esa ECOSPHERE

Landscape influence on the local distribution of western pond turtles

ROBERT B. HORN[1] AND JENNIFER A. GERVAIS[2,3,]†

[1]Bureau of Land Management, 777 NW Garden Valley Boulevard, Roseburg, Oregon, USA
[2]Oregon Wildlife Institute, PO Box 1061, Corvallis, Oregon 97339 USA
[3]Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, Oregon 97331 USA

Citation: Horn, R. B., and J. A. Gervais. 2018. Landscape influence on the local distribution of western pond turtles. Ecosphere 9(7):e02346. 10.1002/ecs2.2346

Abstract. Spatial and temporal scales are important for understanding habitat associations because organisms have neither unbounded mobility nor perfect knowledge of their environment, but still must make decisions on where to seek food, shelter, and mates. Semi-aquatic turtles exemplify the need to evaluate potential habitat characteristics at a range of scales, because their ectothermy makes these animals particularly sensitive to local environmental conditions, yet their limited mobility spatially constrains selection of microsites. Microsite choice may also be sensitive to larger geographic context. We explored site occupancy and abundance of western pond turtles (*Actinemys [Emys] marmorata*) as a function of environmental variables over a range of spatial scales up to that of the entire watershed. We modeled occupancy at ponds and abundance at river sites using data from surveys conducted at 50 ponds and 58 river locations throughout the South Umpqua, Umpqua, and North Umpqua watersheds in western Oregon, USA in 1999–2000. The South Umpqua supported the greatest abundance of western pond turtles in rivers and the highest rates of occupancy in ponds. No turtles were detected in rivers of the North Umpqua, and only low numbers were detected in ponds in that watershed. Increasing amount of potential relative solar radiation was associated with increased probability of pond occupancy, particularly in the North Umpqua watershed. Pond turtle abundance in rivers increased with increasing distance to nearest pond, decreasing area of nearby ponds, and increasing area of nearby wetland habitat of all types, particularly in the Klamath Mountain and Coast Range physiographic provinces, which dominate the South Umpqua and Umpqua watersheds, respectively. Western pond-turtle occupancy and abundance varied with both broad-scale and fine-scale habitat features, not solely to the fine-scale features that are most often measured.

Key words: abundance estimation; *Actinemys marmorata;* ecological scale; *Emys marmorata;* landscape context; occupancy; Oregon; Umpqua River Basin; western pond turtle.

Received 26 January 2018; revised 17 May 2018; accepted 6 June 2018. Corresponding Editor: George Middendorf.

† **E-mail:** jen@oregonwildlife.org

INTRODUCTION

Scale is recognized as an important issue in ecological studies because different patterns may be observed at different levels of resolution through both space and time (Senft et al. 1987, Wiens 1989, Schneider 2001). At a very broad level, a species is bound by its geographic range, and individuals of that species are limited within their range ultimately by their dispersal capacity. Individuals make a series of hierarchical decisions by first selecting a home range, then selecting habitat within that home range (Johnson 1980). Further, available habitat is likely to be spatially and temporally nested, such that habitat available at short time scales is constrained by decisions made over larger spatial scales and longer time frames (Rettie and Messier 2000, Mayor et al. 2009).

Understanding the hierarchy of temporal and spatial scales at which an organism must make decisions requires consideration of its life history, sensory abilities and perception, physiological limitations, and movement capabilities. Most studies of resource selection that have examined multiple spatial or temporal scales have involved either large, mobile terrestrial animals such as ungulates (Boyce et al. 2003, Anderson et al. 2005, Dussault et al. 2005, Godvik et al. 2009) or smaller but even more vagile organisms such as birds (Martin 1998, Becker and Beissinger 2003, Cushman and McGarigal 2004). These animals might reasonably be expected to sample a large extent of habitat before selecting home ranges, or features within them, and to move throughout their home ranges with relative ease.

Habitat use by less vagile ectothermic organisms such as turtles may be far more constrained on short time frames by choices made at larger temporal and spatial scales. The slow, cumbersome movements of semi-aquatic turtles over land may force individuals to select among less-than-optimal habitat conditions in the short term to better meet habitat requirements over the course of the season or year, or to optimize one requirement temporarily at the expense of another (Compton et al. 2002). Ectotherms must regulate their body temperatures behaviorally so they can forage, avoid predators, and assimilate their food (Huey 1991). Ectothermy therefore further restricts suitable habitat conditions to those where appropriate body temperatures can be maintained. Constraints imposed by larger-scale landscape characteristics may exist to an even greater extent for species such as semi-aquatic turtles, especially for those whose life history is complex and requires seasonal use of highly disparate aquatic and terrestrial habitats.

The difficulty of balancing physiological requirements at disparate temporal and spatial scales may be mediated by lack of specialization in specific habitat such that suitable conditions, particularly thermal conditions in the case of ectotherms such as reptiles, can be more easily found (Harvey and Weatherhead 2006, Rasmussen and Litzgus 2010, Paterson et al. 2012). A greater degree of flexibility in use of microhabitat characteristics could also lessen the constraints imposed by limited mobility in a changing environment. This would be particularly important in an organism with limited movement capacity whose life history requires it to use very different habitat elements throughout its life cycle. Therefore, we predict that patterns of occupancy and abundance will be functions of geographic characteristics at both larger and finer spatial scales. Consideration of only fine-scale features in explaining occupancy or abundance could overlook patterns created by the driving factors that are ultimately responsible for the distribution of animals on the landscape (Orians and Wittenberger 1991, Ciarniello et al. 2007). Further, fine-scale patterns may be dependent on the larger geographic context.

The semi-aquatic western or Pacific pond turtle, *Actinemys* [*Emys*] *marmorata* (Iverson et al. 2017), typifies an organism with limited mobility whose habitat requirements vary dramatically throughout its life cycle. Western pond turtles use both terrestrial and aquatic environments on a seasonal basis (Rathbun et al. 2002, Ultsch 2006, Bury and Germano 2008). They inhabit a wide variety of both permanent and ephemeral aquatic habitats, including ponds, lakes, reservoirs, irrigation ditches, sloughs, streams, and rivers (reviewed in Ernst and Lovich 2009) and occur in highly modified environments such as sewage ponds (Germano 2010). Features such as emergent basking sites, muddy substrate, undercut banks, and woody debris are frequently present where western pond turtles are found, and the turtles will bask on a wide variety of structures (Reese and Welch 1998*a*, *b*, Ernst and Lovich 2009). However, larger-scale geographic factors that may be contributing to the pattern of distribution over such a wide range of aquatic habitats are not well understood.

The terrestrial surroundings of aquatic habitat may be particularly important to western pond turtles because they nest on land, and unlike most other North American semi-aquatic turtle species, often overwinter in terrestrial locations as well as underwater (Rathbun et al. 2002, Ultsch 2006, Bury and Germano 2008). Western pond turtles may also resort to terrestrial refugia to estivate during drought conditions (Rathbun et al. 2002, Pilliod et al. 2013). In addition, based on limited data from Oregon, hatchling western pond turtles typically overwinter in their nests before first moving to water in the spring (Holte 1998, Rosenberg and Swift 2013). If terrestrial overwintering sites are used, western pond turtles may spend up to 10 months a year out of water (Ultsch 2006, Ernst and Lovich 2009).

Although western pond turtles frequently remain within 500 m of water (Rathbun et al. 1992, Reese and Welsh 1997, Lucas 2007, Pilliod et al. 2013), they are capable of traveling up to 2 km over land (Bury 1972, Ryan 2001, Bury and Germano 2008). Within aquatic habitats, western pond turtles have been observed to move up to 3 km a day (Bury 1979) or 7 km in the course of a season (Rathbun et al. 2002). However, such long-distance movements are typically made only during specific stages of the turtles' life cycle such as during nesting season or when searching for overwintering locations. Movements are typically <3 km on an annual basis (Bury 1972, Ryan 2001, Bury and Germano 2008). Over the course of their lifespans, however, individual turtles could sample and likely remember habitat conditions over a broad geographic scale, even if they are quite sedentary for much of their annual life cycle.

Although much work has described microhabitat use in this species such as for basking (Holland and Goodman 1996, Lambert et al. 2013), nesting (Rathbun et al. 1992, 2002, Holte 1998, Lucas 2007), terrestrial habitat use by hatchlings (Reese and Welsh 1997, Rosenberg and Swift 2013), and overwintering and estivation (Reese and Welsh 1997, Ryan 2001, Rathbun et al. 2002, Pilliod et al. 2013), little work has explored the potential for larger-scale, landscape features to influence western pond turtle distributions (but see Compton et al. 2002, Marchand and Litvaitis 2004). We analyzed data from two large-scale surveys for western pond turtles that used a probabilistic sampling design to identify habitat features associated with western pond turtle occurrence and abundance. We evaluated a combination of geographic attributes to characterize site occupancy and abundance at scales that incorporate all aspects of their life history. We ask whether the microsite scale of inquiry adequately describes western pond turtle distributions or whether a larger geographic context is also needed. We hypothesized that the lack of consistent, specific microsite associations of western pond turtles (Ernst and Lovich 2009) may be a consequence of factors operating on broader geographic scales and the limited mobility of this species. Therefore, landscape characteristics would be needed in addition to those measured at finer spatial scales to account for patterns of occupancy and abundance of western pond turtles within the landscape. Further, microsite associations may vary with larger landscape-level context.

