# EVALUATING THE CONSERVATION POTENTIAL OF URBAN AND RURAL ECOSYSTEMS FOR AQUATIC-BREEDING AMPHIBIANS: A CASE STUDY OF TWO NATIVE FROGS IN SOUTHWESTERN BRITISH COLUMBIA

by

Jemma Green
B.Sc., University of British Columbia, 2011

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the School of Environmental Studies

University of Victoria

# Supervisory Committee

Evaluating the Conservation Potential of Urban and Rural Ecosystems for Aquatic-breeding Amphibians: A Case Study of Two Native Frogs in Southwestern British Columbia

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# Abstract

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The conservation of aquatic-breeding amphibian populations and their habitats is increasingly challenged by urban and rural development, which is occurring more intensively and more rapidly than ever before. Some species are now impacted by development throughout their range. This has forced a re-evaluation of the potential of developed landscapes for providing habitat and contributing to regional conservation strategies. For many amphibians, little is known about the criteria necessary for persistence in a developed landscape. Considerable variation in the physiology, habitat requirements, and movement behaviour of amphibians suggests that responses to habitat loss, alteration, and fragmentation are species-specific. In this thesis, I investigate species-habitat relationships for the northern red-legged frog (*Rana aurora*) and the Pacific chorus frog (*Pseudacris regilla*) in a mixed urban-rural landscape in southwestern British Columbia to evaluate the potential for species persistence despite urban and rural development throughout their range. I used repeat auditory surveys of the species' breeding chorus to determine presence or absence at potential breeding wetlands. I then related species occurrence and abundance to characteristics of the aquatic and terrestrial environment measured at multiple spatial scales. Both species were found to use rural and urban wetlands, though *R. aurora* were rarely detected while *P. regilla* were common. Occurrence was best explained by characteristics of the terrestrial environment, rather than within-wetland characteristics, though influential terrestrial characteristics and their scale of impact differed between species. Within the context of the developed landscape, I identify species-specific positive and negative habitat associations and suggest the spatial scales at which management of these habitat characteristics will be most effective. These criteria may help to explain the species' current distribution, prioritize management strategies, predict the effectiveness of habitat conservation and restoration projects, and inform development in municipalities seeking to maintain or enhance amphibian diversity.

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# Dedication

*This thesis is dedicated to the biologists, ecologists, restoration practitioners, and others working to conserve amphibians, and to the amphibians themselves, whose amazing forms, behaviours, life histories, and global plight inspire our life's work.*

# Chapter 1 Introduction

## 1.1 Amphibian conservation and restoration challenges

More so than any other taxonomic group, amphibians are experiencing dramatic population declines in every region of the globe (Houlahan et al. 2000; Stuart et al. 2004; Hof et al. 2011). Growing recognition of the severity and widespread nature of this conservation problem in the 1980s and ‘90s led to the first Global Amphibian Assessment by the International Union for the Conservation of Nature (IUCN) in 2004, which determined that over 40% of the world’s amphibian species were experiencing some form of decline; this included populations found within protected areas (Stuart et al. 2004). The most recent assessment of 91% of the world’s more than 7,000 described amphibians, completed by the IUCN in 2008, paints a bleaker picture: one third of the world’s amphibian species are threatened with extinction or have already become extinct, while another 25% are too data deficient to determine their conservation status (IUCN 2018). The primary causes of global amphibian decline include:  habitat loss and fragmentation caused by land use change; chytridiomycosis, a fatal disease caused by the amphibian chytrid fungi (*Batrachochytrium* spp.); climate change; and interactions between these threats (Hof et al. 2011). Unless rapid action is taken to mitigate the host of threats facing amphibians at local, regional, and global scales, hundreds of species are expected to become extinct in the coming decades (Stuart et al. 2004).

One of the leading causes of amphibian decline in North America is habitat loss and fragmentation due to urban and rural development (Lehtinen et al. 1999; Baldwin & DeMaynadier 2009; Scheffers & Paszkowski 2012). Landscape development by European settlers occurred disproportionately in productive, low-lying areas that were once prime aquatic and terrestrial habitat. As development intensified with industrialization and a growing human population, many amphibians began to disappear from areas in which they were once abundant (e.g. Fisher and Shaffer 1996, Davidson et al. 2001, Price et al. 2006). While most native species are negatively impacted by urban activity (Mckinney 2002), aquatic-breeding amphibians are particularly vulnerable due to their requirement of complimentary aquatic and terrestrial habitat to support their complex life histories

(Baldwin & DeMaynadier 2009), their sensitivity to environmental contaminants and stressors due to their unique physiology (Feder & Burggren 1992), and their relatively low vagility (Cushman 2006). In addition to direct loss of habitat, urban and rural development has been shown to negatively impact amphibians through physical and chemical habitat alterations, by limiting habitat connectivity and matrix permeability via buildings, roads and other structures, and by facilitating the spread of non-native, invasive predators and competitors (Mckinney 2002; McKinney 2006; Hamer & McDonnell 2008).

The conservation of amphibian populations and their habitats is likely to be increasingly challenged by urban expansion, which is occurring more intensively and more rapidly than ever before. The United Nations predicts that the world's urban population will grow by 2.5 billion by 2050 (2014). As the global urban population expands, so too will the area of urban ecosystem transformation. This is particularly true in industrialized nations, where natural and agricultural land is being converted to urban and suburban uses at an even faster rate than the urban population is growing (Pickett et al. 2001), with urban cores densifying as the developed landscape sprawls. Thus, a new reality of conservation biology is the management of native species for long-term persistence in ecosystems highly modified by urban and rural development (Hamer & McDonnell 2008). Sound management will require knowledge of the mechanisms underlying species distributions and population trends as well as the criteria for habitat suitability and population persistence in human-modified landscapes.

The first decades of urban ecological research on amphibians have confirmed that, in general, aquatic-breeding amphibians respond negatively to urban and rural development, but that responses are species-specific (Cushman 2006; Scheffers & Paszkowski 2012). Amphibians tend to decline in abundance and diversity with declines in forest cover and increases in urban development (Knutson et al. 1999; Simon et al. 2009; Quesnelle et al. 2015). Negative relationships are also common between species abundance or diversity and indicators of habitat fragmentation: aquatic habitat isolation from terrestrial habitat and proximity or density of roads (Fahrig et al. 1995; Cushman 2006). One of the greatest advancements in amphibian research is the understanding that the extent, configuration, and quality of terrestrial habitat in a heterogeneous landscape is as important as the quality of aquatic breeding sites for many species (Semlitsch & Bodie

2003; Cushman 2006). In addition to these generalizations, we now know that the direction, strength, and scale of relationships between a species' distribution or abundance and landscape development are determined by reproductive effort, dispersal ability, home range size, specific habitat associations, and other species-specific factors (Cushman 2006; Hamer & McDonnell 2009). Some amphibians have shown remarkable behavioural plasticity in habitat selection and resilience to landscape change (e.g. Brand and Snodgrass 2010, Saarikivi et al. 2013, Holzer and Lawler 2015). Furthermore, researchers have documented cases in which urban wetlands have supported abundant amphibian populations (e.g. Riley et al. 2005), high species richness (e.g. Holzer 2014), and genetic diversity similar to habitats outside of urban areas (e.g. Garcia-Gonzalez and Garcia-Vazquez 2012). This research has encouraged cautious optimism about the oft overlooked conservation potential of urban ecosystems for amphibians.

Consensus on the species-specific nature of amphibian responses to urbanization implies that further research is needed on many species. Throughout the world, conservationists are faced with management of amphibian declines concurrent with encroachment of urban development into remaining habitat, yet they are armed with only limited knowledge of how species of concern will respond to changes in habitat area and configuration, roads, and aquatic-terrestrial habitat isolation, as well as the landscape scale at which these relationships may have an impact (Cushman 2006). In British Columbia, and indeed throughout Canada, hypotheses about species responses to urbanization are confounded by limited knowledge of life history, habitat selection, and movement behaviour in even optimal, undisturbed habitats.

## 1.2 Managing the whole landscape

Urban and rural areas are characterized by landscape heterogeneity. Native species that persist on the developed landscape may find habitat in remnant, undisturbed ecosystems (e.g. mature forests and wetlands), in ecosystems that are diverging from their pre-development state due to direct or indirect human impacts (e.g. managed forests, wetlands inundated with invasive plants, dammed waterways), and in ecosystems that have no historical precedent, whether by human design (e.g. stormwater ponds, ornamental ponds, botanical gardens) or negligence (e.g. abandoned farmland or brownfield sites). These ecosystems exist along a continuum in terms of native species diversity and, from a human perspective, management intensity and purpose (Aronson et al. 2017; Higgs 2017). Each ecosystem type demands a different management approach (Higgs 2017). In response to the complexity and dynamism of developed landscapes, and in recognition of the biodiversity conservation value of every ecosystem type, it has been suggested that ecosystem managers embrace a conservation and restoration framework that considers the challenges and opportunities of the whole landscape (Hobbs et al. 2014).

Within the disciplines of restoration ecology and conservation biology, the terminology used to frame the various approaches to ecosystem management differs. An emerging framework within the ecological restoration community differentiates ecosystems based on their resemblance to a historical state, their means of assembly and persistence, and whether ecosystem changes are reversible through restoration (Hobbs et al. 2009, 2013). According to this framework, ecosystems are termed historical, hybrid, or novel. Higgs (2017) proposes a distinction between self-assembled ecosystems—those that assemble and function largely without regular human intervention and management (e.g., historical, hybrid, and novel ecosystems)—and designed ecosystems. Designed ecosystems, which address human problems or provide primarily human benefits, are becoming increasingly common on the developed landscape and may benefit biodiversity (e.g. food forests, green roofs, stormwater ponds) (Higgs 2017). Conservation biologists, on the other hand, have commonly described ecosystems according to where they fall on the continuum between intact and heavily degraded (e.g. Homan et al. 2003; Schwitzer et al. 2011; Caves et al. 2013), implying optimal, suboptimal, and poor biodiversity conservation values. Moreover, in place of 'designed' ecosystems, the terms 'constructed' and 'created' are used, sometimes interchangeably, to describe environments (ecosystems, habitats, features) that were created for human purposes and/or ecosystems created with the purpose of conserving biodiversity or focal species (e.g. Rannap et al. 2009; Brown et al. 2012; Holzer 2014). In this thesis, I adopt terminology from both of these frameworks as they apply to the ecosystems encountered in the study area. I describe ecosystems as intact or degraded to explain their current biodiversity value, or as novel or hybrid to explain their restoration potential. I refer to ecosystems that are not natural in origin as created or constructed depending on whether their purpose as habitat was/is intentional or unintentional, respectively. Research sites were randomly selected from across the study area in an effort to capture this ecosystem heterogeneity.

## 1.3 Thesis overview

In this thesis, I endeavour to build on the body of knowledge of amphibian responses to urban and rural development by investigating species-habitat relationships for two native frog species in an urbanizing region of southwestern British Columbia. The focal species were chosen for their seemingly different levels of disturbance tolerance and for their ease of detection. The Pacific chorus frog (*Pseudacris regilla* Baird and Girard, 1852) is an adaptable, widespread, common species whose populations have remained stable in spite of development throughout its range (Rorabaugh & Lannoo 2005), while the northern red-legged frog (*Rana aurora* Baird & Girard, 1852) is a federally-listed species whose populations have declined in areas of urban and rural development (COSEWIC 2015). Both species vocalize during a defined breeding season and their presence at breeding wetlands is readily detected using established auditory survey methods. I conducted separate repeat calling surveys for each species to determine presence or absence at potential breeding wetlands and relate occurrence to local (within-wetland) and landscape characteristics measured in the field and in GIS, respectively. Based on the observed relationships, I make general recommendations for assessing habitat suitability for conservation and for designing or restoring breeding habitats within the developed landscape.

Chapter 2 reports on the findings of *R. aurora* surveys. I observe that *R. aurora* are rarely present in lentic[1] wetlands and absent from lotic[2] wetlands in both urban and rural areas. Due to the small number of detections, no occupancy analyses are performed; rather, observations of similarities in local and landscape features among occupied sites are made and related to the published literature on *R. aurora*. The species' use of a constructed pond and its absence from lentic wetlands is discussed. I estimate detection probability for *R. aurora* based on the detection history from repeat surveys and discuss the limitations of

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[1] Lentic refers to still freshwater, or lacustrine, habitat. I use the terms *lentic* and *pond* to describe pond, lake, and marsh sites.

[2] Lotic refers to flowing freshwater, or riverine, habitat. I use the terms *lotic* and *waterway* to describe stream and ditch sites.

the auditory survey method for the species. I conclude that *R. aurora* breeding habitat occupancy is likely driven primarily by forest cover and habitat connectivity at the landscape scale and secondarily by aquatic vegetation cover at the local scale. Recommendations are made regarding habitat suitability, survey methods, created/restored wetland design, and further research.

In Chapter 3, I conduct a correlative study of *P. regilla* occupancy and relative abundance in relation to local and landscape habitat variables using occupancy and ordinal regression modeling frameworks, respectively. Landscape variables are measured within eight nested buffers around survey sites to determine the scale of greatest impact for each variable. I structure models around competing hypotheses, suggesting that *P. regilla* occupancy and relative abundance may be driven by variables associated with either (1) aquatic habitat quality, (2) the presence of non-native, invasive predators, (3) complementary terrestrial habitat availability, (4) habitat connectivity, or (5) a combination of variables from among competing hypotheses.

I observe that *P. regilla* are common among rural lentic wetlands, occupy nearly half of urban lentic wetlands, and are absent from lotic wetlands. My findings indicate that the proportion of impervious cover at a scale of 250 metres around a wetland has the strongest impact on *P. regilla* occupancy and relative abundance, rendering all other factors relatively unimportant. I also demonstrate that the most supported models for both responses include variables representing multiple habitat relationships at multiple spatial scales. Factors that impact detection probability are identified and discussed, and *P. regilla* detection probability is estimated. I conclude Chapter 3 with considerations for habitat conservation and design and a discussion of possible motivations for such initiatives.

In Chapter 4, I outline general management recommendations based on my findings. I then discuss how my research can be applied to advance conservation of *P. regilla* and *R. aurora* in urbanizing regions. I conclude with recommendations for further research.

## 1.4 Study area

This study was conducted in Saanich, British Columbia, a 104 km$^2$ municipality in the heart of the Greater Victoria area of southern Vancouver Island (Figure 1.1). Saanich lies in the Coastal Douglas-fir biogeoclimatic zone, influenced by the rain shadow of the Olympic Mountains to the south and west, and the Salish Sea to the east. Winters are mild and wet (~ 500 mm precipitation) and summers are warm and dry (~ 100 mm precipitation) (Government of Canada 2018). Monthly average temperatures do not drop below 0°C (Nuszdorfer et al. 1991). Historically, Douglas-fir forest, interspersed with wetland and open prairie ecosystems, was the dominant land cover (Bjorkman & Vellend 2010). Historical marshes, vernal pools, streams, lakes, and wet meadows are thought to have supported high amphibian abundance (Purnima Govindarajulu, pers. comm.). Since European settlement, much of the landscape has been converted for agricultural and urban development; consequently, it is estimated that over 75% of historic wetlands and 95% of open prairie in the region have been lost (GOERT 2003; Cox & Cullington 2009). Present-day Saanich is situated within the second-most populous metropolitan area in the province. It is divided approximately equally into Rural Saanich and an Urban Containment, a zoning arrangement that has tempered ongoing and intensifying development pressures. Nevertheless, throughout Saanich, many remnant lakes, ponds, marshes, and streams, as well as constructed ponds and ditches, are impacted directly or indirectly by urban and rural development.

