Herpetological Conservation and Biology 8(3):688−706.
Submitted: 5 September 2012; Accepted: 2 April 2013; Published: 31 December 2013.

Defining Conservation-relevant Habitat Selection by the Highly Imperiled Oregon Spotted Frog, *Rana pretiosa*

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***Abstract*.—We tested the degree of habitat selection at two spatial scales by captive-raised Oregon Spotted Frog (*Rana pretiosa*) individuals released at two sites in British Columbia to inform translocation and habitat-based recovery actions for this highly imperiled species. Telemetry of captive-raised adults during the post-breeding season (2009 and 2010) suggests that Oregon Spotted Frogs selected for herbaceous and shrub macrohabitats (delineated from high-resolution aerial imagery) that form continuous floating mats or mats interspersed with water. At the microhabitat level, frogs consistently selected for taller vegetation (= 122.9 ± 8.0 cm) and thicker submerged vegetation (= 23.5 ± 2.4 cm), based on comparisons with paired random locations (= 99.2 ± 9.4 cm, and = 13.8 ± 1.9 cm, respectively). Within two study wetlands, microhabitats with < 50% cover of semi-open herbaceous or shrub vegetation were also associated with higher frog presence. These results provide support for the hypothesis that Oregon Spotted Frogs at these sites select for taller, less dense vegetation, irrespective of the floristic composition at the microhabitat scale, but not at the macrohabitat scale. These results from captive-reared animals corroborate findings from habitat-selection studies that used wild-collected animals. Differences in selection at the macrohabitat scale between years suggest that a wide range of wetland types could be considered as candidates for reintroduction efforts. Our results emphasize the need for methods that transcend site-specific floristic differences among wetlands to inform potential reintroduction sites and guide habitat restoration activities.**

Key Words.—amphibian declines; critical habitat; Canada; habitat selection; imperiled species; Oregon Spotted Frog; *Rana pretiosa*; recovery plan

Introduction

Reversing or stemming the decline of endangered species is a ubiquitous goal of conservation biology, yet remains one of the most challenging tasks to achieve (Foin et al. 1998). Populations of imperiled and declining species are usually small and exceedingly vulnerable to both demographic and environmental stochasticity (Lande 1993), rendering it logistically difficult to diagnose the mechanisms of decline (Caughley 1994). Moreover, recovery efforts are often hindered by limited information about the ecology and natural history of declining species, and the lack of adequate monitoring exacerbates this problem (Campbell et al. 2002). In many cases, managers depend on two general types of recovery actions to arrest further declines, even in the absence of a mechanistic understanding of declines (Tear et al. 1993; Snyder et al. 1996; Taylor et al. 2005; Gascon et al. 2007): direct population management through population augmentation (e.g., captive breeding, hatcheries, translocation), and habitat protection or restoration.

Amphibians have undergone dramatic declines over the past three decades, and are among the most imperiled taxa on Earth (Stuart et al. 2004; Collins and Halliday 2005). A suite of diverse stressors are often cited as causes for declines (Alford and Richards 1999; Blaustein and Kiesecker 2002; Collins and Storfer 2003), and the vulnerability of some amphibians is magnified by biphasic life cycles with potential impacts occurring in both aquatic and terrestrial habitats (Wilbur 1980). Many imperiled amphibians represent a classic conservation dilemma where management actions to reverse declines are often needed well before a full understanding of the underlying causes of declines. In light of such uncertainty, many management and conservation efforts to reverse amphibian declines focus on increasing habitat availability and quality, or directly augmenting populations (Semlitsch 2000, 2002), as habitat and population abundance can be more feasible to manipulate compared to modifying or eliminating environmental stressors. However, direct actions to improve habitat or translocate captive-raised or wild-type animals require knowledge of habitat selection by focal species.

In addition, legislation to aid species recovery (Canada's Species at Risk Act, U.S. Endangered Species Act, and E.U. Habitats and Birds

Directives) often focuses on the management of habitat that encompasses the space required for behavior and reproduction, food resources, and cover attributes necessary for the survival of listed species (Hodges and Elder 2008). Though the role of critical habitat designation in predicting species improvement remains equivocal (Clark et al. 2002; Hoekstra et al. 2002; Taylor et al. 2005), such designations are essential to legislated recovery planning efforts. Definitions of critical habitat are often limited by a lack of species-specific data on habitat use and movement both within individual sites (microhabitat selection) as well as at the landscape-scale (macrohabitat selection; Morrison et al. 2006; Börger et al. 2008). When combined with translocation efforts of captive-raised animals, critical habitat designation becomes more difficult given the uncertainties surrounding habitat selection (resource use relative to resource availability; Johnson 1980; Aebischer et al. 1993; Manly et al. 2002) by animals released in a novel environment. In this study we evaluated the strength of habitat selection at two spatial scales by the endangered Oregon Spotted Frog (*Rana pretiosa*) raised in captivity and released at two sites in British Columbia, as a means to inform species recovery efforts, which currently include habitat restoration as well as translocation.

Oregon Spotted Frogs, extirpated from 90% of historic wetland sites across their range (southern British Columbia to northern California), are listed as vulnerable by the IUCN (Hammerson and Pearl 2004). Moreover, the species is currently listed as endangered under the Species at Risk Act in Canada (COSEWIC 2011) and is a likely candidate for listing under the US Endangered Species Act. Four Oregon Spotted Frog populations remain in Canada, the northern-most extent of the species' range, and all four locations have low numbers and occur in remnant habitats heavily modified by anthropogenic activities that span a wide range of physical, hydrologic, and vegetation characteristics (Canadian Oregon Spotted Frog Recovery Team. 2012. Recovery strategy for the Oregon Spotted Frog (*Rana pretiosa*) in British Columbia. Available from http://www.env.gov.bc.ca/wld/recoveryplans/recovery_doc_table.html [Accessed 30 January 2013]). A previous habitat selection study of a larger US population (Watson et al. 2003) showed that during summer, Oregon Spotted Frogs selected for herbaceous and shrub-dominated habitats with a complex architecture, which offered both cover (e.g., tall vegetation interspersed with open water and floating mats) and basking microhabitats (e.g., medium stem densities and/or canopies). We investigated habitat selection using radiotelemetry of Oregon Spotted Frogs at two sites located at the northern limit of the geographic distribution in 2009 and 2010, where we aggregated habitat data into ecologically-based categories of plant growth forms (Harris and Harris 2001). We focused our analysis at two levels of resolution, the first being contiguous macrohabitat patches (≥ 100 m^2) delineated from high-resolution aerial imagery, which were used to assess use versus availability at the wetland scale. The second was the microhabitat associations recorded within 1-m^2 plots centered on frog telemetry locations and paired random plots, which identified habitat selection at the scale of daily movements. If strong habitat selection exists at the macrohabitat scale, reintroduction and translocation efforts for this species could be focused on wetlands that contain broad characteristics most strongly selected for that would require relatively low effort to identify (e.g., new sites for introductions within the current range using aerial imagery and rapid habitat surveys). If selection occurs more strongly at the microhabitat scale, management could focus on maintaining or restoring fine-scale attributes (e.g., manipulate vegetation height and density, water depth) prior to augmentation efforts. Consistent selection at both scales could provide the most specific guidelines for habitat management, but it would also be the most limiting in terms of conservation actions for species recovery due to higher cost associated with active management at both spatial scales (e.g., identifying specific macrohabitats across existing wetlands, followed by active management of structural attributes).

Our overarching goal was to examine the interplay between two scales of habitat selection by the endangered Oregon Spotted Frog in two remnant British Columbia populations to help inform species recovery. Based on existing studies which found that vegetation structure strongly influenced habitat selection, we predicted that Oregon Spotted Frogs would exhibit strong selection at the microhabitat level, while macro-scale selection would be relatively weak. Specifically, the study objectives were: to evaluate the strength of habitat relationships at two levels of resolution, macro- and microhabitat, and to present a framework to inform habitat management practices that can be broadly applicable across sites with different vegetation characteristics.

Materials and Methods

Study sites.—We worked at two wetland sites with remnant Oregon Spotted Frog populations in British Columbia, Canada (Fig. 1), Maria Slough and Maintenance Detachment Aldergrove (henceforth Aldergrove). These wetlands are located 62 km apart in the Fraser River Valley (Fig. 1). Maria Slough is a 7-ha wetland (UTM 10: 593998E, 5461631N, elev. = 16 m) and contains an estimated breeding population of 400 to 500 adult Oregon Spotted Frogs based on a mark-recapture study conducted in 2011 (Amanda Kissel, unpubl. data). Maria Slough was historically a large side channel of the Fraser River now disconnected at its upstream end. Water levels at Maria Slough are dynamic (0.3–1 m change seasonally) and largely driven by those in the Fraser River, but also affected by beaver dams and water extraction for local agriculture. Wetland vegetation at Maria Slough is dominated by herbaceous species including Cattail (*Typha* spp.) and invasive Reed Canarygrass (*Phalaris arundinacea*), the latter forming continuous floating and submerged mats (Appendix I). The surrounding landscape is dominated by agriculture (row crops), the transition of which is marked by a narrow, discontinuous riparian buffer.

