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THE INFLUENCE OF HABITAT COMPOSITION, SEASON AND GENDER ON HABITAT SELECTION BY WESTERN TOADS (*ANAXYRUS BOREAS*)

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Abstract.—The Western Toad (*Anaxyrus boreas*) is a species of conservation concern in much of its range. We used radio-telemetry to track 116 adult toads in three study areas that were dominated by parkland, pasture, or boreal forest, respectively. We created resource selection function (RSF) models to evaluate the influence of habitat composition, season, and gender on habitat selection by toads. Overall, toads were found more often in open habitats (e.g., wet shrubland, crop/hay fields) than predicted by their availability. This pattern was most evident during the foraging season (July-August). Toads were more likely to be found close to breeding ponds in May-June and near hibernation sites in September-October. Female toads selected open habitat more than males, whereas males were more closely associated with water. Habitat in the northern part of the Western Toad's range is undergoing rapid change associated with resource development. Our study identifies key habitat features that should help managers protect this species in these landscapes.

INTRODUCTION

Understanding habitat use and movement patterns is essential for conserving declining animal species. In parts of its range, populations of the Western Toad (*Anaxyrus boreas* [= *Bufo boreas*]) have decreased markedly and it is recognized as a species of conservation concern broadly (Wind and Dupuis 2002). Habitat use and movements have been examined in some areas, but Western Toads are widely distributed, and habitat use can vary regionally, seasonally, and with gender (e.g., Bartelt et al. 2004; Bull 2006; Browne and Paszkowski 2010a). Data on Western Toads in their northern range remain limited and these areas are changing rapidly as a result of resource development.

We used Resource Selection Function (RSF) models to examine habitat selection by Western Toads in Alberta, Canada. Resource Selection Function models are statistical models designed to compare use of a resource to its availability (Manly et al. 2002). We created separate RSF models for male and female toads for three seasons in each of three study areas. We sought to identify habitat elements that were consistently selected by Western Toads and likely to define critical habitat in our region. We predicted that habitat types selected by toads would vary among study areas, but that the most important elements would be more consistently selected among all three. We predicted that habitat selection would change with season, with toads selecting locations close to breeding ponds early in the year, locations close to hibernation sites late in the year, and locations favorable to foraging and growth (e.g., warm

with abundant prey) in mid-summer. We predicted that habitat selection would differ between male and female toads because: (1) males remain at breeding ponds longer than females in spring; (2) females may use summer foraging habitat farther from breeding ponds than males (e.g., Muths 2003; Goates et al. 2007); and (3) Western Toads are sexually dimorphic in size and we found that large toads move to hibernation sites later in the year than small toads (Browne and Paszkowski 2010b). Observations elsewhere led us to predict that female toads would more strongly select open habitat types than males, and that males would select habitat types associated with water more often than females (Bartelt et al. 2004; Bull 2006).

MATERIALS AND METHODS

Study areas.—All three study areas were in northern Alberta, but differed in land use. The parkland area is within the Aspen Parkland natural region and within Elk Island National Park (EINP; Alberta Government 2005). This study area is undeveloped and centered on toad breeding sites in two shallow lakes (10−20 ha) and primarily surrounded by upland forest (*Populus tremuloides, P. balsamifera, Picea glauca, Corylus cornuta*) and marsh.

The pasture area, located 3.5 km west of EINP and 10 km from our parkland area, was set in an agricultural landscape with patches of forest and peatland. Agricultural uses included cattle grazing, cultivation of hay and crops (e.g., wheat, barley, oats, canola, timothy, alfalfa), and rural housing. Forest patches included *Populus tremuloides, P. balsamifera, Picea glauca, P.*

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mariana, *Betula papyrifera*, *Larix laricina*, and *Pinus banksiana*. This study area was centered on four man-made ponds (0.09−0.4 ha) used by toads for breeding. Ponds were created during sand extraction and are currently surrounded by sparsely vegetated pasture grazed by cattle later in the season.

The boreal forest area is located near Lac La Biche, approximately 150 km north of our parkland study area and within the Boreal Forest natural region (Alberta Government 2005). This region is influenced by the forestry and oil/gas industries (e.g., forest cut-lines made during seismic exploration, pipelines; Fig. 1) and comprises 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, Salix spp.*, and *B. nana*. This study area was centered on a 0.07-ha, shallow stream-fed pond used by toads for breeding. The pond was next to a gravel road and within a major utility corridor.

We used the distance between the study area center (the midpoint of the breeding pond[s]) and its most distant toad location as the radius to define each circular study area; this distance was 983 m for the parkland area, 1,145 m for the pasture, and 2,239 m for the boreal forest area. Study areas encompassed 3.0, 4.1, and 15.7 km^2, respectively. See Appendix I for the proportion of each land-cover type at each study area.

Radio-telemetry.—We captured 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 to nearest mm), mass (to nearest g), and gender of each toad at the time of capture. Toads captured between May and August were given unique toe clips (1−2 toes; thumbs never clipped) for identification and aging via skeletochronology (Chris Garrett, unpubl. report; Michelle Mark, unpubl. report).

