# Identification Of Habitat Controls On Amphibian Populations:
## The Northern Red-Legged Frog In The Pacific Northwest

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A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2013

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Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

University of Washington

# Abstract

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Historically, research addressing vulnerability of stillwater-breeding amphibians focused on reproductive (aquatic) habitat. However, in the Pacific Northwest (PNW), terrestrial (active-season) habitat is also important to many stillwater-breeding amphibians though its importance has rarely been evaluated. Locally, these terrestrial habitats are rapidly shrinking with increasing urbanization, placing most PNW stillwater-breeding amphibians at an unidentified level of risk. The Northern Red-legged Frog (*Rana aurora*) is a sentinel species in the PNW and is the focus of my research because it is prevalent in mesic areas and known to migrate extra-kilometer distances into terrestrial habitat seasonally. Both characteristics make it more likely that progressive urbanization will influence its abundance and distribution. The overarching goal of my research was to determine the relationship between *R. aurora* occupancy and abundance in each of the aquatic and terrestrial compartments of its habitat. I used egg mass counts to survey

30 stillwater aquatic habitats in King County, WA for *R. aurora* occupancy and abundance. I categorized wetlands across two strata: (1) within five categories of development to maximize the urbanization gradient and ensure gradient evenness; and (2) within three size categories of aquatic habitat to ensure sufficient variation in aquatic habitat size and evenness across the aquatic habitat size gradient. I then used GIS and regression analysis to determine the relationship of *R. aurora* within each of their aquatic and terrestrial habitat footprints. My results suggest that *R. aurora* abundance largely reflects the amount of forested area surrounding breeding wetlands. Occupancy was determined to be related to connectivity, area of available emergent vegetation, forested perimeter of wetlands, fish, and percent forest. Predators, including fishes and the American bullfrog (*Rana catesbeianus*) did not have an effect on *R. aurora* abundance. Results support and expand on previous findings on *R. aurora* relationships to their habitat requirements and inform refining previous management suggestions linking wetland breeding ponds to the surrounding forested landscape.

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# ACKNOWLEDGEMENTS

I am eternally grateful for the guidance and support of my supervisory thesis committee: Dr. Kristiina Vogt, Dr. Daniel Vogt, and Dr. Marc Hayes. Members of the Vogt lab were crucial to the completion of this research and providing moral support; thank you very much to Angel Klock, Jason Scullion, Jig-Han Jeong, Llyod Nackley, Maura Shelton, Maria Sandercock, and Stephan Gmur. Study design, site selection, and field techniques were enhanced by the involvement of Christopher Anderson, Daniel Vogt, Elissa Ostergaard, Jo Wilhelm, Klaus Richter, Kristiina Vogt, and Marc Hayes. Statistical support was provided by Marc Hayes, Loveday Conquest, and U.W. Statistical Consulting Services. A very big thank you to Jenny Mears and the Woodland Park Zoo's Amphibian Monitoring Program for providing citizen volunteers to complete amphibian surveys within my research sites. A special thank you to Garret Brendon for enduring long and cold field work days throughout the entirety of the breeding season. Additional field support was also provided by Tara Wilson, Lana Dalton, Chris Brewer, Nai Saetern, Hannah Litzenberger, Yuting Li, Robyn Turner, Amanda Beaty, Nathan Johnson, Yu-Chi Huang, Maura Shelton, Lisa Hannon, and Amy Yahnke. Last, but not least, thank you to my family and friends for their unconditional love, support, and encouragement throughout this fulfilling graduate school experience.

# INTRODUCTION

Vertebrate animal taxa are disappearing at high rates all around the world with amphibians representing the group with the largest number of species threatened with extinction (Stuart et al. 2004; Beebee and Griffiths 2005; Wake and Vredenburg 2008). Multiple factors have been implicated in causing amphibian species population declines which can lead to local extirpations. The primary causes for these declines and local extirpations are the loss, degradation, and fragmentation of habitats (Marsh and Trenham 2001; Homan et al. 2004). Human alteration of amphibian habitat can lead to changes in their occupancy, abundance, and species richness (Peterson et al. 1998). Of particular importance to ecologists and landowners is obtaining quantitative knowledge on precisely which impacts human activities impose on remaining fragmented natural habitats to ultimately understand what landscape changes push amphibian populations over tipping points that induce potentially irreversible declines in abundance.

## Amphibians: An Indicator for Biodiversity and Ecosystem Health

Understanding mechanisms of amphibian population declines can enhance our understanding of ecosystem degradation on multiple levels, and consequently offer an early warning sign for a decrease in ecosystem health. Amphibians are sensitive to the surrounding environment and therefore considered indicators for biodiversity and ecosystem health (Noss 1990; Blaustein et al. 1994). The ability of amphibians to absorb water easily through their skin magnifies their response to chemicals and temperature (Blaustein et al. 2003; Hillman et al. 2009), potentially affecting their occupancy and abundance in polluted ecosystems. Many amphibians also require both an aquatic and terrestrial habitat for survival, contributing to their sensitivity to disturbance.

If the causes for amphibian species declines are better understood, planners and land managers may more appropriately plan restoration efforts to an entire ecosystem.

## Landscape Changes Impacting Amphibians

Dramatic transformations of coniferous and boreal forest composition and structure in North America are largely a result of European settlement (White and Mladenoff 1994, Schoonmaker et al. 2007). Forest land has been, and continues to be converted to farmland, rangeland, urban settlement and young forests. More recently, rapid increases in human population densities have been expediting this process. In Washington State alone, the human population density has grown by 13% between 2000 (817.03 persons/ sq mile) and 2012 (925.05 persons/ sq mile) (WOFM 2012). King County is already the most populous county, with a total population in 2010 of 6,724,540, in Washington State and is expected to grow by two million people by the year 2040 (WOFM 2012). This extraordinary population growth projection is cause for concern on an already fragmented urbanizing landscape. Unplanned growth along with limited understanding of wildlife ecosystem requirements poses a threat to the viability of wildlife populations and the environment as a whole.

Population growth of this magnitude commonly comes with habitat loss, fragmentation, and degradation. Forests become replaced by roads and buildings while wetland breeding sites are filled in. These forms of habitat alteration have been found to cause local population declines for lentic breeding amphibians that require the adjacency of forest habitat types (Semlitsch 2000; Semlitsch and Bodie 2003). Many lentic-breeding amphibians in the PNW require aquatic and terrestrial habitats to complete their lifecycles; connectivity between these two habitats is essential to maintain local populations. Consequently, these lentic breeding amphibians are threatened in human altered landscapes at multiple scales: loss of wetland breeding pools, clearing and conversion of adjacent non-breeding terrestrial habitat, loss of landscape connectivity, and degradation to either the aquatic or terrestrial habitat (Gibbs 2000).

Throughout the greater Puget Sound region, over 70% of the wetlands have been lost or significantly degraded primarily due to urban expansion, intensive forestry operations and/or agricultural practices (Kentula et al. 1992; Lane and Taylor 1996; Thom et al. 2001). Development can degrade or eliminate wetlands in which amphibians reproduce by changing hydrological and thermal regimes, and facilitating the spread of contaminants. Urbanized wetlands have fewer native amphibian and plant species, the latter are important for amphibian breeding, than less urbanized wetlands (Richter and Azous 1995; 2001). Increased impervious surfaces such as pavement and roof tops prevent water from infiltrating the ground. This urban runoff increases water temperatures which can decrease dissolved oxygen levels that may increase mortality of amphibian eggs and larvae (Yi and James 2004; Yahnke 2011).

Increased runoff and reduced infiltration also cause unstable hydrologies, mostly by increasing the magnitude of water fluctuations in wetlands (Horner et al. 1997; Richter and Azous 2001). These fluctuations change water velocities which decrease the likelihood that lentic sites will be used for breeding, strip eggs from oviposition sites, or can expose eggs above the waterline which increases their mortality from desiccation or freezing (Reinelt et al. 1998; Ostergaard et al. 2008). Higher water fluctuations can also cause temporary wetlands to remain flooded all summer which increases the likelihood that these altered habitats may be used by exotic predators, e.g., warm-water fishes and American Bullfrog (*Rana catesbeianus* ), requiring permanent waters (Adams 1999; Adams et al. 2003; Kentula et al. 2004).

Urban runoff frequently contains pesticides, metals, and petroleum and may be detrimental to amphibian populations that utilize wetlands in more urbanized landscapes (King County 2006; 2007; Voss et al. 1999). Herbicides and fertilizers (including ammonium nitrate and ammonium sulfate) kill frogs early in their developmental stages at concentrations lower than the EPA's maximum allowed application levels (Marco et al. 1999).

Loss and fragmentation of non-breeding habitat in urbanizing landscapes may pose other risks to amphibian populations. Conversion to urban development increases habitat loss for amphibians and decreases connectivity because the landscape becomes a matrix of suitable and unsuitable habitat patches (Hels and Buchwald 2001; Chan-McLeod 2003). Conversion increases road densities and building structures. These structures are a major threat to amphibian populations during migration because they increase casualties from road kill and expose amphibians to non-suitable microclimates (Lehtinen et al. 1999). Large-scale forestry practices, especially those that include clearcut-harvesting, can be barriers to amphibian movement (Chan-McLeod 2003). These physical changes in the landscape also have the potential to alter available food resources (Marra and Edmonds 1998). Currently, the effects of land use change on amphibians have been extensively studied in the aquatic portion of their life, but research on the life history behavior of amphibians in their terrestrial habitats is deficient.

Most of the terrestrial research on amphibians to date has focused on the relationships between amphibian populations and the area of forest or urban development and roads in the surrounding landscape (Cushman 2006). However, there have been relatively few landscape-level studies of amphibian density and their movements. Cushman (2006) noted that reliable inferences about amphibian habitats require more research on species-specific ecological characteristics and their interactions with environmental conditions at multiple spatial scales.