Aldergrove is an 18-ha headwater wetland (UTM 10: 537349E, 5345981N, elev. = 105 m) with extensive emergent shrub vegetation dominated by Hardhack (*Spiraea douglasii*) and abundant floating vegetation, mainly Watershield (*Brasenia schreberi*) and Water-starwort (*Callitriche* sp.). Water levels at Aldergrove vary seasonally by 0.5–1 m, driven by precipitation and groundwater, and are also influenced by weirs and beaver dams. Surrounding land consists of forested wetlands, agricultural lands, and extensive mowed fields. No breeding activity has been detected at Aldergrove since 2007, but individual adults continue to be found, indicating that the population persists at low levels.

Radiotelemetry.—To elucidate the habitat correlates of Oregon Spotted Frog movement at two scales, we followed post-metamorphic individuals using radiotelemetry. Over the course of the study, we tracked 45 Oregon Spotted Frogs (Maria Slough: n = 14 in 2009 and n= 13 in 2010; Aldergrove: n = 10 in 2009 and n = 8 in 2010), one of which was a female that was used in both 2009 and 2010. Study animals (14

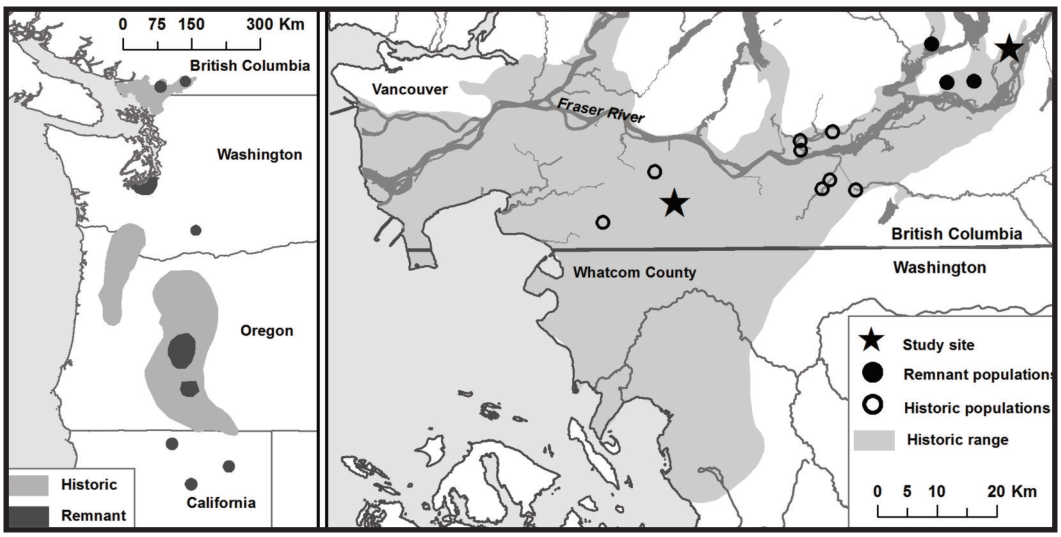

Figure 1. Historic and current geographic distribution of Oregon Spotted Frogs (*Rana pretiosa*) in North America (left), and in British Columbia, Canada (right). Historic and current ranges were redrawn from IUCN range maps (International Union for Conservation of Nature and Natural Resources. Digital distribution maps of the world's amphibians. Available from http://www.iucnredlist.org/technical-documents/spatial-data#amphibians [Accessed 1 February 2013]), with edits from Marc Hayes (pers. comm.).

females and 30 males) were 1–2 years of age and captive-raised from wild eggs at the Greater Vancouver Zoo (Aldergrove, British Columbia) and Mountain View Conservation and Breeding Center (Langley, British Columbia) as part of a head-start recovery program. All individuals had been collected as wild embryos from Maria Slough in 2007 and 2008. We used captive-raised frogs as opposed to wild adults to limit impacts to the already small remaining wild Oregon Spotted Frog populations in the region. We selected frogs for the telemetry study based on median size (mass = 28.45 g, range = 20.1–71.7 g; snout-vent length = 59 mm, range = 53–91 mm), which reflected their ability to carry a Model BD-2T radio transmitter (Holohil Systems Ltd., Carp, Ontario, Canada) with minimal stress; radio transmitters (0.9–3.0 g) did not exceed 5% of the mass of each frog. We attached radio transmitters using a waist-belt system in which we threaded a small belt either made of jewelry cord threaded with small beads or folded Opsite Flexifix (Smith and Nephew, London, UK) through the transmitter and tied the belt around frog's waist. We tracked frogs from September 2009 to February 2010, and from July to November 2010 at both sites. We relocated frogs 1–4 times per week (relocations per frog = 8) during the study period to within approximately 10 cm of their actual location or until visual contact, and recorded their locations using hand-held global positioning system unit (number of relocations Maria Slough: 126 in 2009 and 69 in 2010; Aldergrove: 136 in 2009 and 36 in 2010). Only 14 frogs were relocated ≥ 10 times. The median and range of the number of relocations per frog varied by year and site: Maria Slough 2009: = 13 (range = 6–29), Maria 2010: = 7 (range = 5–16), Aldergrove 2009: = 16 (range = 9–24), and Aldergrove 2010: = 6 (range = 5–7). Few telemetry locations per frog limited our ability to define individual home ranges; consequently, we focused the analysis on aggregated (i.e., population-level) habitat selection (2nd-order selection; Johnson 1980; Thomas and Taylor 2006) for each site separately. Frogs were released at known and historic breeding locations within the wetlands, and we conducted analyses separately for each year. To allow individuals introduced to new wetland habitats to acclimatize and reduce the likelihood of handling and release effects, we excluded the first three days of relocation data from our analyses.

***Macrohabitat delineation*.**—To determine if Oregon Spotted Frogs selected habitat at a macrohabitat level, we delineated coarse macrohabitat types based on 2004 ortho-imagery (1 × 1 m resolution) at Aldergrove, and 2009 ortho-imagery at Maria Slough (20 × 20 cm resolution) (GeoBC, Digital Image Service, Victoria, British Columbia, Canada) followed by ground-truthing. We defined macrohabitat patches by the presence of contiguous areas dominated (> 80%) by a particular vegetation structure (e.g., herbaceous, culm, floating), which could be resolved to a minimum size of approximately 100 m^2 (i.e., the minimum size of any given macrohabitat patch delineated from aerial imagery). Based on our knowledge of the sites, and after consulting Harris and Harris (2001), we identified a total of four macrohabitat categories: Herbaceous, Culm, Shrub, and Floating (macrohabitat definitions and area occupied at each site are provided in Table 1). Notably, the first two categories form continuous mats that are partially or totally submerged. Shrubs can be completely emergent, or partially submerged depending on local topography and water levels. Besides these macrohabitat categories, we also scored macrohabitat patches as Open Water, as well as selected combinations (e.g., Culm/Herbaceous, Shrub/Floating) in cases where different categories were highly interspersed (e.g., where individual macrohabitat patches were not distinguishable at the 100-m^2 minimum mapping unit). Several macrohabitats were represented at both sites, but some site-specific types (Fig. 2) reflected fundamental differences in vegetation between the two sites. Specifically, Maria Slough was dominated by Herbaceous and Culm, whereas Aldergrove was dominated by Shrub. Previous studies have shown that Oregon Spotted Frogs remain in wetlands throughout the active season, only rarely moving into upland habitat (Watson et al., 2003), so our habitat selection analyses were confined to wetted areas within the landscape.

