random location to represent available habitat. We selected each random location within a circular area surrounding the previous location of the toad as recorded 1–6 d earlier. The distance moved by the toad from its previous to current location was used as the radius for this circle. To determine the random location, we generated two random numbers between 0 and 1. We multiplied the first number by 360 to determine a random bearing and multiplied the square-root of the second number by the distance the toad travelled between its previous and current location to determine a random distance (Skalski 1987). Random distances used for our analyses ranged from 0.08 to 231 m (mean = 22.3 ± [SE] 1.91 m) at the Parkland in 2004, 0.13 to 304 m (mean = 38.2 ± 3.64 m) at the Pasture in 2004, 0.20 to 543 m (mean = 36.0 ± 2.32 m) at the Boreal Forest in 2005, and 0.06 m to 563 m (mean = 30.6 ± 1.58 m) at the Pasture in 2006.

We recorded five continuous habitat variables (air temperature, percentage cover of woody debris, distance to water, vegetation height, and percentage cover of vegetation) and two categorical variables (substrate type and dominant vegetation type) in 2004. In 2005 and 2006, we recorded 11 continuous variables (air temperature, soil moisture, percentage cover of woody debris, distance to water, herbaceous vegetation height, percentage cover in dead herbaceous vegetation, percentage cover in live herbaceous vegetation, shrub height, percentage cover in dead shrub, percentage cover in live shrub, and canopy cover) and four categorical variables (habitat type, substrate type, dominant vegetation type, and shelter type).

We recorded habitat type surrounding each plot using the ecosites key of Beckingham and Archibald (1996) for northern Alberta for areas that appear natural and by disturbance type (e.g., road, cutline, cut-block, burn) for altered areas. This habitat variable was recorded in the field and characterized the habitat immediately surrounding the toad (within 25 m). The advantage of measuring this variable in the field, versus extracting it from a map, was that small pockets of preferred habitat within other habitat types could be identified even if they were too small to detect on landcover maps. We combined similar habitat types to reduce the number of categories for data analysis. We merged natural habitat categories based on similarities in soil moisture. We merged ecosite codes B, C, and D of Beckingham and Archibald (1996) to form the category mesic/submesic; E, F, G, and H were merged into hygric/subhygric; I, J, and K were merged into subhydric. Ecosite code L (hydric) rarely occurred, so we placed it in the category Other. Upland shrub was retained as a distinct ecosite. Altered areas included burnt or cut-block; linear corridor (e.g., gravel road, paved road, cutline, utility corridors, railroads, or ditches); crop or hay fields; cattle or goat pasture; and pond edge in cattle pasture. Linear corridor rarely occurred in 2004 and 2006, so we placed it in the category Other for these years. Habitat type was not recorded systematically in 2004, but locations in crop/hay fields could be easily identified from the vegetation data recorded. Crop/hay fields were frequently used at the Pasture area in 2004, so we added a habitat type variable with two categories (crop/hay and Other) for the Pasture 2004 models.

We recorded soil texture for mineral soils (e.g., clay, sand, silt, loam) and substrate type (organic, peat/moss, rock, pavement, woody debris, etc.) for all other

Figure 1. Western Toad (*Anaxyrus boreas*) using woody debris for shelter. (Photographed by Constance L. Browne).

ground surfaces. We merged substrate types into four categories for the categorical variable, substrate type, for 2005: mineral soils, organic, peat, and other. Peat was not common at the Parkland or Pasture study areas, so we placed this substrate in the category Other for 2004 and 2006. We recorded family, genus, or species for the three most abundant plant taxa present in each plot. We reclassified these based on which vegetation type was most abundant in the plot to form the dominant vegetation type variable with four categories: forbs, graminoids, trees/shrubs, and not applicable.

Air temperature was recorded in degrees Celsius using a hand-held thermometer at the actual locations of the toad (e.g., in the open, in a tunnel, under debris) for used plots and in the middle of the grid at soil surface for random plots. Percentage cover of woody debris was the percentage of the grid covered by woody debris, which included sticks, logs, bark, etc. Distance to water (m) was the distance to the nearest open water source deep enough to cover the pelvic patch of a toad.

We collected soil moisture data using two methods: gravimetric, and a Kelway soil pH and moisture meter (Forestry Suppliers, Jackson, Mississippi, USA). For the gravimetric method, we calculated percentage soil moisture using the formula: ([soil field weight–soil dry weight]/soil field weight) × 100. We collected soil samples weighing 10–63 g near the soil surface (top 7 cm), below the location of the toad for used plots and in the middle of the grid for random plots for the gravimetric method. We dried samples in a drying oven at 105° C for at least 2 d. We used both methods for 560 samples in 2005 and 1012 samples in 2006. There was considerable variation between the two methods but generalized linear model results showed that the two methods were significantly correlated (2005: Wald X^2 = 464.46, df = 1, $P < 0.001$; 2006: Wald X^2 = 120.41, df = 1, $P < 0.001$). The gravimetric method is considered to be the more reliable method (Johnson 1992), thus we used these measurements when available (n = 668 in 2005, 1028 in 2006). We collected soil moisture data using only the moisture meter for 368 samples in 2005 and 287 samples in 2006. We calibrated the soil moisture meter data using the generalized linear model results with the formula: Soil moisture = ([Coefficient for the soil moisture meter reading] × [Soil moisture meter reading] + [Coefficient for the constant]). We recorded the percentage cover and approximate height (cm) of vegetation (herbaceous plants and shrubs) in 2004. In 2005 and 2006 our measurements were more detailed, and we split these two variables into six: herbaceous vegetation height, percentage cover in dead herbaceous vegetation, percentage cover in live herbaceous vegetation, shrub height, percentage cover in dead shrub, and percentage cover in live shrub.