Such characterization is essential if scientists are to evaluate the effects of habitat loss on specific populations. In this paper, species-specific habitat needs of the Northern Red-legged Frog (*Rana aurora*) are being assessed to develop causal relationships between the frog and the coupled aquatic-terrestrial habitat that they need to survive. While a number of the questions addressing the natural history of *R. aurora* have been answered, the quality and distribution of forest habitat needed to support healthy populations of this species is still unknown (Hayes et al. 2008).

### ***Rana aurora* Natural History**

*Rana aurora* is a sentinel species in the Pacific Northwestern United States and is the focal species of this research for several reasons. It must undergo both local and landscape-level population movements to maintain viable populations at both scales. It is prevalent in mesic areas and is the most terrestrial of the Pacific Northwest amphibians, migrating the farthest distances (5km) into terrestrial habitat seasonally (Hayes et al. 2008). Both characteristics make *R. aurora* more likely to be influenced by habitat loss and fragmentation (Hayes et al. 2008). The increase in impervious surfaces and fragmentation that is occurring in the Puget Sound portion of *R. aurora's* geographic range likely contributes to losses of *R. aurora* habitat (Hayes et al. 2008). Collective observations of the frog's decline are consistent with regional trends in habitat losses (Lehmkuhl and Ruggiero 1991; Noss and Peters 1995). The positive association with forest cover and negative association with road density suggest this species may serve as a biotic indicator of urbanization (Pearl et al. 2005).

*Rana aurora* is distributed along the Pacific coast of North America from southwestern British Columbia to northern California (Jones et al. 2005). Stillwater aquatic habitat with a minimum hydroperiod of 6 months is necessary for egg laying by adult females (Storm 1960;

Licht 1969; Hayes and Miyamoto 1984; Richter and Azous 1995). Eggs are typically attached to rooted aquatic vegetation, dead branches or twigs. Eggs are commonly found at a minimum depth of 30.5cm and as deep as 3m in areas exposed to sunlight for most of the day (Licht 1969a, Calef 1973). The eggs generally hatch after about 30-45 days (Brown 1976). Larvae consume algae (Dickman 1968) and utilize dense vegetation as cover (Pearl et al. 2005). Larvae metamorphose after 11-14 weeks (Brown 1976). Juvenile *R. auroras* remain on the edges of the wetland only days to weeks before dispersing into the surrounding riparian vegetation and forests. *Rana aurora* disperses considerable distances (5km) into the adjacent forests and will not return until the next breeding season (Licht 1986a; Jennings and Hayes 1994).

Once frogs reach the terrestrial habitat they move short distances of less than 10 m daily (Haggard 2000; Ritson and Hayes 2000; Hayes et al. 2001). *Rana aurora* is strongly associated, or even limited to forest habitat, and uncommonly move more than 12.5 m from vegetation cover (Haggard 2000; Chan-McLeod 2003). Forests with a complex understory consisting of down woody debris (Aubry and Hall 1991; Haggard 2000; Ritson and Hayes 2000) and sword fern (Haggard 2000) are preferred. These understory characteristics provide appropriate shelter from predators, moisture in the form of relative humidity and standing water (Licht 1986), foraging opportunities and appropriate temperature conditions between breeding seasons.

## Study Objectives and Hypotheses

Despite multiple studies of amphibian communities demonstrating strong associations between amphibian richness and the composition of the surrounding landscape (Laan and Verboom 1990; Koloszvary and Wigart 1999; Knutson et al. 1999; Lehtinen et al. 1999), protection and restoration of wetlands is often disassociated from preservation or restoration of surrounding uplands.  This issue is particularly important for lentic-breeding amphibians in the Pacific Northwest that use forest as their primary upland habitat during their non-breeding active season (Nussbaum et al. 1983; Martin and McComb 2003; Pearl et al. 2005; Hayes et al. 2008). Therefore, both the presence and arrangement of landscape features such as forests can influence population levels.  If specific habitat relationships can be identified, it is possible to project how future land use change might affect amphibian populations (Cole et al. 1997; White et al. 1997).

The overarching goal of this research is to examine the association between the amount of available habitat (aquatic and upland forest) and the occupancy and abundance of *R. aurora* within King County, Washington.  The influences of local wetland characteristics, forest area, and forest connectivity have on the distribution of *R. aurora* were investigated in this study. More specifically, this study sought to (1) describe the relationship between *R. aurora* occupancy and abundance and the terrestrial habitat including forest area and forest connectivity, (2) to describe the relationship between *R. aurora* occupancy and abundance and wetland characteristics including wetland area, emergent vegetation area, and length of forested wetland perimeter, (3) determine if *R. aurora* exhibits a threshold of tolerance to forest area within a 5km radius, and (4) determine the distance at which forest area has the greatest effect on *R. aurora* abundance.  It was hypothesized a priori that *R. aurora* occupancy and abundance (1) increase as the proportion of undeveloped land increases up to some intermediate distance from breeding sites, but (2) changes in aquatic habitat size do not influence *R. aurora* occupancy or abundance. It was also hypothesized that (3) there exists a threshold of forest area beyond which *R. aurora* might be predisposed to local extinction, and (4) there is a distance from breeding wetlands at which the correlation of *R. aurora* abundance and forest area will maximize.

# METHODS

## Site Description and Selection

Sites to be surveyed for *R. aurora* density were selected in western King County near Seattle, Washington. King County, bordered by the Puget Sound in the west and the Cascade crest on its eastern side, is the most urbanized and largest county in Washington State. The undeveloped area of the region is dominated by temperate moist forests and is abundant in wetland areas (Franklin and Dyrness 1973).

Geographic Information System technology (GIS) and water body data from the King County data portal were used to identify potential stillwater wetlands for the survey (ESRI 2011; King County 2010). All potential wetlands were located west of the Cascade Mountain foothills and below 800 meters in elevation in order to avoid wetlands beyond *R. aurora's* range. Wetlands within 200 meters of a neighboring wetland were excluded from this study in order to ensure that independent populations of *R. aurora* were being considered. Artificial stormwater ponds were also excluded from this survey, but not natural wetlands currently used as stormwater facilities.

Wetland area was measured for all 1,006 wetlands that fulfilled the selection criteria. Wetlands above 1.5 hectares were removed because wetlands of this size are less likely to be used by *R.* aurora and to increases sampling efficiency. The remaining 883 wetlands less than 1.5 hectares (ha) in area were then labeled with the percentage of the surrounding forest area within a 5km radius from the edge of the wetland. A 5km maximum distance was used because *R. aurora* has been recaptured at straight line distances over 5km (Hayes et al. 2001; Hayes et al. 2007). Wetlands were then categorized across two strata to ensure evenly capturing the range of variability in forest cover and wetland size among study wetlands. These strata included: (1) five categories of surrounding forest cover (0-17%, 17-33%, 33-50%, 50-66%, 66-100%); and (2) three size categories of aquatic habitat area (≤0.5 ha, 0.5-1.0 ha, and 1.0-1.5 ha). This resulted in 15 different combined forest cover and area categories.

From this pool of sites, two wetlands were chosen at random to fill each of the 15 different combined forest cover and area categories. This resulted in a total of 30 sites for this survey (Figure 1). Sites were then visited to assure that they satisfied *R. aurora* habitat requirements. Wetlands that were less than 0.6 m in depth and/or wetlands with emergent vegetation that was shaded for most of the day were replaced by another site within the same wetland area and percent forest categories (Licht 1969).

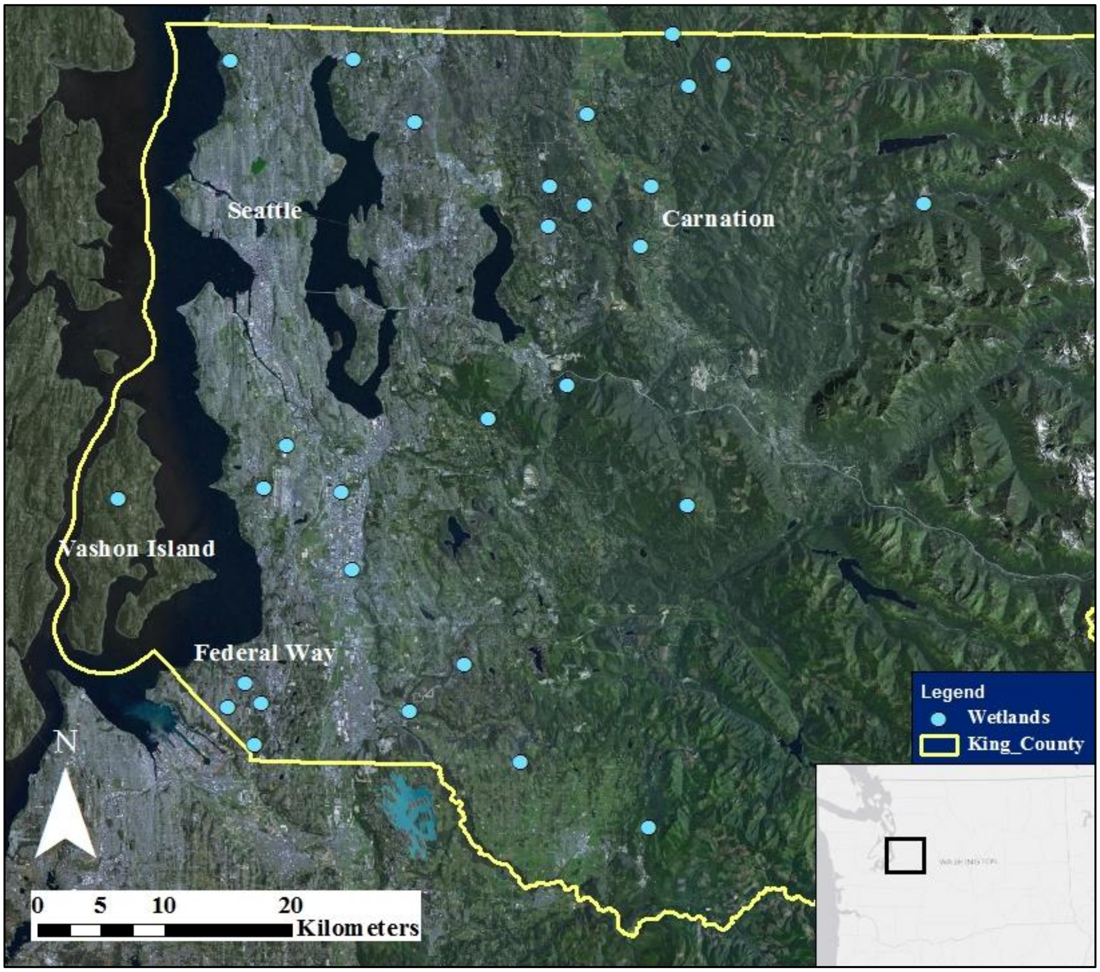

Figure 1. Study site locations within the habitat area of *Rana aurora* in King County, WA.