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), which had minimum battery lives of 28 d to 3 mo (Holohil Systems Ltd., Carp, Ontario, Canada). 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). 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). One hundred sixteen toads were radio-tracked; 92 toads yielded at least four relocations and were
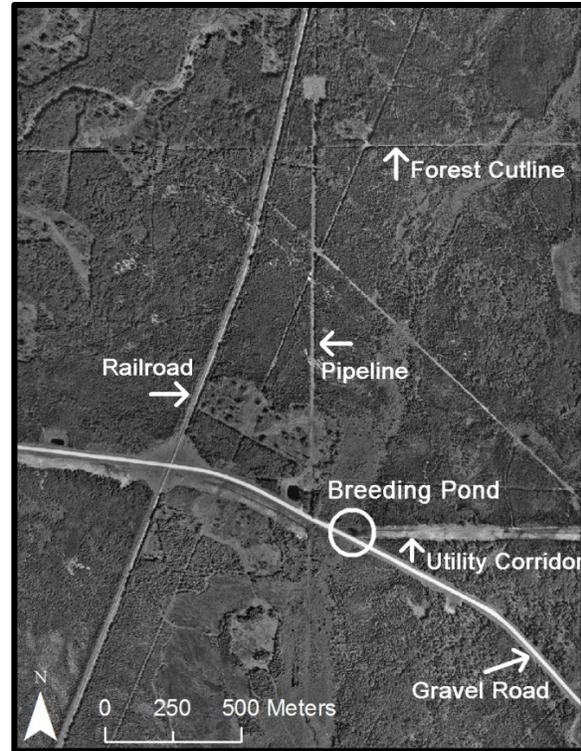

FIGURE 1. Boreal forest study area located north of Lac La Biche in north-central Alberta. Western Toads (*Anaxyrus boreas*) were radio-tracked at this site in 2005. This study area contained large proportions of natural land-cover types, but also was influenced by several human-produced linear features.

included in analyses. We analyzed data from 6 females/6 males in parkland; 29/26 in pasture; and 13/12 in boreal forest.

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).

Landscape data.—We used aerial photographs taken in 2001 (parkland), 2005 (pasture), and 2006 (boreal forest) to create land-cover layers for our study areas (ArcGIS 9.2, ESRI, Redlands, California, USA; see Appendix III of Browne and Paszkowski (2010a) for methods and descriptions of land-cover types). We digitized photos at a resolution of 1:1,890 (a pixel size of 0.5 m^2 when converted to raster). We created a polygon layer for toad breeding ponds by digitizing all known

TABLE 1. Sample sizes (females/males) from radio-telemetry of Western Toads (*Anaxyrus boreas*) in north-central Alberta, 2004−2006. Ten random locations were paired with each telemetry location to produce the available habitat locations. Final sample sizes consisted of available habitat locations that were of a land-cover type examined in Resource Selection Function models.

Site	Season	Toads tracked	Average telemetry fixes/toad (range)	Total telemetry fixes	Available habitat locations	Final sample sizes
Park	Breeding	3/ 4	10.3(5–20)/ 14.0(5–20)	31/ 56	310/ 560	191/ 348
	Foraging	3/ 3	22.7(13–29)/13.0(5–26)	68/ 39	680/ 390	489/ 239
	Pre-hib.	3/ 3	9.0(4–14)/ 9.0(5–12)	27/ 27	270/ 270	182/ 89
Pasture	Breeding	22/23	9.6(4–15)/ 10.3(4–16)	210/236	2,100/2,360	2,078/2,258
	Foraging	20/15	11.9(4–25)/ 13.0(5–18)	238/195	2,380/1,950	2,232/1,803
	Pre-hib.	13/ 8	7.7(4–13)/ 7.5(4–10)	100/ 60	1,000/ 600	949/ 292
Boreal	Breeding	8/12	11.8(7–14)/ 11.9(8–13)	94/143	940/1430	893/1158
	Foraging	8/10	10.6(5–14)/ 11.8(7–15)	85/118	850/1180	692/ 980
	Pre-hib.	11/ 8	5.8(4–9)/ 7.4(6–9)	64/ 59	640/ 590	550/ 430

breeding ponds at each study area. We also created a point layer for all toad hibernation sites (39 sites for 50 toads radio-tracked to confirmed hibernacula) at each study area. We are fairly confident that all breeding sites were digitized, but some hibernation sites were not located. Assembled layers quantified land-cover type, distance to nearest breeding pond, and distance to nearest hibernation site for all toad locations and random points.

We used the join function (based on spatial proximity) in ArcGIS 9.1 (ESRI, Redlands, California, USA) to calculate the straight-line distance to nearest breeding pond and nearest hibernation site. We used Hawth's Tools (ArcGIS 9.1) to generate random points to characterize available habitat. We drew these points from within a circular buffer with a radius of 300 m; this distance was the mean of the upper 5% of distances between consecutive locations for all toads (n = 2,143 location pairs). We compared habitat type at each toad location with the habitat at 10 random points within the buffer around the toad's previous location.

Model creation and evaluation.—We created separate RSF models for each study area, season, and gender. We collected data from 1,850 toad locations that were suitable for analysis; numbers of locations per analysis category are in Table 1. We used conditional logistic regression to compare used to available habitat (Compton et al. 2002). This analysis pairs available points with the respective used point and the difference between paired points is calculated for each variable and used in the regression calculations. 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 because a predator or scavenger could have moved the transmitter); and (3) locations for toads that had entered

hibernation sites (we continued to monitor toads for several days to weeks into hibernation).