We measured canopy cover using a convex spherical densiometer (Model No. 43887, Forestry Suppliers, Jackson, Mississippi, USA) with standard methodology (Forestry Suppliers, Inc. 2008. Instructions: Using Forest Densiometers. Forest Suppliers, Inc., Jackson, Mississippi, USA. Available from http://www.forestry-suppliers.com/Documents/1450_msds.pdf [Accessed 15 November 2016]). We held the spherical densiometer directly over the grid plot at elbow height while standing and took measurements facing each cardinal direction. We converted the average of these four measurements to a percentage and used this for percentage canopy cover. We often found toads within shelters, so we recorded used and available shelter types in 2005 and 2006. Categories included open (no shelter used or available), coarse woody debris (e.g., Fig. 1), tunnel (any hole

extending under ground, most were produced by small mammals), dead vegetation/leaf litter, and dense live vegetation.

Model creation and evaluation.—We created separate RSF models for each year, study area, season, and sex. Several statistical approaches are appropriate for RSF analyses but must align with the study design. Previously, we used generalized linear models with a binomial distribution and logit link function to examine land-class selection within the range of the local population (second-order selection of Johnson 1980) by comparing used locations to available points (delineated using toad movement distances from each site and ranging from 0.98 to 2.24 km) at three study areas (Browne 2010). To examine land class selection within the home range of individual toads (third-order selection of Johnson 1980), we used conditional logistic regression to compare used locations to paired available points drawn from within 300 m of the previous use location of a toad (Browne 2010; Browne and Paszkowski 2014). For this study, we chose a matched case, used-available design and conditional logistic regression analysis (Compton et al. 2002; Chan 2005) because to examine fourth-order selection, used points must be paired with available points based on the movement abilities of study-animals at this fine spatial scale. This analysis pairs available points with their respective used point, and the difference between paired points is calculated for each record and used in regression calculations. We incorporated data from 1,670 toad locations that were suitable for analysis (see Table 1). We excluded: (1) first capture locations for each toad because they may be biased towards sites with greater visibility (e.g., open areas); (2) locations where actual use by the toad was unclear (e.g., points where only transmitters were found and possibly moved there by a predator or scavenger); (3) locations for toads that had entered hibernation sites; (4) aquatic points; and (5) any used point that lacked a paired available point, or vice versa.

Categorical variables cannot be used in logistic regression analysis, so we converted our categorical variables (habitat type, substrate type, vegetation type, and shelter type) to binary variables (0 = absent, 1 = present) for each category type (Hosmer and Lemeshow 2000). For each categorical variable, we selected one category type as the reference variable for each model and omitted this variable from the model. As a result, each of the other binary variables associated with that categorical variable were indirectly compared to the reference variable. When possible, we selected a category that was abundant and present in most subsets (year, study area, season, sex) as a reference variable. We considered all other category variables for entry into the models. Categories were either merged with others or dropped from the model if their low frequency of occurrence made them inappropriate for inclusion in analyses.

We excluded variables if they were highly correlated ($r \geq 0.6$) with other predictor variables. When correlation was high, we excluded the variable that was suspected to be of lesser biological importance. Biological importance was assessed using the literature, field observations, and also by screening each variable to determine its individual contribution (running a conditional logistic regression model with only this

Table 1. Sample sizes for data suitable for analysis from radio-telemetry of Western Toads (*Anaxyrus boreas*) in north-central Alberta, Canada, 2004–2006. Each sample consists of a telemetry point and a paired available point. Total sample size indicates the number of samples that met our analysis criteria. Seasons are Breeding, Foraging, and Pre-Hibernation (Pre-Hib). Sex is indicated by F for females and M for males. NA indicates not applicable.

			Toads tracked		Average telemetry fixes/toad (range)		Total sample size for locations	
Year	Study Area	Season	F	M	F	M	F	M
2004	Parkland	Breeding	4	4	8.5 (3–16)	5.3 (2–11)	34	21
		Foraging	3	3	21.0 (9–29)	11.0 (1–24)	63	33
		Pre-Hib	4	4	6.8 (2–13)	6.3 (3–10)	27	25
	Pasture	Breeding	4	3	14.5 (14–15)	10.7 (8–14)	58	32
		Foraging	4	4	20.0 (10–24)	6.5 (4–9)	80	26
		Pre-Hib	3	0	8.3 (2–13)	NA	25	NA
2005	Boreal Forest	Breeding	8	13	10.4 (5–13)	8.8 (1–12)	83	115
		Foraging	12	11	7.4 (1–13)	10.4 (1–15)	89	114
		Pre-Hib	13	9	5.2 (1–9)	6.6 (1–9)	67	59
2006	Pasture	Breeding	22	19	5.5 (1–11)	6.7 (1–11)	120	128
		Foraging	19	14	8.5 (1–18)	12.0 (2–18)	162	168
		Pre-Hib	14	8	5.9 (1–10)	7.4 (4–10)	82	59