MATERIALS AND METHODS

Study area

The study area included much of the Umpqua River basin, southwest Oregon. The basin is 12,081 km^2, and the elevation varies from sea level to 1827 m (Table 1). The basin includes five physiographic provinces, three of which dominated the study area: Coast Range, Western Cascades, and Klamath Mountains (also called Siskiyou Mountain province, Wallick et al. 2011). These provinces largely but incompletely overlap the river drainages (Fig. 1).

Table 1. Characteristics of the physiographic provinces within the Umpqua Basin study area in southwestern Oregon, USA.

Characteristic	Coast Range province	Klamath Mountains (Siskiyou) province	Western Cascades province
Summer climate	Temperate	Hot, dry	Hot, dry
Winter climate	Moderate, wet	Mild, wet	Cold, snow
April–June temps (°C)	6.1–14.9	3.9–18.7	3.3–15.2
January temps (°C)	3.1–10.27	1.7–8.7	−4.8–3.8
Annual precip (cm)	190	60–170 (mostly non-growing season)	215 (mostly snow)
Dominant trees	Douglas-fir† Western hemlock‡ Red alder¶	Douglas-fir Ponderosa pine§ Incense cedar# Oaks (*Quercus* spp.)	Douglas-fir Western hemlock Fir (*Abies* spp.)

Notes: Western pond turtles were surveyed April–September along rivers in 1999 and on ponds in 1999 and 2000. Data from Anderson et al. (1998), Verts and Carraway (1998), and Wallick et al. (2011).

† *Pseudotsuga menziesii.*

‡ *Tsuga heterophylla.*

§ *Pinus ponderosa.*

¶ *Alnus rubra.*

\# *Calocedrus decurrens.*

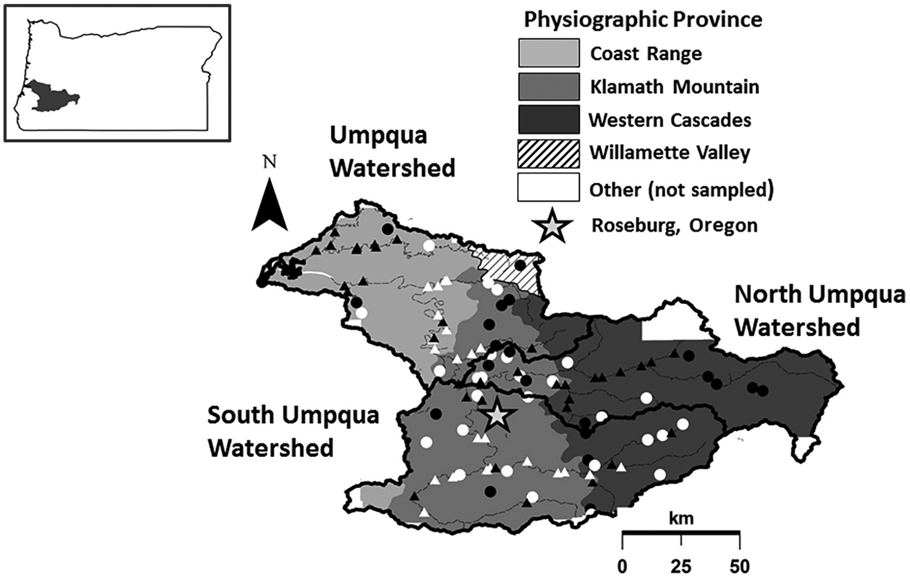

Fig. 1. Umpqua Basin in southwestern Oregon, USA, showing major watersheds and physiographic provinces. Western pond turtles were surveyed April–September along rivers in 1999 and on ponds in 1999 and 2000. Triangles denote river survey sites, and circles denote ponds. White symbols indicate sites at which pond turtles were observed during surveys.

Each province has different rainfall and temperature regimes, and the dominant vegetation and seasonality also vary (Table 1). The Coast Range province is characterized by low mountains with steep slopes (Anderson et al. 1998, Verts and Carraway 1998). The Klamath Mountains province includes the Klamath and Siskiyou mountains as well as western slopes of the Cascades. This region is marked by steep terrain with dendritic drainage patterns (Anderson et al. 1998). The Western Cascades province is one of high mountains with steep slopes (Hughes et al. 1987). These three provinces converge near the city of Roseburg (Fig. 1).

The watersheds of the South Umpqua, Umpqua, and North Umpqua, which make up the Umpqua Basin, have strikingly different temperature and flow regimes. The North Umpqua, which is dominated by the Western Cascades province (Fig. 1), is fed largely by groundwater and resulting spring complexes. Consequently, the North Umpqua River has the least variable flows throughout the year, with peak flows less than seven times those of the mean August flows (Wallick et al. 2011). The geology underlying the South Umpqua River in the Klamath Mountains and Western Cascades provinces generates much more extreme river flows because it lacks extensive groundwater storage (Wallick et al. 2011). The Umpqua River's peak flows are most influenced by winter storm events (Wallick et al. 2011). The South Umpqua is split between the Klamath Mountains and Western Cascades provinces whereas the Coast Range province dominates the Umpqua River watershed (Fig. 1). There are no dams on the mainstem Umpqua and South Umpqua Rivers. A small dam on the North Umpqua near Roseburg allows water to flow over the top such that the downstream water temperatures are not decreased from the dam. The North Umpqua River has eight hydroelectric installations on its upper reaches, but these do not strongly influence peak flows because their storage capacity is limited (Wallick et al. 2011).

Site selection and survey methods

We considered waterways and bodies of water below 1524 m (5000 feet) elevation to be potential pond-turtle habitat within the Umpqua basin (Nussbaum et al. 1983). Riverine surveys were conducted along 15 rivers and creeks (hereafter rivers) of the basin, spread throughout the three fourth-field watersheds (Umpqua, South Umpqua, and North Umpqua; Seaber et al. 1987). River length was divided by 20 km to determine the number of sampling stations on each river. That number of survey stations was then randomly placed on the river's length. For example, if a river was 40 km long, two survey stations were randomly placed along the 40 km. Numbers of survey stations on any tributary varied from 1 to 11 for a total of 58 survey stations (Fig. 1). The minimum distance between river survey stations was 600 m (Fig. 1). Station locations were adjusted initially as needed either up or downstream to the closest viable alternative point that allowed access and maximized the amount of river visible. These locations were then maintained for all future surveys. No two survey stations fell within the same river reach or segment (see *Site covariates* below).

We selected ponds and reservoirs (hereafter ponds) from a comprehensive list of 226 ponds within the Umpqua Basin. The list was generated using US Geological Survey 7.5-min series topographic maps. We only included ponds viewable from public land and at least 0.2 ha in size. This was the smallest pond that was reliably depicted on maps and that could be easily located in the field. The final list of ponds to be included in the study was generated based on surrounding land use and habitat quality as described below. Ponds were randomly selected to represent four development-intensity categories and habitat-quality scores (described below) in as balanced a manner as possible, as not all combinations of characteristics were represented. A total of 35 ponds were surveyed in 1999. Four of these ponds were dropped from further work because of access difficulties, such that only 31 of the original ponds were surveyed again in 2000. Additional ponds were selected randomly from the list of eligible ponds generated initially, and any nearby ponds that could be easily surveyed with minor additional logistical effort were also added to the survey list regardless of their surrounding land use or habitat-quality scores. This increased the total ponds surveyed in 2000 to 46. Survey stations for each pond were situated to maximize amount of water and shoreline visible and were maintained throughout the study. The minimum distance between study ponds was 800 m (Fig. 1). Ponds ranged in size from 0.2 to 210 ha, with 9 larger than 10 ha.

Survey protocols remained constant throughout the study. All surveys were conducted by a single observer using binoculars. The observer scanned the visible aquatic areas every 3 min and recorded all newly detected turtles seen along with the time of the observation during the 35 min of the survey. Care was taken to avoid double-counting individuals. If a turtle returned to the water and a similar-sized turtle appeared in the water or climbed out again in the same location within a few minutes, it was considered to be the same individual. Observer identity was not recorded, although several people collected data each year. Surveys were carried out between 08:00 and 14:00 h on partly sunny to sunny days during months when turtles were expected to be active. River surveys were conducted between 23 April 1999 and 1 October 1999. Pond surveys were carried out between 14 April 1999 and 22 September 1999 and 6 April 2000 to 19 September 2000. Four rounds of surveys were completed in 1999 for river stations and in each year for pond stations. Each round of surveys was completed at all pond or river survey stations before any were resurveyed, such that each round of surveys did not overlap in time. At least 1 week had elapsed before surveys were repeated at any particular station.

Data analysis

Site covariates.—We identified a set of covariates at a range of spatial scales that we hypothesized would affect turtle abundance. Many of these covariates were measures of characteristics within 500 or 1000 m of either rivers or ponds. River covariates were determined relative to either river segments (averaging 1400 m in length) as identified by the NORWEST database (http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html) or the shorter stream reaches (averaging 140 m; Clarke et al. 2008). For ponds, characteristics were measured at distances from pond edges. We gathered covariate data from a combination of GIS, maps, aerial photographs, and site visits.