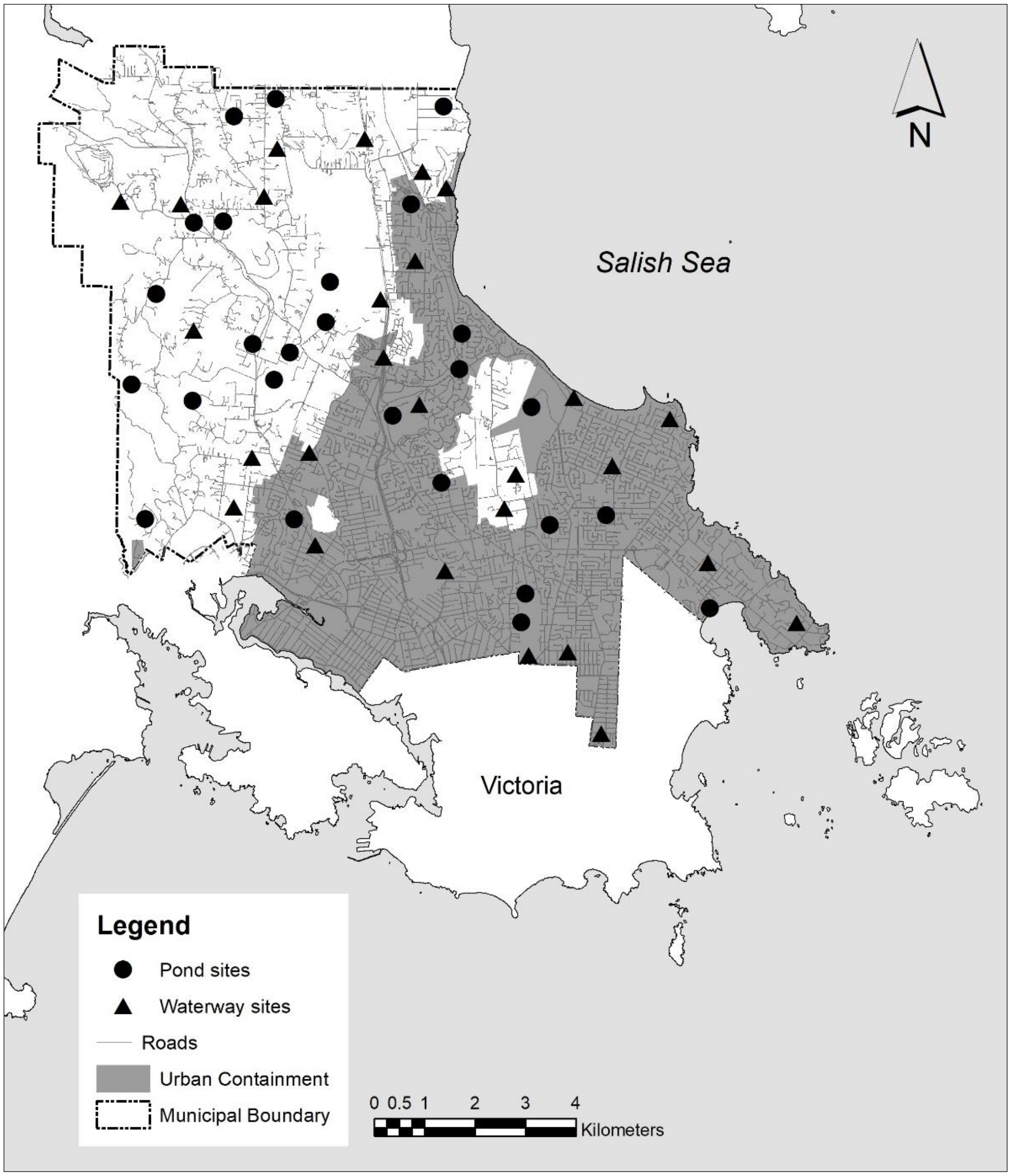

**Figure 1.1** Distribution of study sites throughout urban and rural Saanich, British Columbia. White polygons within the Urban Containment are rural "islands." Descriptions of study site selection are provided in Chapters 2 and 3.

# Chapter 2 Northern Red-legged Frog Auditory Survey and Assessment of Breeding Habitat in Urban and Rural Saanich, Vancouver Island

## 2.0 Abstract

This research was intended to facilitate the identification of potential northern red-legged frog (*Rana aurora*) habitat in the face of an expanding urban population and intensifying development pressures in the southern Vancouver Island region, as well as to help guide habitat restoration and enhancement activities. With the objectives of estimating occupancy and detectability, I conducted a repeat calling survey of 52 natural and constructed lentic and lotic wetlands in urban and rural Saanich during the *R. aurora* breeding season in 2017. I complemented these presence-absence surveys with measurements of habitat variables at the local (wetland) scale and within multiple nested landscape scales to investigate which habitat variables and scales of analysis best explain species occurrence.

*R. aurora* was absent from lotic sites and detected at only four of 26 lentic sites. Occupied sites included both natural and constructed ponds in both urban and rural contexts. Due to the small number of occurrences, occupancy, detectability, and species-habitat relationships could not be modeled. While the inferences that can been drawn from this study are limited, the similarities among occupied ponds are notable: *R. aurora* were present in ponds that had moderate aquatic vegetation cover and that were structurally connected to a large patch of forest. These observations support the findings of recent studies in Washington and Oregon. Thus, I add to the weight of evidence that *R. aurora* will select rural and urban ponds, including constructed ponds, as breeding sites but that their distribution in developed landscapes is limited primarily by the availability and connectivity of complementary terrestrial habitat.

The occurrence of *R. aurora* in fragmented, developed landscapes, including constructed ponds not intended as habitat, is indication of the potential for unconventional landscapes and novel habitats to contribute to regional species conservation. Linking protected area populations through constructed and restored habitats could promote metapopulations that are more resilient in the face of cumulative global threats to

amphibians. Further research on the ecology of *R. aurora* in an urban and rural context, including terrestrial habitat requirements and the permeability of the landscape to migration and dispersal, would advance creative and pragmatic conservation and habitat restoration initiatives for this species.

## 2.1 Introduction

The northern red-legged frog (*Rana aurora*) is a medium-sized frog belonging to the family Ranidae (COSEWIC 2015). Adults typically have a snout-vent length of 50-70 mm, though females may reach lengths of 100 mm (COSEWIC 2015; B.C. MOE 2018). *R. aurora* have gold-coloured eyes from which prominent dorsolateral folds extend down the sides of the back. Dorsally, *R. aurora* has smooth, brown or reddish-brown skin flecked with small, black spots. Ventrally, the species is characterized by distinctive transparent, pale red skin on its long hind legs. *R. aurora* only vocalize during the breeding season, when males make low, grunting underwater calls to attract females (Licht 1971).

It is estimated that one-third of the species' global population is found in Canada (B.C. MOE 2015), in the coastal lowlands of southwestern British Columbia including Vancouver Island, the Gulf Islands, and the adjacent mainland from Vancouver east to Hope (Blaustein et al. 1995a, COSEWIC 2015). *R. aurora*'s historic range, which extends south of the border along the Pacific coast to Baja California (Matsuda et al. 2006), overlaps heavily with regions of intensive urban and agricultural development and rapidly growing human populations. Widespread *R. aurora* declines (IUCN 2017) coincide with habitat loss and fragmentation, the introduction of non-native predators and competitors, and the emergence of diseases (Kiesecker & Blaustein 1997, 1998; Adams 1999; Kiesecker et al. 2001; Pearl et al. 2007; Hayes et al. 2008). In recognition of downward population trends and the species' vulnerability to a host of threats throughout its range, *R. aurora* is listed as a species of "Special Concern" in British Columbia (B.C. MOE 2015), Canada (COSEWIC 2015), and California (Thomson et al. 2016), and as "Sensitive" in Oregon (ODFW 2016).

Like other aquatic-breeding amphibians, *R. aurora* is sensitive to habitat degradation and fragmentation due to its complex habitat requirements. While the frog spends most of the year in riparian and upland terrestrial habitats, where it will forage, estivate, and overwinter, it must have access to suitable aquatic habitat during the breeding season. Aquatic environments provide the necessary habitat for oviposition, embryo and larval development, and the metamorphosis of juveniles prior to dispersal. In British Columbia, *R. aurora*'s breeding season occurs over two to three weeks in February and early March when adults, responding to temperature cues (Storm 1960), emerge from a state of torpor and migrate to permanent and seasonal aquatic habitats where they call to attract potential mates (Licht 1969; COSEWIC 2015). Identified breeding habitats include still or slow-flowing rivers, streams and ditches, temporary ponds, permanent water bodies, and marshes (Storm 1960; Licht 1969; Blaustein et al. 1995). For a wetland to be suitable breeding habitat, it must have the following basic requirements: standing water until at least June (Storm 1960, Guderyahn et al. 2016); circumneutral pH, low salinity, and low pollutant levels (Hayes et al. 2008; COSEWIC 2015); minimum water depth of 30 cm (COSEWIC 2015); low or no flow (< 5 cm/s) (Storm 1960; Hayes et al. 2008b); emergent or submerged vegetation (Storm 1960; Cary 2010); and at least partial sunlight exposure (Hayes et al. 2008; COSEWIC 2015).

Less is known about *R. aurora* movement and terrestrial habitat requirements outside of the breeding season. Because of its terrestrial habitat associations, *R. aurora* is strongly associated with mature forest ecosystems. Telemetry studies of *R. aurora* have demonstrated the use of habitats with a complex understory structure characterized by abundant woody debris and herbaceous vegetation cover (Haggard 2000), which may provide optimal moisture and temperature conditions in addition to protective cover, as well as the avoidance of newly regenerating clearcut patches under hot, dry conditions (Chan-McLeod 2003). Moreover, *R. aurora* may be more abundant in mature deciduous forests than coniferous forests (Gómez & Anthony 1996; Martin & McComb 2003). Because *R. aurora* spends most of the year in terrestrial environments hundreds and sometimes thousands of metres from its aquatic breeding and rearing habitat (COSEWIC 2015), it has been described as an umbrella species for aquatic-breeding amphibian conservation in the region (Hayes et al. 2008).

The typical home range size and migration and dispersal distances of *R. aurora*, even in intact habitats, are not well understood. A small number of studies have observed that *R. aurora* tend to remain in close proximity (270-312 m) of breeding sites (Haggard

2000; Shean 2002) and move less than 10 metres per day once they reach suitable terrestrial habitat (Chan-McLeod 2003). However, individuals are capable of moving hundreds of meters in a short timeframe; for example, radio-tagged *R. aurora* placed in various clearcut regeneration treatments moved more than 300 m over terrestrial habitat in 24 hours (Chan-McLeod 2003). Over a period of several months, Hayes et al. have documented adult *R. aurora* movements of up to 4.8 km (2007). Though there has been little research to confirm juvenile dispersal abilities, juvenile *R. aurora* have been captured up to 500 m from their natal wetland (as cited in COSEWIC 2015).

Given the species' association with forested habitats, its reliance on terrestrial-aquatic habitat complexes, and its large potential home range, developed landscapes have generally been considered unsuitable habitat for *R. aurora*. However, it may be possible for *R. aurora* populations to persist within urban and rural areas under certain conditions. Indeed, the possibility that urban and rural ecosystems are overlooked opportunities for wildlife conservation has prompted numerous ecological studies in recent years, including those with a focus on aquatic-breeding amphibians (e.g. Brand and Snodgrass 2010, Hamer and Parris 2011, da Silva et al. 2012). These studies have documented the use of urban and rural wetlands, including novel habitats such as ornamental ponds, agricultural ditches, and stormwater treatment ponds, by many amphibian species (e.g. Brand and Snodgrass 2010, Saarikivi et al. 2013). Furthermore, certain studies have demonstrated the potential for urban and rural habitats to support population abundance (Riley et al. 2005), species richness (Holzer 2014), and genetic diversity (Garcia-Gonzalez and Garcia-Vazquez 2012) similar to adjacent undeveloped areas.

Recently, researchers have begun to explore the potential for *R. aurora* persistence in developed landscapes. Holzer (2014) found that *R. aurora* were present in 30% of ponds surveyed in Portland, Oregon, despite the species being reported as absent from ~70% of historical sites in the greater Willamette Valley. Further north, Grand et al. (2017) observed *R. aurora* egg masses in 75% of wetlands surveyed in greater Seattle. These studies identified a positive relationship between *R. aurora* presence and abundance and forest metrics at coarser scales, such as forested perimeter around a wetland (Grand et al. 2017), connectivity to forest habitat (Grand et al. 2017), and the amount of forest cover on the surrounding landscape (Holzer 2014; Grand et al. 2017). Also, negative impacts of roads and impervious surfaces have been documented for *R. aurora* and other amphibians (e.g. Pillsbury and Miller 2008, Van Buskirk 2012). Holcomb (2012) found that *R. aurora* breeding effort in western Washington was significantly lower at sites with a high-traffic road within 400 m. Guderyahn et al. (2016) observed a significant negative impact of impervious surface cover on *R. aurora* at multiple scales in northwest Oregon.

To extend this investigation of the distribution and breeding habitat associations of *R. aurora* in urbanizing areas to British Columbia, I conducted a single season of presence-absence surveys in a mixed urban-rural landscape on southern Vancouver Island in 2017. The goals of this pilot study were to (1) determine whether *R. aurora* are using urban and rural wetlands in the region as potential breeding sites and, if so, (2) investigate relationships between site occupancy and local- and landscape-level habitat characteristics. Species distribution information can be used to inform habitat management and protection while species-habitat relationships can be used to predict habitat suitability and guide enhancement/restoration design. By identifying opportunities to protect, restore, or create habitat within the developed landscape matrix, it may be possible to manage populations of *R. aurora* within the developed landscape and facilitate connectivity of urban or rural populations with populations in undisturbed, protected areas.

## 2.2 Methods

### 2.2.1 Sampling design & site selection

I began the process of site selection by creating a current, detailed map of all identifiable freshwater habitat features, hereafter referred to as wetlands (UNESCO 2014), on the landscape using GIS data and a 2015 aerial orthophoto provided by the District of Saanich. Using ArcMap (ESRI 2017), I categorized wetlands as either ponds (lentic habitats, such as ponds, lakes, and flats) or waterways (lotic habitats, such as streams and ditches) and as either natural or constructed. I followed a stratified random design for initial site selection using the NOAA’s Sampling Design Tool for ArcGIS (NOAA 2013). Based on a literature review of movement behaviour and distances, I concluded that it is extremely unlikely that *R. aurora* would move a distance of 500 metres between ponds within the breeding season (2-3 week period; Grand et al. 2017); therefore, I programmed the Sampling Design Tool to generate an equal number of random points within urban and rural wetlands layers while keeping a minimum distance criteria of 500 metres between each point to ensure spatial independence (Petranka et al. 2004). The randomly selected wetlands were vetted in GIS using the 2015 aerial orthophoto. To facilitate comparative analyses, I selected an equal number of urban and rural, natural and constructed ponds and waterways.

Site suitability was confirmed on the ground in autumn 2016. The greatest uncertainty during site selection was whether waterways would have the 6-month hydroperiod necessary for egg survival and larval development (Storm 1960; Richter & Azous 2001; Guderyahn et al. 2016). I considered only streams and ditches of at least 100 m in length, with still water or low flow, water depth exceeding 15 cm, and a hydroperiod extending until at least midsummer. If a waterway did not have standing water at the time of site selection, a minimum channel depth of 0.5 m and the presence of hydrophytic vegetation (e.g. skunk cabbage, sedges, cattail; Cox & Cullington 2009) were used as indicators of suitability. Apart from minimum hydroperiod, there were no selection criteria for ponds. Final site selection was determined by whether access was granted by the private landowner or public park agency. Figure 1.1 shows the distribution of sample sites across the study area.