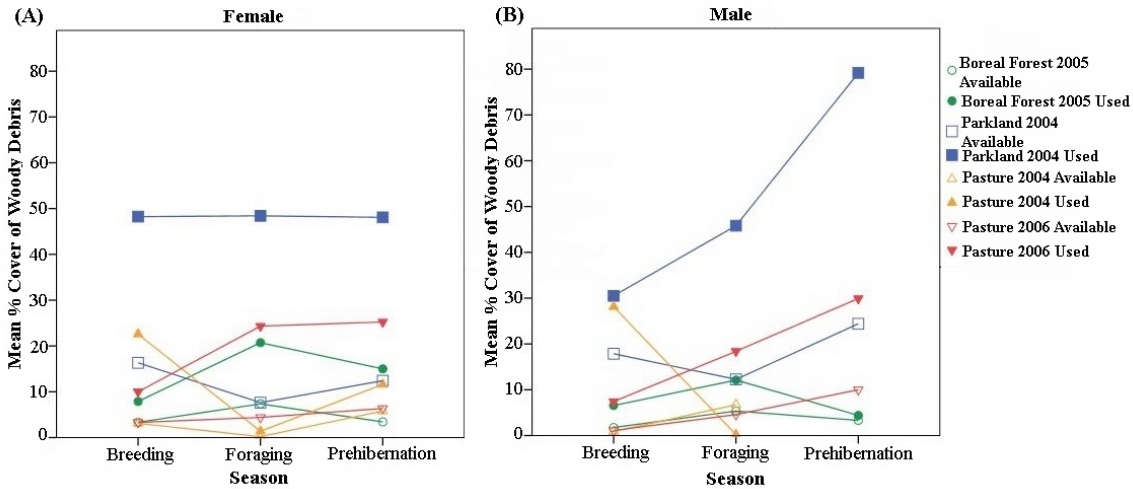

Figure 2. Mean percentage cover of woody debris for used (filled symbols) and available (hollow symbols) sites among study areas and seasons for female (A) and male (B) Western Toads (*Anaxyrus boreas*). Lines connecting points simply serve to link data; no trends are implied.

variable included). If both variables were of similar importance, then we retained the variable that performed best in the model (e.g., some variables had more missing values than others).

Ideally, habitat selection analyses should use individual animals as sample units rather than individual locations because use of multiple locations from the same individuals is pseudoreplication (Otis and White 1999). However, although we tracked a large number of toads, our sample sizes were limited within each analysis and for each individual (Table 1) because we divided our data into subsets to assess selection patterns at a finer scale, i.e., among study areas, years, seasons, and sex. We could not resolve the pseudoreplication using common approaches (e.g., Alldredge and Ratti 1986, 1992; Aebischer et al. 1993; Compton et al. 2002); however, we were conservative when interpreting our results, and only concluded that predictor variables played important roles in microhabitat selection if they proved significant in multiple analysis categories.

We created two models for each analysis subset (year, study area, season, and sex): a microhabitat selection model (full and final versions produced) and a shelter selection model. The full microhabitat selection model included all of the continuous variables plus the categorical variables habitat type, substrate type, and vegetation type. The microhabitat selection model contained a large number of variables, so we created a second model (called final model) that only contained the variables that significantly contributed to the first model. We used Akaike Information Criterion (AIC) to determine which variables significantly contributed to the full model (Boyce et al. 2002; Burnham and Anderson 2002); if a variable did not significantly contribute, then it was excluded from the final model. The shelter selection model included the categorical variable shelter type. We merged the shelter types woody debris and tunnel for our analysis because these categories often caused singularities in the Hessian matrix when entered on their own, which means that one of the predictors is constant for one category of the dependent variable. We used Likelihood Ratio tests to assess significance and considered $\alpha < 0.05$ to indicate statistical significance. We used IBM SPSS Statistics Version 24 for statistical tests (IBM Corp., Armonk, New York, USA).

Results

Woody debris and tunnels.—Woody debris was the microhabitat feature that was most consistently selected (Table 2; Fig. 2). Woody debris contributed to all but two (Pasture 2004 foraging season female and male) of the final microhabitat models and was significantly selected for ($P < 0.05$) in 17 of the 23 final models (All Parkland and Boreal Forest models except pre-hibernation season males; Pasture 2004 breeding season females and males; All Pasture 2006 models except for breeding season males). Woody debris was used as a shelter type more often than expected based on its availability on the landscape for all seasons and study areas, and by both sexes (Table 3; Supplemental Information 1). The merged shelter category, woody debris/tunnel, was statistically significant in 10 of the 12 models (Supplemental Information 2). Tunnels were relatively rare on the landscape, present in 0–2% of available sites; however, 4–54% of observations among subgroups based on study site, season, and sex were in tunnels (Table 3; Supplemental Information 3).