## Data collection

### *Landscape and Aquatic Habitat*

All aquatic habitat and landscape features were estimated in ArcGIS 10.0 (ESRI 2010). Wetland areas were estimated using the Geometry Field Calculator. Percent forest covers were estimated using the 2006-era classification of the U.S. West Coast Region, zone 1 Landsat raster data with an accuracy of 86.1% (Department of Commerce 2008). These Landsat data were differentiated into 21 class types (Table 1).

Table 1. Land cover categories (2006) converted to forest for this study's analysis of wetlands in King County, WA.

| | Landsat Classification | Conversion Category |
|---|---|---|
| **1** | Background | |
| **2** | Unclassified | |
| **3** | High Intensity Developed | |
| **4** | Medium Intensity Developed | |
| **5** | Low Intensity Developed | |
| **6** | Developed Open Space | |
| **7** | Cultivated Land | |
| **8** | Pasture/Hay | |
| **9** | Grassland | |
| **10** | Deciduous Forest | Forest |
| **11** | Evergreen Forest | Forest |
| **12** | Mixed Forest | Forest |
| **13** | Scrub/Shrub | |
| **14** | Palustrine Forested Wetland | Forest |
| **15** | Palustrine Scrub/Shrub Wetland | |
| **16** | Palustrine Emergent Wetland | |
| **17** | Estuarine Forested Wetland | |
| **18** | Estuarine Scrub/Shrub Wetland | |
| **19** | Estuarine Emergent Wetland | |
| **20** | Unconsolidated Shore | |
| **21** | Bare Land | |
| **22** | Open Water | |

Four Landsat Classification classes (Deciduous Forest, Evergreen Forest, Mixed Forest, and Palustrine Forested Wetland) were reclassified into one category, Forest (Table 1). After reclassification, the percent forest area of the landscape surrounding each wetland was calculated using FRAGSTATS (v4.0) (McGarigal et al. 2012). Percent forest was also calculated at 19 different distances from the wetlands in concentric footprints that extended out from the edge of the wetlands every 50 m up to 500 m, and from every 500 m up to 5 km (Figure 2).

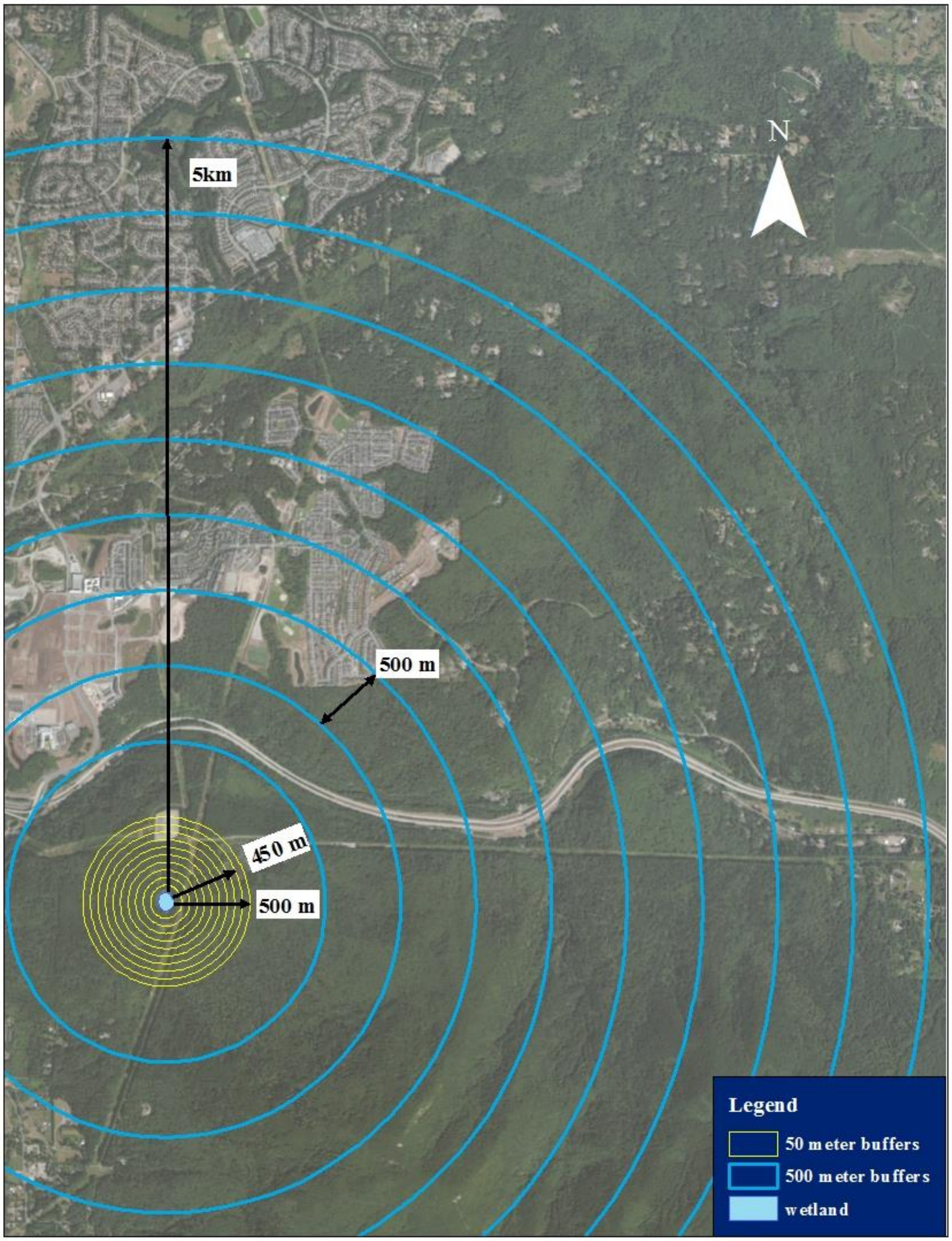

Figure 2. A GIS representation of the concentric circles used to identify landscape spatial extents. The blue circle represents the wetland. Buffers at 50 and 500 meter intervals radiate out from the edge of the sampling site.

These nested landscape footprints were used to identify the maximum spatial extent used by *R. aurora* during migration. Length of forested perimeter, connectivity, and area of emergent vegetation were also calculated. Length of forested perimeter was assessed to identify if the amount of forest adjacent to the wetland had an effect on occupancy or abundance. The total perimeter of each of the wetlands was measured for forest adjacency in meters. The area of emergent vegetation was also calculated using GIS to understand the potential importance of the area of the potential breeding habitat within the wetland. Google's imagery base map (2010) was used to create polygons with GIS Editor. These polygons included only the area within the stillwater wetland which had live or dead vegetation that could be considered an egg mass brace. Live vegetation included reeds, grasses, cattails, and young shrubs. Dead vegetation included fallen trees in which branches could be used as braces. Connectivity was calculated using the COHESION metric in the program FRAGSTATS (v4.0) (McGarigal et al. 2012). COHESION estimates the connectivity of habitat as perceived by *R. aurora* dispersing into the binary landscape (forest/no forest) (Schumaker 1996). This metric was used to quantify the effects of fragmentation on occupancy and abundance of *R. aurora* within study sites.

### *Amphibian Presence and Abundance*

Amphibian species occupancy and relative abundance were estimated from visual encounter surveys of egg masses (Heyer 1994). In the case of *R. aurora*, one egg mass corresponds to one breeding female and hence is an effective estimate of the breeding population size of females and is a good surrogate for adult breeding population size (pers. comm. M. Hayes 2012). Surveys were completed between February and May 2012. One site was resurveyed twice in February and March 2013 due to the questionability of the original survey. Given that adult *R. aurora* have an estimated longevity of 10-12 years (Licht 1974 ), variation in egg mass numbers is typically very low from year to year unless there has been a dramatic habitat change that will influence population size (Adams 1999; pers. comm. M. Hayes 2013).

Seven sites were surveyed by volunteer citizen science groups. All sites, not completed by these volunteer citizen science groups, utilized the double observer approach as described by Grant et al. (2005). The surveys were completed by walking around the edge of the wetland up to a depth of 1 meter. In wetlands where the perimeter was impassable due to thick woody vegetation and/or the water was too deep to effectively monitor from the shore, a floatation device was used to navigate around the shoreline to count egg masses.

Each egg mass was identified by species and geographically located using a handheld Garmin GPS unit with an accuracy of 3m. The vegetation type and water depths were also noted. Each wetland was surveyed a minimum of two times to ensure obtaining an estimate of the maximum egg masses. If a wetland was surveyed twice and still showed signs of fresh egg masses (i.e., egg masses with round embryos) next to more developed egg masses (i.e., having elongated embryos), it was surveyed a third time. Additionally, each site was visually surveyed for aquatic predators including the exotic American Bullfrog (*Rana catesbeianus)*; and fishes.