***Microhabitat sampling*.**—To evaluate microhabitat selection of Oregon Spotted Frogs, we quantified the structural attributes of vegetation within circular 1-m^2 plots centered on the frog locations (i.e., telemetry points), as well as paired random plots located in a random direction 5–20 m from the frog location. We chose this range of distances based on the range of daily movements inferred from the 2009

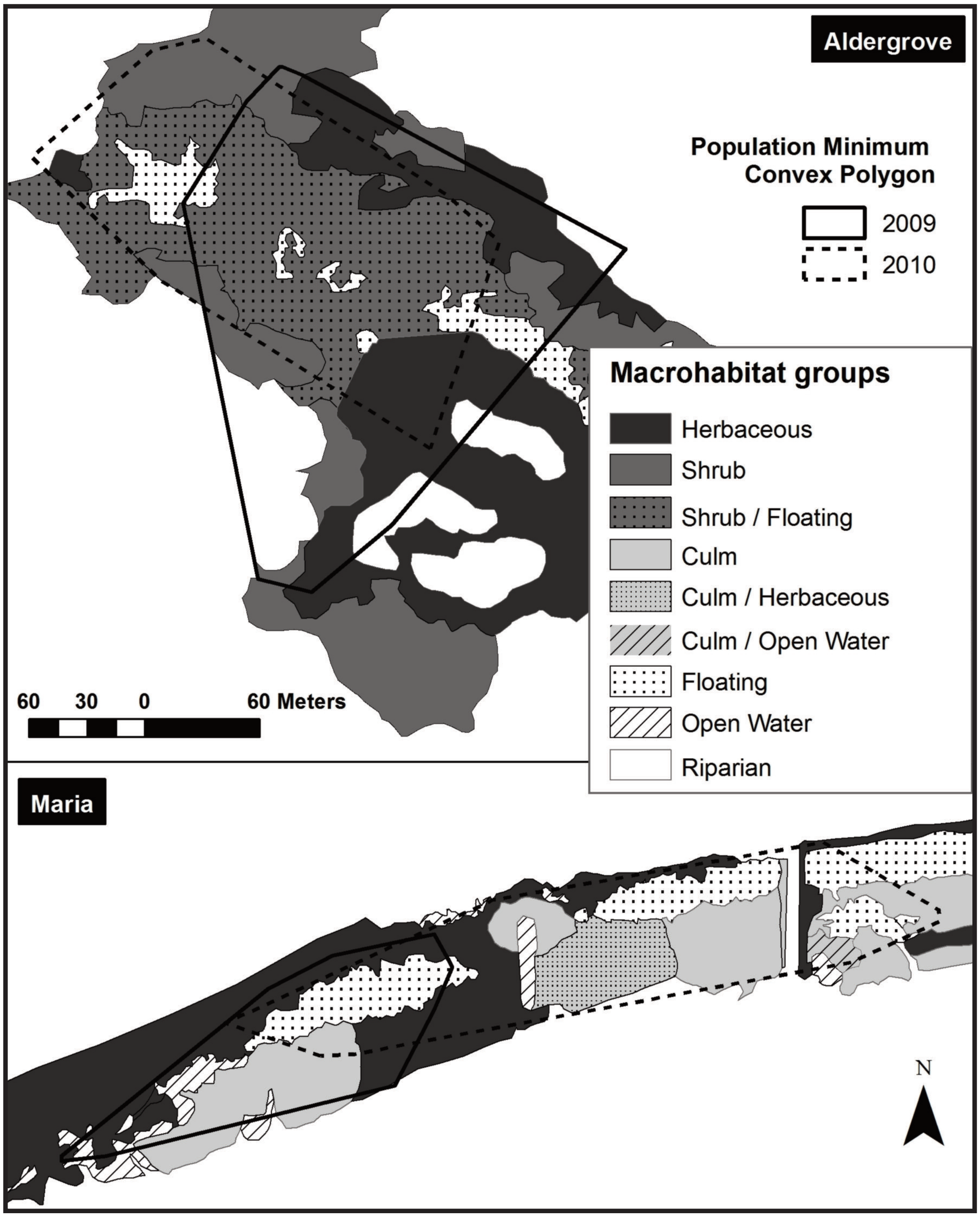

FIGURE 2. Macrohabitat types and 2009–2010 Oregon Spotted Frog population Minimum Convex Polygons at Maria Slough and Aldergrove sites, British Columbia, Canada.

telemetry data: 4–32 m/day (Monica M. Pearson, unpubl. data). This type of habitat sampling was performed at both Maria Slough (n = 158 plots) and Aldergrove (n = 72 plots) only in 2010. We categorized vegetation into microhabitat types based on growth form (e.g., herbaceous vs. shrub and emergent vs. submergent vs. floating) and stem density (e.g., dense, semi-open, or open;

Table 1. Macrohabitat types and area (ha) covered within population yearly minimum convex polygons encompassing all frog relocations (proportions of MCP for each year and site are shown in parentheses and italics).

Macrohabitat	Definitions	Maria Slough		Aldergrove	
		2009	2010	2009	2010
Herbaceous	Areas dominated (> 50% cover) by grass species (Poaceae) with continuous submerged root mats	0.514	0.663	0.555	0.194
		(0.37)	(0.26)	(0.18)	(0.08)
Culm	Areas dominated (> 50% cover) by tall culm (e.g., *Typha* spp.) with continuous submerged root mats	0.423	0.631	--	--
		(0.31)	(0.25)	--	--
Culm/Herbaceous	Areas dominated by a mix of Culm and Herbaceous, with continuous submerged root mats	–	0.361	--	--
		--	(0.15)	--	--
Shrub	Areas dominated by tall, woody, emergent vegetation, with little or no standing water	–	–	0.516	0.418
		--	--	(0.16)	(0.16)
Shrub/Floating	Areas dominated (> 50% cover) by shrub vegetation (e.g., *Spiraea* spp.) interspersed with water channels with floating vegetation, with continuous submerged root mats	–	–	1.915	1.716
		--	--	(0.60)	(0.67)
Floating	Areas dominated by floating vegetation (e.g., *Nuphar*, *Brasenia* spp.), with complex submerged structure	0.306	0.733	0.174	0.230
		(0.22)	(0.29)	(0.06)	(0.09)
Culm/Open Water	Areas dominated by a mix of Culm and Open Water, with continuous submerged root mats within the Culm portions	--	0.044	--	--
		--	(0.02)	--	--
Open Water	Areas with no vegetation	0.124	0.077	--	--
		(0.09)	(0.03)	--	--
	Total Minimum Convex Polygon (ha)	**1.367**	**2.533**	**3.160**	**2.559**

Harris and Harris 2001) regardless of plant species composition (Table 2). We recorded percent cover of microhabitats present in the 1-m^2 sampling plots (adding to 100% cover for each plot). Microhabitat categories used were often nested within the macrohabitat categories described above. For example, emergent shrub microhabitats were found only within Shrub macrohabitat, while dense, semi-open, and open emergent herbaceous microhabitats could be found within Herbaceous or Culm/Herbaceous macrohabitats. We considered the submerged portions of the Herbaceous and Culm categories as part of these respective macrohabitats, rather than a separate "submerged" category. At the same time, open water, as a microhabitat, could be found within all macrohabitat categories. We also recorded maximum vegetation height (*VegHeight*) above the surface of the water, the maximum depth that emergent vegetation extended into the water column from the surface (*VegDepth*), and water depth (*WatDepth*). The latter two variables were highly correlated (r > 0.8), and we selected *VegDepth* for the microhabitat selection analyses. Oregon Spotted Frogs often burrow into submerged vegetation mats (Amanda Kissel and Monica Pearson, pers. comm.), thus the depth of the vegetation would be more informative of habitat selection compared to water depth.

Macrohabitat selection analysis.—We used a Euclidean Distance (ED)-based analysis (Conner and Plowman 2001, Conner et al. 2003) to investigate selection of broad macrohabitat types within the population home range, defined as the

Table 2. Microhabitat types used for the conditional logistic habitat selection analysis. Plants were first classified into their dominant growth form and then assigned a microhabitat type based on botanical features. The table also shows the median (range) percentage cover of each microhabitat type in the frog telemetry plots and paired random plots.

Vegetation growth form	Microhabitat	Example	Definition	Median and Range Percentage			
				Maria Slough		Aldergrove	
				Frog Plot	Random Plot	Frog Plot	Random Plot
Emergent	Culm (*ECulm*)	Cattail (*Typha* spp.)	Plants with single stems >2 cm in diameter	2 (0−95)	0 (0−95)	−	−
	Dense Herbaceous (*EDHerb*)	Reed Canary Grass *(Phalaris arundinacea)*	Herbaceous plants with narrow leaves and high-density single stems (i.e., >50% cover)	0 (0−100)	0 (0−100)	−	−
	Semi-Open Herbaceous (*ESOHerb*)	Poaceae	Herbaceous plants with single stems and narrow leaves that would not otherwise be categorized as Dense or Open Herbaceous (i.e., <50% cover)	10 (0−50)	0 (0−45)	0 (0−40)	0 (0−25)
	Open Herbacous (*EOHerb*)	Horsetail (*Equisetum* spp.)	Low-density herbaceous plants with one or a few stems	0 (0−40)	0 (0−20)	−	−
	Shrub (*EShrub*)	Hardhack (*Spiraea douglasii*)	Any shrub-like growth form: multiple, woody stems, shorter in height than a tree	−	−	10 (0−30)	1 (0−30)
Floating	(*Float*)	Watershield (*Brasenia schreberi*)	Plants that have a growth form in which leaves float on the surface of the water	−	−	0 (0−50)	0 (0−80)
Submergent	(*Submergent*)	Watershield roots, Water Milfoil (*Myriophyllum* spp.)	Loosely interwoven roots, stems, or leaves that form a web-like structure beneath the water	0 (0−60)	0 (0−95)	−	−
Floating Debris	(*FltDeb*)	Downed Cattail	Vegetation which was no longer growing or attached to roots or stems of a plant that was floating on the surface of the water	10 (0−90)	0 (0−92)	5 (0−50)	2 (0−50)
Open Water	(*OpenWat*)	−	No vegetation above, below, or floating on the water surface that may have provided cover for a frog	40 (0−98)	30 (0−100)	70 (25−89)	60 (0−100)