GIS-generated covariates included physiographic province (http://spatialdata.oregonexplorer.info/geoportal/details;id=3e072de595134d36a0e1c5b5e50907d3) and extent of aquatic habitat, which included the area of all wetland types (hereafter wetlands) including riparian areas, and area of lentic wetlands (hereafter ponds) within 500 and 1000 m of the river reach and edge of pond based on the National Hydrography Dataset (https://viewer.nationalmap.gov/basic/?basemap=b1&category=nhd&title=NHD%20View). We used the National Land Cover Class (http://www.mrlc.gov/nlcd2011.php) to quantify potential human impact within 500 and 1000 m of the river segment or the perimeter of the pond. These included proportions of the landscape in developed areas and covered by forest. We also included the proportion of lands in private ownership, as conservation and management options can vary dramatically on private vs. public lands. We obtained mean elevation for ponds and river reaches, and distance to the nearest stream of any size for each pond. The mean index value of the potential relative solar radiation each pond or river reach receives was estimated using the method of Pierce et al. (2005). This method estimates the amount of radiation a site would be expected to receive assuming skies are clear each hour of the day, summed over the growing season, into a unitless measure originally developed for use in vegetation community studies (Pierce et al. 2005). It is based on landscape topography and includes the potential for land forms to shade sites. It does not account for possible shading by existing vegetation.

Additional reach-scale variables for river sites included distance to the nearest pond, average water depth, mean bank river width, mean valley width, and mean gradient along the reach (Clarke et al. 2008). Distance to the edge of the nearest pond was computed using pond distribution data from the National Hydrography Dataset. We also included a composite variable assessing habitat suitability for coho salmon (*Oncorhynchus kisutch*) at the reach scale (Burnett et al. 2007), under the hypothesis that western pond turtles would be associated with the low-flow, low-gradient reaches unconstrained by valley width that were associated with coho (Burnett et al. 2007).

We used somewhat different covariates for the ponds. We estimated the proportion of potential nesting habitat within 500 m of the survey station based on aerial photographs at the time of the surveys. We defined nesting habitat as areas of low, sparse vegetation structure or bare ground (Reese and Welsh 1997, Rathbun et al. 2002, Ernst and Lovich 2009). American bullfrogs (*Lithobates catesbeianus*) were scored as present or unknown for each pond based on observations taken during surveys. Bullfrogs are non-native predators of turtle hatchlings and have been hypothesized to have negative impacts on western pond turtles (Buskirk 2002). Additional covariates included the following: pond depth (<4–5 m or greater) which was estimated based on the presence of emergent vegetation, local topography, and hydrological characteristics when available; size (<2 ha or ≥2 ha); basking site availability on a scale of <5 or ≥5 rocky outcrops or woody debris features; and basking quality on a five-point categorical scale that was weighted by the size of viewable area to control for area (for a midscale viewing area, 0 emergent basking sites, 1–2, 3–7, 8–14, ≥15). We created a composite variable for overall habitat quality for analysis, which was a four-point categorical scale based on summing each pond's rankings in the categories of pond size, depth, and basking features. Top ranking was given to small, shallow ponds with abundant basking sites. Large, deep bodies of water with few basking sites were lowest ranked.

We used aerial imagery to classify land use immediately surrounding each pond as agricultural, natural/forested, lightly developed, or heavily developed. The agricultural category included ponds that had grazing near or next to the pond's edge, received agricultural runoff, or whose immediate uplands were altered by farming activities. The light-development category included ponds that fell within city limits, were near permanent dwellings, or near major roads. Heavily developed ponds were classified as those with two or more of the light-development criteria. The category of natural/forested was assigned if the site was forested with no development nearby, with the exception of access roads that did not lead to developed areas or recreational sites and abandoned or uninhabited structures such as abandoned barns or sheds away from inhabited areas.

Finally, each pond was classified by watershed and physiographic province. The one pond that fell at the edge of the Willamette Valley province was reassigned to the Klamath province (Fig. 1).

There were some general differences in pond and river survey station characteristics among the watersheds (Fig. 2). The Umpqua watershed's river survey stations were lower in elevation, occurred in broader sections of valley, and differed in topography overall from its northern and southern tributaries. The North Umpqua pond sites were surrounded by more forest within 500 m of the survey sites and the pond sites in the Umpqua watershed had less forest as an immediate land-use category. Similar patterns also existed by physiographic province (Fig. 3). Ponds in the Klamath Mountain province, which falls primarily in the South Umpqua basin (Fig. 1), were surrounded by less forest, more development, and more ponds and wetland nearby than focal ponds in other provinces. Despite these general differences, covariate characteristics of individual ponds and river survey sites broadly overlapped across physiographic provinces and watersheds.

Modeling.—We reduced the number of covariates considered in modeling river and pond habitat associations to avoid including highly correlated variables. We calculated correlation coefficients for each set of continuous covariates and coefficients of determination between categorical and continuous variables. We eliminated one covariate of any pair whose correlation was >0.6. We chose to retain the covariate that we felt was most directly related to habitat features used by turtles. Five river covariates (mean river width, depth, elevation, and gradient of the river reach, and wetlands within 500 m of the reach) were highly correlated. They described conditions that together suggest characteristics of topography affecting river current, to which turtles seem likely to respond. We therefore conducted a principal components analysis (PCA) with these five covariates using a correlation matrix (Tabachnick and Fidell 1989). The gradient variable was log-transformed prior to analysis to better meet the assumption of normality. The first two PCA axes explained 85% of the variance of the original data and were used as covariates in subsequent analyses of the river data.

We then evaluated variance inflation factor scores for linear combinations of all variables and removed variables with scores >3.0 (Zuur et al. 2009). We evaluated relationships between continuous and categorical variables using a linear modeling approach to estimate correlations. We retained 10 covariates to model turtle abundance at river sites and 12 covariates to model turtle occupancy of ponds. We did not use watershed for river data because no turtles were ever detected during river surveys within the North Umpqua watershed. We centered and scaled all continuous variables following screening and prior to analysis.

River surveys had a maximum count of 14 western pond turtles, and turtles were never observed at many survey stations. We therefore modeled abundance using the zero-inflated Poisson distribution to model residual error within the Pcount fitting function in Unmarked (Fiske and Chandler 2011). However, because of the extreme skew in the count data created by very large numbers of turtles in just two ponds (Fig. 3), we modeled pond-turtle occupancy of ponds rather than abundance using the occu fitting function in the Unmarked package in R (R Version 3.2.4, R Core Team 2016; Royle 2004, Fiske and Chandler 2011).

We first combined all covariates into global models for river and pond data, respectively. We used Akaike's information criterion (AIC, Burnham and Anderson 2002) to select the covariates for estimating detection probability based on the global model because we had a very limited model set that included non-nested models. We modeled detection probability by (1) comparing week of survey based on the Julian calendar, which captured the well-described seasonal change in detection in semi-aquatic turtles (Litzgus and Brooks 2000, Grayson and Dorcas 2004), (2) constant detection probability, and (3) for the pond data, year of survey because surveys were conducted over 2 yr. We also examined week of survey and year in the same detection model for the pond data.

We had no basis for restricting the set of possible candidate models based on the variables we were examining, as we surmised that all of the variables we examined had a biological rationale for inclusion. This left us with hundreds of possible candidate models in the absence of specific hypotheses regarding the variables and potential models. Further, our intent was to explore whether variables encompassing a variety of spatial scales adequately described pond turtle