The total number of sites that could be sampled was primarily constrained by seasonal and diurnal calling period lengths, which determined the number of possible survey hours and sites that could be resampled by a single observer. In British Columbia, the breeding season of *R. aurora* typically begins in the last week of January or first week of February and lasts for a period of 2-3 weeks. As *R. aurora* are thought to chorus primarily during nighttime hours (Nelson et al. 2017a), I followed the call survey timing recommended by the North American Amphibian Monitoring Program, which is 30 minutes after sunset until 0100 hours (Weir & Mossman 2005). Most sampling methods detect the target species imperfectly, thereby underestimating species presence at a site (MacKenzie et al. 2006). To account for a probability of detection less than 1, I followed the standard occupancy study design described by MacKenzie and Royle (2005). An occupancy study design relies on initial estimates of occupancy and detection probabilities which are, in the absence of published estimates, based on knowledge and experience (MacKenzie et al. 2006). Most sites were estimated to have a probability of occupancy of 0.1, while detection probability was expected to vary greatly between wetland types

(Appendix A). Ditch sites, which had the lowest estimated probability of detection, required resampling seven times, while streams and pond sites required resampling five and two times, respectively (Appendix A). As all ditch sites were shallow enough that frogs were likely to be seen if not heard, I averaged the probability of detection between stream and pond sites for the initial study estimate. Thus, this study was designed with initial, assumed estimates of 0.1 for occupancy probability and 0.5 for detection probability (MacKenzie and Royle 2005; Appendix A). Using these values, I calculated that sites would need to be resampled three times to yield the most precise estimate of occupancy possible: a standard error for occupancy of 0.05 and a probability of detecting the species at least once of 0.88 (MacKenzie and Royle 2005: 1110; Appendix B). Thus, the maximum number of sites that could be resampled three times by a single observer during the available survey hours was fifty-seven[3]. Fifty-six sites were selected to allow an equal number of urban and rural wetlands to be surveyed.

### 2.2.2 Site characterization

*Local characteristics*

Between January and May 2017, prior to the onset of the summer drought and substantial lowering of water level, surveys were opportunistically conducted at each site to collect data on 12 local habitat variables that have been recognized for their importance in explaining either *R. aurora* occurrence or general ranid frog occurrence in aquatic habitat (Table 2.1). I followed the provincial government's *Interim Hygiene Protocols for Amphibian Field Staff and Researchers* to reduce the risk of disease transmission between sample sites (B.C. MOE 2008). With the exception of predator surveys, all local variables were measured at multiple points and then averaged: for ponds, data were collected at the approximate cardinal direction points (north, east, south, and west) around the shore, using a 1 $m^2$ quadrat frame spanning 0-1 meters from the shore; for waterway transects, data were collected from within the 1 $m^2$ quadrat frame placed at 0 m, 50 m, and 100 m points along the 100-meter transect. At all measurement points, location data were collected using a

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[3] Based on an estimate of 150 survey hours and 52 minutes per survey, including travel and equipment disinfection between sites.

Garmin GPSMAP® 60CSx handheld GPS unit. Collection of more detailed water chemistry data was beyond the scope of this study. Flow was measured at four representative waterway sites using a Swoffer 3000 flow meter and was found on average to be below the tolerance of 5 cm/s for *R. aurora* oviposition microhabitat (Hayes et al. 2008).

**Table 2.1** Local habitat variables considered, their definition and measurement method, and the literature that supports their inclusion.

| **Habitat variable** | **Definition/Measurement Method** | **Reference** |
|---|---|---|
| Aquatic footprint | Total area ($m^2$) of surface water at the site. For ponds, calculated in GIS using a 2015 aerial photo; for waterway transects, calculated as the average width multiplied by the length (100 m). | Babbitt 2005,<br>Pillsbury and Miller 2008 |
| Distance to tree cover | Distance (m) to the nearest patch of 3 or more trees with overlapping canopies, measured with a field tape (< 10 m range) or Nikon® Forestry 550 laser rangefinder (10-500 m range). | Chan-McLeod and Moy 2007 |
| Canopy density | Percent cover of canopy over the wetland, estimated with a spherical densiometer as described by Denton and Richter (2013). | Licht 1971,<br>Rezansoff and Tripp 2010,<br>Adams et al. 2011 |
| Aquatic vegetation cover | Percent cover of emergent and submerged aquatic vegetation in the littoral zone, visually estimated with the aid of a vegetation cover comparison chart (Appendix C). | Adams et al. 2011,<br>Guderyahn et al. 2016 |
| Water depth | Measured in cm at one metre from the shore/banks for ponds and for waterways wider than 2 m. Measured at the midpoint of the channel for waterways narrower than 2 m. | Storm 1960,<br>Guderyahn et al. 2016 |
| Shore/bank slope | Angle of pond margin or stream/ditch bank. For ponds, equivalent to the inverse of water depth/100. For waterways, average of angles measured at both banks at 0, 50, and 100 m along the transect using a clinometer (Gordon 2004). | Adams 1999 |
| Nitrate/nitrite concentration | Gauged using WaterWorks™ Nitrate/Nitrite Nitrogen colormetric test strips. | Marco et al. 1999,<br>Holzer 2014 |
| pH | Measurements were taken with a handheld water quality meter (Oakton® PC Testr 35). | Pope et al. 2000 |
| Conductivity | Measurements (µS) were taken with a handheld water quality meter (Oakton® PC Testr 35). | Hamer and Parris 2011 |
| Hydroperiod | Permanent or temporary, as determined by a site visit during the dry season. | Rubbo and Kiesecker 2005,<br>Guderyahn et al. 2016 |

| | | |
|---|---|---|
| Fish presence/absence | Presence or absence of non-native predatory fish, determined by incidental observation or minnow trap survey. | Hecnar and M'Closkey 1997,<br>Kiesecker and Blaustein 1998,<br>Pillsbury and Miller 2008,<br>Guderyahn et al. 2016 |
| American bullfrog presence/absence | Presence or absence of the non-native, invasive American bullfrog, determined by incidental observation during auditory surveys (bullfrogs rest at the water's surface and have a yellow-green eye glow upon illumination by a flashlight or headlamp) or by minnow trap survey. | Kiesecker and Blaustein 1997, 1998;<br>Govindarajulu 2004 |

To determine the presence of non-native fish and American bullfrogs within potential tadpole habitat at permanent pond sites, I conducted minnow trap surveys in June and July, 2017. Minnow trap surveys were not conducted at waterway sites because non-native fish and bullfrogs are known only to breed in permanent ponds. Minnow traps were deployed only at pond sites where American bullfrogs and non-native fish had not previously been detected during preceding habitat and auditory surveys. If no non-native fish or bullfrogs were observed during a quick visual survey from the shore, minnow traps were deployed in the late afternoon (16:30-18:30) and left overnight. I used galvanized steel wire minnow traps (6 mm mesh) 0.5 m in length and 0.3 m in diameter tapering to a 3-5 cm-diameter entrance hole at either end. The number of traps used at a site was proportional to pond area, and ranged from 1-3. Though unbaited (Adams et al. 1997; BC MELP 1998), traps were positioned to increase the likelihood of fish capture: traps were randomly placed along the shores with the greatest evening sunlight exposure and oriented parallel with edges of patches of aquatic vegetation. To ensure the safety of trapped animals, traps were tethered within 2 m of the shore and kept partly afloat using a foam float (Figure 2.1). Traps were retrieved the following morning before 9:00 to prevent temperature stress to trapped animals. The contents of the trap were quickly transferred to a bucket of local pond water and any captured individuals were identified, photographed, and released alive at the location of capture. Non-native fish and bullfrogs were determined to be present if they were found in the minnow traps or if they were otherwise detected (visually or aurally) at any time during the field season.

**Figure 2.1** Deployed minnow trap oriented parallel to littoral vegetation and kept partly submerged with foam float.

### *Landscape characteristics*

A literature review identified several landscape characteristics and associated scales of analysis that may explain *R. aurora* occurrence. Using GIS (ArcMap version 10.5.1, ESRI) to analyze spatial data provided by the District of Saanich and the Capital Regional District, I measured five characteristics within eight nested buffers around each site; these included: number of ponds (Rubbo & Kiesecker 2005), total pond area (Houlahan & Findlay 2003), percent tree cover (Rubbo & Kiesecker 2005), percent impervious surface cover (Guderyahn et al. 2016), and road density (Houlahan & Findlay 2003). A high-resolution aerial orthophoto enabled the detection, and inclusion, of ponds as small as 2 $m^2$. The eight scales of analysis ranged from the scale of immediate riparian habitat to a scale approximating the maximum within-season movement distance expected in a fragmented landscape: 50, 100, 150, 250, 500, 1000, 1500, and 2000 meters. I measured additional landscape characteristics that were not scale-dependent; these included: distance to nearest pond (Petranka & Holbrook 2006), distance to nearest forest patch (Guderyahn et al. 2016), and area of nearest forest patch (Holcomb 2012; Grand et al. 2017). The smallest forest patch had an area of 2705 m$^2$, which is large enough to serve as a stepping stone or short-term refuge (but highly unlikely to provide adequate long-term habitat) (Chan-McLeod & Moy 2007).

### 2.2.3 Auditory surveys

Auditory surveys for chorusing males were conducted during the breeding season, between February 1 and March 22, 2017. The breeding calls of *R. aurora* are made underwater, therefore surveys were conducted with the aid of a handheld hydrophone (DE 200, DolphinEar Hydrophones). A survey consisted of listening for 5 minutes at 1-4 randomly selected, approximately evenly spaced locations near the water's edge (Dorcas et al. 2010). For pond sites, the number of listening points was proportional to area. Listening points were spaced ≥ 50 m apart and 0.5-10 m from the shoreline depending on the extent of shoreline vegetation. Along each transect, waterway sites were surveyed from three listening points located at approximately 0, 50, and 100 metres. The exact listening points were selected to optimize the range of detection of the omnidirectional hydrophone (which increases with increasing water depth, decreasing flow, and decreasing density of aquatic vegetation and other soundwave barriers). More listening points would have been preferable had time permitted; however, given the sensitivity of the hydrophone to *R. aurora* call frequencies (commonly 450-1300 Hz) and range at which *R. aurora* calls can carry through water (> 9 m radius) (Licht 1969), the number of listening points should be sufficient to sample the area surveyed. To minimize effects of any seasonal or temporal anomalies that were unaccounted for, sites were not resampled within a week of the previous survey and sites were not revisited at the same time of night.

Environmental data were collected at the time of each survey, to be used in models of detectability. Sampling variables included start and end time, air temperature, water temperature, wind speed, cloud cover, and precipitation (Appendix D). Any interference by environmental (e.g. rain drops) or anthropogenic noise (e.g. road traffic) was also noted.

### 2.2.4 Statistical analysis

I used the Mann-Whitney U Test in R (Version 3.4.3; R Core Team 2017) to test for significant differences in local and landscape variables between urban and rural ponds and between natural and constructed ponds, as all variables were non-normally distributed. It was intended that site-occupancy relationships and detectability would be analysed using an occupancy modeling framework and implemented in R using the package 'unmarked' (Fiske & Chandler 2011). However, complex statistical analyses could not be conducted because of the small number of occurrences. Instead, I used the program PRESENCE (version 2.12.10; Hines 2006) to estimate northern red-legged frog detection probability based on detection history alone (i.e., without inclusion of detection covariates).

## 2.3 Results

### 2.3.1 Local and landscape characteristics of occupied ponds

I detected *R. aurora* at four of the 26 ponds sampled. *R. aurora* were not detected at any waterway sites sampled in this study, which included 13 urban and 13 rural randomly selected transects representing a range of habitats from undisturbed forest streams, to marshy floodplains, to highly channelized streams, to park and roadside ditches. As the data were readily available, I investigated whether the non-detection of *R. aurora* at waterways could be explained by within-wetland differences between waterways and ponds by testing for significant differences between the two wetland types. Waterways were significantly shallower and shadier, with significantly higher conductivity, than ponds (Appendix E). Although the difference in aquatic vegetation cover between waterways and ponds was not significant, mean aquatic vegetation cover was 10% lower among waterway sites (Appendix E). Due to these significant differences, I hypothesized that the non-detection of *R. aurora* at waterway sites may have been due to differences in aquatic habitat alone and did not pursue additional landscape-scale analyses of waterways.

*R. aurora* were detected in one urban pond and three rural ponds, including one constructed pond. The local and landscape variables associated with occupied and unoccupied ponds, as well as the different pond types, are summarized in Table 2.2 and 2.3. There were few significant differences between urban and rural ponds and between natural and constructed ponds at the local (pond) scale (Table 2.2). Tests for statistically significant differences between occupied and unoccupied ponds were not possible due to the small number of detections. All occupied ponds had a minimum aquatic vegetation cover of 30% (Figure 2.2). There were no other outstanding similarities among occupied ponds: measurements of aquatic footprint, water depth, shore slope, canopy density, distance to tree cover, conductivity, and the occurrence of one or both types of predators varied widely (Table 2.2). With one exception, pH and nitrate/nitrite values were similar between occupied and unoccupied ponds (Table 2.2).

**Table 2.2** Descriptive statistics for local variables measured at pond sites. All categories are subsets of the total sample population (n=26). Values represent median (range) unless otherwise noted. Bold values marked with an asterisk indicate a statistically significant difference between pond categories (urban vs rural, natural vs constructed), as determined by a Mann-Whitney U-test ($p<0.05$).

| **Variable** | **Occupied (n=4)** | **Unoccupied (n=22)** | **Urban (n=12)** | **Rural (n=14)** | **Natural (n=12)** | **Constructed (n=14)** |
|---|---|---|---|---|---|---|
| Aquatic footprint ($m^2$) | 21,342 (4,582–75,236) | 1,293 (36-84,266) | 1,983 (36-32,226) | 4383 (63-84,266) | **5547 (344-84,266)*** | **876 (36-10,458)*** |
| Distance to tree cover (m) | 21(1.5-67) | 7.8(0-501) | 8.2(0-501) | 7.8(0.63-78) | 4.7(0.56-37) | 13(0-501) |
| Canopy density (%) | 34(0.16-85) | 67(0.16-96) | 76(0.16-96) | 61(0.16-92) | 69(0.16-95) | 33(0.16-96) |
| Aquatic veg. cover (%) | 42(30-63) | 21(0.5-74) | 21(0.5-74) | 39(9-74) | 21(6-69) | 39(0.5-74) |
| Water depth (cm) | 30(16-55) | 37(15-68) | 27(15-68) | 41(20-63) | **25(15-57)*** | **46(25-68)*** |
| Shore slope | 0.30 (0.16-0.55) | 0.37 (0.15-0.68) | 0.27 (0.15-0.68) | 0.41 (0.20-0.63) | 0.25 (0.15-0.57) | 0.46 (0.25-0.68) |
| Nitrate/nitrite concentration | 0(0)/0(0) | 0(0-22)/0(0) | 0(0)/0(0) | 0(0-22)/0(0) | 0(0-22)/0(0) | 0(0-2.2)/0(0) |
| pH | 8.0(7.2-8.7) | 7.8(6.6-8.5) | 7.9(7.2-8.7) | 7.7(6.6-8.5) | 7.7(6.6-8.7) | 7.8(6.9-8.4) |
| Conductivity (µS) | 254 (115-470) | 244(76-505) | 340(76-505) | 208(115-383) | 232(76-505) | 253(127-368) |
| Hydroperiod (temp/permanent) | 1/3 | 2/20 | 3/9 | 0/14 | 1/11 | 2/12 |
| Non-native fish (present/absent) | 2/2 | 7/15 | 2/10 | 7/7 | 5/7 | 4/10 |
| American bullfrog (present/absent) | 3/1 | 14/8 | **4/8*** | **13/1*** | 8/4 | 9/5 |

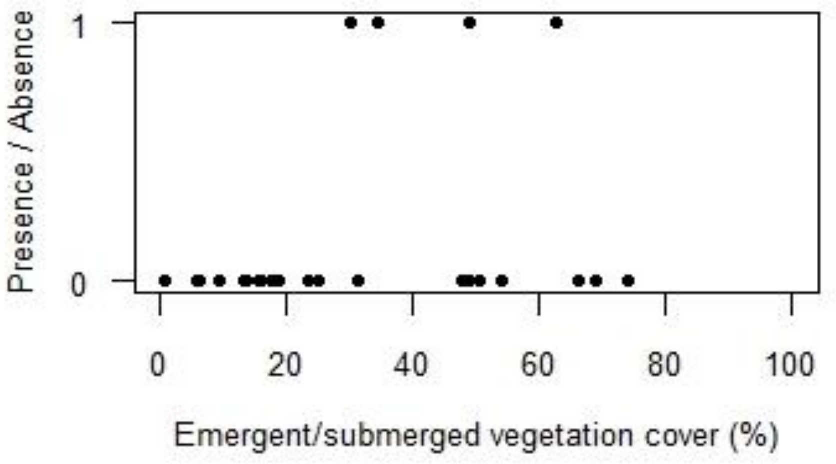

**Figure 2.2** Percent cover of emergent/submerged vegetation in ponds in which Rana aurora was present (1) and not detected (0). Note that the sample maximum is 74% (n=26).