Land-cover was a categorical variable with 22 land-cover types; however, categorical variables cannot be used in logistic regression analysis, so we converted this variable to binary variables (0 = absent, 1 = present) for each land-cover type. We selected one land-cover type as the reference variable for each model and omitted this variable from the model. As a result, each of the other land-cover type variables was indirectly compared to the reference variable. We selected deciduous forest as the reference land-cover for our parkland and pasture models and coniferous forest as the reference for our boreal forest models (unless otherwise noted) because these land-cover types were prevalent at the respective study areas and were used by toads in most categories. All other land-cover types were considered for entry into the models if they were used by toads more than once in the category of interest (study area, season, and gender). We included the continuous variables "distance to nearest breeding pond" and "distance to nearest hibernation site" in all models. We set the maximum number of step-halvings (a stopping criteria in the regression algorithm) to 30 for all models; we increased this from the default setting of 5 to avoid separation in the data set, which can be a problem with samples that have a high number of parameters relative to sample size (Heinze and Ploner 2003). We tested for collinearity and considered it not to be a concern because correlations between predictor variables within a model were always < 0.6. We considered α < 0.05 to indicate statistical significance. We used SPSS version 15 for statistical tests (SPSS Inc., Chicago, Illinois, USA; Chan 2005) unless otherwise noted.

We used five-fold cross-validation to compare the internal consistency of each model following the methods described in Johnson et al. (2006). We used an equal-interval classification to reclassify our RSF maps into 10 equal-interval bins ranked from low- to high-

TABLE 2. Predictors of Western Toad (*Anaxyrus boreas*) locations in north central Alberta, 2004−2006. Study areas are A) Parkland, B) Pasture, and C) Boreal Forest. Seasons are Breeding (Bre), Foraging (For), and Pre-Hibernation (PHib). Models were created for each season and gender (F or M) combination. Values are beta coefficients (SE) from Resource Selection Function models. Signs indicate selection (+ beta coefficient) or avoidance (- beta coefficient) of a predictor relative to deciduous forest for Parkland and Pasture study areas, or to conifer forest for the Boreal Forest study area. Fonts are regular ($P > 0.05$), *italic* ($0.05 \geq P \geq 0.001$), or **bold** ($P < 0.001$). Predictors include distance to nearest breeding pond (DistBre), distance to nearest hibernation site (DistHib), and land-cover types: marsh/wet meadow (Marsh), emergent vegetation (EmgtVeg), wet shrubland (WetShr), disturbed grass (DisGra), dry meadow (Meadow), conifer forest (ConFor), mixed-wood forest (MixFor), dry shrubland (DryShr), crop field/hay field (CropHay), pasture/sparsely vegetated (Pasture), water, mowed lawn (MowLwn), deciduous forest (DecFor), moss/peat wetland (Moss), Burn, cut-block tree/shrub dominated (CutTre), cut-block grass-dominated (CutGra).

A) Parkland

Model	DistBre	DistHib	Marsh	EmgtVeg	WetShr	DisGra	Meadow
Bre F	**-0.01(0.00)**	**-0.01(0.00)**	0.36(0.31)				
Bre M*	**-0.03(0.00)**	**-0.01(0.00)**	**2.60(0.32)**	0.73(0.47)			
For F	**-0.01(0.00)**	-0.00(0.00)	**-3.35(0.37)**		**1.01(0.28)**	*1.65(0.56)*	
For M	**-0.05(0.01)**	*-0.01(0.00)*	-0.93(0.79)		*2.32(0.85)*		
PHib F	*-0.01(0.00)*	**-0.01(0.00)**	-0.12(0.30)		*3.08(0.98)*		*1.89(0.83)*
PHib M**	*-0.10(0.04)*	*-0.02(0.01)*					

B) Pasture

Model	DistBre	DistHib	Marsh	EmgtVeg	WetShr	DisGra	ConFor
Bre F	**-0.01(0.00)**	-0.00(0.00)	**2.49(0.44)**	**2.77(0.30)**	**2.41(0.37)**	**1.85(0.27)**	*0.61(0.21)*
Bre M	**-0.02(0.00)**	0.00(0.00)		**2.01(0.35)**			**1.69(0.30)**
For F	**-0.01(0.00)**	**-0.01(0.00)**				**1.11(0.19)**	*-0.43(0.16)*
For M	**-0.01(0.00)**	**-0.01(0.00)**		*0.89(0.31)*	**2.67(0.44)**	-0.46(0.28)	
PHib F	**-0.01(0.00)**	**-0.02(0.00)**				**1.68(0.43)**	0.17(0.31)
PHib M	-0.00(0.01)	**-0.20(0.06)**					*-2.30(1.03)*