## Data Analyses

All statistical analyses of the data were evaluated in R (v2.14.1) (2011) and significance was accepted at $\alpha \leq 0.05$. Two sites were removed from this study due to the lack of certainty in the species identification of the egg masses. Where several surveys were performed, and since egg masses were not individually marked, egg masses within 2m of another egg mass were considered to represent the same egg mass. If the accuracy of the GPS coordinates was above 13m, the maximum egg mass counts for a wetland were used as my estimate.

Habitat and landscape variables were assessed for skewness by plotting each variable with the egg mass count. The ‘percent forest’ variable was log transformed due to the right skew of the data. This transformation was confirmed because the relative variance of the model identifying the relationship between log of percent forest and abundance was lower than the relative variance in the model assessing the relationship between percent forest and abundance.

Mann-Whitney U tests were used to compare eggs masses between various groups of wetlands. The tests compared wetlands with bullfrogs to wetlands without bullfrogs; wetlands with fish to wetlands without fish; wetlands with either bullfrogs or fish to wetlands with neither bullfrogs nor fish; and wetlands with both bullfrogs and fish to wetlands without both bullfrogs and fish.

Generalized linear models (GLMs) were then used to identify the individual relationship between the variables (percent forest (PCF), connectivity (CHN), area of emergent vegetation (EMG), forested perimeter (FRP), and wetland area (AREA)) and *R. aurora* egg mass abundance and occupancy. GLMs were used because the two response variables represented count and binomial data (abundance and occupancy respectively). A Poisson (log) in the case of abundance (count data) and binomial (logit) in the case of occupancy (presence/absence) were used. These analyses report the parameters as a log transformation in order to control the mean that it uses to calculate variance. Quasi models were applied because they use the notion that variance is proportional to the mean rather than equal to the mean – this makes the test less restrictive (Wedderburn 1974). This was done because the data are over-dispersed resulting in a greater residual deviance than the residual degrees of freedom ($\hat{c} > 1$).

A global model was created for both the abundance and occupancy data. An analysis of deviance (ANODEV) was used to evaluate significance of the parameters. ANODEV uses maximum likelihood rather than least-square estimation as used by an analysis of variance (ANOVA) (McCullagh and Nelder 1989). This allows for accommodation to other error distributions including count and binomial distributions. All variables with a relationship at a significance of $\alpha \leq 0.1$ were used in the global model for a multi-regression analysis. An $\alpha$ of 0.1 was used to reduce the likelihood of making a Type II error as a result of a relatively small sample size.

The R package, Multi-Model Inference (MuMIn), was used to run all possible combinations of the model (Bartoń, 2013). The models were compared by ranking the Quasi-Akaike Information Criterion ($QAIC_c$) values. The best model possessed the lowest reported $QAIC_c$. $QAIC_c$ is an estimate of the expected, relative distance between the fitted model and the unknown true mechanism that generated the observed data. The “Q” represents the AIC calculated for the use of the “quasi” model and the subscript “c” is the corrected values. Corrected values were used because the ratio of [N/k] of the sample size to the number of parameters is less than 40 [$N/k < 40$] – for this reason the AIC corrected is recommended (Burnaham and Anderson 2002). All models within a difference of two units of the lowest $QAIC_c$ model were considered.

As described by Burnham and Anderson (2002), Akaike weights ($w_i$) were used to assess the fit for each model within the subset of best models. As $w_i$ values approach one, the model is considered to better support the data. If the $w_i$ values are closer to zero, there is weak support for the best model and variation may increase in the selected best model from sample to sample. To establish evidence for the importance of each independent habitat variable, a relative importance estimate was calculated by adding $w_i$ values for all of the best fit models containing that variable. The variables with the largest cumulative weights provided evidence for the importance of that variable in the context of the entire set of models considered. A model averaging procedure was then performed in R package MuMIn based on the $w_i$-likelihood for each model in the subset of best models. Lastly, a ‘goodness of fit’ test was done to confirm the results of the Akaike weight analysis.

A regression tree, which is a type of binary recursive partitioning, was fit to the *R. aurora* populations in order to estimate potential thresholds of the predictor variable categories using the recursive partitioning package (RPART) in R (v2.14.1) (Therneau et al. 2011). This analysis splits the population based on a significant difference in one of the predictor variables. The break is chosen for the best or ‘purest’ division of the population among all of the predictor variables with respect to the values of the response variable. This process is then repeated with the new subset population being considered individually until a sub group can no longer be provided. These subsets maximize homogeneity of the mean response (egg abundance) by minimizing the deviance within each group. This process is visually represented as a tree-like structure. Each node or leaf represents a portion of the original population. The relative error of a tree is calculated as $1\text{-}R^2$ and can range between zero (representing a good prediction) and one (representing a poorer prediction) (Cukjati et al. 2001). Using the *printcp* command within RPART, the complexity parameter is selected. The complexity parameter is the measure of cost for adding additional predictors to the model and serves to minimize the cross-validation prediction error (Everitt 2010 and Therneau and Atkinson 2012). The regression tree was cross-validated to ensure replication in the fitted response variables. Regression trees are a non-parametric analysis which does not make assumptions about the underlying distribution of the predictor variables (Lewis 2000 and Tittonell et al. 2008).

A Spearman Rank correlation was used to identify the relationship of percent forest with the *R. aurora* egg mass counts within each of the 19 concentric rings. A non-parametric test was used because observed count data typically lacks a normal distribution.

## RESULTS

*Rana aurora* egg masses were found in 21 of the 28 breeding wetland sites surveyed. Individual wetlands contained between 0 and 369 egg masses. Bullfrogs were present in nine of the wetlands and fish were present in three of these nine wetlands. Fish were also present in six wetlands without bullfrogs. The presence of bullfrogs and/or fish did not differ significantly the number of egg masses found from those without bullfrogs and/or fish (Table 2).

Table 2. Results of the Mann-Whitney U test reported no significant differences in the *R. aurora* egg mass abundance between ponds with or without bullfrogs, fish, both bullfrogs and fish, and either bullfrogs or fish. $\bar{x}$ represents the mean of each group, $\tilde{x}$ represents the median, and IQR is the interquartile range of the median.

| Predator presence | egg masses with predator group present | | | egg masses with predator group absent | | | p-value |
|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | $\tilde{x}$ | IQR | $\bar{x}$ | $\tilde{x}$ | IQR | |
| Only Bullfrog | 65 | 7 | 254 | 44 | 15 | 76 | 0.980 |
| Only Fish | 50 | 28 | 70.5 | 54 | 3 | 69 | 0.137 |
| Bullfrog and fish | 22 | 11 | 42 | 54 | 12 | 79.5 | 0.822 |
| Bullfrog or Fish | 64 | 24 | 143 | 35 | 3 | 54.5 | 0.236 |

### ***Rana aurora* Occupancy**

There were five variables that individually had a significant ($p \leq 0.1$) relationship with occupancy ($\varphi$) of *R. aurora* egg masses (Table 3). These variables (PCT, CHN, EMG, FSH, and

FRP) were included in the global model for "best fit model selection." All possible models including the significant covariates and a null model were assessed. The subset of best models ($\Delta QAIC_c \leq 2$) predicting *R. aurora* occupancy included six models (Table 4; Figure 3). The relative importance estimates identified occupancy to be a function of connectivity (CHN), area of emergent vegetation (EMG), fish (FSH), length of forested perimeter (FRP), and percent forest (PCF) (Table 5). PCT, CHN, EMG, and FSH had a positive relationship with occupancy, while FRP had a negative relationship with occupancy. A goodness-of-fit test indicated that all models statistically fit the data (Table 6). Because all models statistically fit the data, a model merge was done with the subset of best models. The merged model is as follows:

$$\varphi = -81.96 + 1.063 * \mathrm{CHN} + 0.0012 * \mathrm{EMG} + 20.07 * \mathrm{FSH} + 3.779 * \mathrm{PCT} - 0.0577 * \mathrm{FRP}$$

Table 3. Covariates used in *R. aurora* egg mass occupancy models. An asterisk indicates a significant p-value when ($p \leq 0.1$).

| Type | Covariate | Description | p-value |
|---|---|---|---|
| **Wetland** | AREA | Area of the breeding wetland in hectares | 0.79 |
| | EMG | Area of the emergent vegetation square meters | 0.017* |
| **Vegetation** | PCF | The natural log of the percent of the landscape with in the 5km buffer categorized as forest | 5.9e-5* |
| | FPR | Length of the perimeter of the breeding wetland adjacent to forest cover type | 0.022* |
| **Spatial** | CHN | Metric representing the habitat connectivity in a binary landscape | 2.9e-4* |
| **Predator** | BULL | Bullfrog occupancy | 0.821 |
| | FSH | Fish occupancy | 0.003* |

Table 4. *Rana aurora* egg mass occupancy models and their coefficients ranked according to lowest Quasi-Akaike Information Criterion ($QAIC_c$) values. The variable identifiers are defined as: connectivity (CHN), emergent vegetation (EMG), fish (FSH), forested perimeter (FRP), percent forest (PCF).