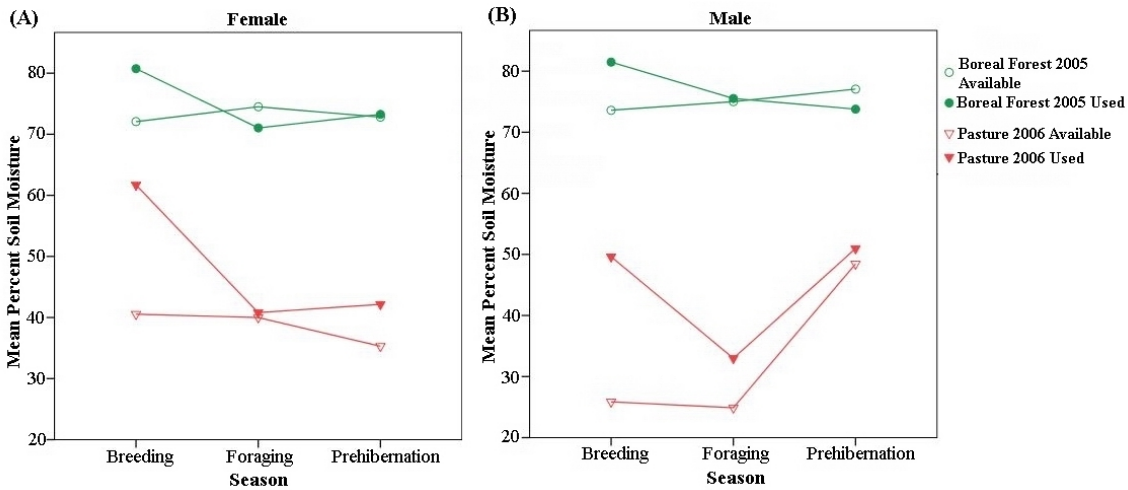

Figure 3. Mean percentage soil moisture for used (filled symbols) and available (hollow symbols) sites among study areas and seasons for female (A) and male (B) Western Toads (*Anaxyrus boreas*). Lines connecting points simply serve to link data; no trends are implied.

Moisture, water and temperature.—The Boreal Forest area had much higher soil moisture levels on average than the Pasture (Fig. 3). Soil moisture was a significant variable in one model (Pasture breeding season females; Table 2). Toads selected sites closer to water in six subgroups (males during the breeding season at the Parkland and Pasture in 2004; females at the Pasture during the breeding and pre-hibernation season in 2004 and foraging season in 2006; and pre-hibernation season at the Boreal Forest); however, sites farther from water were selected for by female toads during the foraging season at the Pasture in 2004 (Supplemental Information 2, 4). Air temperature was a significant variable in six of the 23 models; in these cases, sites with lower air temperatures were selected (Table 2).

Table 2. Significance rates of variables as predictors of Western Toad (*Anaxyrus boreas*) locations in north central Alberta, Canada, 2004–2006, from 23 multivariate microhabitat models created for each year, study area, season, and sex combination. The categorical variable Shelter Type was modeled separately for 12 study area, season, and sex combinations. Significance rates (% Significant) were calculated using the number of models in which a variable was significant (# Significant) divided by the number of models in which that variable was included (# Models). The number of positive (#+) and negative (#-) relationships are indicated for significant continuous variables under column # Significant (#+/#-). Full model details can be found in Supplemental Information 2.

Variable	# Models	# Significant (#+ / #-)	% Significant
Habitat type	17	6	35
Air temperature	23	6 (0/6)	26
Substrate	21	4	19
Soil moisture	11	1 (1/0)	9
% Woody debris cover	21	17 (17/0)	81
Distance to water	23	7 (1/6)	30
Vegetation Type	22	6	27
Vegetation height	8	2 (2/0)	25
Vegetation % cover	9	2 (0/2)	22
Herbaceous height	12	3 (3/0)	25
Herbaceous % dead cover	12	0 (0/0)	0
Herbaceous % live cover	12	3 (0/3)	25
Shrub height	7	1 (1/0)	14
Shrub % dead cover	12	3 (3/0)	25
Shrub % live cover	9	2 (2/0)	22
Canopy cover	12	5 (2/3)	42
Shelter Type	12	11	92

Vegetation and substrate.—Canopy cover was a significant variable in all breeding season models and all models for males at the Pasture; however, selection for sites with higher or lower canopy cover varied depending on the study area, season, and sex (Supplemental Information 2; Fig. 4). Vegetation characteristics were significant in 12 of 23 models (Supplemental Information 2). When these variables were significant, toads selected for sites with taller vegetation (Supplemental Information 5, 6), lower percentage cover of herbaceous vegetation (Supplemental Information 7), and higher percentage cover of shrubs (Supplemental Information 8). Vegetation type (i.e., forbs, graminoids, trees/shrubs) did not show consistent patterns of selection (Supplemental Information 2, 9). Substrate type was a significant variable in four of the 23 models (Table 2). When this variable was significant, mineral soils were generally avoided and organic substrate or substrate consisting of accumulated woody debris were selected (Supplemental Information 10). Mean soil moisture levels were higher in organic substrate than in mineral