Model	MixFor	DryShr	CropHay	Pasture	Water	MowLwn
Bre F	-0.17(0.15)	0.33(0.36)	**0.80(0.18)**	**-0.66(0.16)**	**1.71(0.26)**	
Bre M	0.18(0.22)	**3.31(0.45)**	**1.98(0.32)**	**-0.92(0.23)**	**1.51(0.32)**	
For F	-0.19(0.12)		**1.08(0.14)**	**-1.59(0.16)**		
For M	**-0.72(0.14)**	**1.20(0.25)**	**0.95(0.18)**	**-1.00(0.17)**	0.31(0.34)	**2.30(0.50)**
PHib F	*0.56(0.23)*	0.24(0.66)	**1.85(0.34)**	**-1.96(0.37)**		
PHib M	*-2.42(1.03)*	1.88(14.89)				

C) Boreal Forest

Model	DistBre	DistHib	WetShr	DisGras	MixFor	Water	DecFor
Bre F	**-0.00(0.00)**	**-0.01(0.00)**	**2.42(0.24)**	**1.72(0.23)**	*0.78(0.28)*		**0.99(0.24)**
Bre M	**-0.01(0.00)**	**0.01(0.00)**	**0.65(0.18)**	**-0.89(0.23)**		0.45(0.52)	
For F	*-0.00(0.00)*	**-0.01(0.00)**	**2.75(0.27)**	**2.20(0.29)**			**1.38(0.26)**
For M	*0.00(0.00)*	-0.00(0.00)	**1.21(0.18)**	*-0.66(0.21)*	**1.30(0.27)**		
PHib F	0.00(0.00)	**-0.02(0.00)**	0.51(0.32)	-0.39(0.39)			0.36(0.36)
PHib M	0.00(0.00)	**-0.01(0.00)**	0.31(0.40)				

Model	Moss	Burn	CutTre	CutGras
Bre F	**2.98(0.28)**	**4.32(0.50)**	**2.93(0.56)**	
Bre M	**1.57(0.19)**			**2.12(0.40)**
For F	*1.03(0.43)*		0.29(0.56)	
For M	**-1.27(0.25)**	-0.46(0.25)		*0.60(0.30)*
PHib F	-0.24(0.57)	**-2.80(0.70)**		
PHib M	*-1.35(0.50)*			*1.31(0.66)*

*Water was used as the reference variable because only one toad observation was in deciduous habitat.

** Land-cover types were not evaluated because all toad locations were in marsh except for one in wet shrubland.

suitability. We used linear regression to assess model fit and followed Howlin et al.'s (2004) method for assessing model predictive ability. However, not all of the 180 datasets used in this analysis met the assumptions of normality. We used General Linear Models (GLM) in IBM SPSS Statistics 21 (IBM Corp., Armonk, New York, USA) to compare the predictive power (using R^2_{adj} values from the cross-validation) among model groups. These data were not significantly different from a normal distribution (Kolmogorov-Smirnov test for normality: $P = 0.590$).

Throughout our work we use the word "selected" when a land-cover type was used more than would be expected based on availability, "avoided" when a land-cover type was used less than expected based on availability, and "used" when an animal location was

recorded in a land-cover type (irrespective of availability). We cannot rule out the possibility that some differences in habitat use among study areas reflected temporal variation in behavior as we tracked toads in different areas in different years.

RESULTS

General patterns of habitat selection.—Our 18 analysis categories contained data from three to 23 toads with a mean of 10.45 (range = 4−29) telemetry fixes per toad (Table 1). Toads used 17 of 22 land-cover types that occurred on study areas. Unused land-cover types were inaccessible (building) or provided no overhead cover (railroad, gravel road, paved road, and exposed land). Three land-cover types were consistently selected or avoided: wet shrubland, crop/hay fields, and pasture (Appendix II). Toads significantly selected wet shrubland in nine of 11 models (Table 2). Toads selected crop/hay fields and avoided pasture in all five models where these cover types were used. Distance to nearest breeding pond was significant in 15 of 18 models. Toads selected locations closer to breeding ponds in all of the models where this variable was significant except for the boreal forest foraging male model (Appendix III). Toads also selected locations closer to hibernation sites in all but three models; the boreal forest breeding-male model was the only model that showed a significant reverse trend. Fourteen of 18 models were validated to be good or acceptable (Table 3). Model fit adjusted R^2 values ranged from 0.582 to 0.967 for these models.
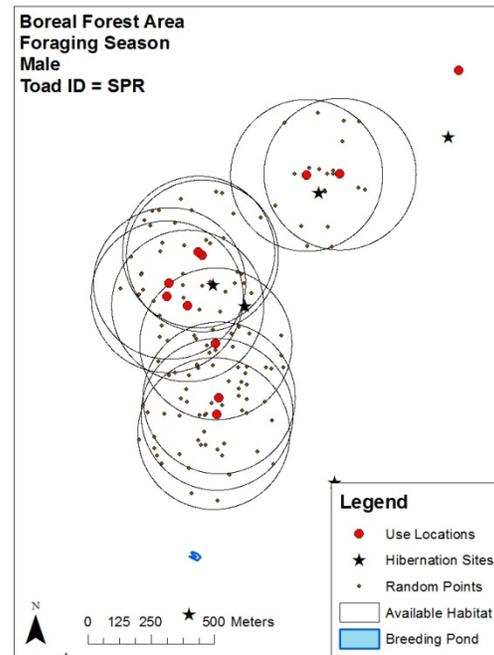
FIGURE 2. Telemetry fixes and available habitat locations for one male Western Toad (*Anaxyrus boreas*) in foraging season in the boreal forest study area in north-central Alberta, 2005. This toad moved north and northeast along wet shrubland habitat; it wintered at the hibernation site in the northeast corner of this image.