| **Model #** | **Intercept** | **CHN** | **EMG** | **FSH** | **FRP** | **PCF** | **df** | **loglink** | **$QAIC_c$** | **$\Delta$ $QAIC_c$** | **weight** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **8** | -0.0102 | 1.03 | 0.0012 | 20.8 | | | 4 | -5.34 | 20.4 | 0.0 | 0.142 |
| **6** | -0.8981 | 0.927 | | 18.42 | | | 3 | -6.78 | 20.6 | 0.13 | 0.133 |
| **2** | -0.8824 | 0.916 | | | | | 2 | -8.45 | 21.4 | 0.95 | 0.088 |
| **17** | -0.1217 | | | | | 3.812 | 2 | -8.59 | 21.7 | 1.23 | 0.076 |
| **16** | -0.1636 | 1.683 | 1.6e-3 | 22.04 | -0.058 | | 5 | -4.75 | 22.2 | 1.79 | 0.058 |
| **19** | -0.1288 | | 6e-4 | | | 3.732 | 3 | -7.67 | 22.3 | 1.91 | 0.055 |
| **4** | -7.867 | 0.808 | 6e-4 | | | | 3 | -7.74 | 22.5 | 2.06 | 0.051 |

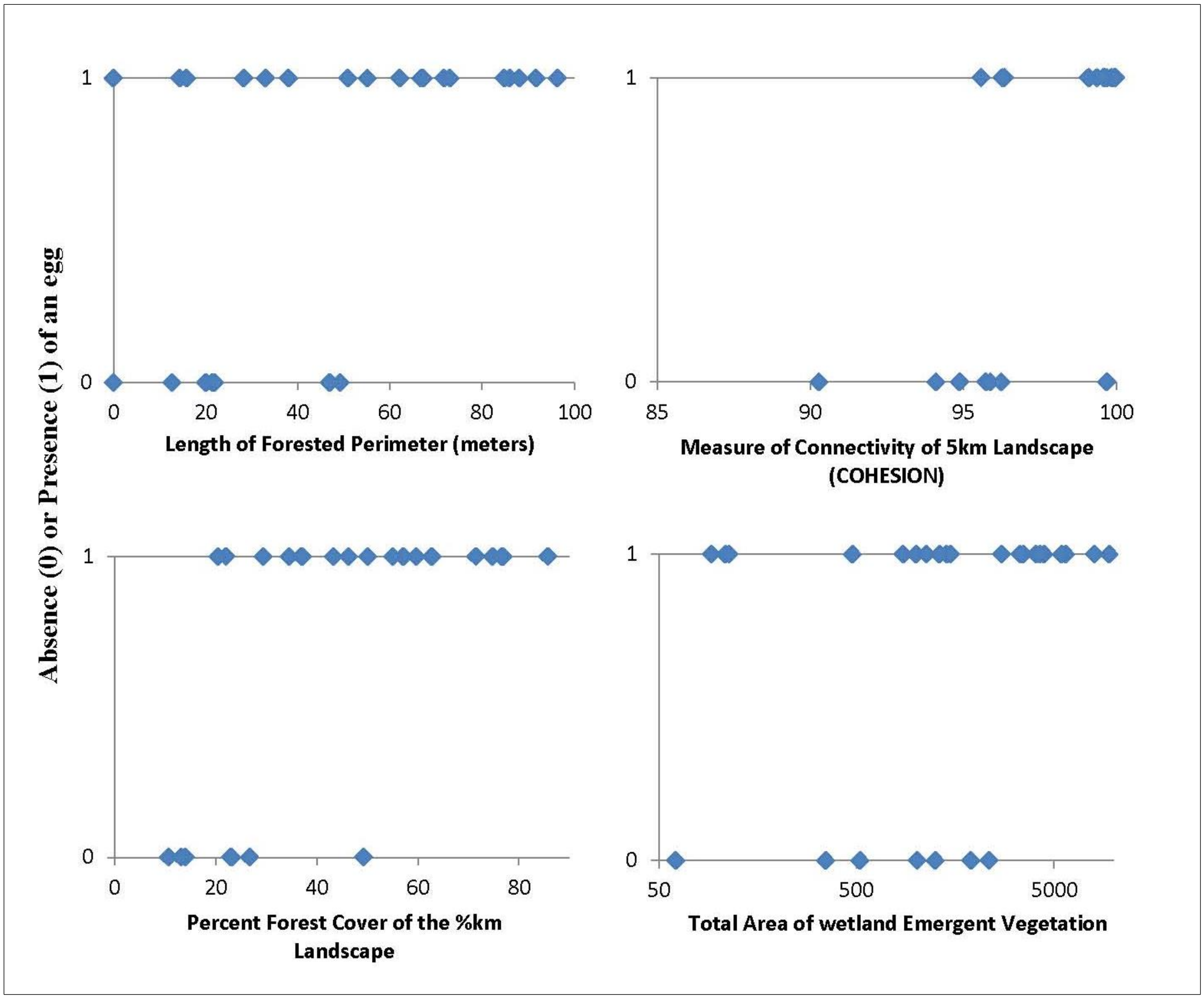

Figure 3. The relationship between *R. aurora* egg mass presence/absence and (-) forested perimeter (*p=0.017*), (+) connectivity (*p=2.9e-4*), (+) percent forest (*p=5.8e-5*), and (+) area of emergent vegetation (p=*0.023*) (n=28 for all cases). Total area of wetland emergent vegetation is presented on a log scale.

Table 5. Relative importance of habitat variables included in logit regression models predicting *Rana aurora* occupancy. Relative importance quantities are different than the sum of weights in Table 3 because the weights below were recomputed for the newly defined set of six best fit models (Burnham and Anderson 2002). Values increase in importance as they approach 1 and decrease in importance as they approach 0.

| Variable | Relative importance |
|---|---|
| Connectivity | 0.762 |
| Fish | 0.602 |
| Emergent vegetation | 0.461 |
| Percent forest | 0.248 |
| Forested perimeter | 0.105 |

Table 6. Goodness of fit chi-sq values for the top six occupancy models ($QAIC_c \leq 2$). See Table 3 for variable definitions.

| Model | Residual Deviance | $X^2$ |
|---|---|---|
| CHN + EMG +FSH + PCF | 10.134 | 0.998 |
| CHN +FSH | 13.556 | 0.978 |
| CHN | 16.893 | 0.912 |
| PCF | 17.181 | 0.904 |
| COH + EMG +FSH + FRP | 9.4907 | 0.999 |
| EMG + PCF | 15.334 | 0.951 |

### ***Rana aurora*** **Abundance**

As hypothesized, wetland area does not have a relationship with *R. aurora* egg mass abundance ($p$=0.859), but percent forest does have a relationship with *R. aurora* egg mass abundance within a 5km radius of the wetland ($p$=0.0012). This result was validated with a 95% confidence interval of the percent forest slope term. The confidence interval of the wetland area slope term incorporates zero (CI(-9.54e-5 ; 80.5e-5)), while the percent forest slope term does not incorporate zero (CI(0.905 ; 3.976)).

Only three variables were found to have an individually significant ($p \leq 0.1$) relationship with the abundance ($\gamma$) of *R. aurora* egg masses (Table 7). These co-variates include the PCF, CHN, and FRP. Analysis of the global model revealed abundance to be a positive function of PCT ($QAIC_c$ = 29.8; $w_i$=57.9%). Table 8 lists the two models with the lowest $QAIC_c$ of the total eight possible models. The second model has a $\Delta$ $QAIC_c > 2$ and is therefore not in contention for best fit model (Burhnam and Anderson 2002). As a result the best model representing the abundance of *R. aurora* in this study is:

$$\gamma = -5.760 + 2.441 * PCF$$

This model has an intermediate $w_i$ value and may be slightly varied from samples to sample. This is supported by the goodness of fit test (residual deviance = 1545.2; p-value = $2.79e^{-310}$).

Table 7. Covariates used in *R. aurora* egg mass abundance models. The asterisk indicates a significant p-value when ($p \leq 0.1$).

| Type | Covariate | Description | p-value |
|---|---|---|---|
| **Wetland** | AREA | Area of the breeding wetland in hectares | 0.859 |
| | EMG | Area of the emergent vegetation square meters | 0.855 |
| **Vegetation** | PCF | The natural log of the percent of the landscape with in the 5km buffer categorized as forest | 1.9e-5 * |
| | FPR | Length of the perimeter of the breeding wetland adjacent to forest cover type | 0.050 * |
| **Spatial** | CHN | Metric representing the habitat connectivity in a binary landscape | 0.002 * |
| **Predator** | BULL | Bullfrog occupancy | 0.519 |
| | FSH | Fish occupancy | 0.961 |

Table 8. *R. aurora e*gg mass abundance models and their coefficients ranked according to lowest QAICc. FRP represents forested perimeter and PCF represents percent forest.

| **Model** | **Intercept** | **FRP** | **PCF** | **df** | **loglink** | **$QAIC_c$** | **$\Delta QAIC_c$** | **weight** |
|---|---|---|---|---|---|---|---|---|
| **5** | -5.760 | | 2.441 | 2 | -825.46 | 29.8 | 0.00 | 0.579 |
| **7** | -5.494 | 0.002319 | | 3 | -822.56 | 32.5 | 2.66 | 0.153 |

## Identifying Terrestrial Habitat Thresholds: Regression Tree Analysis

*Rana aurora* abundance regression tree models were used as an alternative tool to explore relationships between predictor variables and *R. aurora* egg mass counts. This tree has two nodes, the first representing the entire population and the second splitting the population by percent forest (Figure 4). In order to minimize the cross-validation prediction error and thus choosing the best fit tree, a cp value of 0.5 was chosen (Table 9). This would prune the tree to one node representing the original population, decreasing the possibility of over-fitting the data. Therefore, the best fit tree that represents these data do not show that percent forest can significantly predict *R. aurora* egg mass abundance. Before pruning, the regression tree reported one split positively associating percent forest with *R. aurora* egg abundance (Figure 4). The predicted number of egg masses below 56 percent forest is low, with an average of 10.6 egg masses among 17 sites. The predicted number of egg masses above 56 percent forest is higher, with an average of 113 egg masses among 11 sites.