Occupied ponds shared more similarities at landscape scales. Occupied ponds were located adjacent, or in close proximity, to a forest patch on the scale of thousands or millions of square metres (Table 2.3). Occupied ponds were also located within 200 m of another pond (Table 2.3). With the exception of the urban pond, *R. aurora* were detected at ponds in areas of high tree cover (≥ 48%) and low impervious surface cover (<13%).

Many statistically significant differences in landscape variables emerged between urban and rural ponds, particularly at scales larger than 50 m (Table 2.3). Though the difference in proximity and size of the nearest forest patch was not significant, tree cover was significantly higher around rural ponds at many scales (Table 2.3). Conversely, many of the statistically significant differences between natural and constructed ponds occurred at scales within 250 m (Table 2.3). For example, natural ponds were closer to a larger patch of forest than constructed ponds (Table 2.3).

**Table 2.3** Descriptive statistics for landscape variables measured at occupied and unoccupied ponds, urban and rural ponds, and natural and constructed ponds. All categories are subsets of the total sample population (n=26). Three of eight landscape scales are displayed. Bold values marked with (*) indicate a statistically significant difference between pond categories (urban vs rural, natural vs constructed), as determined by a Mann-Whitney U-test ($p<0.05$).

| **Variable** | **Occupied (n=4)** | **Unoccupied (n=22)** | **Urban (n=12)** | **Rural (n=14)** | **Natural (n=12)** | **Constructed (n=14)** |
|---|---|---|---|---|---|---|
| Distance to nearest pond (m) | 93(63-159) | 87(6-621) | 157(6-621) | 83(7-274) | 44(6-507) | 169(8-621) |
| Distance to nearest forest (m) | 0(0-93) | 11(0-780) | 9(0-780) | 2(0-116) | **0(0-239)*** | **47(0-780)*** |
| Nearest forest area ($m^2$) | 452,353(137,716-1,327,039) | 31,269(2705-1,293,563) | 31,269(2705-1,293,563) | 39,980(3211-1,327,039) | **167,126(6,523-1,327,039)*** | **20,730(2705-708,169)*** |
| Road density (50/ 500/2000 m) | 0.002(0-0.009)/ 0.002($3.0e^{-4}$-0.01)/ 0.004 (0.002-0.009) | 0(0-0.027)/ 0.006(0.008-0.01)/ 0.005(0.002-0.01) | **0.004(0-0.008)*/ 0.009(0.007-0.01)*/ 0.009(0.005-0.01)*** | **0(0-0.01)*/ 0.003($9.0e^{-4}$-0.004)*/ 0.003(0.002-0.005)*** | 0(0-0.015)/ 0.005(0.002-0.012)/ 0.005(0.002-0.011) | 0(0-0.03)/ 0.006($3.0e^{-4}$-0.011)/ 0.005(0.003-0.012) |
| Number of ponds (50/500/ 2000 m) | 1(1)/19(6-23)/ 109(70-147) | 1(1-6)/ 11(1-21)/ 99(37-206) | 1(1-6)/ **8(1-12)*/ 48 (37-160)*** | 1(1-3)/ **18(3-23)*/ 134(74-206)*** | **2(1-6)***/ 12(1-23)/ 116(44-156) | **1(1-2)***/ 11(1-21)/ 87(37-206) |
| Pond cover (50/500/2000 m) (%) | 29(16-53)/ 5(3-8)/ 4(3-6) | 9(0.39-59)/ 1(0.005-42)/ 2(0.1-17) | 11(0.39-36)/ **0.8(0.006-2.8)*/ 0.71(0.1-17)*** | 17(0.86-58)/ **2.9(0.21-42)*/ 6(1-16)*** | **21(2.7-58)***/ 3.7(0.13-42)/ 3.1(0.19-16) | **8(0.39-21)***/ 1(0.005-3.3)/ 2(0.1-17) |
| Tree cover (50/500/2000 m) (%) | 48(37-73)/ 60(23-73)/ 59(29-73) | 36(5-83)/ 34(9-80)/ 41(18-73) | 34(7-83)/ **25(9-80)*/ 28(18-42)*** | 47(5-73)/ **47(27-73)*/ 53(24-73)*** | **52(19-83)***/ 43(23-80)/ 44(20-73) | **32(5-62)***/ 28(9-61)/ 37(18-66) |
| Impervious surface cover (50/500/2000 m) (%) | 7.5(0-13)/ 6.5(2-34)/ 8.5(3-26) | 9.5(0-65)/ 11(0-42)/ 13 (3-41) | **17(0-65)*/ 28(0-42)*/ 27(13-41)*** | **5(0-29)*/ 6(1-12)*/ 7(3-12)*** | **3(0-34)***/ 6(0-37)/ 12(3-37) | **17(0-65)***/ 16(1-42)/ 13(5-41) |

### 2.3.2 Detection histories

The detection histories from auditory surveys at occupied ponds were highly variable in both the number and sequence of positive detections (Table 2.4). Based on this detection history, and assuming a constant detection probability across sites and surveys, I estimated detection probability to be 0.28 (SE 0.21). At three sites, breeding calls were detected with the hydrophone during one or more surveys. At one site, however, breeding calls were not detected during auditory surveys at all; rather, *R. aurora* was later confirmed as present when a tadpole was captured in a minnow trap in July (Figure 2.3). The number of positive detections did not vary with pond type. No calls were heard before February 17th and no calls were heard when the water temperature at the start time of the survey was below 5.3°C (Table 2.4).

**Table 2.4** Detection histories of *Rana aurora* at occupied sites.

| Site | Survey | Detection | Date | Water temp. at start-end time (°C) | Pond type |
|---|---|---|---|---|---|
| 1 | 1 | 0 | Feb. 1, 2017 | 2.3 | Rural, constructed |
| | 2 | 1 | Feb. 23, 2017 | 6.1-2.6 | |
| | 3 | 1 | Mar. 7, 2017 | 5.3-4.2 | |
| 2 | 1 | 0 | Feb. 1, 2017 | 0.2 | Rural, natural |
| | 2 | 0 | Feb. 23, 2017 | 4.2-2.5 | |
| | 3 | 1 | Mar. 14, 2017 | 8.4-8.0 | |
| 3 | 1 | 1 | Feb. 17, 2017 | 7.7-7.4 | Urban, natural |
| | 2 | 0 | Feb. 27, 2017 | 1.2-0.7 | |
| | 3 | 0 | Mar. 13 2017 | 9.1-9.0 | |
| 4* | 1 | 0 | Feb. 13, 2017 | 3.3 | Rural, natural |
| | 2 | 0 | Feb. 26, 2017 | 4.6 | |
| | 3 | 0 | Mar. 16, 2017 | 8.5-7.5 | |

* *R. aurora* presence was later confirmed by minnow trap survey (a tadpole was live-captured).

**Figure 2.3** *Rana aurora* tadpole, live-captured at a site at which breeding calls had not been detected by auditory surveys.

## 2.4 Discussion

This research demonstrated that *R. aurora*, though rare, can occur in ponds in both urban and rural areas on southern Vancouver Island, including constructed ponds. The small number of *R. aurora* occurrences prevents any direct inferences about species-habitat relationships, occupancy, or detectability. Nevertheless, the results of this study provide further support to the findings of other researchers that *R. aurora* will use both constructed ponds and ponds in a developed landscape as breeding habitat under certain conditions (Hayes et al. 2008; Holzer 2014; Guderyahn et al. 2016). Specifically, *R. aurora* occurrence appears to be driven primarily by the size, proximity, and connectedness of complementary terrestrial habitat and secondarily by the availability of oviposition sites at the pond scale. Another important finding of this study is the apparent absence of *R. aurora* from all waterway sites sampled, regardless of associated landscape conditions. This may be due to a failure of the sampling design, or to the unsuitability of waterways in the developed landscape as breeding habitat for *R. aurora*, or because *R. aurora* preferentially select lentic habitat where population density is low and such habitat is available. Finally, I demonstrate the importance of using multiple means of detecting *R. aurora* instead of relying on auditory surveys alone.

### 2.4.1 Potential causes of non-detection at waterway sites

The most unexpected outcome of this study was the absence of *R. aurora* from all waterway transects sampled, which reduced the effective sample size from 52 to 26. The earliest accounts of *R. aurora* breeding site selection describe the use of slow flowing streams and rivers (Storm 1960; Licht 1969, 1974) and these primary sources are cited in the most recent government reports on the species (e.g. COSEWIC 2015). If the non-detections in this study represent true absences, the most likely explanation is that the waterways were too shallow to be suitable for *R. aurora*: average waterway depth ranged from 3-80 cm and more than half of the sites did not reach the minimum oviposition depth of 15 cm, as described by Storm (1960) and others, at the time of measurement. Furthermore, I observed a positive relationship between waterway depth and flow, suggesting that suitably deep waterways experience unsuitably high flow. In either case, waterway depth likely fluctuated widely during the survey period and may not be well-represented by my one-time measurement.

There are three additional reasons why waterways in this region may not be suitable breeding sites for *R. aurora*. First, water levels may fluctuate widely due to high surface water runoff from impervious surfaces, stranding eggs (Richter & Azous 2001; Hayes et al. 2008). Second, in the short term, high volumes of stormflow can dislodge egg masses (Hayes et al. 2008) and hamper the ability of juveniles and even adults to maintain their position in otherwise suitable microhabitats; in the long term, high stormflow can alter stream geomorphology with impacts on habitat (Paul & Meyer 2008). Third, urban and rural waterways have been shown to transport elevated loads of fertilizers, metals, pesticides, and other pollutants (Paul & Meyer 2008); thus, streams in the developed landscape can become a toxic environment for *R. aurora* and other amphibians. Though a thorough water quality assessment was not within the scope of this study, I measured the greatest nitrate/nitrite concentrations and highest conductivity levels at waterway sites (Appendix E).

Alternatively, the non-detections may represent false absences. If *R. aurora* does indeed breed in any of the waterways sampled, it is possible that the species went undetected. The depth of waterway transects sampled, which averaged 21.3 cm, may have been too shallow for the hydrophone to effectively detect calls. Or, calls may also not have been detected because of noise interference: ditches were located along roads with associated traffic noise and streams often generated ambient noise through water flow over substrates such as rocks or through structures such as culverts (which amplified sounds). However, as water flow (ambient noise) was generally low across sites and anthropogenic noise was inconsistent across repeat surveys, this latter explanation is not likely. It is also possible that *R. aurora* breeds in Saanich waterways but it is distributed in such low densities that a random sample of 26 sites (9 sites if only those waterways with > 15 cm average depth are included) was insufficient to detect its presence in the study area—or that a 100-metre transect was too small to constitute a representative sample of a waterway.

### 2.4.2 Within-pond habitat considerations

Where the availability and connectivity of terrestrial habitat meets the requirements of *R. aurora* at landscape scales, the species' occurrence in a given pond will depend on local variables. Of the 12 local habitat variables measured in this study, only a possible association with aquatic vegetation cover was indicated. Other studies have identified aquatic vegetation as an important local factor driving *R. aurora* occurrence. For example, Holzer (2014) found that amphibian species richness in ponds in Portland, Oregon, was best predicted by aquatic vegetation cover. In Humboldt County, California, Cary (2010) found that *R. aurora* egg masses occurred at significantly greater densities in ponds with high emergent and floating vegetation cover. Richter and Azous (2001) asserted that the most important local habitat feature for the suite of native aquatic-breeding amphibians in King County, Washington, was the zone of emergent vegetation. This relationship is easily explained: *R. aurora* attach their egg masses to a submerged support and have demonstrated a preference for stiff, vertical stems of emergent or submerged vegetation (Storm 1960), though use of floating vegetation (Cary 2010) and woody debris (Govindarajulu, pers. comm.) has also been observed. The more stable the aquatic vegetation, the greater the chance of survival of embryos (Licht 1974). As the amount of vegetation cover increases, so too does the availability of oviposition sites as well as the amount of protective cover when the pond becomes a nursery to hatched tadpoles.

This study's small sample size and even smaller number of detections explain the failure to detect a pattern between species presence and other local habitat variables. It is highly likely that water quality is a limiting factor for *R. aurora* in developed landscapes, due to increased runoff and inputs of fertilizers, pesticides, road salt, metals, and other pollutants. In their experimental study of the impacts of nitrate and nitrite concentrations on amphibian larvae, Marco et al. (1999) found that two species sympatric with *R. aurora* exhibited negative physiological responses to increasing nitrate concentrations, with a marked increase in mortality above 2 mg $NO_3$/L (though *R. aurora* was not tested). This same study demonstrated sensitivity of *R. aurora* larvae to nitrite, with lethal concentrations reached at < 2 mg $NO_2$/L. Sub-lethal concentrations of nitrite reduced feeding and swimming activity and caused disequilibrium, physical abnormalities, and paralysis among *R. aurora* (Marco et al. 1999). Similarly, elevated conductivity may have deleterious effects on *R. aurora*, as it can interfere with the maintenance of water and ion balance across the skin (Ultsch et al. 1999). While responses to conductivity are species-specific and the conductivity tolerance of *R. aurora* has not been investigated, field- and lab-based studies of other species of *Rana* have demonstrated negative behavioural and physiological responses to increasing conductivity (Dougherty & Smith 2006; Sanzo & Hecnar 2006; Karraker et al. 2008), including on survival once conductivity levels reached 2000-3000 µS. While the conductivity and nitrate concentration measurements taken at the ponds sampled in this study are likely within the tolerance of *R. aurora* (Table 2.2), this may not be the case in other urban and rural wetlands and other regions. Further research is needed to identify the species' pollutant tolerances so that inputs can be mitigated against in ponds managed for *R. aurora*.

Other local variables, including aquatic footprint, hydroperiod, shore slope, water depth at 1 meter, water pH, canopy cover, and the presence of American bullfrogs and non-native fish predators, ranged widely between occupied ponds, suggesting, first, that conditions were within the tolerance of *R. aurora* and, second, that *R. aurora* has a wide range of tolerance for these variables. While it is possible that a sufficiently large sample size would reveal further species-habitat relationships at the local scale, others have also failed to detect a relationship between *R. aurora* occurrence and aquatic footprint (Richter & Azous 1995, 2001; Grand et al. 2017), hydroperiod (Holzer 2014), and American bullfrog occurrence (Kiesecker & Blaustein 1998; Pearl et al. 2005; Holzer 2014; Grand et al. 2017). There is greater disagreement over whether non-native fish predators have a direct negative impact on *R. aurora* occurrence: some studies failed to detect a relationship (e.g. Kiesecker and Blaustein 1998, Cary 2010, Adams et al. 2011, Grand et al. 2017) while others detected a negative relationship (e.g. Pearl et al. 2005; Rowe and Garcia 2014; and Guderyahn et al. 2016). It is likely that complex interactions between fish, other invasive predators, and the environment confound consensus on the impacts of non-native fish on *R. aurora*. Then again, it is possible that life history characteristics, such as the short duration of aquatic habitat use by adults and anti-predator behaviour developed in response to native fish predators, allow *R. aurora* to co-occur with non-native fish predators despite increased mortality from predation.