Differences among study areas.—Habitat composition differed greatly among study areas. The three most abundant land-cover types were deciduous

TABLE 3. Five-fold validation results for Resource Selection Function models of Western Toad (*Anaxyrus boreas*) habitat use in north-central Alberta, 2004−2006. Study areas are Parkland, Pasture, and Boreal Forest. Seasons are Breeding, Foraging, and Pre-Hibernation (Pre-Hib). Linear regression was used to assess model fit and predictive ability was assigned per Howlin et al. (2004). A good model should have $B_0 = 0$ and $B_1 = 1$.

Area	Season	Gender	B_0	P	B_1	P	Adjusted R^2	Validation
Parkland	Breeding	F	0.001	0.823	0.991	0.009	0.648	Good
		M	0.002	0.503	0.976	0.049	0.690	Good
	Foraging	F	0.042	0.462	0.583	0.120	0.380	Unacceptable
		M	0.066	0.167	0.337	0.255	0.372	Unacceptable
	Pre-Hib	F	0.003	0.422	0.971	0.001	0.908	Good
		M	0.085	0.168	0.146	0.388	0.119	Unacceptable
Pasture	Breeding	F	0.028	0.082	0.705	<0.001	0.937	Acceptable
		M	0.039	0.184	0.575	0.001	0.773	Acceptable
	Foraging	F	0.031	0.329	0.692	0.002	0.765	Acceptable
		M	0.012	0.548	0.884	<0.001	0.945	Acceptable
	Pre-Hib	F	0.017	0.284	0.829	<0.001	0.967	Acceptable
		M	0.026	0.181	0.742	<0.001	0.940	Acceptable
Boreal Forest	Breeding	F	0.012	0.727	0.877	0.001	0.851	Good
		M	0.069	0.049	0.306	0.161	0.272	Unacceptable
	Foraging	F	0.029	0.294	0.708	0.002	0.795	Acceptable
		M	-0.064	0.248	1.637	0.001	0.766	Good
	Pre-Hib	F	0.028	0.445	0.719	0.042	0.582	Acceptable
		M	0.020	0.285	0.800	0.030	0.591	Acceptable

forest, marsh, and water at the parkland area; crop/hay field, pasture, and deciduous forest at the pasture area; and conifer forest, deciduous forest, and mixed-wood forest at the boreal forest area (Appendix I). Moss, burn, grass-dominated cut-block (forestry area recently cleared of trees), and tree-dominated cut-block (forestry area cleared of mature forest, dominated by young trees) only occurred at the boreal forest area. Mowed, crop/hay, and pasture only occurred at the pasture area. Most land-cover types were used infrequently (Appendix II). Only deciduous forest, conifer forest, wet shrubland, and disturbed grass occurred in more than half of the models. Some land-cover types that were extensive on the landscape were used frequently (e.g., marsh at the parkland area, conifer at the boreal forest area). However, toads showed significant selection for land-cover types more often when these features were rare on the landscape and when alternate habitat choices were poor (e.g., selection for conifer forest, marsh, emergent vegetation, and water in the pasture area). Model predictive power differed significantly among areas (GLM: $F_{2,15} = 4.746$, $P = 0.025$). Predictive power was greatest for models at the pasture area (mean $R^2_{adj} = 0.888 \pm 0.038$ SE), followed by boreal forest (mean $R^2_{adj} = 0.643 \pm 0.087$) and parkland (mean $R^2_{adj} = 0.520 \pm 0.115$; Table 3).

Differences among seasons.—We detected several qualitative patterns that suggest habitat selection differs among seasons. Wet shrubland occurred in five of the six foraging season models, but only occurred in three breeding season models and three pre-hibernation season models (Table 2). Toads selected wet shrubland in all five of the foraging season models in which it occurred. The foraging season model in which wet shrubland was not used was for pasture females; these toads selected crop/hay fields and disturbed grass. Toads only used water and pond sites with emergent vegetation during the breeding season, except for foraging pasture-males. Distance to nearest breeding pond was not significant in three pre-hibernation season models, indicating that, at least in some circumstances, hibernation sites are selected independent of the location of breeding ponds. All foraging season models contained a greater or equal number of significant land-cover variables compared to the corresponding pre-hibernation model and only two foraging season models contained fewer significant variables than the corresponding breeding season model. Selection for certain habitat types became weaker (larger P-values) in several pre-hibernation season models compared to foraging season models. Model predictive power was similar among seasons (Breeding: mean $R^2_{adj} = 0.695 \pm 0.095$ SE; Foraging: mean $R^2_{adj} = 0.671 \pm 0.097$; Pre-hibernation: mean $R^2_{adj} = 0.685 \pm 0.133$; GLM: $F_{2,15} = 0.013$, $P = 0.987$).