100% Minimum Convex Polygon (MCP) encompassing all frog relocations. Euclidean distance based-approaches integrate both areal and linear habitat features (Conner et al. 2003), such as pond edges, which are known to be important attributes for many pond-breeding aquatic amphibians (Semlitsch 2002). Although ED techniques have been successfully used for assessing habitat selection in reptiles (e.g., DeGregorio et al. 2011; Rozylowicz and Popescu 2013), this is the first study to apply ED to an amphibian. First, we used the Geospatial

Modeling Environment (GME; Hawthorne L. Beyer, Spatial Ecology LLC. 2010. Available from www.spatialecology.com [Accessed 20 May 2012]) with ArcGIS 10 (ESRI, Redlands, California, USA) to simulate points from a uniform random distribution within the population MCP footprint in a 5-meter uniform pattern (detailed enough to capture small, ≈ 100 m^2, macrohabitat patches). Because we analyzed each year and site separately, the number of simulated points was: 549 from Maria Slough in 2009; 1,067 from Maria Slough in 2010; 1,412 from Aldergrove in 2009; and 1,050 from Aldergrove in 2010. We measured the straight-line distance from each random point to the nearest representative of each macrohabitat type, and calculated a habitat availability vector (a) as the average distance between random points and each macrohabitat. Second, we measured the straight-line distance from the known locations of each individual (i.e., telemetry points) to the nearest representative of each macrohabitat, and calculated a habitat use vector (u_i) as the average distance between telemetry points and each macrohabitat type. These distances were calculated using the *Near* tool in ArcGIS 10. We created a vector of ratios for each frog with ≥ 5 telemetry locations, by dividing each element in the vector of habitat use by the vector of habitat availability ($d_i = u_i/a$). Lastly, we calculated the average of vector ratios (vector = ρ) for each macrohabitat.

To test whether frogs exhibited landscape-scale macrohabitat selection we performed a multivariate analysis of variance (MANOVA) under the null hypothesis that the mean ratios vector r did not differ from a vector of 1 (i.e., habitat selection did not occur). The alternative hypothesis was that the mean vector r differed from a vector of 1, (i.e., habitats were preferred non-randomly and habitat selection occurred). If the MANOVA test rejected the null hypothesis, we then used a two-tailed Wilcoxon signed rank test to determine which macrohabitats were used disproportionately and obtained a ranking matrix of all macrohabitats in the study area. If the mean vector for a certain habitat ($\rho_{habitat}$) was significantly < 1, the corresponding habitat was used more than expected. If $\rho_{habitat}$ was significantly > 1, the corresponding habitat was avoided more than expected (Conner and Plowman 2001). This pattern can be interpreted as selected ($\rho_{habitat} < 1$) or avoided ($\rho_{habitat} > 1$) habitats. Because ranking macrohabitats did not reveal information on whether a particular macrohabitat is used proportionately more than other macrohabitat types, we performed t-test pairwise comparisons among all macrohabitat types, under the null hypothesis: $\rho_{habitat\,A} - \rho_{habitat\,B} = 0$. A significant test statistic indicates that one macrohabitat type was used proportionately more than the other. Analyses of 2nd-order habitat selection were performed using code adapted from Conner and Plowman (2001) for program SAS/STAT 9.3 (SAS Institute, Inc., Cary, North Carolina, USA).

Microhabitat selection analysis.—We used conditional logistic regression to analyze selection of microhabitat features for 2010, the only year for which data were available. Conditional logistic regression takes advantage of data collected in a matched design to identify differences between habitat features at the location of animal occurrences (habitat used) and paired random locations (habitat available) measured at the same time (Breslow and Day 1980; Hosmer and Lemeshow 1989). For species with limited mobility, including many amphibians, conditional logistic regression tends to better represent habitat choices compared to traditional logistic regression or multivariate techniques (Compton et al. 2002; see Rittenhouse and Semlitsch 2007 and Gorman and Haas 2011 for use of this technique with terrestrial and aquatic anurans). Estimated coefficients (betas) are interpreted similarly to those of simple logistic regression: an *n*-unit increase in the explanatory variable results in an $\exp(n \times beta_1)$ increase in the odds ratio (Compton et al. 2002). Because explanatory variables in conditional logistic regression are differences between paired observations, not the observations themselves, the model is interpreted in terms of differences in habitat rather than absolute measured values of habitat variables (Compton et al. 2002). We only used data from animals with > 6 telemetry relocations.

We applied a model selection approach (Burnham and Anderson 2002) and selected a set of eight candidate models for each of the two sites containing combinations of percent cover of various microhabitat types, vegetation height, and water depth. The candidate models included microhabitat types only (percent of microhabitat within sampling plot), structural information only (*VegDepth* and *VegHeight*), or a combination of both. These sets of models also included the full (all-variables) and null (intercept-only) models. We first ran microhabitat type only and structural only models, and compared them to the full and null models to test whether microhabitat type or structure alone can be used to explain microhabitat selection. The full model proved to have better explanatory power, and we iteratively removed microhabitat types until we obtained a set of models that varied in complexity. We then used likelihood ratio tests to test whether simpler models (containing fewer variables) performed better than more complex models (Royle and Dorazio 2008) and ranked the candidate models based on their AIC_c values (Akaike Information Criterion corrected for small sample sizes; Burnham and Anderson 2002). We performed conditional logistic regression analyses using function *coxph* in package '*survival*' (Therneau and Lumley 2011) in program R Version 2.14 (R Core Team 2012).

Most telemetry data was collected during the wet season (September - January) as per Watson et al. (2003), so we did not attempt to characterize seasonal (dry versus wet season) habitat selection. Thus, this analysis provides a preliminary characterization of post-breeding, active-season habitat associations of 1−2 year old frogs after their release following captive rearing. Throughout the manuscript, we present means ± standard errors.

Results

Minimum Convex Polygon population home range sizes varied between 1.37 and 3.16 ha (Table 1). At the macrohabitat level, two categories were present at both study sites, Herbaceous and Floating, but they differed in proportions within the yearly population MCPs (Fig. 2). Each of the Herbaceous, Culm, and Floating macrohabitats accounted for > 20–25% of the total MCPs areas at Maria Slough, while the combination Shrub/Floating dominated Aldergrove in 2009 and 2010 (60–70%; Table 1). Open Water was limited at both sites throughout the study (Table 1).

Microhabitat diversity reflected differences in floristic composition between the two sites (e.g., herbaceous versus shrub species), as well as local differences in vegetation structure (e.g., stem density; Table 2). Only the Semi-open Herbaceous and Floating Debris microhabitats were represented at both sites.

***Macrohabitat selection*.—**Oregon Spotted Frogs exhibited strong habitat selection at the population home range level (2nd-order habitat selection) at both sites during the study period. The distances between random locations and macrohabitat types were different from distances between telemetry locations and macrohabitat types for both sites and years (MANOVA; Wilk's Lambda U statistic, $P < 0.05$, range = 0.000–

Table 3. Use versus availability mean ratios (r) and standard errors for landscape scale (2nd order habitat selection) at Maria Slough and Aldergrove sites, British Columbia, Canada. Values for r < 1 indicate macrohabitats that animals selected for (locations were closer in terms of Euclidean distance to the respective macrohabitat than expected). Values in bold depict significant selection (r < 1) or avoidance (r > 1) of macrohabitats (using Wilcoxon signed rank tests); n = the number of frogs used in the macrohabitat selection analysis (different individuals each year).

Maria Slough	2009 (n = 10 frogs)			2010 (n = 10 frogs)		
	ρ	SE	*P*-value	ρ	SE	*P*-value
Herbaceous	**0.21**	0.07	0.002	1.05	0.45	0.322
Culm/	–	–		**1.55**	0.20	0.019
Culm	**1.86**	0.33	0.027	**0.38**	0.13	0.009
Culm/Open Water	–	–		**0.49**	0.11	0.004
Floating	0.80	0.25	0.375	0.86	0.19	0.492
Open Water	**1.72**	0.40	0.014	**0.60**	0.10	0.025

Aldergrove	2009 (n = 8 frogs)			2010 (n = 8 frogs)		
	ρ	SE	P-value	ρ	SE	P-value
Shrub/Floating	**0.27**	0.19	0.029	2.06	1.04	0.985
Herbaceous	**0.66**	0.12	0.039	0.64	0.17	0.148
Floating	0.66	0.18	0.148	**1.70**	0.12	0.008
Shrub	1.31	0.24	0.312	0.45	0.21	0.055

0.041). However, the patterns of habitat selection differed both between years at each site and between sites.

At Maria Slough, the population Minimum Convex Polygons for 2009 and 2010 were different in their extent, with < 50% overlap (Fig. 2), which led to different proportions of available macrohabitat types each year (Table 1). For example, 2009 frogs showed habitat selection ($\rho < 1$; Table 3) towards Herbaceous, and avoided Open Water and Culm (Table 3). At the same site in 2010, frogs preferred Culm, Culm/Open Water, and Open Water ($P < 0.025$), and avoided Culm/Herbaceous (Table 3). The pairwise comparison of distance ratios associated with each habitat indicates that Herbaceous was preferred over all other macrohabitat types in 2009, and Culm/Herbaceous was avoided in 2010 (Table 4).