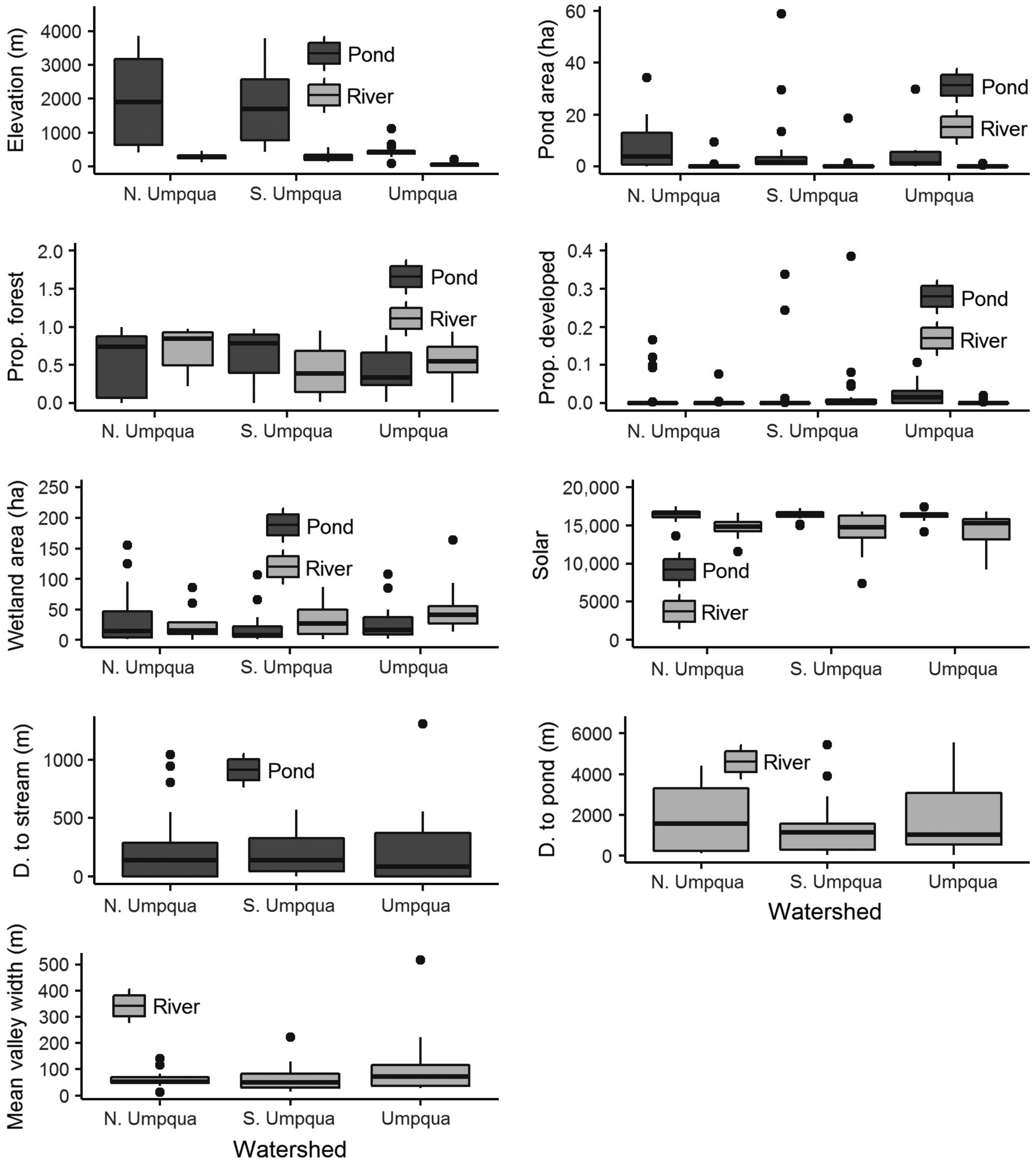

Fig. 2. Boxplots of watershed-level covariate values for all sites at which western pond turtles were surveyed in the Umpqua River Basin in southwestern Oregon, USA. Western pond turtles were surveyed April–September along rivers in 1999 and on ponds in 1999 and 2000. The boxes enclose the inter-quartile range, the horizontal bar indicates the median, and whiskers represent the upper quartile. Sample sizes are 19, 18, and 13 ponds and 12, 20, and 26 river sites in the North Umpqua, South Umpqua, and Umpqua watersheds, respectively.

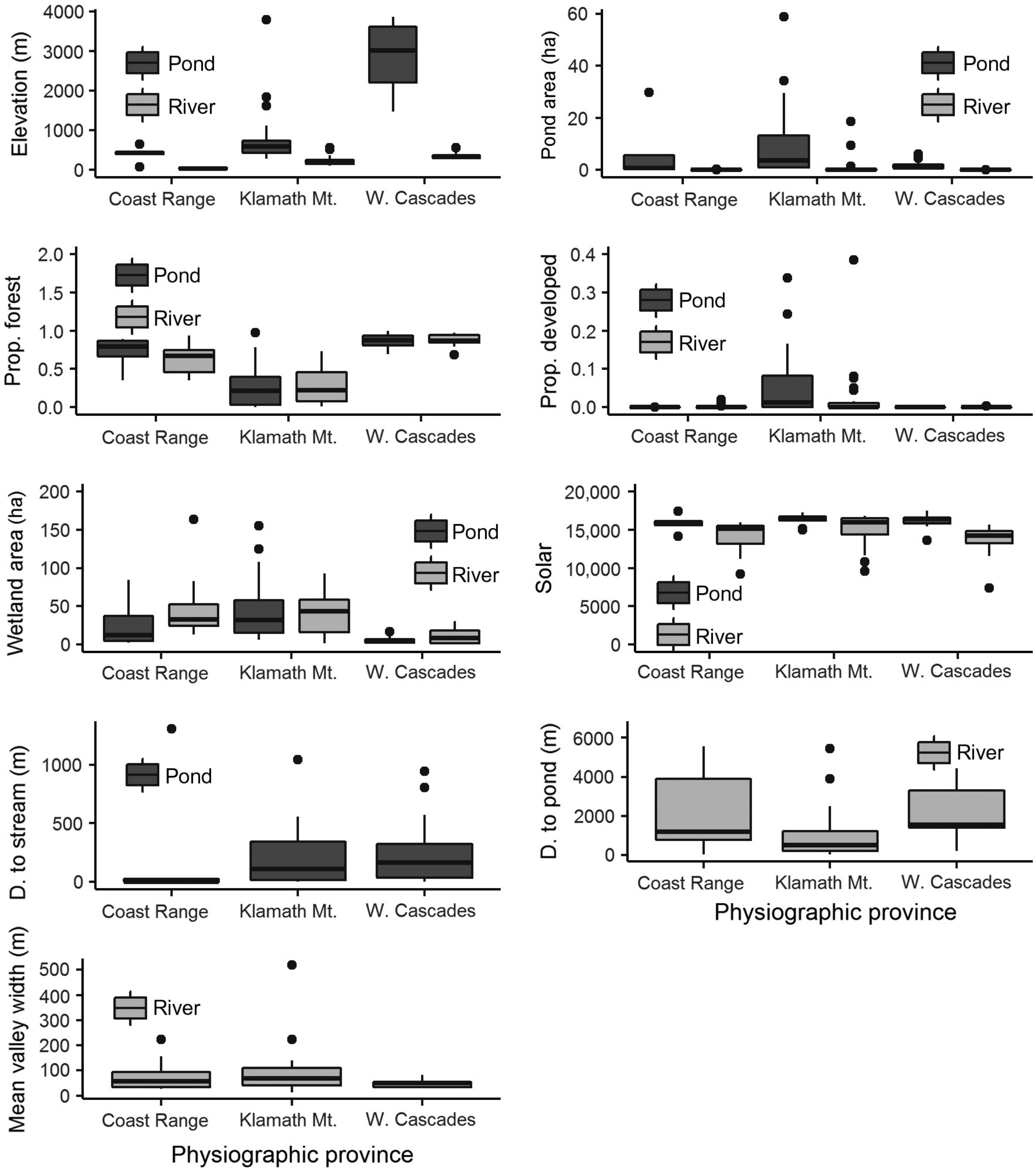

Fig. 3. Boxplots of covariate values at the physiographic province level for all sites at which western pond turtles were surveyed in the Umpqua River Basin in southwestern Oregon, USA, by physiographic province. Western pond turtles were surveyed April–September along rivers in 1999 and on ponds in 1999 and 2000. The boxes enclose the inter-quartile range, the horizontal bar indicates the median, and whiskers represent the upper quartile. Sample sizes are 5, 27, and 18 ponds and 21, 25, and 12 river sites in the Coast Range, Klamath Mountain, and Western Cascades physiographic provinces, respectively.

abundance and distribution better than small-scale variables alone. Therefore, we performed our exploratory analysis using a stepwise elimination and substitution strategy starting with the global model to evaluate independent variables in models of western pond turtle presence and abundance (Steidl 2006, 2007). The global river model contained the variables distance to nearest pond, coho suitability index, mean valley width of the river reach, pond area within 500 m of the reach, mean elevation of the reach, area of all wetland types within 1000 m of the reach, mean potential relative solar radiation, proportion of forest and development within 500 m of the river segment, and the scores for the first PCA axis of reach log gradient, river depth, and river width of the river reach. For ponds, the global model included total habitat quality, bullfrog presence, pond condition, nesting habitat within 500 m of the pond edge, pond elevation, mean potential relative solar radiation, area of lentic wetlands within 500 m, area of all wetlands within 1000 m, proportion of developed land within 500 m, distance to nearest stream, physiographic province, and watershed. We also included interaction terms between watershed and solar radiation, land use and solar radiation, and watershed and land use one at a time in the global pond model. We hypothesized that the impact of solar radiation would vary by watershed because of broad differences in topography in each watershed, such that it would be more important in the steeper mountainous areas. We also hypothesized that the effects of solar radiation would interact with adjacent land use, such that although forested sites might have less solar radiation, their relative lack of human activity would make such ponds more attractive to turtles than ponds with greater solar radiation but surrounded by development. Finally, we hypothesized that the impact of land use on turtles would vary among watersheds, such that watersheds with greater levels of development would lead to habituation to human activity and thus otherwise suitable ponds would still be used by turtles.

We used a multi-step approach in building models to provide greater assurance that we were not excluding predictive habitat covariates from consideration. We first examined the parameter estimates for the global model and dropped all variables whose estimates were not significantly different from zero at $P \leq 0.1$ to create a reduced model. We selected this criterion for greater assurance that covariates would not be excluded from consideration as a result of the sparse data. We then added the dropped variables back individually to the reduced model and built a second model that included all of the first set of retained covariates and any of the variables that were significant when added to the first set of retained covariates. This second model's covariates were again examined for nonzero parameter estimates, and covariates that did not meet this criterion were dropped. We ran the final habitat covariate model a second time with each of the detection covariate models and compared them using AIC to confirm the initial selection of the detection probability model. Lastly, we examined parameter estimates and predictions generated from them for the final models and assessed model fit with parametric bootstrapping, using the parboot function in the Unmarked package in R.