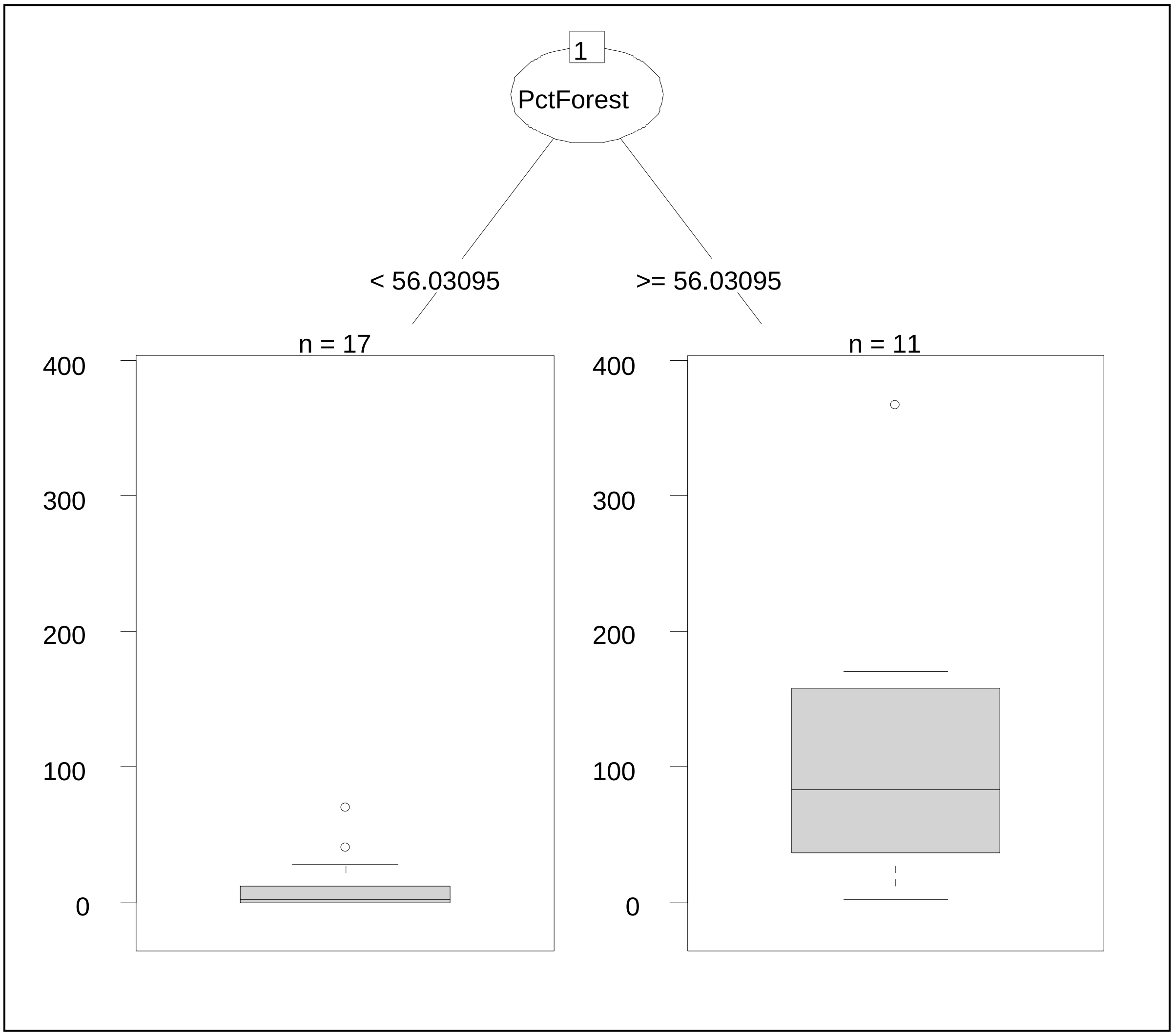

Figure 4. *Rana aurora* abundance as explained by environmental variables using a regression tree (n=28). Labels indicate decision rules used to separate abundance into two groups. Median values for groups are at the terminal (bottom) nodes. Relative amount of deviance in *R. aurora* abundance explained by split is represented by the box plots. Circles in the box plots are potential outliers to the group.

Table 9. Complexity parameter (Cp) table for the regression tree presented in Figure 4. This table identifies if the tree is appropriate or if some of the branches need to be subjected to pruning. The xerror column estimates the cross-validated prediction error for different numbers of splits. The best tree has 0 splits.

| | **CP** | **Number of splits** | **Relative error** | **Xerror** | **Standard Error** |
|---|---|---|---|---|---|
| **1** | 0.5116314 | 0 | 1.0 | 1.067224 | 0.3257875 |
| **2** | 0.5000000 | 1 | 0.4883686 | 1.167854 | 0.3620566 |

### Spatial Extent of *Rana aurora* Terrestrial Habitat Use.

Percent forest was quantified at each site for nested spatial footprints every 50m from 50 to 500m and every 500m from 500 to 5000m (Figure 2). A Spearman Rank correlation was computed for each site within each spatial footprint. Percent forest is positively correlated with the number of *R. aurora* egg masses at every distance ($p<0.01$ for all distances except 100m where $p<0.02$). The correlation coefficient peaks at a distance of 450m with an $r_s = 0.778$ (Figure 5).

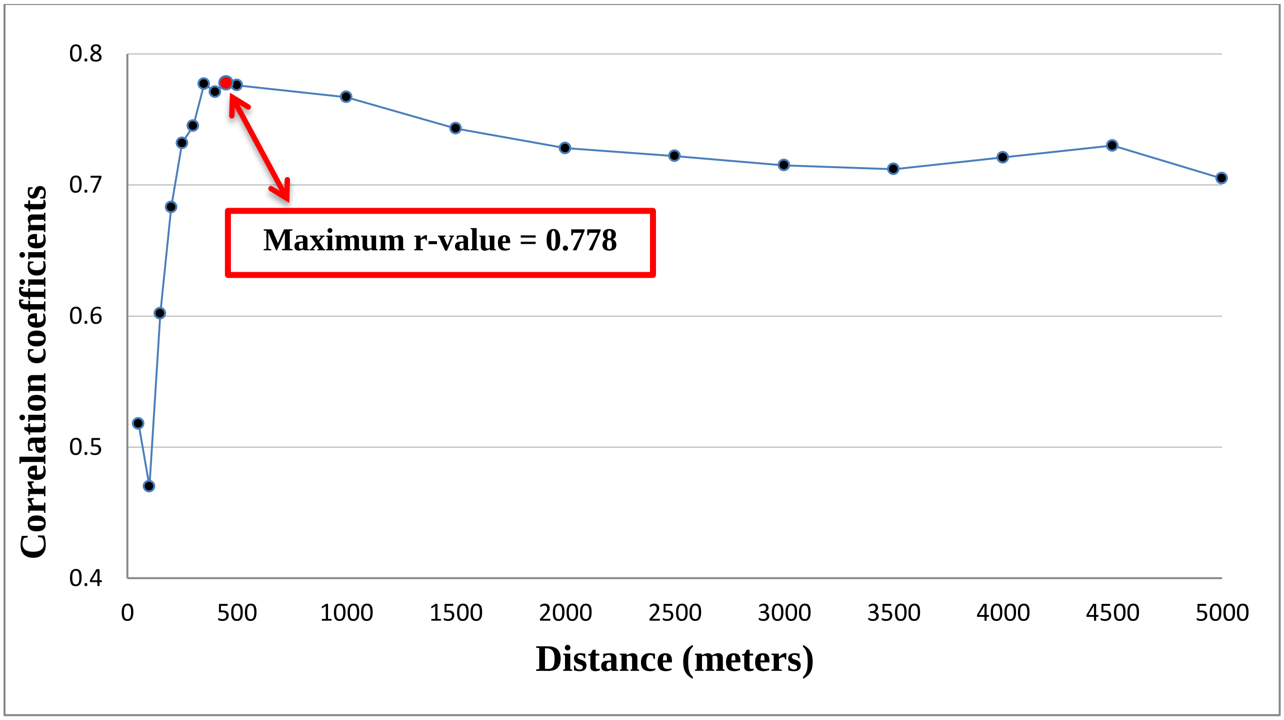

Figure 5. Variation in the relationship between *R. aurora* population size and percent forest as a function of distance from wetland breeding sites.

## DISCUSSION

### ***Rana aurora*** **Occupancy and Abundance in the Terrestrial Habitat**

The most consistent landscape habitat association reported in the literature today is the positive association between forest and amphibian occupancy (Porej et al. 2004; Cushman 2006). This study also supports this relationship with not only *R. aurora* occupancy, but abundance as well. Though percent forest is the best fit predictor for the abundance for *R. aurora*, the model presented above describes the data less well than was expected with an intermediate Akaike weight of 57.9%. This suggests that variables or interactions associated with those variables that may not have been included in the analysis are important predictors of *R. aurora* breeding. However, it is intuitive that percent forest would be the leading determinant in *R. aurora* abundance because forests provide the resources necessary for *R. aurora* survival. In a telemetry study of *R. aurora*, Haggard (2000) found that the frogs spend most of their time in thicket/forest habitats and detections of frogs in grasslands were within short distances of the edges of either thickets or forb patches. Additionally, Aubry and Hall (2001) found *R. aurora* to be positively associated with cover by woody debris and water. This may reflect mature forest structure. More mature stands tend to have more woody debris, water resources, food availability, shelters, and fewer predators.

Several possible explanations exist to why *R. aurora* prefers to travel so far into their terrestrial habitat even in cases where percent forest is high close to the breeding wetlands. One factor to their migration may be to take advantage of the decrease of competition between *R. aurora* individuals for shelter and the variety of prey organisms. Woody debris is positively associated with *R. aurora* (Aubry and Hall 2001). Down debris may provide moist shelters for *R. aurora* and increased access to small invertebrates such as spiders and insects that make up their main diet (Nussbaum et al. 1983; Hayes and Tennant 1985; Licht 1986). *Rana aurora* has also been found to be positively associated with sword fern (Haggard 2000), a common understory plant in the Pacific Northwest conifer forests (Franklin and Dryness 1973). Sword fern provides shelter and moisture for *R. aurora* under their drooping fronds where relative humidity is likely high. Dispersing into the forest for these resources instead of remaining close to the wetland may decrease the intraspecific competition for food. Additionally, if the frogs stay on or near the wetlands they might be at greater risk of predation by raccoons or avian predators (Licht 1974, 1986).