Similar macrohabitat types were available to Oregon Spotted Frogs during both 2009 and 2010 at the Aldergrove site (> 50% overlap in MCP; Table 1; Fig. 2). In 2009, frogs strongly selected for Herbaceous and Shrub/Floating ($\rho < 1$; Table 3), and no macrohabitat type was selected against. The pairwise comparisons of distance ratios indicate that Herbaceous and Shrub/Floating were preferred over all the other macrohabitat types (Table 4). In 2010, habitat selection was slightly different as animals marginally selected for Shrub, and against Floating macrohabitats; Table 3).

Selection of microhabitat features.—Oregon Spotted Frogs selected for specific microhabitat attributes at the telemetry vs. paired random location scale at both Maria Slough and Aldergrove. For Maria Slough, three competing models had similar support ($\Delta AIC_c < 2$), and contained similar combinations of structural and

Table 4. Pairwise comparisons of use versus availability mean ratio (r) for 2nd-order (landscape scale) distance-based selection by Oregon Spotted Frogs at Maria Slough and Aldergrove sites, British Columbia, Canada. We present t-statistics and associated *P*-values (in parentheses). For each column, negative values denote selection of the habitat in the column header over the habitats in the row headings within the same column (values in bold denote significant selection at $\alpha \leq 0.05$).

Maria Slough 2009	Herbaceous	Culm	Floating
Herbaceous			
Culm	**-4.17 (0.002)**		
Floating	-1.81 (0.104)	1.82 (0.103)	
Open Water	**-5.97 (<0.001)**	0.55 (0.595)	-1.69 (0.126)

Maria Slough 2010	Herbaceous	Culm/ Herbaceous	Culm	Culm/Open Water	Floating
Herbaceous					
Culm/Herbaceous	-1.67 (0.130)				
Culm	1.38 (0.200)	**5.44 (< 0.001)**			
Culm/Open Water	1.14 (0.282)	**3.73 (0.005)**	-0.63 (0.542)		
Floating	0.37 (0.717)	1.95 (0.083)	-1.72 (0.120)	**-2.80 (0.020)**	
Open Water	0.97 (0.356)	**4.62 (0.001)**	**-2.78 (0.021)**	-0.62 (0.553)	1.02 (0.336)

Aldergrove 2009	Shrub/Floating	Herbaceous	Floating
Shrub/Floating			
Herbaceous	-1.56 (0.162)		
Floating	-1.56 (0.161)	-0.01 (0.993)	
Shrub	**-2.86 (0.024)**	**-3.49 (0.010)**	-1.65 (0.143)

Aldergrove 2010	Shrub / Floating	Herbaceous	Floating
Shrub/Floating			
Herbaceous	1.47 (0.184)		
Floating	0.37 (0.722)	**-4.32 (0.003)**	
Shrub	1.43 (0.196)	0.59 (0.575)	**5.46 (< 0.001)**

microhabitat cover variables (Table 5). The top model had the most support, with an AIC_c weight = 0.349, and contained vegetation height (*VegHeight*), submerged vegetation depth (*VegDepth*), and two emergent microhabitat types: Culm (*ECulm*) and Semi-open Herbaceous (*ESOHerb*; Table 5). Coefficients of the top model (Table 6) suggest that Oregon Spotted Frogs at Maria Slough select microhabitats that have higher vegetation depth (23.5 ± 2.4 cm), taller vegetation (122.9 ± 8.0 cm), and higher percent of Semi-open Herbaceous microhabitat (15.8 ± 1.9%) compared to paired random locations (13.8 ± 1.9 cm, 99.2 ± 9.4 cm, and 5.9 ± 1.2%, respectively; Table 6, Fig. 3A,B). The odds ratios indicate that at this site on a relative basis every 10 cm increase in vegetation depth results in a 45% increase in selection, that every 10 cm of additional vegetation height results in a 10% increase in selection, and that a 5% increase in percent cover of Semi-open Herbaceous results in a 40% increase in selection (Table 6).

At Aldergrove, three competing models had similar support ($\Delta AIC_c < 2$; Table 5) and contained combinations of structural and cover attributes, similar to Maria Slough. The top model provided most support (AIC_c weight = 0.453), and included vegetation height (*VegHeight*), percent open water (*OpenWat*), and two emergent microhabitat variables: Shrub (*EShrub*) and Semi-open Herbaceous (*ESOHerb*; Table 5). Of these, only *VegHeight* was significant, and the model coefficients and,

Table 5. Candidate conditional logistic regression models of Oregon Spotted Frog microhabitat selection at Maria Slough and Aldergrove sites in British Columbia, Canada in 2010. LogLik = model log-likelihood; K = number of parameters; ΔAIC_c = difference in Akaike Information Criterion corrected for small sample size from the top model; higher AIC_c weights denote models that are supported among the set of candidate models.

Model	LogLik	K	ΔAICc	AICc weight
Maria Slough				
VegDepth + VegHeight + ECulm + ESOHerb	-35.437	4	0	0.349
VegDepth + VegHeight + EDHerb + ECulm + ESOHerb	-34.828	5	0.782	0.231
VegDepth + VegHeight + ESOHerb	-36.936	3	0.998	0.211
VegDepth + VegHeight + DHerb + ECulm + ESOHerb + OpenWat	-34.467	6	2.06	0.124
VegDepth + VegHeight + EDHerb + ECulm+ Submerged + OHerb + FltDeb + ESOHerb + OpenWat [Full model]	-31.960	9	3.046	0.076
EDHerb+ ECulm + ESOHerb	-41.744	3	10.614	0.001
VegDepth + VegHeight	-45.208	2	15.542	0.000
1 [Null model]	-54.759	1	32.644	0.000
Aldergrove				
VegHeight + EShrub + ESOHerb + OpenWat	-12.165	4	0	0.453
VegDepth + VegHeight + EShrub + FltDeb + ESOHerb + OpenWat [Full Model]	-11.699	5	1.315	0.234
EShrub + VegHeight	-15.206	2	1.781	0.185
VegDepth + VegHeight + EShrub	-14.869	3	3.226	0.090
VegDepth + VegHeight	-17.326	2	6.021	0.022
EShrub + ESOHerb + OpenWat	-17.197	3	7.882	0.008
EShrub + FltDeb + ESOHerb	-17.849	3	9.186	0.004
1 [Null model]	-24.953	1	19.217	0.000

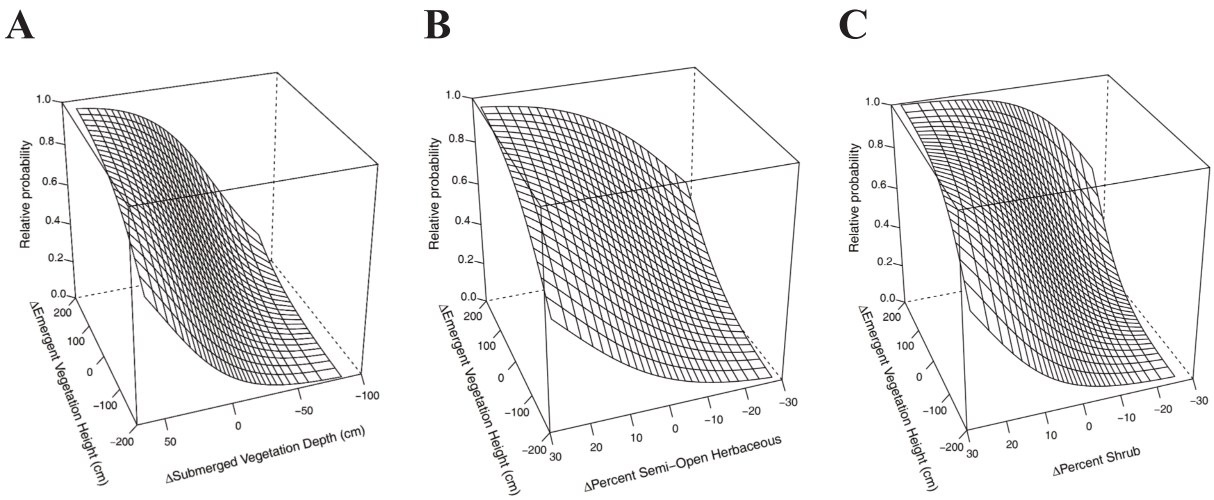

FIGURE 3. Relative probability of occurrence of Oregon Spotted Frogs given the difference between (A) values for vegetation height and water depth (Maria Slough), (B) values for vegetation height and percent Semi-open Herbaceous vegetation (Maria Slough), and (C) values for vegetation height and percent shrub vegetation (Aldergrove) between frog telemetry locations and random locations. Maria Slough: odds ratio for *EClum* is 0.967; Aldergrove: odds ratio for *ESOHerb* is 1.191, and for *OpenWat* is 1.016.

similar to Maria Slough, odds ratios (Table 6) suggest that at Aldergrove Oregon Spotted Frogs select microhabitats with taller vegetation (129.5 ± 11.2 cm compared to 60.6 ± 10.2 cm at random locations): every 10 cm of additional height results in a 14% increase in selection of any given microhabitat type (Fig. 3 C).