Results

We observed western pond turtles in 23 of 58 river survey stations and 26 of 50 ponds (Fig. 1). No western pond turtles were observed at river sites in the North Umpqua watershed (Fig. 3). Very few turtles were seen along rivers in the Western Cascades physiographic province, which largely covered the North Umpqua watershed. Western pond turtles were observed in ponds throughout all three watersheds and physiographic provinces (Figs. 1, 3). However, far more individuals were seen in the South Umpqua watershed than in the other two (Fig. 4). Two ponds consistently had much larger counts of western pond turtles than any other sites in the region, ranging from 15 to 76 for one pond and 26–84 for a second pond. Of the remaining 48 ponds, only four others had counts of >10 western pond turtles, and all maximum counts of these four ponds were <20.

Rivers

Counts of turtles declined with survey week at river locations. The detection covariate survey week was the most parsimonious and was therefore used in all subsequent models (Fig. 5a).

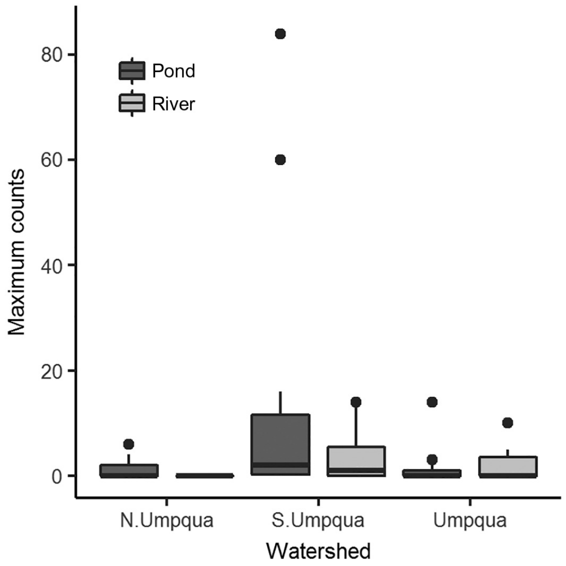

Fig. 4. Boxplots of the maximum counts of western pond turtles in river sites and ponds in the Umpqua River Basin watersheds in southwestern Oregon, USA. Western pond turtles were surveyed April–September along rivers in 1999 and on ponds in 1999 and 2000. The boxes enclose the inter-quartile range, the horizontal bar indicates the median, and whiskers represent the upper quartile. Note the two outliers for ponds in the South Umpqua watershed. Sample sizes are 19, 18, and 13 ponds and 12, 20, and 26 river sites in the North Umpqua, South Umpqua, and Umpqua watersheds, respectively.

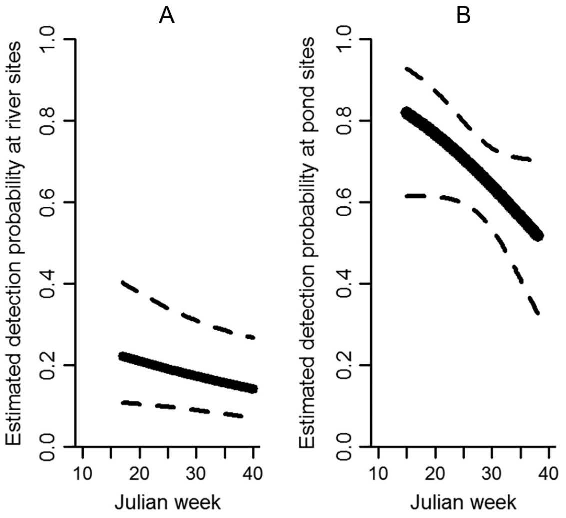

Fig. 5. Estimated detection probabilities through time for western pond turtles within the Umpqua River basin, Oregon, USA. Western pond turtles were surveyed April–September along rivers in 1999 and on ponds in 1999 and 2000. Dashed lines represent standard errors. Week is Julian week, with week 25 falling in the middle of June. The abscissa is limited to the actual range of observed data. (A) Estimated detection for abundance at river sites. (B) Estimated detection for occupancy of pond sites.

Detection probability was much lower at river locations than at ponds, however, and the decline in detection throughout the survey season was less pronounced (Fig. 5b).

Physiographic province, distance to nearest pond, area of pond habitat within 500 m, and area of all wetland types within 1000 m of the river reach were significant in the global model (Table 2). None of the eliminated variables had parameter estimates different from 0 when added individually to this reduced model, and all four variables remained significant in the reduced model. The final model predicted that western pond turtle abundance in river sites increases with increasing distance to the nearest ponds and with the area of surrounding wetland habitat but decreases with increasing area of pond habitat (Fig. 6). The effects were greatest in the Klamath Mountain and Coast Range

Table 2. Parameter estimates for the top model predicting probability of occupancy of ponds by western pond turtles in the Umpqua River basin, Oregon, USA, in 1999–2000.

Parameter	Estimate	Standard error	*z*	*P* (>$\lvert z \rvert$)
(Intercept)	0.846	0.575	1.471	0.141
South Umpqua	−0.647	0.771	−0.839	0.402
Umpqua	−1.671	0.862	−1.939	0.053
Mean solar radiation†	1.008	0.438	2.302	0.021

Notes: The top model was identified by backwards elimination and substitution of factors in a regression model. Detection probability varied over the course of the survey season (see Fig. 5). The global model contained the parameters total habitat quality, known presence of bullfrogs, mean potential relative solar radiation†, elevation, surrounding land use, proportion of nesting habitat within 500 m, area of ponds within 500 m, area of wetland within 1000 m, distance to nearest stream, proportion of development within 500 m, physiographic province, and watershed. The North Umpqua Basin is the reference value for watershed.

† Mean potential relative solar radiation index value calculated using the methods of Pierce et al. (2005).

provinces, which dominate the South Umpqua and Umpqua watershed, respectively (Fig. 1). Turtles were predicted to be most abundant in the Klamath Mountain Province, and least abundant in the Western Cascades province (Fig. 6).

Ponds

Detection probability at ponds was best modeled as a function that declined throughout the season (Fig. 5b). Detection probability was greater at ponds than at river sites and declined