### 2.4.3 A case for created ponds

Another local factor that does not appear to influence breeding pond use by *R. aurora* is pond origin; that is, whether a pond is natural or constructed. The occupied constructed pond in this study had high littoral zone vegetation cover (63%), an average depth at 1 m of 55 cm, and no nitrate/nitrite pollution. Water pH was relatively high (8.4), but within the tolerance of *R. aurora* (Hayes et al. 2008). Conductivity was 368 µS, also likely within the tolerance of *R. aurora*. The pond had a permanent hydroperiod and both bullfrogs and non-native fish were present. The forest patch neighbouring the occupied constructed pond was located less than 100 m away and was the third-largest neighbouring forest patch among the ponds sampled. Moreover, the permeability of the intervening landscape can be assumed to be high because impervious surface cover within 100 m of the pond was very low (11%), there were no road barriers[4] between the pond and the forest patch, and road density was zero within 250 m of the pond.

While no constructed ponds sampled in this study were managed to provide amphibian habitat, my measurements indicate that constructed ponds had developed local characteristics similar to relict natural ponds over time. Indeed, I found that aquatic footprint and depth at 1 m were the only variables that differed significantly between natural and constructed ponds, and although the depth of constructed pond margins tended to be greater (Table 2.2), even the deepest littoral zone (68 cm) encountered at a constructed

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[4] However, a single-lane gravel road used only by golf carts does run between the occupied pond and the forest.

pond was still well within the range of depths documented for *R. aurora* oviposition (Licht 1971; Cary 2010). Furthermore, pond size is not known to limit *R. aurora* breeding activity; the species is known to breed in small seasonal pools and even potholes (Blaustein et al. 1995), provided there is a sufficient hydroperiod to permit tadpoles to complete metamorphosis.

The use of constructed ponds by aquatic-breeding amphibians is well documented (Simon et al. 2009; Shulse et al. 2010; Saarikivi et al. 2013), but responses are thought to be species-specific (Brown et al. 2012). The case of constructed pond use in this study adds to the weight of evidence that *R. aurora* do not discriminate between constructed and natural ponds when selecting breeding habitat (Cary 2010; Holzer 2014; Guderyahn et al. 2016). Of course, one would not expect a frog to select habitat based on a categorical difference of origin, but rather on the local- and landscape-scale features that support necessary life history functions such as breeding, oviposition, embryo and larva development, survival of metamorphosed individuals, migration, and dispersal. I suggest that there were fewer *R. aurora* detections at constructed ponds not because of local habitat features, which were similar to natural ponds (Table 2.2), but because, like urban ponds, constructed ponds tended to be more isolated from suitable terrestrial habitat and because neighbouring forest habitats tended to be smaller—possibly too small to sustain a local population. There is considerable evidence to support the creation of ponds as a conservation measure for *R. aurora*. However, it is clear that landscape conditions must be met for created ponds to be colonized and used to support *R. aurora* breeding activity over the long term.

### 2.4.4 Terrestrial habitat availability and connectivity

Each of the four occupied ponds was located adjacent to, or within 100 metres of, a patch of forest, suggesting that the availability of terrestrial habitat within close proximity of a pond is a determining factor for *R. aurora* in a developed landscape. This observation is consistent with the results of other studies, which have identified a negative relationship between *R. aurora* occurrence and the distance to the nearest forest patch (Guderyahn et al. 2016) and a positive relationship between *R. aurora* egg mass abundance and adjacent forest patch size (Holcomb 2012). Mathias (2008) recommended a minimum forest patch size of 2,000,000 m$^2$ to support functional connectivity for *R. aurora* in an urbanizing landscape. However, I detected *R. aurora* in a pond complemented by a forest patch of 130,000 m$^2$. This may be because forest patches with a width of over 400 metres provide core habitat that is free of detrimental edge effects like lower relative humidity, reduced soil moisture, and increased solar radiation, which are known to penetrate > 200 m into the forest (Chen et al. 1992, 1995; Chan-McLeod & Moy 2007). While forest patches of this size may provide a hospitable climate, their ability to provide the foraging opportunities and diversity of microhabitats required to support sustainable populations of *R. aurora* is unclear. Further investigation is needed into the minimum forest patch size that will support *R. aurora* in a developed landscape. In any case, the positive relationship between *R. aurora* occurrence and abundance and neighbouring forest patch size reflects the importance of protecting, and even expanding on, relict forest patches in a developing landscape if it is to support *R. aurora*.

In addition to the size of the nearest forest patch, the amount of tree cover on the landscape also appears to be a determining factor for *R. aurora* occurrence. I found that occupied rural ponds were surrounded by a minimum of 37% tree cover at scales of 50-250 m and 50% tree cover at scales of 500 m and larger. The urban occupied pond was surrounded by over 40% tree cover within a range of 100 m, above which percent tree cover declined and remained at approximately 25%. These observations support the more robust inferences of other landscape-scale studies of *R. aurora*, which have identified significant positive relationships between *R. aurora* occurrence and/or abundance and forest cover. Grand et al. (2017) and Holzer (2014) found that percent forest cover was a strong predictor of both *R. aurora* occurrence and abundance at scales of 5 km and 1 km, respectively. Ostergaard et al. (2008) found a positive relationship between *R. aurora* and the amount of forest cover within 200 m. My results add to the weight of evidence that a critical threshold of approximately 50% forest cover exists at multiple scales, below which probabilities of occurrence and abundance of *R. aurora* decline (Gibbs 1998; Newcomb Homan et al. 2004; Grand et al. 2017).

Habitat connectivity or, conversely, habitat fragmentation, has been identified as another primary determinant of *R. aurora* occurrence at breeding ponds in a developed landscape (Grand et al. 2017). *R. aurora* is capable of moving great distances, and the greater the distance travelled, the more barriers will be encountered (Cushman 2006). One of the greatest contributors to habitat fragmentation in urban and rural environments is roads (Fahrig et al. 1995). Roads negatively impact *R. aurora* by increasing mortality of individuals, either by traffic collision or by desiccation, and by acting as a movement barrier. Such barriers limit migration and dispersal activity, increasing the risk of localized extinction and reducing the likelihood of recolonization (Vos & Chardon 1998). In this study, there were no roads or other known barriers between occupied ponds and the nearest patch of forest. This may explain why the urban pond in this study retained *R. aurora* even though it was in close proximity to a highway and in an area of moderate road density.

Pond isolation is a product of habitat fragmentation (Cushman 2006). Negative relationships between pond isolation and amphibian presence or, conversely, positive relationships between amphibian presence and proximity of terrestrial or alternative wetland habitat have been observed for *R. aurora* (Guderyahn et al. 2016) and other amphibian species (Vos & Chardon 1998; Lehtinen et al. 1999; Guerry & Hunter Jr. 2002; Veysey et al. 2011). Although *R. aurora* are capable of moving great distances, this may not be possible in a fragmented, developed landscape. If a breeding pond is dredged, developed, or otherwise dried up, *R. aurora* will benefit from alternative ponds in close proximity (Bulger et al. 2003). It is therefore not surprising that the occupied ponds in this study were located within close proximity (< 200 m) of both the nearest forest patch and the nearest pond (Table 2.3).

Rather than discrete habitat corridors, an alternative conceptualization of connectivity is matrix permeability. The concept of the landscape matrix, which arose out of the theories of island biogeography and metapopulation dynamics (Ricketts 2001), can be defined as the non-habitat space between discrete habitat patches. Factors that facilitate an individual's movement through the landscape matrix contribute to permeability, while factors that slow or impede an individual's movement, thereby increasing energetic costs or exposure to mortality risk, contribute to matrix impermeability (landscape resistance). For *R. aurora* and many other amphibians, tree cover can be considered one of many indicators of matrix permeability (Quesnelle et al. 2015). Even small groups of trees may be used as stepping stones, providing a temporary refuge for *R. aurora* as it disperses across the landscape (Chan-McLeod & Moy 2007). In contrast, impermeable surfaces, roads, parking lots, and other anthropogenic structures associated with urbanization, have been shown to negatively impact *R. aurora* (Richter & Azous 2001; Guderyahn et al. 2016) and other amphibians (e.g. Pillsbury and Miller 2008, Simon et al. 2009, Van Buskirk 2012) by increasing the impermeability of the landscape (in addition to displacing habitat). This is because paved substrates warm quickly, resulting in rapid surface moisture evaporation which can strand *R. aurora* with high risk of mortality from heat stress or desiccation. Consistent with other landscape-scale studies of *R. aurora* (e.g. Richter and Azous 1995, Holcomb 2012, Guderyahn et al. 2016), I observed that tree cover was higher and impermeable surface cover lower around occupied ponds than unoccupied ponds in the same landscape context.

In undisturbed habitats, *R. aurora* is unlikely to have a metapopulation structure because of its high vagility and the apparent low site fidelity of females (Calef 1973; Smith & Green 2005; Hayes et al. 2007); however, metapopulation dynamics may develop for *R. aurora* in highly fragmented landscapes, as are found on southern Vancouver Island. If this is the case, a positive relationship between species occurrence and nearest pond proximity would be expected because the likelihood of recolonization of ponds following localized extinction increases with increasing proximity of other occupied ponds (Hanski 1998). For *R. aurora* to persist in a developed landscape, it is important for individuals dispersing from breeding ponds to encounter as little resistance as possible when seeking suitable foraging, aestivation, and overwintering habitat.

### 2.4.5 The limitations of auditory surveys for *Rana aurora*

Another valuable outcome of this research was the improved understanding of the limitations of auditory surveys for *R. aurora*. First, the weather-triggered breeding behaviour of *R. aurora* can make auditory surveys hard to time; if surveys do not coincide with the onset of the breeding season, the brief calling period may be missed in whole or in part, leading to false absences and an underestimation of the number of occupied ponds. Second, daily calling activity appeared to be influenced by water temperature, so one’s ability to detect the presence of *R. aurora* during a given survey is vulnerable to environmental stochasticity. These limitations are exemplified in the detection histories of Sites 1, 2 and 3 (Table 2.4), and reflected in the low estimate of detection probability (0.28).

In this study, surveys began on February 1st and the first calls at occupied sites were not detected until February 17th, though the breeding season typically begins in the last week of January or first week of February in this region (P. Govindarajulu, pers. comm.). Auditory surveys were conducted during an unseasonably cold winter (Figure 2.4) and it is likely that the onset of the *R. aurora* breeding season was delayed for this reason. The first detection was heard at the urban pond (Site 3), possibly because it was at least 2 degrees warmer than any rural pond sampled around that same time. It is likely that calls were not heard at the urban pond during the second survey because of a cold snap (the water had dropped to 1.2 °C; Table 2.4), and that calls were not heard during the third survey – which took place almost one month after the first survey – because the breeding season had ended at that site. Comparing the detection histories of Sites 1 and 2 in Table 2.4 with water temperature further supports the hypothesis that chorusing behaviour is influenced by water temperature, as calls were detected only at the site with warmer water even though the surveys were conducted on the same day and the ponds were only 2.3 km apart. This pattern is consistent with one of the earliest studies of *R. aurora* breeding behaviour, which reports that breeding calls in southwestern British Columbia did not start until water temperature had remained above 6°C for more than 5-7 days (Licht 1969).

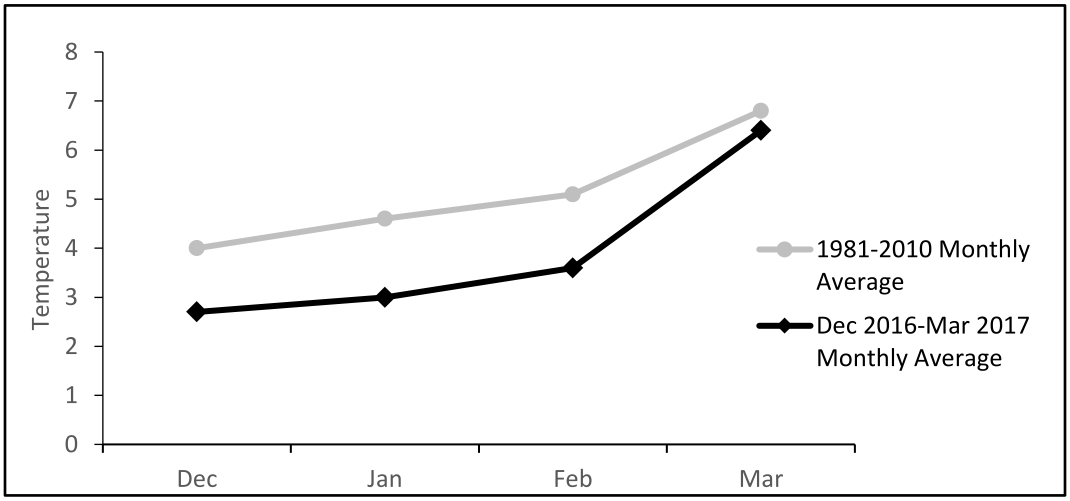

**Figure 2.4** Comparison of monthly average temperatures during the survey period and monthly averages for the period of 1981-2010 for the Saanich area (VISN 2018, Government of Canada 2018b).

The experience of Site 4 demonstrates another limitation of auditory surveys as the sole means of *R. aurora* detection. The most plausible explanation for three false absences at Site 4 (Table 2.4) is that the hydrophone was unable to detect calls because the emergent vegetation was so dense. Similar to other occupied ponds, the amount of aquatic vegetation cover in the littoral zone at Site 4 was high (49%); however, unlike other sites, the aquatic vegetation was dense throughout the pond, with few areas of open water through which sound might travel. It is likely that calls would not have been heard at this site with additional repeat surveys unless the number of listening points was increased dramatically. At sites with dense emergent or submerged vegetation throughout, an auditory survey must consist of a large number of listening points to increase the likelihood of detection.

The detection histories of the occupied ponds show that the effectiveness of three repeat surveys, temporally separated by a minimum of one week and conducted irrespective of water temperature, is poor for detecting *R. aurora*. A control site with high abundance of breeding *R. aurora* from year to year should be used as a reference and monitored closely to determine breeding season onset; this control site should have a similar microclimate to that of other study sites to ensure its representativeness. Given the species' short breeding season, all surveys should be completed within the span of three weeks once calling is detected. Furthermore, surveys should only be conducted when water temperature is above 6°C. Finally, I suggest that auditory survey effort should be proportional to the density of aquatic vegetation rather than wetland area, as calls carry great distances through open water but are extremely hard to detect in the presence of soundwave barriers. Ultimately, the best strategy may be to conduct the minimum number of surveys at the minimum number of sites to obtain the desired level of precision with regards to the occupancy estimate (as was the design used in this study; Mackenzie and Royle 2005) but supplement auditory surveys with larval surveys, which are not as seasonally- or diurnally-restricted nor weather-dependent.

### 2.4.6 The rarity of *Rana aurora*

I suggest that the absence of *R. aurora* from the remaining 85% of ponds sampled can be explained by the same local and landscape determinants that have explained their presence: nearest forest patch size and proximity, percent tree cover, and within-pond aquatic vegetation cover. Among the 22 unoccupied ponds, only five were complemented by a patch of forest exceeding 130,000 m$^2$, the patch size required to achieve core habitat that is free of most edge effects (Chen et al. 1995). One of these ponds was located 275 m from the nearest forest patch in a landscape with less than 27% tree cover at all scales, so overall landscape permeability and terrestrial habitat availability is assumed to be low. Another three of these ponds had less than 20% aquatic vegetation cover, suggesting that oviposition and rearing habitat is limited. The fifth pond was anomalous in that it was located on a mountaintop separated from the nearest pond by over 500 m; if the pond was historically occupied by *R. aurora*, the probability of recolonization is low due to low population density coupled with pond isolation.