DISCUSSION

We used techniques for evaluating habitat selection at two different scales that allowed us to compare relevant habitat attributes across two sites of conservation concern for Oregon Spotted Frogs, and that can provide support for management actions currently being considered

TABLE 6. Conditional logistic regression models that best explains microhabitat selection by Oregon Spotted Frogs at Maria Slough and Aldergrove sites in British Columbia, Canada. Values in bold denote significant selection at α = 0.05.

Variable	Measured values (mean ± SE) Frog Plot	Random Plot	Model coefficient ± SE	*P*-value	Odds ratio	Unit increase
Maria Slough						
VegHeight	122.9 ± 8.0 cm	99.2 ± 9.4 cm	0.009 ± 0.004	**0.019**	1.100	10 cm
VegDepth	23.5 ± 2.4 cm	13.8 ± 1.9 cm	0.037 ± 0.016	**0.022**	1.206	5 cm
ECulm	6.8 ± 1.5%	9.4 ± 1.9%	-0.032 ± 0.021	0.123	0.720	10%
ESOHerb	15.8 ± 1.9%	5.9 ± 1.2%	0.069 ± 0.021	**0.001**	1.416	5%
Aldergrove						
VegHeight	129.5 ± 11.2 cm	60.6 ± 10.2 cm	0.013 ± 0.005	**0.007**	1.138	10 cm
EShrub	9.6 ± 1.4%	3.8 ± 1.0%	0.099 ± 0.052	0.056	1.640	5%
ESOHerb	4.3 ± 1.6%	1.6 ± 0.9%	0.175 ± 0.107	0.103	1.191	1%
OpenWat	65.2 ± 2.6%	60.9 ± 3.9%	0.016 ± 0.019	0.401	1.173	10%

for the species (e.g., identifying new wetlands for translocation, managing habitat within extant sites). Our analyses suggest that released Oregon Spotted Frogs are variable in the macrohabitats selected at the wetland-scale (i.e., population home range), but make use of microhabitats with more consistent structural attributes. At the macro-level, Oregon Spotted Frogs selected for habitats that form continuous mats with emergent vegetation (emergent Herbaceous and Culm vegetation, but Herbaceous was preferred over Culm) or mats interspersed with water covered by floating aquatic vegetation (emergent Shrub/Floating, characteristic of Aldergrove). Animals mostly avoided contiguous areas of Open Water habitat in the absence of interspersed emergent or floating vegetation. However, we identified strong differences in macrohabitat selection among years at each site, potentially caused by differences in seasonality, or the physical location of where captive-raised frogs were initially released. The rate of movement of Oregon Spotted Frogs in our study was low (range = 4–32 m/day; Monica M. Pearson, unpubl. data), and thus individuals mostly used the area in the vicinity of release locations. This resulted in small population MCPs, and only partial overlap of MCPs between years. These findings are supported by other Oregon Spotted Frog telemetry studies (Watson et al. 2003). Slightly different results at Maria Slough for years 2009 and 2010, as well as selection at Aldergrove for a habitat type that does not exist at Maria Slough (Shrub/Floating) indicate that Oregon Spotted Frogs may have some flexibility in habitat utilization. While Oregon Spotted Frogs appear to avoid certain macrohabitats outside the breeding season (e.g., Open Water, Floating), we did not observe strong positive selection of any one macrohabitat over the others. This suggests that Oregon Spotted Frogs may be plastic in their selection of habitat at the wetland scale, and show flexibility in their macrohabitat requirements based on structural vegetation composition. Other Oregon Spotted Frog studies in Washington and Oregon also suggest some plasticity. For example, Watson et al. (2003) found that Oregon Spotted Frogs selected for shrub/scrub macrohabitats with intermediate cover at Dempsey Creek, Washington during late summer.

The variation in macrohabitat use outlined above was in contrast to relatively consistent selection for specific structural attributes common to both sites at the microhabitat level. Higher vegetation was positively associated with frog presence, and vegetation height was the best microhabitat predictor of presence at both sites (Fig. 3 A, C). Vegetation height measurements, as well as the odds ratios associated with this variable were similar at both sites (Table 6). In addition, frog presence was also associated with higher percent cover of certain semi-open vegetation types: Semi-open Herbaceous (dominated by Poaceae) at Maria Slough and Shrub (dominated by *Spiraea* sp.) at Aldergrove (Table 6). At Maria Slough specifically, we found higher probability of occurrence in areas of thick submerged vegetation, which was the extent to which vegetation extended down into the water column from the surface of the water (Fig. 3 B). Oregon Spotted Frogs preferred submerged vegetation that extended 23.5 cm below water surface (compared to 13.8 cm at random locations), suggesting that underwater structural complexity is an important attribute for Oregon Spotted Frogs. These results are similar to Watson et al. (2003), who found that mean water depth at frog locations was significantly greater than depth at random locations during late summer (23.6 cm and 16.3 cm, respectively). These results provide support for the hypothesis that Oregon Spotted Frogs select for taller, but less dense vegetation, irrespective of the differences in floristic composition present at these two sites. Frogs preferred tall grasses and shrubs (mean height = 122–129 cm) that form mats, where emergent stem densities do not impede movements (interspersed with water), but that have high underwater (submergent) complexity (e.g., *Brasenia* sp., *Myriophyllum* sp.). Such habitats may be used for predator avoidance, cover, feeding, and basking. Our results corroborate the findings of other studies of Oregon Spotted Frogs habitat selection. For example, microhabitats with standing water interspersed with moderate canopies (approximately 50% shrub cover) have been identified as particularly important for post-breeding adults, especially during the dry season, and Oregon Spotted Frogs tended to avoid dense herbaceous vegetation (> 50–75% cover; Watson et al. 2003). In addition, Watson et al. (2003) have suggested that water with submergent vegetation that forms dense mats (e.g., *Utricularia vulgaris* and *Potamogeton* spp.) and can attain higher temperatures during summer (e.g., > 20° C), can be important for Oregon Spotted Frogs as foraging, basking, and escape habitat.

Our study was conducted using 'head-started' frogs raised in captivity from eggs collected in the wild, not wild animals from the study sites. Given the endangered status of the species in Canada and the large uncertainties surrounding the total abundance of each remnant population, it was not possible to use wild frogs for studying habitat selection because of concerns about potential stress and harm from carrying radio-transmitters. General recognition exists that captive-breeding across several or even one generation may reduce individual fitness and survival upon release in the wild (Frankham 2008). However, our study animals were not captive-bred, but instead released following being raised from egg masses collected from the wild. Thus, we expect that the deleterious effects of captivity may be less severe in these animals, though comparisons with wild individuals once recovery goals are met in the future would be a worthwhile effort. Additionally, the introduction of captive individuals to a novel natural environment may have affected the behaviors we identified (e.g., strong habitat associations at the microhabitat scale). However, we excluded a 3-day acclimatization period from our analysis to account for the short-term handling and release stress.

Given the low number of relocations for the majority of the frogs in our study, we could not investigate individual home ranges, and potential gender-based differences in habitat selection. As such, we analyzed yearly site data pooled together across all relocations (for conditional logistic regression), and used only frogs that had > 6 relocations for the Euclidean distance-based analyses. Despite these shortcomings we believe that our microhabitat selection analysis, which reflects choices at the daily activity level, complements the coarser-scale macrohabitat (landscape-scale) analysis. Strong selection for habitat structural attributes (i.e., vegetation height and percent semi-open vegetation regardless of plant species composition) among all frogs at both sites suggests that individual variation in microhabitat use based on habitat structure might be relatively low. Condensing data to several macro- and microhabitat types (as opposed to using species-specific vegetation data) might oversimplify habitat selection by Oregon Spotted Frogs. However, the presence of strong habitat selection despite this aggregation suggests that a practical advantage may exist in adopting this approach more broadly for habitat selection studies. Testing the appropriateness of this possibility is needed.