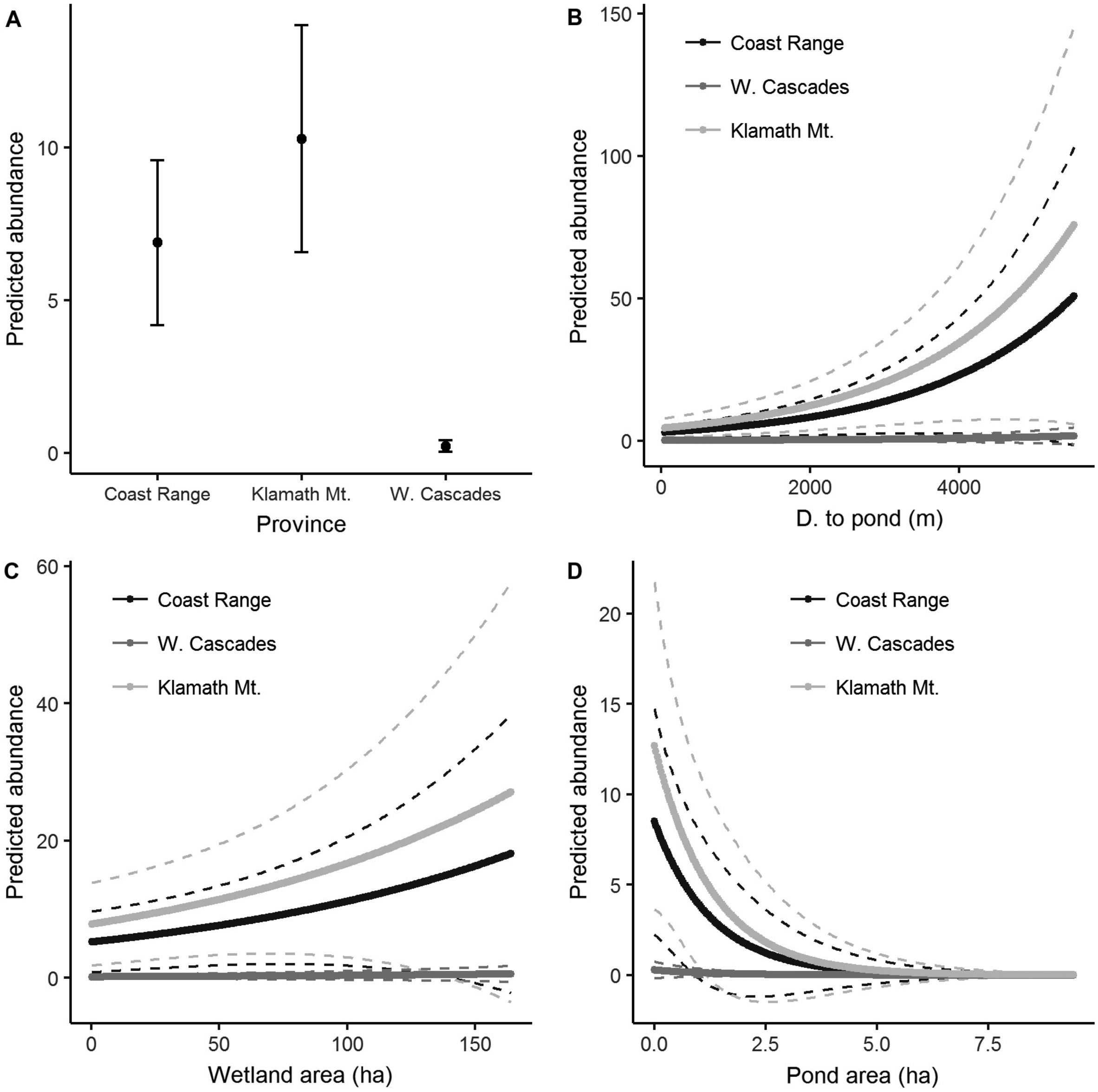

Fig. 6. Effects of the top model's covariates on predicted abundance of pond turtles at river survey sites within the Umpqua River basin, Oregon, USA. Western pond turtles were surveyed April–September along rivers in 1999. The top model included physiographic province, distance to nearest pond, pond habitat within 500 m, and area of all wetland types within 1000 m. Dashed lines indicate standard errors. Each covariate was varied while the other three were held at their mean. (A). Estimated mean abundances and standard errors by physiographic province. (B) Effect of distance to the nearest pond. (C) Effect of area of all wetland habitat within 1000 m. (D). Effect of area of pond habitat within 500 m.

more markedly as the season progressed (Fig. 5). Initially, none of the interactions tested in the global model were significant, and the pond condition by watershed interaction could not be estimated. We therefore dropped the interaction terms. Without the interactions, total habitat quality, pond area within 500 m, and mean potential relative solar radiation were significant and formed the basis of the first reduced model. Of the remaining variables that were added back one at a time to this base model, watershed was also significant. When the other variables were added singly to the first reduced model, neither those variables nor total habitat quality were significant, leaving only mean potential relative solar radiation and area of pond habitat within 500 m. We thus reduced the model to pond habitat within 500 m and mean potential relative solar radiation. In that model, only mean potential relative solar radiation was significant. We added back each variable singly to the model with only mean potential relative solar radiation, and only watershed was significant in addition to solar radiation. Our final model therefore contained watershed and mean solar radiation (Table 3) to model occupancy with week of survey to model detection probability. Increases in solar radiation led to increases in the probability of pond occupancy by western pond turtles (Fig. 7a). When solar radiation was held constant, ponds within the North Umpqua watershed had the highest predicted occupancy rates and the Umpqua watershed the least (Fig. 7b).

DISCUSSION

Western pond turtles showed strong geographic patterns in their abundance among river sites and occupancy of ponds, which were not related to most fine-scale habitat characteristics frequently associated with semi-aquatic turtle habitat. Further, finer-scale patterns were best explained in the context of larger-scale geography. Western pond turtles were more abundant at river sites throughout the Umpqua basin that were farther from ponds and had less pond habitat nearby, although greater area of all wetland habitat types was associated with increased abundance. No turtles were observed on any river sites within the North Umpqua watershed, which is characterized by cold, spring-fed waters. Ponds were more likely to be occupied if they had greater solar exposure; potential relative radiation had the greatest influence on pond occupancy within the North Umpqua watershed.

Western pond turtles use a very broad range of aquatic habitats (reviewed in Ernst and Lovich 2009). Such behavior may arise from the need to find suitable aquatic conditions adjacent to the upland habitat required by the species to complete its life cycle. The use of a disparate set of habitats by an animal with limited movement capacity (typically <3 km on an annual basis; Bury 1972, Ryan 2001, Bury and Germano 2008) leads to the expectation of flexibility in selection of specific habitat characteristics provided that physiological needs are met. This may be a factor behind the pattern of occurrence of western pond turtles in aquatic habitat within the Umpqua River basin, where larger-scale geographic patterns in addition to finer-scale site characteristics were descriptive of pond-turtle occupancy and abundance.

Table 3. Parameter estimates for the top model predicting abundance of western pond turtles at river sites in 1999 within the Umpqua River basin, Oregon, USA.

Parameter	Estimate	Standard error	z	P (>|z|)
(Intercept)	2.681	0.361	7.43	<0.001
Distance to nearest pond	0.825	0.123	6.73	<0.001
Area of all wetlands within 1000 m	0.227	0.111	2.05	0.041
Area of pond habitat within 500 m	−0.970	0.461	−2.10	0.035
Western Cascades province	−3.427	0.856	−4.01	<0.001
Klamath Mountains province	0.402	0.191	2.11	0.035

Notes: The top model was identified by backwards elimination and substitution of factors in a regression model. Detection probability varied over the course of the survey season (see Fig. 5). The global model contained an index of coho salmon habitat suitability, mean valley width of the reach, distance to nearest pond, the amount of pond habitat within 500 m, the proportion of forested habitat within 500 m, the proportion of developed habitat within 500 m, the amount of wetland within 1000 m, potential relative solar radiation†, and principal components analysis scores for the first axis of the combination of reach gradient, depth, elevation, and mean river width along the river reach, and wetland area within 500 m of the reach. The Coast Range physiographic province is the baseline.

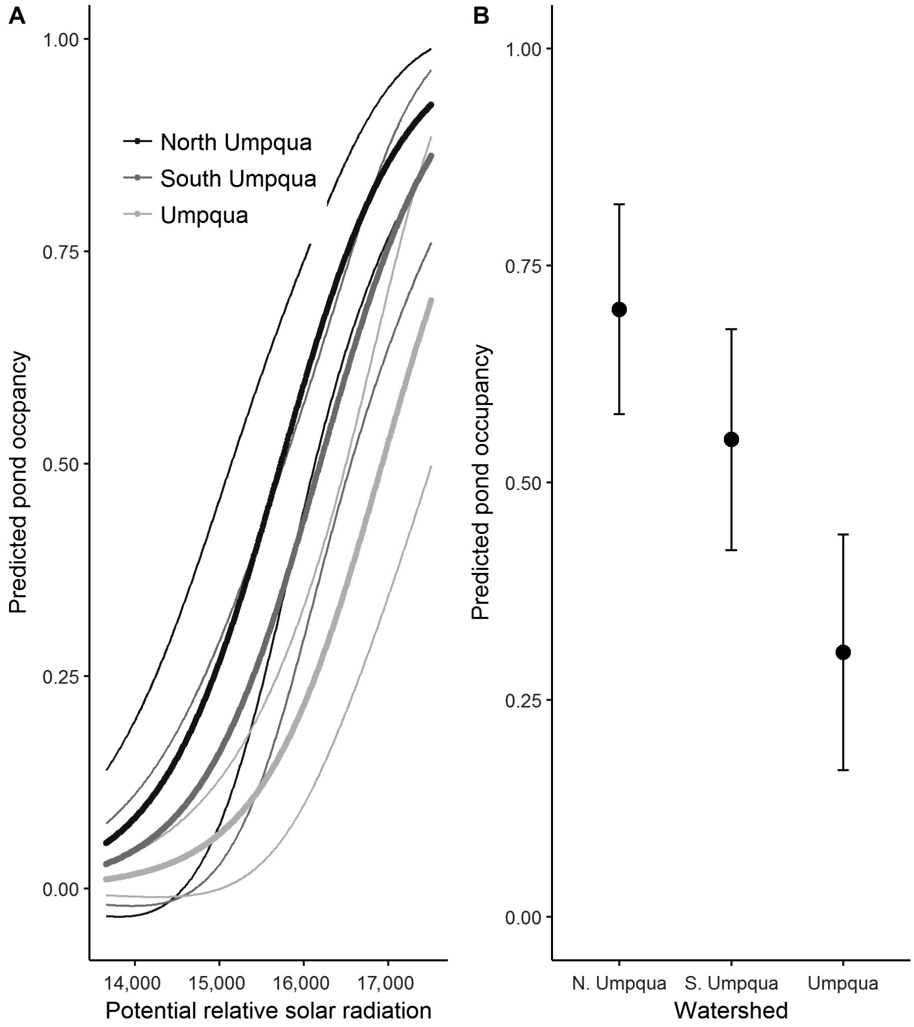

Fig. 7. Effects of the top model's covariates on predicted pond occupancy by pond turtles in the Umpqua River basin, Oregon, USA. Western pond turtles were surveyed April–September on ponds in 1999 and 2000. The top model included the covariates watershed and mean potential relative solar radiation, a unitless measure (Pierce et al. 2005). (A) Impact of increasing mean potential relative solar radiation on predicted probability of pond occupancy by watershed. Broken lines indicate standard errors. (B) Predicted probability of occupancy for each watershed when solar radiation was held constant at its mean value. Error bars are standard errors of the mean.