Differences between genders.—We detected differences in habitat selection between males and females for some variables. Six of our models suggested female toads were selecting disturbed grass (parkland: foraging; pasture: breeding, foraging, and pre-hibernation; and boreal forest: breeding and foraging). For male toads, disturbed grass was either avoided (two models) or its use was not significant (one model) compared to the reference variable (Table 2). Only foraging pasture males used water and emergent vegetation habitat outside of the breeding season. Predictive power was slightly higher for models of female habitat selection (mean $R^2_{adj} = 0.759 \pm 0.064$ SE) than for males (mean $R^2_{adj} = 0.608 \pm 0.098$), but the difference was not statistically significant (GLM: $F_{1,16} = 1.682$, $P = 0.213$).

DISCUSSION

General patterns of habitat selection.—Similar to the findings of Long and Prepas (2012) in western Alberta, we found that Western Toads used a variety of habitat types. Only land-cover types that were inaccessible or provided no cover were never used, but some land-cover types were selected more frequently than others. Wet shrubland was the most frequently selected land-cover type in our study. Western Toads in Idaho also selected shrub habitat (Bartelt et al. 2004). The shelter provided by shrubs and accompanying accumulations of litter and woody debris on saturated soils may facilitate water conservation in toads with breaks in the canopy creating areas warmed by the sun (Tracy et al. 1993; Bartelt et al. 2004).

Crop/hay fields and pasture were the most abundant land-cover types at our pasture study area. Both male and female toads selected for crop/hay fields but avoided pasture. The pasture at this site was sparsely vegetated and probably provided little cover for toads or their invertebrate prey. Katie Thompson (unpubl. report) found higher invertebrate abundance in crop/hay fields than deciduous or conifer forest at our pasture study area; pasture had fewer invertebrates than did deciduous forest. Toads may have selected crop/hay fields because of more abundant prey and warmer daytime temperatures, which could facilitate growth (Lillywhite et al. 1973).

Toads selected locations closer to breeding ponds or hibernation sites in all models, and 11 of 18 models showed significant selection for locations closer to both of these features. Selection was expected as breeding ponds and hibernation sites are essential resources; however, two models showed opposite trends (boreal forest breeding males farther from hibernation sites than expected; boreal forest foraging males farther from breeding ponds). Reversed patterns were likely observed for boreal forest males because hibernation

sites were far from the breeding pond and males' movements were fairly direct; thus, when males moved towards one seasonal resource they moved away from another.

Most of our models were validated and deemed acceptable, so these findings should be useful to land-managers for assessing habitat quality. Three of the four unacceptable models were from our parkland area. We suspect that sample size within study area affected model predictive power, as the parkland had the lowest sample size and power and the pasture area had both the largest sample and best predictive power.

Differences among study areas.—Land-cover composition differed greatly among our study areas (Appendix I). We thus expected selection by toads to vary among study areas if preference was conditional upon availability. Toads may use certain patch types, even if rare, if they contain a limited resource not available in other settings (see Orians and Wittenberger 1991; Mysterud and Ims 1998). Our results are consistent with this premise, as toads generally used land-cover types more often when they were abundant on the landscape yet selected some cover types more strongly when they were rare.

Selection or avoidance of deciduous and coniferous forest did differ among models. Conifer forest was rare at the pasture area and was selected over deciduous forest in two models. Otherwise, deciduous forest was generally selected or used equally to conifer forest. In another study in northwestern Alberta, we documented a negative relationship between Western Toad abundance at breeding ponds and percent coverage of conifer stands surrounding these ponds (Browne et al. 2009). Deciduous forest may be selected over coniferous forest during the active period because deciduous forests have greater understory vegetation and invertebrate densities (Willson and Comet 1996; Ferguson and Berube 2004), which provide cover and food for toads. However, toads in this area often hibernate in conifer stands (Browne and Paszkowski 2010a). Conifer forest may also provide resources not found in certain deciduous forest patches, such as standing water (many conifer stands at our study areas were poorly drained and dominated by black spruce) and refuge (e.g., Red Squirrel, *Tamiasciurus hudsonicus*, tunnels). These attributes could have contributed to the selection of conifer patches within the open, dry pasture area.

Another example of selection for a land-cover type being influenced by alternate choices was use of emergent vegetation. Emergent vegetation occurred along the edges of breeding ponds at both the parkland and pasture areas. It was more abundant at the parkland area (5.1% cover) than pasture area (0.8% cover), but was used more often in the pasture area (e.g., 22% vs. 5% of breeding male locations) and selected for in

several pasture models but no parkland models. Breeding ponds in the parkland area were surrounded by marsh habitat, whereas ponds at the pasture area were surrounded by grazing land.

Differences among seasons.—Throughout the active period, toads tended to select for open environments (i.e., no canopy cover). All foraging season models showed selection for at least one open habitat type (e.g., wet shrubland, disturbed grass, crop/hay). Our results are consistent with other studies: toads selected open forest (vs. closed forest or clear-cuts) in Idaho (Bartelt et al. 2004), sites with little or no canopy cover in Oregon (Bull 2006), severely burned habitat (vs. partially burned or unburned habitat) in Montana (Guscio et al. 2007), clear-cuts and edge habitat (vs. closed forest) in British Columbia (Deguise and Richardson 2009), and open habitat (vs. closed habitat) as activity centers within their home ranges for female toads in Alberta (Long and Prepas 2012). We suspect that toads are seeking the warm temperatures and abundant prey found in open habitat types to facilitate growth and fat accumulation for gamete production and over-wintering. Hossack et al. (2009) showed that microsites in open habitats used by toads in Guscio et al. (2007)'s study were warmer than microsites in nearby forest.