Translocation efforts are inherently related to critical habitat designation. Ensuring that sites for translocation meet critical habitat standards is often a minimum filter for consideration, as the quality of the habitat is essential to the success of the translocation program (Griffith et al. 1989). This tenet is especially important for herpetofauna, whose success rate of translocation is lower than that of mammals and birds (Dodd and Seigel 1991; Wolf et al. 1996), despite an increase in success rate from 19% to 41% after 1990 (Germano and Bishop 2009). As such, critical habitat designations need to incorporate the uncertainties surrounding habitat selection by animals (wild or captive-raised) released into novel environments. However, critical habitat designation is often not completed because of a lack of data; for example, only 10% of species listed under the US Endangered Species Act have critical habitat defined (Hoekstra et al. 2002). Once defined, critical habitat may or may not be correlated with species recovery (positive effect: Taylor et al. 2005; no effect: Hoekstra et al. 2002; Male and Bean 2005), but rather species taxonomy, funding, and recovery priority more often lead to positive change. However, beyond the legislated importance of critical habitat designation, a better understanding of the movement and habitat use by imperiled species can only aid recovery efforts by directing effort to habitats and at scales relevant to the ecology of the species. For Oregon Spotted Frogs in Canada, our findings are novel in that no other habitat use studies have been done in the region. Our results also complement the current definition of critical habitat needed to support Oregon Spotted Frog populations, which is based on published knowledge of habitat characteristics selected by wild Oregon Spotted Frogs from extant populations (Watson et al. 2003; Lisa Hallock and Scott Pearson, unpubl. report; Christopher Pearl and Marc Hayes, unpubl. report; Ken Risenhoover et al., unpubl. report; Marc Hayes et al., unpubl. report). Our findings build on these earlier studies by identifying habitats used by captive-raised and released Oregon Spotted Frogs. Despite potential limitations of our study due to low numbers of relocations and a limited sample size of frogs that were reared in captivity (but from wild embryos), our results provide information that is essential to future decisions about increasing the number of extant populations of Oregon Spotted Frogs in Canada, as translocations to new wetlands (e.g., introductions) will be accomplished through the use of captive-reared or captive-bred individuals.

Despite our motivation to evaluate broad macrohabitat categories that could potentially be identified from high-resolution aerial imagery, our study suggests that the identification of potential wetlands for translocation would be better served by collecting detailed information on microhabitat structural attributes at individual sites. Our study suggests the possibility that structural microhabitat attributes strongly selected by Oregon Spotted Frogs could be manipulated to enhance habitat, and that such management actions could be undertaken as experiments for species recovery. For example, at West Rocky Prairie Wildlife Area, Washington, 3-m diameter herbaceous habitat swaths were mowed to create more open water breeding habitat, which resulted in a higher proportion of egg masses in the enhanced versus un-manipulated habitat (Kapust et al. 2012). Because movements during summer have been found to be small (e.g., Marc Hayes, unpubl. report, found that radio-tracked Oregon Spotted Frogs moved < 100 m from the capture/release locations), microhabitat manipulation for selected attributes within relatively small areas could increase the likelihood of successful introductions. Ultimately, successful introduction of individuals into new habitats will also depend on how habitat attributes affect the survival of sensitive life history stages (Biek et al. 2002). For Oregon Spotted Frogs, successful reintroductions of adults have been linked to high survival in post-breeding and overwintering habitats (Chelgren et al. 2008), but an urgent need remains to follow the success of both wild and captive individuals in our focal populations.

One of the potential threats to Oregon Spotted Frog habitat integrity is thought to be habitat modification by the invasive Reed Canarygrass (*Phalaris arundinacea*). However, at both study sites, Reed Canarygrass dominated the herbaceous macrohabitat category, and our analysis suggests that it was never selected against. Similarly, Watson et al. (2003) found that Reed Canarygrass habitats were extensively used during summer, but not during the wet part of the post-breeding season (i.e., late fall) when Oregon Spotted Frogs preferred shrub/scrub habitats. These lines of evidence suggest that Reed Canarygrass may not pose as great a threat to Oregon Spotted Frog recovery efforts as previously thought, unless Reed Canarygrass occurs at very high densities. Thus, active management, such as mowing (Kapust et al. 2012) might be required to maintain semi-open herbaceous habitat interspersed with open water/floating vegetation channels to address seasonal differences in habitat requirements not directly addressed by our study (e.g., oviposition and over-winter habitat).

Management implications.—The recovery of highly imperiled species often requires a combination approaches tailored to each species. While actions to address site-specific threats are sometimes essential to species persistence, more often achieving recovery goals requires information and actions that transcend site-by-site management (e.g., maintenance of population connectivity and diversity, disease control, and reversing broad drivers of habitat loss). As such the two-tiered approach we used to examine habitat selection by Oregon Spotted Frogs lends support to both regional-scale recovery efforts (e.g., delineation of critical habitat or increasing the number of extant populations) as well as *in situ* management of habitat for this data-deficient species. We find that Oregon Spotted Frogs appear flexible in their use of habitat at the scale of individual wetlands (macrohabitat), suggesting that the number of potentially suitable wetlands for species translocation may be higher than previously thought. At the microhabitat scale, our results suggest that data collection focused on structural habitat attributes may be a useful method for developing critical habitat designations across sites with different vegetation composition. These findings should be interpreted carefully because they rely on habitat conditions that may be altered compared to habitats native to the Fraser Valley, and only represent a temporal snapshot of vegetation succession. Consequently, management actions stemming from our results should be integrated into an adaptive management framework. For example, potential recovery actions could start with small batch, gradual releases of Oregon Spotted Frogs at wetlands that include a combination of shallow pools for oviposition (Watson et al. 2003, Kapust et al. 2012) and refugia, and tall grass or shrub-dominated habitat structures that form emergent and submergent mats, regardless of vegetation species composition. Such introductions followed by active monitoring of released animals, and periodic reassessment of macro- and microhabitat selection based on multiple sites could then be used to refine wetland attributes that relate to successful introductions.

Acknowledgments.—The authors thank Isabell Eischeid, Andrea Gielens, Jill Miners, and Stacey Boks for field assistance. We thank Cindy Hulst at the Greater Vancouver Zoo and Gord Blankstein and Andrea Gielens at the Mountain View Conservation Center for overseeing the Oregon Spotted Frog husbandry program along with the Department of National Defense and Maintenance Detachment Aldergrove for access and support and the British Columbia Oregon Spotted Frog Recovery Team for guidance and support. Laurentiu Rozylowicz provided guidance with the distance-based habitat selection analyses. This study was funded by Interdepartmental Recovery Funds to Christine Bishop, a US Fish and Wildlife Service Competitive State Wildlife Grant to the Washington Department of Fish and Wildlife (Marc Hayes), Canadian Wildlife Federation grants to Wendy Palen, and the Canada Research Chairs Program (Wendy Palen).

Literature Cited

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Alford, R.A., and S.J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30:133–165.

Biek, R., W.C. Funk, B.A. Maxell, and L.S. Mills. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology 16:728–734.

Blaustein, A.R., and J.M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters 5:597–608.

Börger, L., B.D. Dalziel, and J.M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637–650.

Breslow, N.E., and N.E. Day. 1980. Statistical Methods in Cancer Research. Volume I: The Analysis of Case-control Studies. International Agency for Research on Cancer, Lyon, France.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multi-model Inference. 2nd Edition. Springer, Berlin, Germany.

Campbell, S.P., J.A. Clark, L.H. Crampton, A.D. Guerry, L.T. Hatch, P.R. Hosseini, J.J. Lawler, and R.J. O'Connor. 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecological Applications 12:674–681.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Chelgren, N.D., C.A. Pearl, M.J. Adams, and J. Bowerman. 2008. Demography and movement in a relocated population of Oregon Spotted Frogs (*Rana pretiosa*): influence of season and gender. Copeia:742–751.

Clark, J.A., J.M. Hoekstra, P.D. Boersma, and P. Kareiva. 2002. Improving US Endangered Species Act recovery plans: key findings and recommendations of the SCB recovery plan project. Conservation Biology 16:1510–1519.

Collins, J.P., and T. Halliday. 2005. Forecasting changes in amphibian biodiversity: aiming at a moving target. Philosophical Transactions of the Royal Society B: Biological Sciences 360:309–314.

Collins, J.P., and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9:89–98.

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.

Conner, L.M., and B.W. Plowman. 2001. Using Euclidean distances to assess non-random habitat use. Pp. 275–289 *In* Radio Tracking and Animal Populations. Millspaugh, J.J., and J.M. Marzluff (Eds.). Academic Press, San Diego, California, USA.

Conner, L.M., M.D. Smith, and L.W. Burger. 2003. A comparison of distance-based and classification-based analyses of habitat use. Ecology 84:526–531.

COSEWIC. 2011. COSEWIC assessment and

status report on the Oregon Spotted Frog (*Rana pretiosa*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada.

DeGregorio, B.A., B.J. Putman, and B.A. Kingsbury. 2011. Which habitat selection method is most applicable to snakes? Case studies of the Eastern Massasauga (*Sistrurus catenatus*) and Eastern Fox Snake (*Pantherophis gloydi*). Herpetological Conservation and Biology 6:372–382.

Dodd, C.K., Jr., and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

Foin, T.C., S.P.D. Riley, A.L. Pawley, D.R. Ayres, T.M. Carlsen, P.J. Hodum, and P.V. Switzer. 1998. Improving recovery planning for threatened and endangered species. Bioscience 48:177–184.

Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. Molecular Ecology 17:325–333.