Although solar exposure and surrounding wetland features were predictive of occupancy and abundance within the context of watershed, many of the other characteristics at fine spatial scales were not retained in our modeling process. These included basking site availability and surrounding land use. This is consistent with earlier work on habitat selection in semi-aquatic turtles, where few fine-scale features were predictive of turtle occurrence (Compton et al. 2002, Paterson et al. 2012). A broad array of microhabitats was used by wood turtles (*Graptemys insculpta*) within areas with low canopy cover and that were near water. This was in contrast to the study's finding that home ranges were located within the watershed where canopy cover was moderate and there was little open water (Compton et al. 2002). Similarly, snapping turtles (*Chelydra serpentina*) were found in all aquatic habitats in central Ontario, Canada. However, individual turtles were found to specialize in different wetland types (Paterson et al. 2012). This suggests that snapping turtles were able to find suitable conditions in a variety of habitats. Work with the semi-aquatic painted turtle (*Chrysemys picta*) found that landscape context in the form of distance to nearest wetlands was correlated with habitat use (Bowne et al. 2006, Cosentino et al. 2010), but other features such as the amount of forest or road proximity were not (Bowne et al. 2006, Attum et al. 2008). A possible issue in identifying finer-scale patterns of habitat associations is the use of GIS-generated variables, which may not detect habitat characteristics relevant to the turtles (Compton et al. 2002, Tingley et al. 2010). However, we also included covariates based on ground observations and aerial photographs, so that the lack of explanatory ability of most finer-scale habitat covariates cannot be attributed solely to the methodology used to generate them. We did not attempt to quantify length of shoreline that might be used as basking sites, or floating mats of algae, which are also used by western pond turtles in the study region and elsewhere (R. B. Horn and J. A. Gervais, *personal observation*). The ability to bask on a variety of substrate types suggests that although turtles may prefer some fine-scale features over others, the absence of those preferred features may not prevent selection of a site provided that some opportunity to bask is present when the turtle's physiological status requires it, particularly if more preferred conditions are not readily available.

Basking is a crucial behavior in semi-aquatic turtles. Light intensity and daily solar radiation have been shown to influence basking in other turtle species (Boyer 1965, Schwarzkopf and Brooks 1985, Grayson and Dorcas 2004, Edwards and Blouin-Demers 2007). The need to gain body heat from the environment may be the driving factor behind the association of western pond turtles with ponds with greater relative solar radiation. It may also indirectly be a factor in the pattern of turtles occurring on river sites with less pond habitat nearby. If western pond turtles have relatively easy access to ponds or other wetlands, they may use those over river sites, particularly if nearby ponds are warming faster than the flowing waters of rivers and streams.

Human development surrounding ponds did not predict occupancy by western pond turtles. However, our definition of heavy development was based on the proximity of permanent dwellings and major roads, which may not have reflected human disturbance meaningful to turtles. Painted turtles were associated with greater road densities near ponds in New Hampshire, for example (Marchand and Litvaitis 2004). Western pond turtles can live in urban environments (Spinks et al. 2003, Germano 2010), suggesting that this species can acclimate to some level of proximate human activity (but see Lambert et al. 2013). We have observed basking western pond turtles in areas frequented by people, including in a pond in the middle of a busy park (R. B. Horn and J. A. Gervais, *personal observation*). It seems that individual pond turtles can habituate to some levels of human activity nearby at least in some circumstances. However, recreational disturbance has been identified as a cause of population declines in other turtle species (Garber and Burger 1995, Mitchell and Klemens 2000), and semi-aquatic turtles can be highly sensitive to disturbance when basking and nesting (Moll 1974, Mitchell and Klemens 2000). Further work to understand what types of disturbance may affect western pond turtles will aid in conservation efforts as human populations expand and urban conservation increases in importance for species persistence.

Bullfrog presence also was not predictive of pond occupancy. Our inability to confirm that bullfrogs were absent from ponds may have reduced the correct classification of this covariate, although if they were undetected, the bullfrogs were likely at low densities. Bullfrogs are known to prey on very small turtles (Haskell et al. 1996), which is a life stage least important to population persistence in long-lived turtle species (Heppell 1998). Whether this mortality factor is great enough to influence the population persistence of any semi-aquatic turtle species is unknown and worthy of further inquiry.

An important piece of the microsite puzzle that was poorly captured in our data was aquatic habitat characteristics, including water temperature. Detection probability declined as the warm season progressed, which was expected based on both pond turtle biology and research on other semi-aquatic turtle species because basking is less frequent as water temperatures increase (Grayson and Dorcas 2004, Litzgus and

Mousseau 2004, Ernst and Lovich 2009) and turtles were only observed when basking. Water temperature has long been known to influence turtle behavior and growth (Boyer 1965, Reese and Welch 1998*a*). In our study region, data collected incidentally to this study revealed that ponds and reservoirs with turtles had a mean temperature of 18.8° vs. 10.8°C for ponds and reservoirs that did not support turtles (R. B. Horn, *unpublished data*). Although temperature data for river sites supporting turtles are not available, other river sites had a mean water temperature of 13.4°C (R. B. Horn, *unpublished data*), well below that of the mean temperature for occupied ponds. The probability of detection was much greater at ponds than in river sites, and dropped off more dramatically as the season progressed. This may be strongly influenced by water temperature profiles.

Western pond turtles may move among water bodies as temperature differentials between water and air, and among bodies of water, change over the course of their active season. Water temperature data indicated that water temperatures peaked at different ponds in different months. Water temperatures taken incidentally to this study between June and September at ponds within the study region ranged from 10° to 26°C, with a change of 1–8°C at each individual pond. Similarly, river temperature data collected during turtle surveys between June and August ranged from 9° to 26°C, with a maximum difference at a single survey site of 9°C (R. B. Horn, *unpublished data*). Western pond turtles might therefore select a body of water based on the best of a series of options at a spatial scale that is available to them on a time scale of hours to several days. Obtaining thermal profiles of water bodies that capture fine-scale temperature differences within water bodies and how these profiles change through time will greatly enhance our understanding of habitat associations in semi-aquatic turtles and other aquatic species with behavioral thermoregulation.

Semi-aquatic turtles are known to make use of more than one wetland during their active season provided the distances among them are relatively short (Bowne et al. 2006, Cosentino et al. 2010). Our occupancy and abundance models assumed population closure (Royle and Nichols 2003, Royle 2004). We cannot be certain that our surveys fully met the assumptions of closure, particularly when other wetlands were near some survey sites. However, allowing detection probability to vary through time helps correct for the potential bias introduced by nonrandom movements to or from a site (MacKenzie et al. 2006). If individual turtles were counted at more than one survey location, estimated abundances and occupancy will be biased upwards (Rota et al. 2009). As we were interested in exploring geographic variables associated with western pond turtle presence and abundance, and because all covariates were constant over the time scale of the study, violations of this assumption should not greatly affect our results. Given that water temperatures are dynamic, the potential for individual turtles to move within a relatively small area in response to thermal characteristics needs to be considered not only to understand their biology, but to better estimate occupancy and abundance.

Our results make clear the need to consider a range of spatial and temporal scales in order to adequately understand what factors may be influencing the distribution and abundance of a species with limited mobility that requires a disparate series of habitats to complete its life cycle. Turtles may offer particularly interesting insights into how animals perceive scale, because their limited mobility may be offset by their substantial longevity and possibly the memory of the conditions they have encountered throughout their lives (Compton et al. 2002, Litzgus and Mousseau 2004). More work to test the robustness of the patterns revealed in our exploratory analysis, and to understand potential processes behind the patterns we documented here, will be critical to developing a greater understanding of why western pond turtles occur where they do.

Acknowledgments

Tony Dove, Larry Gangle, Justin Hadwen, Angela Hager, Matt Lawhead, Ernie Ortega, Greg Schuerger, and Randy Sisk conducted surveys, and Cindy Barkhurst gave her unflagging support to this project. Funding for fieldwork was provided by the US Forest Service, US Fish and Wildlife Service, and Oregon Department of Fish and Wildlife. D. K. Rosenberg generated the GIS covariates. We also thank D. K. Rosenberg and R. J. Steidl for discussions regarding and assistance with data analysis. We thank the anonymous reviewers whose comments have greatly improved the manuscript. Funding for the analysis and manuscript preparation was largely provided by the Interagency Special Status Sensitive Species Program of the USDI Bureau of Land Management and the USDA Forest Service of Oregon and Washington.

Literature Cited

Anderson, E. W., M. M. Borman, and W. C. Krueger. 1998. The ecological provinces of Oregon. SR 990, Oregon Agricultural Experiment Station, Corvallis, Oregon, USA.

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management 69:298–310.

Attum, O., Y. M. Lee, J. H. Roe, and B. A. Kingsbury. 2008. Wetland complexes and upland-wetland linkages: landscape effects on the distribution of rare and common wetland reptiles. Journal of Zoology 275:245–251.

Becker, B., and S. R. Beissinger. 2003. Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. Marine Ecology Progress Series 256:243–255.

Bowne, D. R., M. A. Bowers, and J. E. Hines. 2006. Connectivity in an agricultural landscape as reflected by interpond movements of a freshwater turtle. Conservation Biology 20:780–791.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fyxell, and P. Turchin. 2003. Scale and heterogeny in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421–431.

Boyer, D. R. 1965. Ecology of the basking habit in turtles. Ecology 46:99–118.

Burnett, K. A., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecological Applications 17:66–80.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Second edition. Springer-Verlag, New York, New York, USA.