Differences between genders.—Bull (2006) reported that female toads selected more open habitat than males, and males were more closely associated with water. We observed comparable patterns; for example, female toads selected disturbed grass in six models. When models for male toads included disturbed grass it was either avoided or not significantly different from the reference variable. Somewhat contradictory to our results, Long and Prepas (2012) found that female Western Toads used wetland habitat significantly more in their activity centers when compared to their 50% core home ranges; however, male toads included a greater proportion of wetland habitat in their 50% core home ranges than did females. Differences in habitat selection between the genders observed by us and others could be: (1) because females are more attracted to habitats that facilitate somatic growth and gamete production (Muths 2003), whereas males focus on locations close to breeding ponds in spring (Gatz 1981; Olson et al. 1986); (2) because males are smaller, and thus more prone to dehydration, which might restrict their ability to use open upland habitat (Bartelt et al. 2004); and/or (3) to reduce intraspecific competition (Johnson et al. 2007).

Conclusions.—Western Toads used a variety of habitat types and differences in habitat selection were observed among study areas, seasons, and genders. Throughout the active period, toads selected habitats that could facilitate growth (warm, open habitat with

abundant prey) and/or provide essential resources (e.g., moisture, shelter, breeding locations). Wet shrubland was the most highly selected land-cover type during the active period. Crop/hay fields were also warm, open habitat with abundant prey and were frequently selected where they occurred in an agricultural setting. Pasture habitat was avoided, possibly because vegetation cover was sparse and invertebrate densities low. Generally land-cover types were used more frequently when common on a landscape, but significant selection was documented for some rare land-cover types, suggesting that valuable resources occurred in these patches.

Our results can help land managers identify essential land-cover types and habitat features for Western Toads in their northern range. Results from our parkland and boreal forest study areas are of direct use for those managing large areas of similar habitat (e.g., park biologists and forestry land managers). However, we find our pasture study area especially interesting as it provides insight on how humans and toads can coexist in a modified landscape. Toads in this area breed in constructed ponds located in cattle pasture and many toads spend much of the foraging season in crop/hay fields. A key feature for the population is scattered patches of mixed deciduous and coniferous woodland used by the toads mostly for hibernation. This system suggests that retention of patches of breeding, foraging, and hibernating habitat may help Western Toad populations persist in agricultural areas.

LITERATURE CITED

Alberta Government. 2005. 2005 Natural Regions and Subregions of Alberta (map). Alberta Sustainable Resource Development, Alberta Environment, Alberta Community Development, and Agriculture and Agri-Food Canada. (http://www.albertaparks.ca/media/442827/nsr2005_final_letter.pdf [Accessed 23 May 2014])

Bartelt, P.E., and C.R. Peterson. 2000. A description and evaluation of a plastic belt for attaching radio-transmitters to Western Toads (*Bufo boreas*). Northwestern Naturalist 81:122–128.

Bartelt, P.E., C.R. Peterson, and R.W. Klaver. 2004. Sexual differences in the post-breeding movements and habitats selected by Western Toads (*Bufo boreas*) in southeastern Idaho. Herpetologica 60:455–467.

Browne, C.L., and C.A. Paszkowski. 2010a. Hibernation sites of Western Toads (*Anaxyrus boreas*): characterization and management implications. Herpetological Conservation and Biology 5:49–63.

Browne, C.L., and C.A. Paszkowski. 2010b. Factors affecting the timing of movements to hibernation sites by Western Toads (*Anaxyrus boreas*). Herpetologica 66:250–258.

Browne, C.L., C.A. Paszkowski, A.L. Foote, A.E. Moenting, and S.M. Boss. 2009. The relationship of amphibian abundance to habitat features across spatial scales in the Boreal Plains. Ecoscience 16:209–223.

Bull, E.L. 2006. Sexual differences in the ecology and habitat selection of Western Toads (*Bufo boreas*) in northeastern Oregon. Herpetological Conservation and Biology 1:27–38.

Chan, Y.H. 2005. Biostatistics 305. Multinomial logistic regression. Singapore Medical Journal 46:259–268.

Compton, B.W., J.M. Rhymer, and M. McCollough. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83:833–843.

Deguise, I., and J.S. Richardson. 2009. Movement behaviour of adult Western Toads in a fragmented, forest landscape. Canadian Journal of Zoology 87:1184–1194.

Ferguson, S.H., and D.K.A. Berube. 2004. Invertebrate diversity under artificial cover in relation to boreal forest habitat characteristics. Canadian Field-Naturalist 118:386–394.

Gatz, A.J. 1981. Non-random mating by size in American Toads, *Bufo americanus*. Animal Behaviour 29:1004–1012.

Goates, M.C., K.A. Hatch, and D.L. Eggett. 2007. The need to ground truth 30.5 m buffers: a case study of

the Boreal Toad (*Bufo boreas*). Biological Conservation 138:474–483.

Guscio, G.C., B.R. Hossack, L.A. Eby, and P.S. Corn. 2007. Post-breeding habitat use by adult Boreal Toads (*Bufo boreas*) after wildfire in Glacier National Park, USA. Herpetological Conservation and Biology 3:55–62.