Another reason that *R. aurora* abundance is high in areas of higher percent forest is possibly due to the microclimatic conditions forests provide. Forests tend to be positively associated with moisture sources because forests absorb and slowly percolate the water that feeds streams, seeps, and ditches throughout the summer. After *R. aurora* start their emigration into the upland forest they were found to spend 90% of their time on land, but commonly not more than five meters from a water source such as a stream, ditch, or seep (Haggard 2000). Forests have a higher relative humidity than vegetation types with more open canopies. Amphibians can absorb moisture through their skin (Hillman et al. 2009) and are therefore less likely to dry out in these moister conditions. Undisturbed forest habitat maintains moderate temperature and evaporation of adjacent aquatic habitats, and moist dispersal corridors for *R. aurora.* These allow *R. aurora* to find shelter and food resources necessary to make the yearly breeding migration back to the wetlands.

The traditional consensus that high dispersing species are the most adaptive to habitat fragmentation (Kareiva and Wennergren 1995; McCarthy et al. 1997) is based on the notion that these species are more able to disperse across unsuitable habitat to new areas of suitable habitat. However, in this study connectivity was positively associated with the occupancy of *R. aurora* egg masses. As connectivity of forest patches increases, so does the dispersal success of *R. aurora* across the landscape. This suggests that fragmentation could be compounding the effects of population declines based solely on habitat loss (Fahrig and Merriam 1985).

Gibbs (1998) found fragmentation remains uniformly high with forest cover below 60%, and that dispersal ability of amphibian species was inversely related to this fragmentation. Increased fragmentation is also the culprit of decrease species richness (Lehtinen et al. 1999). A possible explanation for this relationship is that greater dispersal ability results in a greater mortality risk associated with the frequency of encounters with roads and anthropogenic barriers in fragmented landscapes. Additionally, breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to the high mortality of juveniles during emigration

(Rothermel 2004). This could be of particular concern where local extinction is common and dispersal is critical for recolonization of local populations (Hecnar and M‘closky 1996; Semlitsch et al. 1998; Skelly et al. 1999).

*Rana aurora* has been recaptured in the same season up to five kilometers from their original wetland breeding sites (Reaser and Dexter 1996; Hayes et al. 2007). However, there is little known about their dispersal patterns. The Spearman rank correlation identified that variation in the relationship between *R. aurora* population size and percent forest as a function of distance maximizes at 450m. This suggests that *R. aurora* may migrate as a population on average to a distance of 450m into the upland terrestrial habitat. The steep increase in the correlation coefficients as distance increases over the 50m intervals may imply that *R. aurora* only use the bordering forest habitat to facilitate their migration fully out of the riparian zone and far into the upland habitat during the terrestrial season. In this study it appears that most adults tend to disperse to distances above 300 m where the correlations begin to reach a peak. The correlation coefficients do not decrease much after 450m out to 5000m. This supports the hypothesis that percent forest is more important at greater distances from the breeding wetlands. Further research on the connectivity of the forest patches closer to the wetland edge may provide insight to whether the first couple hundred meters are mainly used as corridors to the further forest patches.

Porej et al. (2004) noted that the most parsimonious models for overall salamander diversity and individual models for the presence of newts, salamanders, and frogs included land-use variables measured outside the immediate habitat surrounding breeding wetlands. In the Pacific Northwest, Richter and Azous (2001) noted the proportion of native species observed related to the percent of forest land within 10, 100, 500 and 1000m of the wetland edge. The significance of this relationship was weakest at 10m (R = 0.57, p = 0.01) and strongest at 500m (R = 0.66, P = 0.004) (Richter and Azous 2001). These results, along with the results of this study, suggest that persistence of local populations depends on the composition of the broader landscape context as well as the immediate breeding habitat.

### ***Rana aurora*** **Aquatic Habitat Relationships**

The preconceived notion that wetland size correlates to amphibian abundance may carry more weight than it should, at least for *R. aurora*. To my knowledge, there have not been any studies that have indicated a positive association of *R. aurora* occupancy or abundance with wetland size. Studies that tested this association either found no association (Richter and Azous 2001), or found a negative association (Adams 1999; Pearl et al. 2005). This study supports the fact that breeding wetland area has no association to *R. aurora* occupancy or abundance. The reason for this lack of association is likely due to *R. aurora's* failure to exhibit territorial behavior when laying egg masses (per. observation). Multiple egg masses have been observed on a single vegetation brace, or within a small area. As a result, a large number of egg masses can fit into smaller wetlands. Negative associations are likely due to a secondary effect of exotic species or inadequate hydroperiods (Adams 1999; Pearl et al. 2005; Richter and Azous 1995). Smaller wetlands are more likely to be ephemeral and therefore do not have the resources to maintain fishes or bullfrogs. Bullfrogs require wetlands to be flooded all year long in order to survive the two years it takes them to metamorphose. Ephemeral wetlands with hydroperiods of less than six months will not support *R. aurora* larvae through metamorphosis and will likely not be able to support a *R. aurora* population.

The realization that wetland size is less important in *R. aurora* occupancy and abundance may be critical information for maintaining the species. Concerns for amphibian species commonly rely more on the status of the breeding wetlands, and less on the upland terrestrial habitat. While wetlands are necessary for the survival of *R. aurora*, choosing them based on location within the landscape forest matrix may be more important than size consideration.

This study along with others found emergent vegetation to be an important predictor of *R. aurora* occurrence within breeding wetlands (Adams 1999; Hazell et al. 2004; Cary 2010). Greater area of emergent vegetation may be important for several reasons. *Rana aurora* attaches their egg masses to emergent vegetation (Nussbaum et al. 1983). Wetlands with greater area of emergent vegetation could potentially hold more egg masses. These vegetation braces also keep egg masses from floating away, becoming stranded, or sinking to the bottom of wetlands. Egg masses that become stranded could dry out and become exposed to predators. Egg masses that fall to the bottom could become exposed to lower temperatures or lower dissolved oxygen concentrations causing slowed development and/or mortality. After metamorphosis to the larval stage, emergent vegetation also provides cover from native and exotic predators (Kiesecker et al. 2001).

Forested perimeter was expected to have a positive association with *R. aurora* occupancy. Forest area that reached the wetland’s edge could imply an increase in connectivity from terrestrial habitat to aquatic habitat. Other studies have also indicated a positive association of *R. aurora* occupancy with decreasing distances to nearest forest patches (Ostergaard 2001). However, in this study the association of *R. aurora* occupancy with forested perimeter of wetlands was negative. In the case of this study, forested perimeter could have been less a function of connectivity, and more of an effect of canopy cover. Increased forested perimeter may have increased canopy cover and as a result decreased sunlight exposure to egg masses. Sunlight is important to embryonic development (Storm 1960; Licht 1969a, 1971; Calef 1973a).

Cary (2010) found a negative relationship of canopy cover with presence of *R. aurora* egg masses. Higher canopy cover can lower water temperatures which slows embryonic development.

Water molds have also been found to invade excessively shaded egg masses resulting in high embryonic mortality (Hayes et al. 2008). Another reason may be reduced food sources - other species, including the pacific tailed frog (*Ascaphus truei*), tend to have increased mortality due to shade because the lack of sunlight reduces the density of algae eaten by the tadpoles (Mallory and Richardson 2005). *Rana aurora* is also believed to have an association with algae that grows inside the egg masses and provides oxygen during embryonic development, and then becomes a food source for the tadpoles (pers. comm. M. Hayes 2012).

The negative relationship between *R. aurora* occupancy and forested perimeter may have also been a side effect of the grain size of the Landsat data. Forested perimeter was measured in ArcGIS (v10.0) (ESRI 2011) with a cell size of 30m by 30m. This is a rather course grain size to measure perimeter. It may be possible that the vegetation type identified by these cells was representative of the 900m area, but not the area directly adjacent to the wetland. In future studies this measurement may require on ground measurements or finer grain sizes within the landscape data used.

### Fishes, American bullfrogs and *R. aurora*

The results of the Mann Whitney analyses revealed that predators (fishes and the exotic American bullfrog) had no significant effect on the number of *R. aurora* egg masses found. Consideration to remove sites that included bullfrogs and fish was high because this research poses a question about the influence of habitat on occupancy and abundance response variables. However, the results of these analyses reviled that the presence of these predators did not significantly differ the abundance of *R. aurora* in my study sites. Instead, bullfrogs and fishes were included as covariates in the influence of *R. aurora* occupancy and abundance. There may be some uncertainty in these data as a result of volunteers failing to report adult frogs, or making note of fish species. In situations where possible, property owners were asked to verify bullfrog and fish presence.

Wetlands with both bullfrogs and fish were expected to show the greatest difference in egg mass abundance, but the difference in population sizes (n=3 and n=25) were too different to compare. The reduction in the average egg mass counts in wetlands with bullfrogs or fish would be consistent with observations linking the frogs' decline with an increase in these exotic predators (Adams 1999). Both bullfrogs and fishes prey on the larvae of *R. aurora* decreasing the number making it to metamorphosis. Bullfrog adults are also known to pray on adult *R. aurora* especially during their breeding period (Pearl et al. 2005). With fewer *R. aurora* larvae making it to adulthood and increased predation on the ones that do, it can be inferred that there will be a decrease in the local population and surveys would result in lower numbers of egg masses.