## 2.5 Conclusion and recommendations

*R. aurora* occurrence has been shown by other researchers to be positively associated with aquatic vegetation cover and the proximity and extent of complementary forest habitat, and negatively associated with roads and impervious surfaces. Furthermore, *R. aurora* is predicted to have greater likelihood of occurrence and greater abundance at ponds surrounded by > 50% forest cover. As further evidence of these positive relationships, I detected *R. aurora* at ponds located within 100 m of forest habitat of a minimum patch size of 130,000 m$^2$, with median tree cover of ≥ 48% at all eight scales of analysis from 50-2000 m. At all scales of analysis, impervious surface cover around occupied sites did not exceed 40% and was more commonly < 10%. No road barriers fragmented the landscape between an occupied pond and complementary terrestrial habitat. *R. aurora* was absent from ponds that did not meet all of these criteria. Based on my observations and a literature review, I make the following recommendations:

(1) When mapping *R. aurora* breeding habitat suitability across the developed landscape, high quality breeding habitat can be defined as a pond that is structurally connected to a patch of forest exceeding 130,000 m$^2$ that is surrounded by a minimum of 50% forest/tree cover at all biologically relevant scales. However, further research, particularly telemetry studies, would confirm minimum patch size and help describe landscape connectivity in the context of *R. aurora*.

(2) In the process of confirming pond occupancy, presence-absence surveys should not be limited to auditory surveys due the rarity of the species in urban and rural areas, the short duration of the breeding season, and limitations of the sampling method. Alternative survey methods, such as egg mass counts and larval sampling, have the additional benefit of confirming breeding activity and/or estimating the number of breeding females and/or estimating offspring survival. If used, auditory surveys should not be conducted when water temperature drops below 6°C.

(3) Pond restoration and creation designs can be flexible in terms of pond area and overall depth, provided minimum hydroperiod is achieved. Instead, design can focus on maintaining moderate aquatic vegetation cover within the range of oviposition depths. Resources permitting, fish and American bullfrogs can be excluded by creating temporary ponds with high habitat complexity and abundant aquatic vegetation that is scattered throughout the pond (rather than clumped in patches) (Kiesecker et al. 2001).

(4) The exclusion of waterways from other urban ecological studies and the failure to detect *R. aurora* in this study suggest that streams and ditches in a developing landscape are unsuitable breeding habitat for *R. aurora*. Further investigation of the suitability of urban and rural waterways could confirm this assumption or possibly reveal the exceptional conditions under which breeding activity occurs. If further study of waterways is undertaken, I recommend the use of alternative sampling methods, such as egg mass surveys, and the extension of transect lengths beyond 100 metres to better capture within-waterway variability. Furthermore, I recommend that a preliminary study of the hydrology of potential sites be conducted such that sites are monitored continuously from January to July to rule out waterways with consistently low or widely fluctuating water levels.

# Chapter 3 Multiscale Determinants of Pacific Chorus Frog Occurrence and Relative Abundance in a Developed Landscape

## 3.1 Abstract

The Pacific chorus frog (*Pseudacris regilla*) could be considered the flagship amphibian species of urbanizing western North America. Unlike most native amphibians with which it historically co-occurred, *P. regilla* has maintained stable populations in spite of urban and rural development throughout its range. Yet it is possible that *P. regilla* will also become extirpated from cities if urbanization intensifies as predicted. Little is known about the set of conditions that enable this species to persist. In this study, I investigated species-habitat relationships for *P. regilla* in a mixed urban-rural landscape in southwestern British Columbia, Canada, to identify potential criteria for habitat suitability. I conducted repeat auditory surveys of chorusing males at 52 potential breeding wetlands, and modeled occupancy and relative abundance using local (aquatic breeding habitat) and landscape (terrestrial habitat) variables representing competing hypotheses and spatial scales. The models that best explained *P. regilla* occupancy and relative abundance included a combination of terrestrial habitat, non-native predator, and habitat connectivity variables. I found that the proportion of impervious cover within 250 metres of a wetland had the strongest negative impact on both occupancy and relative abundance. My findings suggest that terrestrial habitat availability immediately upland from breeding sites is the primary driver of species persistence in the developed landscape. Conservation efforts should seek to limit impervious cover to less than 20% within a 250-meter buffer around breeding wetlands. Further, restored and created wetlands may be more likely to support *P. regilla* if they are designed with a seasonal hydroperiod to exclude non-native aquatic predators and placed in an area of high pond density.

## 3.2 Introduction

Amphibian species around the world face cumulative threats of habitat loss, climate change, disease, and species invasions (Rahel et al. 2008; Hof et al. 2011). One of the primary drivers of habitat loss is urban and rural development (Mckinney 2002; Hamer & McDonnell 2008), which occurs disproportionately in flat, productive, lowland areas that were once wetlands. In these areas, human demands often supersede provisions for wildlife, and small, isolated patches of remnant habitat are all that remain (Sanderson et al. 2002). Aquatic-breeding amphibians are particularly vulnerable to landscape alteration and habitat fragmentation because of their unique requirement for both aquatic and terrestrial habitat to complete their complex life cycle, their relatively low tolerance of environmental stressors, their limited dispersal capabilities, and metapopulation dynamics (Blaustein et al. 2003; Cushman 2006; Willson & Hopkins 2013). Consequently, urban and rural areas have long been overlooked for their potential value in contributing to conservation strategies at a regional scale (Kowarik 2011). Yet these areas must necessarily play an increasing role in supporting biodiversity if human population growth and concurrent rapid expansion of urban areas continues at the predicted pace (United Nations 2014).

In recognition of this new reality of conservation biology, researchers have begun to investigate the impacts of urbanization on aquatic-breeding amphibians. While most have related urbanization to declines in species richness and population abundance (Scheffers & Paszkowski 2012), some have discovered that wetlands in the developed landscape can support abundant amphibian populations (e.g. Riley et al. 2005) and species richness and genetic diversity similar to habitats outside of urban areas (e.g. Garcia-Gonzalez and Garcia-Vazquez 2012, Gabrielsen et al. 2013, Holzer 2014). Responses to urbanization are species-specific; however, some patterns are beginning to emerge. Foremost among these is the opportunistic use of both constructed and relict natural wetlands as breeding sites, including novel, unintended habitats such as ornamental ponds (e.g. Saarikivi et al. 2013), agricultural ditches (Piha et al. 2007), and stormwater treatment ponds (e.g. Hamer et al. 2012). The potential presence of amphibians in the developed landscape is both a management challenge and an opportunity for conservation.

Successful conservation of a species in urbanizing regions requires knowledge of their current distribution as well as the factors that contribute to habitat suitability. Knowledge of how distribution, abundance, and persistence is influenced by local and landscape processes is incomplete for many aquatic-breeding amphibians, even in the context of relatively undisturbed ecosystems (Semlitsch 2002). Still less is known about how these processes change with scale and with urbanization intensity (Hamer & McDonnell 2008; Scheffers & Paszkowski 2012). This knowledge gap can be addressed, in part, with a shift from multi-species, single-scale studies to species-specific, multi-scale studies (Cushman 2006). Such studies can identify whether species occurrence is driven by local factors, such as characteristics of aquatic breeding sites, or by landscape-scale factors that influence terrestrial habitat availability or the processes of migration and dispersal. Furthermore, species-specific, multi-scale studies have the potential to identify the scale at which certain factors have the greatest influence on occurrence (Addicott et al. 1987; Price et al. 2004).

The impacts of urbanization on aquatic-breeding amphibians in western Canada has received little attention. However, several studies on this subject have been completed in American portions of species' ranges. These studies have focused either on the impacts of development on species richness (Richter & Azous 2001; Holzer 2014), on individual species of conservation concern (Adams 1999; Holcomb 2012; Grand et al. 2017), or on native amphibians' associations with broadly applicable variables and scales (Pearl et al. 2005; Goldberg & Waits 2009; Guderyahn et al. 2016). As a result, relatively little is known about the species-habitat relationships of the Pacific chorus frog (*Pseudacris regilla*), a species that is common throughout western North America, from British Columbia to Baja California (Rorabaugh & Lannoo 2005; Matsuda et al. 2006). Unlike other aquatic-breeding amphibians with which it co-occurs, *P. regilla* populations have remained stable despite urban and agricultural development throughout its range (Rorabaugh & Lannoo 2005). *P. regilla* is known to tolerate a relatively wide range of environmental stressors (e.g. Claussen 1973, Ovaska et al. 1997, Marco et al. 1999, Sparling and Fellers 2009) and has been observed in developed landscapes from Los Angeles, California to Greater Victoria, British Columbia (Riley et al. 2005; Holzer 2014). Consequently, *P. regilla* is both a native species to be managed for in urbanizing regions and a flagship species for urban biodiversity.

There is limited or conflicting information on *P. regilla* associations with many of the local and landscape variables commonly considered for aquatic-breeding amphibians. Furthermore, species-specific research to inform design of multi-scale studies is lacking, despite that fact that scale is likely to influence habitat relationships for *P. regilla* due to the species' varied life history processes. This is primarily because terrestrial movements of *P. regilla* remain poorly documented (Rorabaugh and Lannoo 2005, but see Jameson

1956, 1957, Schaub and Larsen 1978, Smith and Green 2005). Urbanization is likely to further complicate questions of scale if home range size is limited by habitat availability and migration and dispersal movements constrained by barriers such as roads and buildings.

In this study, I investigate the local and landscape-scale factors driving breeding habitat occupancy and relative abundance for *P. regilla* at multiple spatial scales in a mixed urban-rural landscape in southwestern British Columbia. My objective was to determine the relative explanatory power and scale of greatest influence of local and landscape-scale habitat variables on occupancy and relative abundance using occupancy models and ordinal regression, respectively. I developed *a priori* hypotheses linked to "proximate ecological mechanisms" (Hamer and McDonnell 2008: 2444), including aquatic habitat quality, predation pressure from non-native species, terrestrial habitat availability, and habitat connectivity. I predicted that both rural and urban wetlands would be used by *P. regilla* and that occupancy and relative abundance would be similar between natural and constructed wetlands. I further predicted that *P. regilla* occupancy and relative abundance would be driven by a combination of local and landscape variables, reflecting the competing importance of multiple life history processes, rather than by variables linked to a single process or scale. Results are used to propose habitat suitability criteria to guide conservation, restoration, and urban ecological design in the region.

## 3.3 Methods

### 3.3.1 Site selection

To address questions of whether species occurrence and habitat relationships differ between urban and rural landscape contexts, between lentic and lotic wetlands, and between natural and constructed wetlands, I used a stratified random sampling design with a balance of sites in each strata. I first created a detailed map of all freshwater features (hereafter referred to as wetlands) in ArcMap using spatial data provided by the District of Saanich. Each wetland was assigned the attributes of urban or rural, lentic or lotic, and natural or constructed. I then used the NOAA's Sampling Design Tool for ArcGIS (NOAA 2013) to generate an equal number of random points within each strata, keeping a minimum distance of 500 metres between points to ensure spatial independence (Petranka et al. 2004;

Grand et al. 2017). Thus, an equal number of random points were allotted to wetlands within the following nested strata: urban vs rural>lentic vs lotic>natural vs constructed. I first vetted these randomly selected wetlands in ArcGIS using a 2015 aerial orthophoto to confirm their presence. I then confirmed each site's suitability with a site visit in autumn 2016. Apart from minimum hydroperiod, there were no suitability criteria for ponds. However, for waterway sites I selected only streams and ditches of at least 100 m in length, with still water or low flow, water depth exceeding 10 cm, and a hydroperiod extending until at least midsummer. If a waterway did not have standing water at the time of the site visit, a minimum channel depth of 0.5 m and the presence of hydrophytic vegetation (e.g. skunk cabbage, sedges, cattail; Cox & Cullington 2009) were used as indicators of suitability. Final site selection was determined by whether access was granted by the private landowner or public park agency.

### 3.3.2 Data collection

*Call surveys*

Call surveys were conducted to determine species presence as well as to provide an index of abundance of calling males. I conducted call surveys over a single season, from mid-March to mid-May 2017. The survey period was timed to coincide with the peak breeding season of *P. regilla* and all surveys were conducted between 30 minutes after sunset and 0100 hours, which approximates the peak calling period of North American anurans (Weir & Mossman 2005).

Although non-invasive and resource-efficient, call surveys introduce a sampling bias because the target species may go undetected even if present. Detectability may vary with survey conditions or site characteristics (MacKenzie et al. 2006). As a way to account for imperfect detection, MacKenzie et al. (2002, 2006) developed a form of occupancy analysis that models probability of occupancy ($\psi$) and probability of detection ($\rho$) simultaneously. Occupancy models work on the premise that by conducting repeat surveys of a site, one can establish a detection history, which can then be used to estimate probability of detection. Detection probability is then integrated into the occupancy modeling framework.

An occupancy study design relies on initial estimates of $\psi$ and $\rho$ which are, in the absence of published estimates, based on knowledge and experience (MacKenzie et al. 2006). I followed MacKenzie and Royle's (2005) standard occupancy study design (in which all sites are surveyed an equal number of times) and referred to their Table 1 (p. 1110) to determine the optimum number of surveys to conduct at each site given initial parameter estimates. I estimated probability of occupancy and detection for each wetland type and intended to base the number of repeat surveys on parameter estimates averaged across types ($\psi = 0.5$ and $\rho = 0.7$; see Appendix F for estimate justifications), which would have been two; however, one type (urban ditches) had parameter estimates that required resampling three times (Appendix F). I therefore decided that all sites would be surveyed three times for equal survey effort. Based on initial parameter estimates and three repeat surveys, the probability of detecting *P. regilla* at least once ranged from 0.88-0.99 (Appendix G), which was an acceptable level of detection. Thus, the total number of sites was determined by the maximum number of sites that could be resampled three times by the same observer during the peak diurnal calling period within the peak seasonal calling period. This amounted to 56 sites which, as previously described, included equal numbers of urban and rural, natural and constructed, lentic and lotic sites (Figure 1.1).

A survey consisted of 5 minutes of listening from a randomly selected point along the water's edge (Dorcas et al. 2010). A site was considered occupied by *P. regilla* if one or more individuals were observed or heard calling from within the pond or transect. In addition to recording species presence or absence, I recorded chorus intensity, which relates to the underlying abundance of the species (Royle 2004). For the latter, I used the North American Amphibian Monitoring Program's (NAAMP) Amphibian Calling Index codes (Weir and Mossman 2005: 312), which are: 1 – individuals can be counted, with periods of silence between calls; 2 – there is some overlapping of calls but individual calls can still be distinguished; and 3 – calls are constant, continuous and overlapping (i.e. a full chorus).

During each survey, I collected data for variables that would be used to model detection probability. I recorded: start time, air and water temperature, wind speed, and ordinal codes for precipitation, moon brightness, and level of anthropogenic noise (Appendix D); if American bullfrogs – a non-native predator and competitor – were heard or observed, this was also noted. In accordance with NAAMP protocol, surveys were not conducted in winds of 20 km/h or higher, if precipitation was heavy enough to impact hearing ability, or if air temperature dropped below 5.6°C (Weir & Mossman 2005). Measurements of relative humidity at the time of each survey and total daily rainfall, collected and published by the Vancouver Island School-Based Weather Station Network, were obtained the following morning.

### *Local characteristics*

Local variables measured for each site were chosen through a literature review and consideration of *P. regilla* life history characteristics. Variables were paired according to two separate hypotheses regarding local drivers of *P. regilla* wetland occupancy: habitat quality and predation pressure from non-native species. For the former, I measured: aquatic vegetation cover (Goldberg & Waits 2009; Holzer 2014; Hossack 2017), littoral water depth (Guderyahn et al. 2016), and canopy cover (Goldberg & Waits 2009). For the latter, I recorded presence/non-detection of American bullfrogs (*Lithobates catesbeianus*; Rowe and Garcia 2014) and non-native fish (Pearl et al. 2005; Rowe & Garcia 2014; Guderyahn et al. 2016). While hydroperiod was also identified as an important factor for *P. regilla* occurrence (Guderyahn et al. 2016), the scarcity of seasonal wetlands in the study area prevented its inclusion.