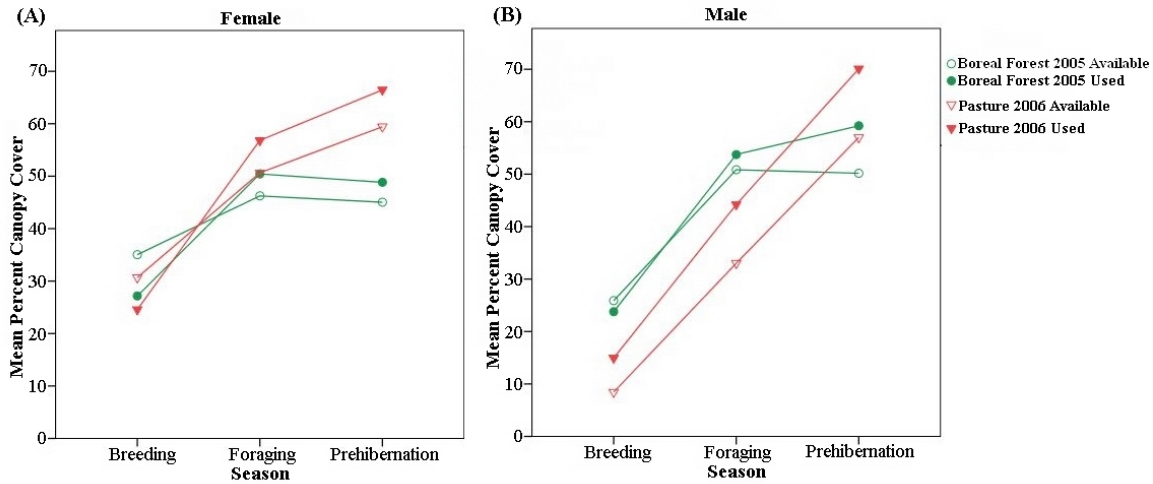

Figure 4. Mean percentage canopy cover for used (filled symbols) and available (hollow symbols) sites among study areas and seasons for female (A) and male (B) Western Toads (*Anaxyrus boreas*). Lines connecting points simply serve to link data; no trends are implied.

soils at our study sites (Boreal Forest: 70 ± [SE] 1.0% versus 46 ± 3.3%, Mann-Whitney U: $P < 0.001$; Pasture 2006: 68 ± 1.3% versus 28 ± 1.0%, Mann-Whitney U: $P < 0.001$).

Habitat type.—Habitat type was a significant variable in six of 17 final models (Table 2; Supplemental Information 11). Pond edge habitat and linear corridor were each significant in two models. Pond edge was selected for in Pasture 2006 breeding female (merged with habitat type Other) and foraging male. Linear corridor habitat was avoided in Boreal Forest males in the breeding and foraging season (Supplemental Information 2). Linear corridors encompassed a variety of vegetation and cover types, which likely influenced use. For example, seismic cut-lines, utility corridors, and roadside ditches offered some cover, but gravel roads none. Linear corridors actually used by males in the Boreal Forest included seismic cut-lines (Breeding season, n = 2 cases; Foraging season, n = 1) and a utility corridor (Foraging season, n = 1). Available habitat choices for the linear corridor habitat type included gravel road (n = 7), roadside ditch (n = 4), utility corridor (n = 5), and seismic cut-line (n = 3) during the breeding season, and utility corridor (n = 3) and seismic cut-lines (n = 6) during the foraging season. Avoidance of gravel roads played a role in the significant patterns seen during the breeding season, but even with the exclusion of these points, linear corridors were still used much less than available.

Discussion

Toads must choose sites that balance their needs for water, food, shelter, and warmth, weigh the advantages/disadvantages of travel to reach ideal sites from other essential habitat patches (e.g., breeding ponds, overwintering sites), and adjust as environmental conditions change. Our results demonstrate the complexity of microhabitat selection choices of Western Toads. Our predictions were partially accepted; we found that toads selected microsites that provided adequate moisture and shelter, such as woody debris, tunnels, and shrub cover, but our analysis did not show selection for warmer microsites. The permeable skin of amphibians and risk of desiccation makes sources of moisture necessary habitat components. Previous studies have measured water availability in different forms, such as soil moisture, relative humidity, distance to water, and as a rule, based on the characteristics of various habitat types, moist environments are reported to be significantly selected (e.g., Bartelt et al. 2004; Bull 2006; Long and Prepas 2012). We were surprised that soil moisture was a significant explanatory variable in only one model in our study (breeding season females at the Pasture). However, moisture may not have been a limiting resource in much of our landscape. The Boreal Forest had high soil moisture levels compared to our Pasture area (average of mean soil moisture at available sites was 74% versus 36%). Additionally, toads may not need moist substrate if standing water is nearby for rehydration as was the case for many individuals; the mean distance to water was < 30 m for nine of the 23 subgroups (Supplementary Information 12). For the remaining individuals, it is possible that they had access to water sources that we failed to detect, or they were obtaining enough moisture from precipitation and nighttime dew and thus were sufficiently hydrated.