Gascon, C., J.P. Collins, R.D. Moore, D.R. Church, J.E. McKay, and J.R.I. Mendelson. 2007. Amphibian Conservation Action Plan. IUCN/SSC Amphibian Specialist Group, Gland, Switzerland and Cambridge, UK.

Germano, J.M., and P.J. Bishop. 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology 23:7–15.

Gorman, T.A., and C.A. Haas. 2011. Seasonal microhabitat selection and use of syntopic populations of *Lithobates okaloosae* and *Lithobates clamitans clamitans*. Journal of Herpetology 45:313–318.

Griffith, B., J.M. Scott, J.W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Hammerson, G., and C.A. Pearl. 2004. *Rana pretiosa*. *In* IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 07 June 2012

Harris, J.G., and M.W. Harris. 2001. Plant Identification Terminology. An Illustrated Glossary. 2nd Edition. Spring Lake Publishing, Spring Lake, Utah, USA

Hodges, K.E., and J. Elder. 2008. Critical habitat designation under the US Endangered Species Act: how are biological criteria used? Biological Conservation 141:2662–2668.

Hoekstra, J.M., J.A. Clark, W.F. Fagan, and P.D. Boersma. 2002. A comprehensive review of Endangered Species Act recovery plans. Ecological Applications 12:630–640.

Hosmer, D.W., and S. Lemeshow. 1989. Applied Logistic Regression. Wiley Interscience, New York, New York, USA.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kapust, H.Q.W., K.R. McAllister, and M.P. Hayes. 2012. Oregon Spotted Frog (*Rana pretiosa*) response to enhancement of oviposition habitat degraded by invasive Reed Canary Grass (*Phalaris arundinacea*). Herpetological Conservation and Biology 7:358–366.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Male, T.D., and M.J. Bean. 2005. Measuring progress in US endangered species conservation. Ecology Letters 8:986–992.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource Selection by Animals. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Morrison, M.L., B.G. Marcot, and R.W. Mannan. 2006. Wildlife-habitat Relationships: Concepts and Applications. 3rd Edition. Island Press, Washington, DC, USA.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rittenhouse, T.A.G., and R.D. Semlitsch. 2007. Postbreeding habitat use of Wood Frogs in a Missouri oak-hickory forest. Journal of Herpetology 41:645–653.

Royle, J.A., and R.M. Dorazio. 2008. Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities. Academic Press, San Diego, California, USA.

Rozylowicz, L., and V.D. Popescu. 2013. Habitat selection and movement ecology of Eastern Hermann's tortoises in a rural Romanian landscape. European Journal of Wildlife Research 59:47–55.

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians.

ournal of Wildlife Management 64:615–631.
Semlitsch, R.D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 16:619–629.
Snyder, N.F.R., S.R. Derrickson, S.R. Beissinger, J.W. Wiley, T.B. Smith, W.D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10:338–348.
Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.
Taylor, M.F.J., K.F. Suckling, and J.J. Rachlinski. 2005. The effectiveness of the Endangered Species Act: a quantitative analysis. BioScience 55:360–367.
Tear, T.H., J.M. Scott, P.H. Hayward, and B. Griffith. 1993. Status and prospects for success of the Endangered Species Act: a look at recovery plans. Science 262:976–977.
Therneau, T., and T. Lumley. 2011. Survival: survival analysis, including penalised likelihood. R package version 2.36-10. http://CRAN.R-project.org/package=survival [Accessed 5 May 2012].
Thomas, D.L., and E.J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.
Watson, J.W., K.R. McAllister, and D.J. Pierce. 2003. Home ranges, movements, and habitat selection of Oregon Spotted Frogs (*Rana pretiosa*). Journal of Herpetology 37:292–300.
Wilbur, H.M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.
Wolf, C.M., B. Griffith, C. Reed, and S.A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

Appendix I. Differences and similarities in species composition and relative frequency in 1-m^2 plots sampled in 2010 at the two sites in British Columbia, Canada (Maria Slough site: n = 158 plots, Aldergrove site: n = 72 plots). Species in bold are represented at both sites.

Species	**Relative Frequency**	
	Maria Slough	**Aldergrove**
Typha latifolia	54.49	0.00
Equisetum spp.	12.92	0.00
Phalaris arundinacea	**62.92**	**18.06**
Spirea douglasii	**4.49**	**72.22**
Nuphar polysepala	7.30	0.00
***Carex* spp.**	**7.87**	**4.17**
Atropa belladonna	1.12	0.00
Poa spp.	**8.99**	**2.78**
Algae	1.12	0.00
***Juncus* spp.**	**2.81**	**4.17**
Mentha spp.	0.56	0.00
Bryophyta	**3.37**	**9.72**
Rubus spp.	1.12	0.00
Lemna spp.	5.06	0.00
Utricularia spp.	6.18	0.00
***Myriophyllum* spp.**	**2.81**	**8.33**
***Callitriche* spp.**	**0.56**	**5.56**
Potamageton spp.	0.56	0.00
Elodea spp.	0.56	0.00
Azolla spp.	0.00	2.78
Brasenia schreberi	0.00	36.11
Menyanthes trifoliate	0.00	1.39
Lysimachia thyrsifola	0.00	1.39

Viorel D. Popescu (left) is a David H. Smith Postdoctoral Fellow in Conservation Research at Simon Fraser University and University of California, Santa Cruz. His current work focuses on estimating the cumulative effects of small hydropower on British Columbia's aquatic and terrestrial ecosystems. He is also a Research Associate at the University of Bucharest where he is working on spatial conservation prioritization and climate change adaptation in Romania. His recent research projects investigated habitat selection of herpetofauna, the effects of forestry practices on vernal pool-breeding amphibians, and the use of dynamic occupancy models for monitoring. Viorel has a B.S. degree in Environmental Science (University of Bucharest, Romania), an M.S. in Conservation Biology (State University of New York - College of Environmental Science and Forestry, Syracuse, New York), and a Ph.D. in Wildlife Ecology (University of Maine, Orono, Maine). (Photographed by Bekka Brodie).

Amanda M. Kissel (right) is a graduate student at Simon Fraser University in Burnaby, British Columbia. Her work focuses on estimating demographic rates of the Endangered Oregon Spotted Frog and combining this information with an economic analysis to inform management decisions for the species in British Columbia. Amanda graduated as an Honors Scholar from Colorado State University with a Bachelor's degree in Wildlife Biology and concentration in Conservation Biology. Prior to joining Wendy Palen's lab at Simon Fraser, she worked as a research assistant on a variety of herpetofauna conservation projects in the western United States. (Photographed by Andrew Wright).

Monica M. Pearson (left) is a graduate student at the University of British Columbia in Vancouver B.C. Her research focuses on identifying partitions in habitat use of Oregon Spotted Frogs and American Bullfrogs to inform wetland restoration. Monica is involved in several restoration projects and conservation organizations in the Fraser Valley of British Columbia. She has a bachelor's degree in Microbiology from the University of Guelph and is a graduate of the Fish, Wildlife, and Recreation program at the British Columbia Institute of Technology. (Photographed by Martin Fietkiewicz).

Wendy Palen (right) is an Assistant Professor and Tier II Canada Research Chair in Aquatic Conservation in the Department of Biological Sciences at Simon Fraser University and a founding member of the Earth to Ocean Research Group (www.earth2ocean.org). Wendy's research focuses on identifying science-based conservation solutions for freshwater species and ecosystems in the Pacific Northwest, British Columbia, and California. Recent research projects integrate her interests in population dynamics, food web ecology, and risk assessment and have focused on the ecology of Pacific salmonids and a wide range of amphibian species. Wendy has a B.A. degree in Biology with highest honors (University of Virginia, Charlottesville, Virginia) and a Ph.D. in Zoology/Biology (University of Washington, Seattle, Washington). (Photographed by Douglas Young).

Purnima Govindarajulu (left) is the small mammal and herpetofauna conservation specialist for the Ministry of Environment in Victoria, British Columbia. She obtained both her B.Sc. (hons.) and M.Sc. from McGill University, where her thesis work focused on how genetic and social relationships influenced agonistic and affiliative behavior in primate matrilineal hierarchies. Her Ph.D. research at University of Victoria examined the impact of introduced bullfrogs on native frogs and her post-doctoral work documented the prevalence of an emerging global amphibian pathogen (*Batrachochytrium dendrobatidis*) in British Columbia. In her current position, she implements applied research projects addressing the management, conservation and population recovery needs of small mammals and herpetofauna in British Columbia through collaborations with academia, non-governmental organizations, students, and volunteers. (Photographed by Jim Foster).

Christine A. Bishop (right) is a Research Scientist with the Canadian federal Department of Environment (Environment Canada Science and Technology Branch), and an adjunct professor at Simon Fraser University and University of British Columbia. Her research focuses on anthropogenic stressors on Species at Risk, with a particular focus on reptiles, amphibians, and birds. Christine holds a B.Sc. (hons.) degree from University of Guelph, a M.S. in Biology from York University, and a Ph.D. in Biology from McMaster University. (Photographed by Annette Potvin).