Fish are predators of both larvae and adult *R. aurora* (Kiesecker and Blaustein 1998; Lawler et al. 1999; Monello and Wright 2001). Multiple studies have determined there to be a negative relationship with *R. aurora* occupancy and exotic fish (Adams 1999; Pearl et al. 2005). The results of this study's multi-regression analysis identified a positive relationship of fish with *R. aurora* occupancy, which was unexpected. This could be for a couple of reasons. One reason may be that the risk of predation of *R. aurora* by fish is site specific and may rely on other habitat features. For example, sites with increased emergent vegetation may provide more shelter for the larvae than sites without. Additionally, fish species observed in this study may have included larger numbers of native fish species than exotic species. This would be consistent with Pearl et al.'s (2005) findings of a positive association of *R. aurora* occupancy with native fish. In this study fish presence was identified, but trappings were not performed to identify fish to the species level.

## Habitat Protection and Land-Use Planning in Urban Environments

Studies of lentic breeding amphibian spatial dynamics have traditionally taken a "ponds-as-patches" view in which subpopulation occupancy is a function of wetland spatial arrangement (e.g., discrete subpopulations; Marsh and Trenham 2000). However, urban land use could increase population decline by creating dispersal barriers between these "patches," such as roads or urban development. Correlational studies demonstrating abundance and probability of occurrence of several amphibian species are lower in wetlands surrounded by little forested area (Clark et al. 2007). Survival of amphibian populations in fragmented landscapes depends on the interaction between the patterns of land cover types (Fahrig 1998; Carr and Fahrig 2001) and needs to be better understood for application into landscape planning.

Habitat protection laws in King County also typically focus more on wetland habitat, than their potentially higher impacted counterpart, forested terrestrial habitat. Therefore, current regulations may be inadequate to maintain the necessary *R. aurora* terrestrial habitat in the face of rapid population growth (Hayes et al. 2008 and Richter et al. 2008). Fixed width buffers are the approach most frequently used to address the impacts caused by adjacent land use (NRC 2001). However, buffer widths in Washington State are commonly determined based on the wetland type, function, and surrounding land use. Little concern is made towards regulation of the condition of adjacent terrestrial habitats for wildlife purposes (Hayes et al. 2008). Wetland buffers in Washington range from 15.2 m to 91.4 m wide (McMillan 1998) depending on wetland quality, function, and size. This is considerably smaller than the 5km distance that *R. aurora* may need to migrate in order to access the necessary resources.

Only within recent years have strides been made to consider more of the surrounding habitat. King County, the most urbanized county in Washington State (King County 2002), has adopted a new ordinance that includes the protection of corridors between wetland complexes in order to reduce isolation of wetland species. Rural landowners were at one point restricted on how much of the area in vegetation could be cleared in order to safeguard the watersheds (King County 2004), but this ordinance was revoked due to discontinuity with laws on development taxation. In 2005, the Washington State Growth Management Act designated critical areas for protection, including fish and wildlife conservation areas, beyond established fixed width buffers (Washington State 2005). However, these regulations are sight specific and jurisdictions rarely consider landscape complementation for *R. aurora* (Hayes et al. 2008). Additionally, private property owners can get out of these regulations by proving that maintaining buffers is an undue burden for them.

Despite the fact that King County's regulations are acknowledged to be the best within *R. aurora* habitat range, they are still unlikely to maintain landscape-level connectivity needed by *R. aurora* (Hayes et al. 2008 and Richter et al. 2008). Therefore, if the goal is to avoid losing *R. aurora* populations in urbanizing areas of the Pacific Northwest, jurisdictions should consider protecting sufficiently large-scale terrestrial and breeding habitat connectivity that can facilitate inter-population dispersal and migration across broader landscapes (Semlitsch and Bodie 1998 and Hayes et al. 2008).

One technique to initiate this process is the identification of forest area thresholds on *R. aurora* occupancy. "A critical threshold exists when the relationship between the amount of suitable habitat and population density or probability of occurrence exhibits a sudden, disproportionate decline as habitat is lost" (Homan et al. 2004). If such thresholds exist, identifying them is essential for understanding extinction processes, and would be important to landscape management and reserve design.

The regression tree analysis provided no evidence of a significant variable that would aid in the prediction of *R. aurora* population sizes, or thresholds in any of the predictor variables. This is likely due to a small sample size. An analysis of this kind would provide excellent information if it was possible to sample wetland breeding sites across the entirety of the *R. aurora* range. However, the tree represented by the over-fitted data does include percent forest as a potential predictor of *R. aurora* abundance. This provides support to the best fit model of *R. aurora* abundance reported above. Percent forest is likely the leading variable in the abundance of *R. aurora* due to their large migration distances into the upland forest.

The over-fitted regression tree identified the *R. aurora* egg mass population associated with less than 56% forest to be significantly different than the egg mass population representing percent forest greater than 56%. This suggests a potential threshold for percent forest. Deforestation to below 56% of the landscape could significantly decrease the number of *R. aurora* egg masses in their associated breeding wetlands. This information would be better tested with a larger sample size across the *R. aurora* range and could be supported by using decision trees and piecewise regression. Though this result is not completely supported by the data in this study, it is in line with previous work looking at thresholds of forest fragmentation. Franklin and Forman (1987) predicted that major thresholds in fragmentation would occur when about 50% of the forest was converted to non-forest as a result of clear-cutting in the Pacific Northwest. Vogelmann (1995) reported the greatest increase in forest fragmentation as the landscape cover changed from 100% to about 80% forest area, with a threshold occurring at 60%, after which only slight increases in fragmentation occurred.

Thresholds of 50-60% forest are also seen with a few other migrating amphibians and the bay breasted warbler. Spotted salamanders have been found to lack occupancy with a 50-60% forest threshold at both 100 and 1000 m spatial scales from breeding wetlands (Homan et al. 2004); red-spotted newt populations did not persist below a forest cover threshold of 50% (Gibbs 1998); and the bay breasted warbler was found to be absent from landscapes with less than 55% forest cover (Drolet et al. 1999). Lastly, amphibian richness was found to be highest in the Puget Sound basin within wetlands that retain at least 60% of adjacent area in forest land up to and exceeding 500m (Richter and Azous 2001). Critical thresholds are species specific, but far-migrating species like *R. aurora*, for which the scale of seasonal habitat use is relatively large, are likely to be sensitive indicators to urbanization effects on habitat fragmentation and loss.

## CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Terrestrial habitat reliance of Pacific Northwest lentic breeding amphibians is underrepresented in current literature. Loss of habitat as a result of urbanization, poses a threat to amphibian persistence and ultimately the ecosystem services they provide. This study provides the first assessment of the association between the amount of available habitat (aquatic and upland forest), and the occupancy and abundance of *R. aurora* within King County, Washington. The potential that terrestrial, rather than aquatic habitat, is the key control on amphibian abundance is a precursor to developing occupancy curves related to the degree of terrestrial habitat development. Better understanding of habitat use adds to effective guidance on jurisdiction that will maintain amphibians on the landscape.

Wetlands with emergent vegetation and decreased forest perimeters surrounded by high areas of connected forest represent desirable *R. aurora* breeding habitat. To maintain *R. aurora* populations it is recommend that managers limit strategies that negatively affect this type of habitat (i.e., maintaining only large deep wetlands in areas of high development and road densities).

Most conservation policies concerning lentic breeding amphibians are dominated by wetland protection and fixed width buffers (Hayes et al. 2008). While core zones have been used as a guide for setting buffers for wetlands and riparian zones (Semlitsh and Bodie 2003), they are inadequate as a conservation strategy for lentic breeding amphibians. This study identified multiple variables that play a role in *R. aurora* occupancy. These variables were not features only found in one of the two habitats required by *R. aurora*. This suggests that conservation plans for amphibians must perceive wetlands and the surrounding terrestrial habitat as one ecological unit.

Additionally, when assessing the spatial extent at which *R. aurora* may migrate in to their terrestrial habitat, the results of this study revealed a potential average migration distance of 450m. These results suggest that *R. aurora* do prefer to migrate fully out of the riparian zone and far into the upland habitat during the upland active season. With this new information it is possible to begin to plan conservation strategies keeping in mind that the area of percent forest is important for *R. aurora* at five times the distance currently protected in wetlands with the largest fixed width buffers in place. The persistence of local populations depends on the composition of the broader landscape context as well as the immediate breeding habitat. Currently, development regulations minimize the threats to wetlands at short distances, but these areas do not extend to distances occupied by the majority of the *R. aurora* population.

In order for *R. aurora* to persist conservation ecology should be linked to land use planning on the landscape scale. This study suggests that forest area, up to at least 450m of the breeding wetlands, is the leading determinant in *R. aurora* population sizes. Neglecting to maintain a sufficient forested habitat will aid us in failing to protect them. This can be of particular concern in fragmented landscapes that inhibit *R. aurora* from accessing breeding wetlands and other water resources. Retention of 50% to 80% forested habitat will have a high probability of ensuring functional habitat connectivity (Gibbs 1998) for the species.

*Rana aurora* makes two long migrations to and from breeding sites yearly. With extensive traveling distances, *R. aurora* is more likely to come into contact with unsuitable habitat types, increasing mortality. In order to control distribution of unfavorable habitat, mapping which integrates the effects of the local landscape on the dispersal and occurrence of *R. aurora* should be done. This in conjunction with friction and cost-distance maps could help King County to create conservation plans before development projects are started. This is preferable to restoration because restoration efforts commonly call for wetland relocation which may displace the current populations. Additionally, these mapping strategies could help to create homogeneity in a landscape currently managed on a parcel by parcel basis. Ultimately, current conservation efforts do not address all the habitat needs of amphibians, especially *R. aurora*. In order to avoid potentially losing this species and others in the landscape it is strongly advised that urban development policies begin to consider maintaining high quality habitat on the landscape scale.

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