Toads selected sites closer to water in six subgroups; however, these patterns may have been driven by

selection for sites close to breeding ponds (i.e., during the breeding season, and for males during the pre-hibernation season at the Boreal Forest), rather than a requirement for water. Toads at the Boreal Forest area often hibernated quite a distance from their breeding pond (mean = 1,086 ± [SE] 128 m; Browne and Paszkowski 2010a), but several males selected sites in/near a wet shrubland area with a small stream that flowed into the breeding pond. Many males would have been in the vicinity of their hibernaculum during this period (Browne and Paszkowski 2010b), and these males may have been selecting sites closer to the stream so that they could use it to return quickly to their breeding pond in spring. Downstream redistribution has been documented for Western Toads in Montana (Adams et al. 2005; Schmetterling and Young 2008).

The selection of sites farther from water by female toads at the Pasture in 2004 during the foraging season seems counterintuitive but can be easily explained. Most toads were initially caught at the breeding pond, but the females did not remain at the pond for long. They laid their eggs and then moved to foraging areas. Our study design selected matched random locations from a circle of available habitat centered on the previous location of the toad. As a result, direct movements to foraging areas showed up as selection for sites farther from water because water bodies were limited in this landscape and these females were moving away from their breeding pond. The reverse pattern (selection for sites closer to water) occurred in the pre-hibernation period for these same females in 2004 as they travelled from their foraging grounds to hibernation sites, which were closer

Table 3. Frequency tables for the categorical variable Shelter Type for Western Toad (*Anaxyrus boreas*) micro-habitat use in north-central Alberta, Canada, 2005–2006. Study areas are Boreal Forest and Pasture. Seasons are Breeding, Foraging, and Pre-Hibernation (PreHib). H or R indicates used habitat (H) versus available habitat (R).

Analysis Categories			Shelter Types					
Season	Sex	H or R	Open	Dead Vegetation	Dense Vegetation	Tunnel	Woody Debris	NA
Boreal Forest 2005								
Breeding	Female	H	56	4	16	3	4	0
Breeding	Female	R	58	15	8	0	0	2
Breeding	Male	H	65	6	29	9	3	3
Breeding	Male	R	54	26	31	0	0	4
Foraging	Female	H	38	6	29	4	11	1
Foraging	Female	R	35	10	37	0	7	0
Foraging	Male	H	31	4	57	5	15	2
Foraging	Male	R	54	6	45	1	6	2
PreHib	Female	H	12	3	21	27	4	0
PreHib	Female	R	37	8	21	0	1	0
PreHib	Male	H	10	6	15	23	4	1
PreHib	Male	R	30	3	25	0	1	0
Pasture 2006								
Breeding	Female	H	49	12	29	13	17	0
Breeding	Female	R	74	8	33	0	5	0
Breeding	Male	H	15	10	25	66	12	0
Breeding	Male	R	105	2	20	0	1	0
Foraging	Female	H	26	9	60	14	52	1
Foraging	Female	R	77	8	67	1	9	0
Foraging	Male	H	18	12	46	54	38	0
Foraging	Male	R	91	8	59	0	10	0
PreHib	Female	H	8	22	9	10	33	0
PreHib	Female	R	24	34	13	0	11	0
PreHib	Male	H	4	8	8	15	24	0
PreHib	Male	R	16	21	11	1	10	0

to their breeding ponds. This pattern was not observed in 2006, possibly because more animals were tracked, leading to greater variation of path trajectories, which included visits to water sources other than the breeding pond by some individuals.

Previously, we found toads used open land-cover types (e.g., wet shrubland, crop/hay fields) more often than predicted by their availability at the home-range scale during the active season (Browne and Paszkowski 2014). Selection for open areas suggests selection for warmer environments. Contrary to our expectations, air temperature was infrequently a significant variable in models (six of 23), and when it was significant, toads selected for sites with lower air temperatures. The mean air temperatures at microsites used by toads ranged from 9.36–21.14° C among subgroups, which is much lower than the preferred body temperature of Western Toads in a laboratory setting (26–27° C; Lillywhite et al. 1973). However, laboratory experiments have shown that toads will select for lower temperatures if food is withheld (Lillywhite et al. 1973), or if kept on a dry substratum (Tracy et al. 1993). Toads in our study may have selected sites with lower temperatures because adequate moisture was limited, food was limited, and/or because they were selecting sites that offered protection from predators, that coincidentally had lower temperatures. Five of the six models where temperature was a significant explanatory variable were from our Pasture area, which was our driest study area. The other significant model was for pre-hibernation females in the Boreal Forest. Forty percent of our observations for this subgroup occurred in tunnels, therefore, these individuals may have been exploring these cool locations as potential hibernation sites. Alternatively, toads may have been using warm open patches, but retreating to sheltered microsites once their preferred body temperatures had been achieved. This could have gone undetected in our analysis if the use of warm open patches was shorter in duration than the use of cooler sheltered sites. The average maximum temperatures recorded across subgroups were above the preferred body temperature (mean = 28 ± [SE] 1.5° C, range = 18–45°C; Supplemental Information 12).