Aquatic vegetation cover, littoral water depth, and canopy cover were measured at multiple points and then averaged: for ponds, data were collected at the approximate cardinal direction points around the pond using a 1 $m^2$ quadrat frame spanning 0-1 meters from the shore; for waterway transects, data were collected from within the 1 $m^2$ quadrat frame placed at 0 m, 50 m, and 100 m points along the 100-meter transect. Aquatic vegetation cover was visually estimated with the aid of a comparison chart (e.g. B.C. MELP & B.C. MF 1998: 9; Appendix C). Water depth was measured with a metre stick at a distance of 1 m from the water's edge. I measured percent canopy cover over each quadrat using a densiometer. To ensure that no wetland sites were toxic to *P. regilla*, I measured conductivity and pH at a depth of 5 cm using a handheld water quality meter (Oakton® PC Testr 35) and gauged nitrate/nitrite concentration using WaterWorks$^{TM}$ Nitrate/Nitrite Nitrogen test strips.

Data collection for the above variables took place from January to May 2017, before the onset of summer drought, with the exception of non-native predator surveys. In June and July 2017, I conducted one-time surveys of American bullfrog and non-native fish presence-absence in tadpole habitat using minnow traps (Shaffer et al. 1994; Skelly & Richardson 2010). As bullfrogs and non-native fish do not breed in seasonal or lotic wetlands, minnow traps were deployed only at permanent pond sites where non-native predators had not been previously detected during research activities. Minnow traps were deployed in the late afternoon and retrieved early the following morning to avoid temperature stress to trapped animals. I used galvanized steel wire (6 mm mesh) minnow traps, 0.5 m in length and 0.3 m in diameter tapering to a 3-5cm-diameter entrance hole at either end. The number of traps used at a site was proportional to pond area (63-84,266 $m^2$), and ranged from 1-3. Though unbaited, traps were positioned to increase the likelihood of fish capture: traps were randomly placed along the shores with the greatest evening sunlight exposure and oriented parallel to edges of patches of aquatic vegetation. To ensure the safety of any mammal or adult amphibian bycatch, traps were tethered within 2 m of the shore and kept partly above water using a foam float (Figure 2.1). Upon retrieving the trap, the contents were quickly transferred to a bucket of local pond water and any captured individuals were identified, photographed, and released alive at the location of capture.

### *Landscape characteristics*

A literature review identified three landscape-scale variables used to describe *P. regilla* terrestrial habitat: tree/forest cover (Pearl et al. 2005; Goldberg & Waits 2009; Holzer 2014), agriculture cover (Goldberg & Waits 2009), and urban/impervious surface cover (Rowe & Garcia 2014; Guderyahn et al. 2016). I identified an additional four landscape-scale variables as having the potential to influence *P. regilla* occupancy based on studies of similar species and probable metapopulation dynamics; these included: percent wetland cover (Johnson et al. 2013), road density (Fahrig et al. 1995), number of ponds (Houlahan & Findlay 2003), and distance to the nearest pond (Marsh & Trenham 2001). With the exception of agriculture cover, which was not considered because it was not applicable across the study area, these variables were grouped according to separate hypotheses of terrestrial habitat availability and connectivity.

The home range size and dispersal ability of *P. regilla* is not well understood. To investigate the scale at which landscape variables influence *P. regilla* wetland use for chorusing, I measured scale-dependent variables within eight nested buffers around each site using ArcMap (version 10.5; ESRI 2017): 50, 100, 150, 250, 500, 1000, 1500, and 2000 metres. I predicted that landscape variables would have a greater influence on wetland occupancy at smaller scales (e.g. 50-250 m from a wetland) due to habitat fragmentation by development.

Forest and impervious surface cover data were originally collected on behalf of the Urban Forest Stewardship Initiative (2008) and provided by the Capitol Regional District (CRD); original percent cover estimates were summarized within 1-hectare grid cells using a 2015 aerial orthophoto provided by the CRD. Forest cover refers to urban forests, which in this case includes relict forest and woodland patches of all stages of maturity, orchards, and ornamental plantings, to the scale of individual trees. I used a detailed waterbodies shapefile supplemented with a 2015 aerial orthophoto, provided by the District of Saanich, to map all wetland boundaries to a minimum area of 2 $m^2$. I then calculated the distance to the nearest neighbour pond, percent wetland cover, and number of ponds at each scale using ArcMap’s Analysis Tools. I derived road density, calculated as summed length of all roads divided by the buffer area ($m/m^2$; Simon et al. 2009), for each scale from the Digital Road Atlas layer published by the B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development. Roads included all single and multi-lane roads and highways current to 2017.

### 3.3.3 Statistical analyses

*Occupancy*

Single-season occupancy models were structured according to five *a priori* hypotheses. I hypothesized that *P. regilla* aquatic habitat occupancy was driven either by: (1) aquatic habitat quality, (2) predation pressure by non-native fish and American bullfrogs, (3) terrestrial habitat availability, (4) habitat connectivity, or (5) an *a posteriori* combination of local and landscape factors. Occupancy analysis was conducted in the R software environment (R Core Team 2017) using the package ‘unmarked’ (Fiske & Chandler 2011). At each stage of the analysis, I used an information-theoretic approach to model selection, ranking models based on $AIC_c$, a second-order variant of Akaike’s information criterion that corrects for small sample size ($n/k < 40$) (Akaike 1973; Hurvich & Tsai 1989; Burnham & Anderson 2002).

I developed a global occupancy model for each hypothesis after completing four preliminary steps. I first explored the data to identify any non-linear relationships between the response and explanatory variables or issues of collinearity between covariates; for the latter I used the package ‘usdm’ (Naimi et al. 2014). Variables with a variance inflation factor (VIF) $\geq 3$ were considered collinear with one or more covariates and modeled separately (i.e., excluded from global models) (Zuur et al. 2010). Tests for collinearity were also done to ensure that pairs of variables with a correlation coefficient $\geq 0.55$ were not combined in final models. Second, all continuous variables were scaled prior to modeling to standardize values across the many different scales of measurement (MacKenzie et al. 2006). The third step was to identify the top detection probability model by comparing models with detection covariates while holding occupancy probability constant (MacKenzie et al. 2006). Detection probability models were limited to one or two covariates to avoid overfitting given the small sample size. Detection covariates included all sampling variables, as well as pond area, bullfrog presence, and fish presence. Pond area was included because the ability to detect calls may diminish with distance from the calling individuals, while bullfrogs and fish were included because there is some indication that *P. regilla* may not vocalize in close proximity to predators (Brattstrom and Warren 1955). The top detection probability model ($\Delta AIC_c=0$) was used in all subsequent occupancy models. Finally, I determined the scale of greatest impact for each landscape variable by comparing occupancy models of each variable at each scale. The scale that appeared in the top model ($\Delta AIC_c=0$) for each variable was used in the global model for the respective hypothesis.

For each hypothesis, the global occupancy model was ranked against more parsimonious subsets using $AIC_c$. Models with $\Delta AIC_c < 2$ from the top ranked model were considered to have similar support in the data (Burnham & Anderson 2002). The top models for each hypothesis were then competed against each other to determine the best explanatory model for *P. regilla* wetland occupancy in the developed landscape. Akaike weights and effect sizes for $\psi$ and $\rho$ were compared to assess the relative explanatory power of each competing model. Finally, I tested the goodness of fit of the global model from which the top model was derived using a parametric bootstrap goodness of fit test (Burnham & Anderson 2002; MacKenzie & Bailey 2004). I used 5000 runs to test goodness of fit and estimate overdispersion (MacKenzie & Bailey 2004).

### *Calling index*

Calling index is related to the underlying abundance of an anuran population at a given sample location (Royle 2004). Thus, I consider calling index to be a proxy of relative abundance. Models of calling index were fit using ordinal logistic regression. I used a single value representing the maximum calling index observed at each site as the response variable. For all analyses, I fitted ordinal regression models using the 'clm' function from the R package 'ordinal,' as the cumulative link model (CLM) accounts for the ordered, categorical nature of the response variable (Christensen 2011). As with occupancy models, the scale of greatest impact for landscape variables on calling index was determined through a preliminary stage of model selection before models were compared within and between hypotheses. I used model $AIC_c$ to determine model rank and Akaike weights to compare the relative likelihood of the model given the data (Burnham & Anderson 2002).

### *A posteriori modeling: combined model and relative variable importance*

After examining the results of the hypothesis model sets for occupancy and relative abundance, I created *a posteriori* global models combining all variables from the top hypothesis models. The global combined model was ranked against the top hypothesis model to determine if a model reflecting the competing importance of multiple life history processes was superior. This model was compared with all possible subsets in order to determine the relative importance of each variable in explaining *P. regilla* occupancy and relative abundance.

## 3.4 Results

Two natural urban ponds had to be removed from the study, one a backwater pond that had become inundated by an adjacent river channel and another a vernal pool that dried sooner than expected. Two urban ditches were removed because they did not meet minimum water depth requirements throughout the survey period. Call surveys were completed at the remaining 52 sites.

Call surveys detected *P. regilla* at 18 of 26 ponds, including 5 (42%) of 12 urban ponds and 13 (93%) of 14 rural ponds. In contrast, *P. regilla* was detected at only 1 of 26 waterways: a rural stream that had, at the transect location, seasonally flooded a field and developed the characteristics of a lentic habitat. Where present, *P. regilla* were detected an average of 2.3 times (median 2.5, range 1-3). The chorus intensity at occupied ponds ranged from 1-3. At ten ponds, the maximum chorus intensity was observed at least once. At six ponds, chorus intensity never increased above 1. Maximum chorus intensity was observed at both urban (n=3) and rural ponds (n= 7) and at natural (n = 6) and constructed ponds (n=4).

There were multiple significant differences between ponds and waterways at the site scale, as determined by a Mann-Whitney U test ($p<0.05$): waterway sites were significantly shallower ($U = 144$, $p = 2.0e^{-4}$) and shadier ($U = 450$, $p = 0.02$) than pond sites and waterways had significantly higher conductivity than ponds ($U = 469.5$, $p = 0.008$). Furthermore, nitrate was more commonly detected in waterways (8/26) than in ponds (2/26). Although the difference in aquatic vegetation cover between waterways and ponds was not significant, mean aquatic vegetation cover was 10% lower among waterway sites. In light of the significant differences between local habitat variables at pond and waterway sites, I reasoned that the categorical absence of *P. regilla* from waterway sites was likely to be attributable to, or at least confounded by, observed habitat differences at the local scale. A similar landscape-scale comparison of ponds and waterways may have presented additional hypotheses for explaining the absence of *P. regilla* from waterways, but was not pursued after weighing this benefit against the additional time and effort required for data collection. As the number of *P. regilla* occurrences in waterways was so low (n=1), waterway sites were excluded from occupancy and CLM analyses, further reducing the sample size to 26.

### 3.4.1 Occupancy

Single-variable models of detection probability suggested that only anthropogenic disturbance, time since sunset, relative humidity, and bullfrog presence had an influence on detection ($\Delta AIC_c < 2$ and more support than constant detection probability model). As these covariates were not collinear, models of all possible two-covariate combinations were fitted. The top detection probability model included minutes after sunset and relative humidity as detection covariates, with minutes since sunset having a positive effect on detectability and relative humidity having a negative effect. This top model received a low Akaike weight ($w_i$=0.18) and six other models were competitive (Table 3.1). Acknowledging this considerable model selection uncertainty, the top detection probability model had three times the support of the constant detection probability model ($w_i$=0.06) and was therefore used in subsequent occupancy models.

**Table 3.1** Detection probability models. ΔAIC<2 indicates substantial support in the data. Models including all other sampling covariates had less support than the null model ($\psi(.)p(.)$) and are therefore not shown here.

| **Model** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i$** | **K** | **-2L** | **$\hat{p}$** |
|---|---|---|---|---|---|---|
| $\psi(.)p$(TIME + RH) | 93.49 | 0.0 | 0.18 | 4 | 83.58 | 0.74 |
| $\psi(.)p$(DIST + BULLFROG) | 93.60 | 0.11 | 0.17 | 4 | 83.70 | 0.68 |
| $\psi(.)p$(DIST) | 93.83 | 0.34 | 0.15 | 3 | 86.74 | 0.68 |
| $\psi(.)p$(RH) | 94.71 | 1.22 | 0.10 | 3 | 87.62 | 0.68 |
| $\psi(.)p$(TIME + DIST) | 95.30 | 1.81 | 0.07 | 4 | 85.40 | 0.75 |
| $\psi(.)p$(BULLFROG) | 95.33 | 1.84 | 0.07 | 3 | 88.24 | 0.74 |
| $\psi(.)p$(TIME + BULLFROG) | 95.43 | 1.94 | 0.07 | 4 | 85.52 | 0.74 |
| $\psi(.)p$(RH + BULLFROG) | 95.60 | 2.10 | 0.06 | 4 | 85.70 | 0.75 |
| $\psi(.)p$(TIME) | 95.67 | 2.17 | 0.06 | 3 | 88.58 | 0.75 |
| $\psi(.)p(.)$ | 95.68 | 2.19 | 0.06 | 2 | 91.16 | 0.75 |

$AIC_c$ = Akaike's information criterion; $\Delta AIC_c$ = difference in $AIC_c$ value from top-ranked model; $w_i$ = $AIC_c$ model weight; K = number of estimated parameters in the model; -2L is twice the negative log-likelihood; $\hat{p}$ = estimated detection probability; TIME is minutes since sunset; RH is relative humidity; DIST is anthropogenic noise disturbance.

Before fitting occupancy models according to the four *a priori* hypotheses (Table 3.2), I first determined the scale of greatest influence for scale-dependent variables. For all variables except tree cover, there was a definitive scale of greatest influence on *P. regilla* occupancy (Table 3.3). Impervious cover and road density were associated with intermediate scales, number of ponds and wetland cover were associated with larger scales, and there was support for tree cover at all scales ≥ 500 m (Table 3.3). The variable measured at its most influential scale was included in the global model for the associated hypothesis. Impervious cover-250 and tree cover-500 had a correlation coefficient of −0.74 and were therefore modeled separately. Within hypotheses, no other covariates were collinear and no covariate had a VIF ≥ 3 (Appendix H).

**Table 3.2** A priori hypothesis summary for occupancy, including covariates and their expected effect on *P. regilla* occupancy.

| **Hypothesis** | **Associated variables (effect)** | **Scale** |
|---|---|---|
| Aquatic habitat quality | Littoral depth (+)<br>Aquatic vegetation cover (+)<br>Canopy cover (−) | Local |
| Predation pressure | American bullfrog P/A (−)<br>Non-native fish P/A (−) | Local |
| Terrestrial habitat availability | Impervious cover (−)<br>Tree cover (+) | 50, 100, 150, 250, 500, 1000, 1500, 2000 |
| Habitat connectivity | Number of ponds (+)<br>Road density (−)<br>Wetland cover (+) | 50, 100, 150, 250, 500, 1000, 1500, 2000 |
| | Distance to nearest pond (−) | Constant across scales |

**Table 3.3** Top occupancy models of scale-dependent landscape variables, using the detection probability model $p$(TIME + RH). Only models with ΔAICc < 2 are shown.

| **Model** | **AICc** | **ΔAIC$_c$** | $\boldsymbol{w_i}$ | **K** | **-2L** |
|---|---|---|---|---|---|
| *Impervious cover* | | | | | |
| $\psi$(250) | 79.48 | 0.0 | 0.79 | 5 | 66.48 |
| *Tree cover* | | | | | |
| $\psi$(500) | 90.25 | 0.0 | 0.32 | 5 | 77.26 |
| $\psi$(1500) | 91.16 | 0.90 | 0.20 | 5 | 78.16 |
| $\psi$(2000) | 91.35 | 1.10 | 0.19 | 5 | 78.36 |
| $\psi$(1000) | 91.60 | 1.35 | 0.16 | 5 | 78.60 |
| *Road density* | | | | | |
| $\psi$(500) | 88.21 | 0.0 | 0.43 | 5 | 75.22 |
| *Number of ponds* | | | | | |
| $\psi$(1500) | 85.04 | 0.0 | 0.75 | 5 | 72.04 |
| *Wetland cover* | | | | | |
| $\psi$(2000) | 90.83 | 0.0 | 0.65 | 5 | 77.82 |

$AIC_c$ is Akaike's information criterion; $\Delta AIC_c$ is the difference in $AIC_c$ value from top-ranked model; $w_i$ is $AIC_c$ model weight; K is the number of estimated parameters in the model; -2L is twice the negative log-likelihood.