Heinze, G., and M. Ploner. 2003. Fixing the nonconvergence bug in logistic regression with SPLUS and SAS. Computer Methods and Programs in Biomedicine 71:181–187.

Hossack, B.R., L.A. Eby, C.G. Guscio, and P.S. Corn. 2009. Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. Forest Ecology and Management 258:1414–1421.

Howlin, S., W.P. Erickson, and R.M. Nielson. 2004. A validation technique for assessing predictive abilities of resource selection functions. Pp. 40–51 *In* Proceedings of the First International Conference on Resource Selection. Laramie, Wyoming, January 13−15, 2003. Resource Selection Methods and Applications. Western Ecosystems Technology, Inc., Cheyenne, Wyoming, USA.

Johnson, C.J., S.E. Nielsen, E.H. Merrill, T.L. McDonald, and M.S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, J.R., J.H. Knouft, and R.D. Semlitsch. 2007. Sex and seasonal differences in the spatial terrestrial distribution of Gray Treefrog (*Hyla versicolor*) populations. Biological Conservation 140:250–258.

Lillywhite, H.B., P. Licht, and P. Chelgren. 1973. The role of behavioral thermoregulation in the growth energetics of the toad, *Bufo boreas*. Ecology 54:375–383.

Long, Z.L., and E.E. Prepas. 2012. Scale and landscape perception: the case of refuge use by Boreal Toads (*Anaxyrus boreas boreas*). Canadian Journal of Zoology 90:1015–1022.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies. 2nd Edition. Kluwer, Boston, Massachusetts, USA.

Muths, E. 2003. Home range and movements of Boreal Toads in undisturbed habitat. Copeia 2003:160–165.

Mysterud, A., and R.A. Ims. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. Ecology 79:1435–1441.

Olson, D.H., A.R. Blaustein, and R.K. O'Hara. 1986. Mating pattern variability among Western Toad (*Bufo boreas*) populations. Oecologia 70:351–356.

Orians, G.H., and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist 137:S29–S49.

Tracy, C.R., K.A. Christian, M.P. O'Connor, and C.R. Tracy. 1993. Behavioral thermoregulation by *Bufo americanus*: the importance of the hydric environment. Herpetologica 49:375–382.

Willson, M.F., and T.A. Comet. 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. Condor 98:350–362.

Wind, E.I., and L.A. Dupuis. 2002. COSEWIC status report on the Western Toad *Bufo boreas in* Canada, in COSEWIC assessment and status report on the Western Toad *Bufo boreas* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada. 31 pp.

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APPENDIX 1. Proportion of land-cover types at three Western Toad study areas in north-central Alberta. Study areas are circular and centered on the breeding pond(s); the radius of each study area was the distance between the study area center and the farthest toad location. See Table 2 for abbreviations.

Land-cover type	Parkland	Pasture	Boreal Forest
ConFor	0.016	0.016	0.412
DecFor	0.397	0.158	0.249
MixFor	0.052	0.099	0.089
DryShr	0.015	0.012	0.006
WetShr	0.032	0.010	0.047
Moss	0	0	0.026
Marsh	0.224	0.014	0.015
Meadow	0.017	0.003	0.001
Burn	0	0	0.017
CutGra	0	0	0.005
CutTre	0	0	0.062
DisGra	0.010	0.028	0.055
Railway	0	0	0.001
Gravel	0.003	0.004	0.006
Paved	0	0.003	0
MowLwn	0	0.004	0
Building	0	0.001	<0.001
CropHay	0	0.411	0
Pasture	0	0.213	<0.001
Exposed soil	0	0.004	0
EmgtVeg	0.051	0.008	<0.001
Water	0.182	0.011	0.007

APPENDIX 2. Summary of results from 18 Resource Selection Function models of Western Toad habitat selection in north-central Alberta. Counts in table are the number of models in which the respective land-cover variable was: selected, used but avoided, used at a level not significantly different from the reference variable, not used but available, not available in the study area, or designated as the reference variable. See Table 2 for definitions of abbreviations of land-cover types.

Land-cover type	Used			Not Used		
	Selected	Avoided	Not Signif.	Available	Not Avail.	Reference
ConFor	2	2	1	7		6
DecFor	2		1	5		10
MixFor	3	2	3	10		
DryShr	2		3	13		
WetShr	9		2	7		
Moss	3	2	1		12	
Marsh	2	1	3	11		1
Meadow	1			17		
Burn	1	1	1	3	12	
CutGra	3			3	12	
CutTre	1		1	4	12	
DisGra	6	2	2	8		
Railway				6	12	
Gravel				18		
Paved				6	12	
MowLwn	1		1	4	12	
Building				12	6	
CropHay	5			1	12	
Pasture		5		7	6	
Exposed soil				6	12	
EmgtVeg	3		1	14		
Water	2		2	13		1

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APPENDIX 3. Distance to nearest breeding pond (top row) or hibernation site (bottom row) from locations used by radio-tracked Western Toads (squares) and random available habitat locations (circles) at three study areas in north-central Alberta (Parkland, Pasture, and Boreal Forest). Distances (mean ± 95% CI; in meters) were compared among three seasons (Breeding, Foraging, and Pre-hibernation = PreHib.) and between females (F) and males (M).

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