Canopy cover can be an important habitat component for amphibians because it reduces daytime temperatures and rates of evaporative water loss (Sweeten and Ford 2016). There appears to be an optimal level of canopy cover for Western Toads, which changes seasonally. Male toads at the Pasture area selected for higher canopy levels in all seasons, but male toads at the Boreal Forest and female toads at both sites (Boreal Forest and Pasture 2006) selected for lower levels of canopy cover during the breeding season. Deguise and Richardson (2009) found that Western Toads in British Columbia selected clearcuts over intact forest in May-June but speculated that very open habitats could be inhospitable later in the year when temperatures are high and precipitation low. Sites with lower canopy cover may have more favorable temperatures during the spring if moisture is not limited. Our Pasture study area was much drier than our Boreal Forest study area, thus moisture may have been a limiting feature throughout the active season in the former landscape. Males may select sites with higher canopy cover compared to females because they are more susceptible to desiccation due to their smaller size (Bartelt et al. 2004). However, toads at the Pasture area bred in man-made ponds in an inactive sand quarry, with very few trees in the area. Thus, the fact that males selected for higher levels, while females selected for lower levels, of canopy cover during the breeding season could simply be because males stayed close to the very open breeding ponds longer than females and canopy cover at available sites were thus much lower for males than females.

At the Boreal Forest area, male toads avoided linear corridors during the breeding and foraging seasons. Browne and Paszkowski (2014) lumped linear corridors into the category disturbed grass; this land-cover type was also significantly avoided by Boreal Forest males during the breeding and foraging seasons. Linear corridors would provide open areas for basking and could facilitate movement (Deguise and Richardson 2009), but might not provide adequate moisture, shelter from predators, and/or foraging opportunities. Female toads have shown stronger selection patterns for open habitat than males (Bull 2006; Browne and Paszkowski 2014) and linear corridors were not avoided by female toads at our study areas.

Woody debris was the most consistently selected microhabitat feature in our study. Although previous studies investigating microhabitat selection by Western Toads have not found woody debris to be significantly selected, several authors have discussed its potential importance for Western Toads (Bartelt et al. 2004; Bull 2006; Long and Prepas 2012). Woody debris may provide more favorable temperature and moisture conditions and/or protection from predators (Harmon et al. 1986). Large pieces of woody debris decompose slowly, and provide stable, moist terrestrial environments (Pilliod et al. 2003). In some cases, rotten wood retains water better than humus (Harmon et al. 1986), and elevated relative humidity is a significant factor in the selection of refugia by Western Toads (Long and Prepas 2012). Woody debris could be important habitat for prey items consumed by toads such as ants (Bull 2006).

Coarse woody debris was the dominant refuge type used by Western Toads at a site in western Alberta; 13 of 26 refugia identified were in, under, or on woody debris (Long and Prepas 2012). Woody debris was not used more than expected based on availability at the study site of Bartelt et al. (2004) in Idaho, but they did find

toads significantly closer to cover (e.g., burrow, woody debris, shrub growth) than at random sites (0.66 ± [SE] 0.08 m versus 1.57 ± 0.1 m). In Oregon, Bull (2006) found that 81% of terrestrial relocations were in refugia, which included rocks (31%), burrows (18%), logs (17%), self-excavated depressions (8%), and stumps, root wads, or bark (6%). It is possible that Bartelt et al. (2004), Bull (2006), and Long and Prepas (2012) did not find a significant selection for woody debris for a variety of reasons including differences among landscapes (woody debris was not limited or more preferred refuges were available) or differences in study design (time of data collection or spatial scale). We suspect that our models that failed to show selection for woody debris reflected low availability of woody debris at the Pasture and strong selection for tunnels by males during the pre-hibernation season at the Parkland and Boreal Forest areas (see below). We observed Western Toads using pre-existing tunnels as hibernacula (Browne and Paszkowski 2010a), and males arrived at hibernacula significantly earlier than females (Browne and Paszkowski 2010b).

Vegetation and substrate characteristics were not strongly selected for overall, but a few consistent patterns emerged. Toads selected for sites with taller vegetation, lower percentage cover of herbaceous vegetation, higher percentage cover of shrubs, and organic substrate over mineral soils. Bartelt et al. (2004) also found that Western Toads selected for shrub habitat and suggested that shrubs would likely provide warm, moist conditions that are preferred by toads because of their low dense structure, large accumulations of litter and woody debris, and breaks in the canopy to allow in sunlight. Organic substrates had higher soil moisture levels than mineral soils at our study sites, and thus might provide higher relative humidity during dry weather and could facilitate water retention.

Tunnels were also highly selected as shelter types for all models in our study, but especially during the pre-hibernation season at the Boreal Forest area and by males at the Pasture (Table 3). Tunnels/burrows offer toads protection from predators, stable temperatures, and high relative humidity (Burda et al. 2007). Tunnels were especially important for males at the Pasture during the breeding and foraging seasons because most of these toads used sites, near the breeding ponds, which were surrounded by very sparsely vegetated cattle pasture in an inactive sand quarry; thus, burrows made by Richardson's Ground Squirrels (*Urocitellus richardsonii*) provided protection from dehydration, temperature extremes, and predators in this hostile environment. Without these burrows, toads attempting to remain close to their breeding sites would likely be limited to the pond edge. The pond edge had a thin band of wetland vegetation that was often used by toads and this habitat was selected for by female toads in the breeding season and male toads during the foraging season in present analyses and also at the home- range scale (Browne and Paszkowski 2014). The stronger selection for tunnels during the pre-hibernation season was likely because many individuals were preparing for winter; toads arrived at their hibernacula gradually from 27 August to 10 October (Browne and Paszkowski 2010b). Bull (2006) also found Western Toads used burrows often (15% of terrestrial observations).