Bury, R. B. 1972. Habits and home range of the Pacific pond turtle, *Clemmys marmorata*, in a stream community. Dissertation. University of California, Berkeley, California, USA.

Bury, R. B. 1979. Population ecology of freshwater turtles. Pages 571–602 *in* M. Harless and H. Maorlock, editors. Turtles: perspectives and research. John Wiley and Sons, New York, New York, USA.

Bury, R. B., and D. J. Germano. 2008. Conservation Biology of Freshwater Turtles and Tortoises. Pages 001.1–001.9 *in* A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Aaumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier, editors. Chelonian research monographs 5. http://www.chelonian.org/crf-publications/

Buskirk, J. 2002. The western pond turtle, *Emy marmorata*. Radiata 11:3–30.

Ciarniello, L. M., M. S. Boyce, D. R. Seip, and D. C. Heard. 2007. Grizzly bear habitat selection is scale dependent. Ecological Applications 17:1424–1440.

Clarke, S. E., K. M. Burnett, and D. J. Miller. 2008. Modeling streams and hydrogeomorphic attributes in Oregon from digital and field data. Journal of the American Water Resources Association 44: 459–477.

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.

Cosentino, B. J., R. L. Schooley, and C. A. Phillips. 2010. Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*. Landscape Ecology 25: 1589–1600.

Cushman, S. A., and K. McGarigal. 2004. Patterns in the species–environment relationship depend on both scale and choice of response variables. Oikos 105:117–124.

Dussault, C., J.-P. Ourllet, R. Courtois, J. Huot, L. Breton, H. Jolicoeur, and D. Kelt. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Edwards, A. L., and G. Blouin-Demers. 2007. Thermoregulation as a function of thermal quality in a northern population of painted turtles. Canadian Journal of Zoology 85:526–535.

Ernst, C. E., and J. E. Lovich. 2009. Turtles of the United States and Canada. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Fiske, I. J., and R. B. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle declines and human recreation. Ecological Applications 5:1151–1162.

Germano, D. J. 2010. Ecology of western pond turtles (*Actinemys marmorata*) at sewage-treatment facilities in the San Joaquin Valley, California. Southwestern Naturalist 55:89–97.

Godvik, I. M. R., E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional response in red deer habitat selection. Ecology 90:699–710.

Grayson, K. L., and M. E. Dorcas. 2004. Seasonal temperature variation in the painted turtle (*Chrysemys picta*). Herpetologica 60:325–336.

Harvey, D. S., and P. J. Weatherhead. 2006. Hibernation site selection by eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) near their northern range limit. Journal of Herpetology 50:66–73.

Haskell, A., T. E. Graham, C. R. Griffin, and J. B. Hestbeck. 1996. Size related survival of headstarted redbelly turtles (*Pseudemys rubriventris*) in Massachusetts. Journal of Herpetology 30:524–527.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367–375.

Holland, D. C., and R. H. Goodman Jr. 1996. *Clemmys marmorata* (western pond turtle) terrestrial habitat use. Herpetological Review 27:198–199.

Holte, D. L. 1998. Nest site characteristics of the western pond turtle, *Clemmys marmorata*, at Fern Ridge Reservoir, in west central Oregon. Thesis. Oregon State University, Corvallis, Oregon, USA.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91–S115.

Hughes, R. M., E. Rexstad, and C. E. Bond. 1987. The relationship of aquatic ecoregions, river basins and physiographic provinces to the ichthyogeographic regions of Oregon. Copeia 87:423–432.

Iverson, J. B., P. A. Meylan, and M. E. Seidel. 2017. Testudines-Turtles. Pages 82–91 *in* B. I. Crother, editor. Scientific and standard English names of amphibians and reptiles of North America North of Mexico, with comments regarding confidence in our understanding. Eighth edition. Herpetological Circular No. 43. Society for the Study of Amphibians and Reptiles, Topeka, Kansas, USA.

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

Lambert, M. R., S. N. Nielsen, A. N. Wright, R. C. Thomson, and H. B. Shaffer. 2013. Habitat features determine the basking distribution of introduced red-eared sliders and native western pond turtles. Chelonian Conservation and Biology 12:192–199.

Litzgus, J. D., and R. J. Brooks. 2000. Habitat and temperature selection of *Clemmys guttata* in a northern population. Journal of Herpetology 34:178–185.

Litzgus, J. D., and T. A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. Copeia 2004:804–807.

Lucas, H. M. 2007. Nest-site selection for the western pond turtle, *Actemys marmorata*, in Washington. Thesis. Western Washington University, Bellingham, Washington, USA.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling. Academic Press, Boston, Massachusetts, USA.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758–767.

Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656–670.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

Mitchell, J. C., and M. W. Klemens. 2000. Primary and secondary effects of habitat alteration. Pages 5–32 *in* J. C. Mitchell, editor. Turtle conservation. Smithsonian Institution Press, Washington, D.C., USA.

Moll, D. L. 1974. Notes on the behavior of Isle Royale painted turtles (*Chrysemys picta bellii*). Journal of Herpetology 8:254–255.

Nussbaum, R. A., E. D. Brodie, and R. M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho, USA.

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

Paterson, J. E., B. D. Steinberg, and J. D. Litzgus. 2012. Generally specialized or especially general? Habitat selection by snapping turtles (*Chelydra serpentina*) in central Ontario. Canadian Journal of Zoology 90:139–149.

Pierce, K. B., T. R. Lookingbill, and D. L. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscale-scale vegetation analysis. Landscape Ecology 20:137–147.

Pilliod, D. S., J. L. Welty, and R. Stafford. 2013. Terrestrial movement patterns of western pond turtles (*Actinemys marmorata*) in central California. Herpetological Conservation and Biology 8:207–221.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, M. L., and J. D. Litzgus. 2010. Habitat selection and movement patterns of spotted turtles (*Clemmys guttata*): effects of spatial and temporal scales of analysis. Copeia 2010:86–96.

Rathbun, G. B., N. Siepel, and D. Holland. 1992. Nesting behavior and movements of western pond turtles, *Clemmys marmorata*. Southwestern Naturalist 37:319–324.

Rathbun, G. B., N. J. Scott Jr., and T. G. Murphy. 2002. Terrestrial habitat use by Pacific pond turtles in a Mediterranean climate. Southwestern Naturalist 47:225–235.

Reese, D. A., and H. H. Welch Jr. 1998*a*. Habitat use by western pond turtles in the Trinity River, California. Journal of Wildlife Management 62:842–853.

Reese, D. A., and H. H. Welch Jr. 1998*b*. Comparative demography of *Clemmys marmorata* populations in the Trinity River of California in the context of dam-induced alterations. Journal of Herpetology 32:505–515.

Reese, D. A., and H. H. Welsh Jr. 1997. Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*: implications for management. Pages 352–357 *in* J. Van Abbema, editor. Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles- An International Conference. New York Turtle and Tortoise Society, New York, New York, USA.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.

Rosenberg, D. K., and R. Swift. 2013. Post-emergence behavior of hatchling western pond turtles (*Actinemys marmorata*) in western Oregon. American Midland Naturalist 169:111–121.

Rota, C. T., R. J. Fletcher Jr., R. M. Dorazio, and M. G. Betts. 2009. Occupancy estimation and the closure assumption. Journal of Applied Ecology 46:1173–1181.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84:777–790.

Ryan, M. 2001. Western pond turtle trapping and telemetry, Hills Creek Reservoir. Unpublished report, US Forest Service, Middle Fork Ranger District, Willamette National Forest, Springfield, Oregon, USA.

Schneider, D. C. 2001. The rise of the concept of scale in ecology. BioScience 51:545–552.

Schwarzkopf, L., and R. J. Brooks. 1985. Application of operative environmental temperatures to analysis of basking behavior in *Chrysemys picta*. Herpetologica 41:206–212.

Seaber, P. R., F. P. Kainos, and G. L. Knapp. 1987. Hydrologic map units. US Geological Survey Water-Supply Paper 2294. USDI Geological Survey, Washington, D.C., USA.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37:789–799.

Spinks, P. Q., G. B. Pauly, J. J. Crayon, and H. B. Shaffer. 2003. Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. Biological Conservation 113:257–267.

Steidl, R. J. 2006. Model selection, hypothesis testing, and risks of condemning analytical tools. Journal of Wildlife Management 70:1497–1498.

Steidl, R. J. 2007. Limits of data analysis in scientific inference: reply to Sleep et al. Journal of Wildlife Management 71:2122–2124.

Tabachnick, B. G., and L. S. Fidell. 1989. Using multivariate statistics. Second edition. Harper Collins, New York, New York, USA.

Tingley, R., T. B. Herman, M. D. Pulsifer, D. G. McCurdy, and J. P. Stephens. 2010. Intra-specific niche partitioning obscures the importance of fine-scale habitat data in species distribution models. Biodiversity Conservation 19:2455–2467.

Ultsch, G. R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Reviews 81:339–367.

Verts, B. J., and L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley, California, USA.

Wallick, J. R., J. E. O'Connor, S. Anderson, M. Keith, C. Cannon, and J. C. Risley. 2011. Channel change and bed-material transport in the Umpqua River Basin, Oregon. US Geological Survey Scientific Investigations Report 2011-5041. USDI Geological Survey, Washington, D.C., USA.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.