Previously we examined selection for habitat types within the home range (third-order selection) and found significant patterns at this scale (Browne and Paszkowski 2014). Habitat type was rarely a significant variable in our current analyses, probably due to the small spatial scale. Random points to characterize available habitat were collected from within 32 m (1.15 SE), on average, of used points. Thus, finer habitat features were the drivers at this scale. In conclusion, tracking with radio-telemetry allowed us to characterize microhabitat use by Western Toads in three areas representing different land use. As predicted, toads at each location selected microsites that offered moisture and shelter. Contrary to expectations, toads did not select warmer microsites. The lack of selection could indicate that exposure to relatively warm temperatures was less important to Western Toads than other requirements, or that toads were shuttling between warm basking areas and sheltered microsites but spending more time in shelters.

Conservation implications.—Woody debris and tunnels/burrows were highly preferred microhabitat features at our study areas. Unfortunately, some land-use practices reduce or eliminate these key features (e.g., fuel reduction; Hirsch and Pengelly 2000; Bull et al. 2005). Forest management schemes that leave some large-diameter snags and down wood, post-harvest, could help conserve toad populations without creating undue risk of wildfire (Pilliod et al. 2006). In agricultural landscapes, burrowing mammals, such as pocket gophers and ground squirrels, are often controlled to reduce damage to croplands (Alberta Agriculture and Rural Development. 2008. Control of Pocket Gophers and Ground Squirrels. Available from http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex897 [Accessed 30 December 2017]). Toads are predators of invertebrates and a useful component in these ecosystems. Practices that could allow rodents and their tunnels to persist, such as choosing crops that are cut at a higher blade height, should be explored for areas where agriculture overlaps with this vulnerable anuran (e.g., Browne 2006).

Acknowledgments.—We thank Leanne Harris, Carol Browne, Katie Thompson, Michelle Mark, Ste-

phen Symes, Drew Osterhout, Leah McGraw, and Eric Brownrigg for their field assistance. Lee Foote, Erin Bayne, Ross Chapman, and Mark Boyce provided valuable advice for our study design and/or data analysis. Financial and in-kind support for data collection was provided by the North American Waterfowl Management Plan, Friends of Elk Island Society, Parks Canada, Alberta Conservation Association, Circumpolar/Boreal Alberta Research, Mountain Equipment Co-op, Alberta Sports, Recreation, Parks, and Wildlife Foundation, Natural Sciences and Engineering Research Council (Postgraduate Scholarships-Doctoral Program, Constance Browne; Discovery grant, Cynthia Paszkowski), Strathcona County, Alberta Fish and Wildlife, Alberta Cooperative Conservation Research Unit, University of Alberta, Alberta-Pacific Forest Industries Inc., town of Lac La Biche, Portage College, and many landowners in Strathcona County. Financial support for data analysis and writing was provided by grants from the Alberta Conservation Association, and the Faculty of Science, University of Alberta. This research was done with approval from the University of Alberta Biosciences Animal Policy and Welfare Committee (Protocol #446604) and Alberta Natural Resources Service (Collection Licence #294 CN and 23154).

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Supplemental Information: http://www.herpconbio.org/Volume_13/Issue_2/Browne_Paszkowski_2018 _Suppl.pdf

Appendix 1. Monthly temperature and precipitation recorded from the Elk Island National Park weather station in 2004 and 2006, and from the Heart Lake, Alberta, Canada, weather station (34 km from our Boreal Forest area) in 2005.

	Mean Temperature (° C)			Total Precipitation (mm)		
Month	2004	2005	2006	2004	2005	2006
May	8.8	8.3	11.7	78.0	112.1	63.2
June	13.7	12.6	15.6	48.4	95.9	67.5
July	16.6	14.8	18.6	162.2	87.7	72.6
August	14.4	12.6	16.0	50.0	86.9	47.6
September	9.0	8.4	11.7	63.6	23.7	72.8
October	2.7	NA	2.3	34.3	NA	38.9

Constance L. Browne is a freelance Ecologist who specializes in conservation, population biology, landscape ecology, and herpetology. She completed a B.Sc. in Biology at the University of New Brunswick in Saint John, Canada, a M.Sc. in Biology at Lakehead University in Thunder Bay, Ontario, Canada, and a Ph.D. in Environmental Biology and Ecology at the University of Alberta in Edmonton, Canada. Currently, she is a Research Associate at the New Brunswick Museum, Honorary Research Associate at the University of New Brunswick, and also serves on the Amphibian and Reptile Specialist Subcommittee of the Committee on the Status of Endangered Wildlife in Canada. (Photographed by Andrew Sullivan).

Cynthia A. Paszkowski is an Emeritus Professor of Biological Sciences at the University of Alberta. She has a Ph.D. in Zoology from the University of Wisconsin-Madison, USA. Cindy and her students have researched the ecology of freshwater fishes, amphibians, and birds. She serves on the IUCN Amphibian Specialist Group. (Photographed by Bill Tonn).