Seven models were fit for the aquatic habitat hypothesis, including the global model and all possible subsets. The top model was a depth-only model, which had almost ten times the support of the constant $\psi$ (occupancy probability) model and no competing models (Table 3.4). For the predation hypothesis, the constant $\psi$ model was the top model, with fish-only and bullfrog-only models competing. The global model including bullfrogs and fish was not competitive (Table 3.4). Between the two models representing the terrestrial habitat availability hypothesis, impervious cover-250 had far more explanatory power than both the tree cover-500 model and the constant $\psi$ model, receiving 100% of the model weight (Table 3.4). The definitive top model for the connectivity hypothesis was the number of ponds-1500 model, which had moderate support (42% model weight; Table 3.4).

**Table 3.4** Within-hypothesis model selection results for occupancy using the detection probability model $p$(TIME + RH).

| Model | AICc | $\Delta AIC_c$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| *Aquatic habitat* | | | | | |
| $\psi$(DEPTH) | 91.23 | 0.0 | 0.43 | 5 | 78.22 |
| $\psi$(DEPTH + CANOPY) | 93.41 | 2.18 | 0.14 | 6 | 76.98 |
| $\psi$(.) | 93.49 | 2.27 | 0.14 | 4 | 83.58 |
| $\psi$(AQVEG + DEPTH) | 93.58 | 2.35 | 0.13 | 6 | 77.16 |
| $\psi$(AQVEG) | 95.28 | 4.05 | 0.06 | 5 | 82.28 |
| $\psi$(CANOPY) | 95.28 | 4.06 | 0.06 | 5 | 82.28 |
| $\psi$(AQVEG + DEPTH + CANOPY) | 96.78 | 5.55 | 0.03 | 7 | 76.56 |
| $\psi$(AQVEG + CANOPY) | 98.10 | 6.87 | 0.01 | 6 | 81.68 |
| *Non-native predators* | | | | | |
| $\psi$(.) | 93.49 | 0.0 | 0.68 | 4 | 83.58 |
| $\psi$(BULFROG) | 96.52 | 0.84 | 0.15 | 5 | 83.52 |
| $\psi$(FISH) | 96.56 | 0.88 | 0.15 | 5 | 83.56 |
| $\psi$(BULLFROG + FISH) | 99.90 | 4.21 | 0.03 | 6 | 83.48 |
| *Terrestrial habitat* | | | | | |
| $\psi$(IMP250) | 79.48 | 0.0 | 1.0 | 5 | 66.48 |
| $\psi$(TREE500) | 90.25 | 10.78 | 0.0 | 5 | 77.26 |
| $\psi$(.) | 93.49 | 14.01 | 0.0 | 4 | 83.58 |
| *Connectivity* | | | | | |
| $\psi$(PONDS1500) | 85.04 | 0.0 | 0.42 | 5 | 72.04 |
| $\psi$(PONDS1500 + WET2000) | 87.32 | 2.28 | 0.13 | 6 | 70.90 |

| | | | | | |
|---|---|---|---|---|---|
| $\psi$(RD500 + PONDS1500) | 87.88 | 2.84 | 0.10 | 6 | 71.46 |
| $\psi$(NEAR + PONDS1500) | 88.11 | 3.07 | 0.09 | 6 | 71.70 |
| $\psi$(RD500) | 88.21 | 3.17 | 0.09 | 5 | 75.22 |
| $\psi$(NEAR + RD500) | 90.34 | 5.30 | 0.03 | 6 | 73.92 |
| $\psi$(NEAR + PONDS1500 + WET2000) | 90.56 | 5.52 | 0.03 | 7 | 70.34 |
| $\psi$(RD500 + PONDS1500 + WET2000) | 90.79 | 5.74 | 0.02 | 7 | 70.56 |
| $\psi$(WET2000) | 90.83 | 5.78 | 0.02 | 5 | 77.82 |
| $\psi$(RD500 + WET2000) | 91.11 | 6.07 | 0.02 | 6 | 74.70 |
| $\psi$(NEAR + RD500 + PONDS1500) | 91.46 | 6.42 | 0.02 | 7 | 71.24 |
| $\psi$(NEAR) | 92.74 | 7.70 | 0.01 | 5 | 79.74 |
| $\psi$(NEAR + RD500 + WET2000) | 93.48 | 8.44 | 0.01 | 7 | 73.26 |
| $\psi$(.) | 93.49 | 8.45 | 0.01 | 4 | 83.58 |
| $\psi$(NEAR + RD500 + PONDS1500 + WET2000) | 94.37 | 9.33 | 0.0 | 8 | 69.90 |
| $\psi$(NEAR + WET2000) | 95.45 | 10.41 | 0.0 | 6 | 79.02 |

$AIC_c$ is Akaike's information criterion; $\Delta AIC_c$ is the difference in $AIC_c$ value from top-ranked model; $w_i$ is $AIC_c$ model weight; K is the number of estimated parameters in the model; -2L is twice the negative log-likelihood; AQVEG is percent aquatic vegetation cover; IMP250 is impervious cover at 250 m; PONDS1500 is number of ponds within 1500 m; RD500 is road density within 500 m; NEAR is distance to nearest pond; WET is percent cover of wetland within 2000 m.

When the best models representing each hypothesis were compared, the definitive top model was that of terrestrial habitat availability, represented by impervious cover-250, which had an Akaike weight of 0.94 (Table 3.5). The parametric bootstrap goodness of fit test on this model showed that there was adequate fit ($\chi^2$ = 3.8, p-value = 0.61) and no indication of overdispersion ($\hat{c}$ = 0.75). Based on the top model, detection probability is estimated as 0.71 and the probability of occupancy is predicted to be 1 for ponds with less than 20% impervious cover, decline precipitously between 25 and 35% impervious cover, and remain 0 at ponds surrounded by over 35% impervious cover (Table 3.5, Figure 3.1).

**Table 3.5** Between-hypothesis occupancy model selection results.

| Model | AICc | $\Delta AIC_c$ | $w_i$ | K | -2L | $\hat{\psi}$ | SE($\psi$) | $\hat{p}$ |
|---|---|---|---|---|---|---|---|---|
| (naïve $\psi$ = 0.69) | | | | | | | | |
| $p$(TIME+RH) $\psi$(IMP250) | 79.48 | 0.0 | 0.94 | 5 | 66.48 | 0.99 | 0.03 | 0.71 |
| $p$(TIME+RH) $\psi$(PONDS1500) | 85.04 | 5.56 | 0.06 | 5 | 72.04 | 0.85 | 0.12 | 0.74 |
| $p$(TIME+RH) $\psi$(DEPTH) | 91.23 | 11.75 | 0.0 | 5 | 78.22 | 0.76 | 0.11 | 0.74 |
| $p$(.) $\psi$(.) | 93.49 | 14.01 | 0.0 | 4 | 83.58 | 0.70 | 0.09 | 0.75 |
| $p$(TIME+RH) $\psi$(BULLFROG) | 96.52 | 17.04 | 0.0 | 5 | 83.52 | 0.67 | 0.16 | 0.74 |
| $p$(TIME+RH) $\psi$(FISH) | 96.56 | 17.08 | 0.0 | 5 | 83.56 | 0.72 | 0.11 | 0.74 |

$\hat{\psi}$ is the estimated proportion of sites occupied (with occupancy covariate set at its mean) and SE($\hat{\psi}$) is the standard error of $\hat{\psi}$; $\hat{p}$ is detection probability; TIME is minutes since sunset; RH is relative humidity; IMP250 is percent impervious cover within 250 m; PONDS1500 is number of ponds within 1500 m.

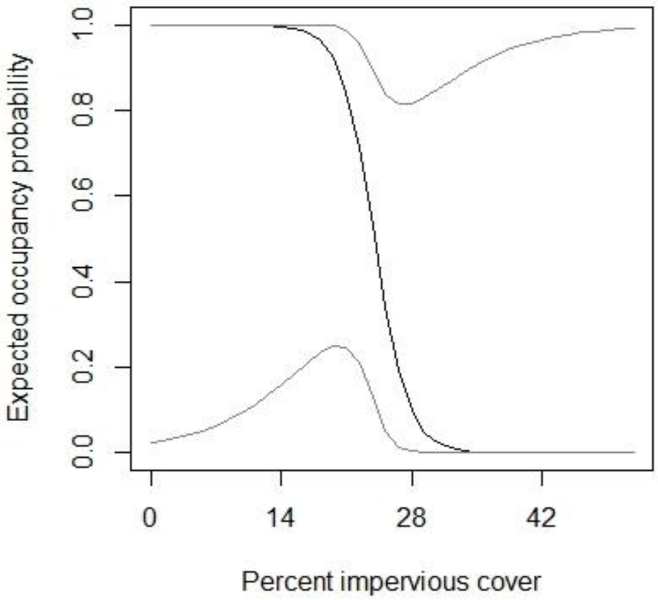

**Figure 3.1** The predicted relationship between occupancy probability and impervious surface cover with 95% confidence intervals. Estimated occupancy probability is based on the model ($p$(TIME+RH)$\psi$(IMP250)), which had an Akaike weight of 0.94.

### 3.4.2 Calling index

Acknowledging that occupancy and abundance may be controlled by different factors, I repeated the process of selecting the scale of greatest influence of scale-dependent variables on calling index using CLMs. The scale of greatest impact of landscape variables on calling index was much less clear. For all variables, two or more scales were competitive; there were four competing scales for tree cover and all eight scales were competitive for wetland cover. I incorporated the top-ranked scale for each variable into the global model for the associated hypothesis. Road density-500 and number of ponds-1500 had a correlation coefficient of −0.70 and were therefore modeled separately. Within hypotheses, no other covariates were collinear and no covariate had a VIF ≥ 3 (Appendix H). Comparison of the global CLMs representing each hypothesis with their respective subsets yielded two competing models for connectivity, one top model for terrestrial habitat availability, two competing models for aquatic habitat quality, and two competing models for predation (Table 3.6). When top models for each hypothesis were competed against each other, the definitive top model was again the terrestrial habitat availability model, again represented by impervious cover at the 250 m scale (Table 3.7).

**Table 3.6** Within-hypothesis model selection results for relative abundance. Note that models that were ill-defined, as indicated by condition of the Hessian, are not shown.

| Model | AICc | $\Delta AIC_c$ | $w_i$ | K | LL |
|---|---|---|---|---|---|
| *Aquatic habitat* | | | | | |
| DEPTH | 73.36 | 0.0 | 0.43 | 4 | -31.73 |
| CANOPY | 75.32 | 1.97 | 0.16 | 4 | -32.71 |
| AQVEG | 75.4 | 2.04 | 0.15 | 4 | -32.75 |
| AQVEG + DEPTH | 76.23 | 2.87 | 0.10 | 5 | -31.61 |
| *Non-native predators* | | | | | |
| BULLFROG | 75.65 | 0.0 | 0.45 | 4 | -32.87 |
| FISH | 75.65 | 0.0 | 0.45 | 4 | -32.87 |
| BULLFROG + FISH | 78.63 | 2.98 | 0.10 | 5 | -32.81 |
| *Terrestrial habitat* | | | | | |
| IMP250 | 64.15 | 0.0 | 0.99 | 4 | -27.12 |
| TREE2000 | 73.16 | 9.02 | 0.01 | 4 | -31.63 |
| *Connectivity* | | | | | |
| RD500 | 67.49 | 0.0 | 0.44 | 4 | -28.79 |
| NEAR + RD500 | 69.39 | 1.90 | 0.17 | 5 | -28.20 |
| PONDS1500 | 70.17 | 2.68 | 0.11 | 4 | -30.13 |
| RD500+WET2000 | 70.48 | 2.99 | 0.10 | 5 | -28.74 |
| NEAR | 72.06 | 4.57 | 0.04 | 4 | -31.08 |
| NEAR + PONDS1500 | 72.21 | 4.72 | 0.04 | 5 | -29.60 |
| NEAR + RD1500 + WET2000 | 72.8 | 5.32 | 0.03 | 6 | -28.19 |
| WET2000 | 73.11 | 5.63 | 0.03 | 4 | -31.60 |
| PONDS1500 + WET2000 | 73.21 | 5.72 | 0.02 | 5 | -30.10 |
| NEAR + WET2000 | 73.99 | 6.50 | 0.02 | 5 | -30.49 |

$AIC_c$ is Akaike's information criterion; $\Delta AIC_c$ is the difference in $AIC_c$ value from the top-ranked model; $w_i$ is $AIC_c$ model weight; K is the number of estimated parameters in the model; LL is the log-likelihood; AQVEG is percent aquatic vegetation cover; BULL is American bullfrog presence; IMP250 is impervious cover at 250 m; TREE is percent tree cover within 2000 m; RD500 is road density within 500 m; NEAR is distance to nearest pond; PONDS1500 is number of ponds within 1500 m; WET is percent cover of wetland within 2000 m.

**Table 3.7** Between-hypothesis model selection results for relative abundance.

| Model | AICc | $\Delta AIC_c$ | $w_i$ | K | LL | Coeff. Est. | Cond. H. |
|---|---|---|---|---|---|---|---|
| IMP250 | 64.15 | 0 | 0.78 | 4 | -27.12 | -0.12 | 2.70e3 |
| RD500 | 67.49 | 3.34 | 0.15 | 4 | -28.79 | -3.26 | 9.70e1 |
| NEAR + RD500 | 69.39 | 5.24 | 0.06 | 5 | -28.20 | 1.77, -2.88 | 9.90e1 |
| DEPTH | 73.36 | 9.21 | 0.01 | 4 | -31.73 | 0.04 | 3.90e4 |
| CANOPY | 75.32 | 11.2 | 0 | 4 | -32.71 | -0.01 | 3.30e4 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| FISH | 75.65 | 11.5 | 0 | 4 | -32.87 | -0.22 | 4.20e1 |
| BULLFROG | 75.65 | 11.5 | 0 | 4 | -32.87 | 0.22 | 6.90e1 |

AIC$_c$ is Akaike's information criterion; ΔAIC$_c$ is the difference in AIC$_c$ value from the top-ranked model; $w_i$ is AIC$_c$ model weight; K is the number of estimated parameters in the model, including thresholds; LL is log-likelihood; Cond. H. is condition of the Hessian; IMP250 is percent impervious cover within 250 m; RD500 is road density within 500 m; NEAR is distance to nearest pond.

### 3.4.3 Relative variable importance

*Occupancy*

When the best occupancy model (impervious cover-250) was compared with a global model that combined all covariates from the top models for each hypothesis, and all possible subset models, it remained the top model but several models were competing, including the global model (Table 3.8). Relative variable importance was calculated from among supported models ($w_i$>0). Impervious cover-250 was identified as the most important factor describing *P. regilla* occurrence ($w_+$= 0.92), with bullfrogs, fish, and number of ponds-1500 receiving moderate support and littoral depth receiving the least support ($w_+$= 0.23; Table 3.8). Several subset models of the global model would not converge and were removed from candidate set.

**Table 3.8** Model selection results for the combined global model (*) and all subsets using the detection probability model $p$(TIME + RH). Note that models without support ($w_i$=0) or that did not converge are not shown. Estimates for occupancy($\hat{\psi}$) and detection probability ($\hat{p}$) are calculated with parameters set at their mean.

| Model | AICc | ΔAIC$_c$ | $w_i$ | -2L | K | $\hat{\psi}$ | SE($\psi$) | $\hat{p}$ |
|---|---|---|---|---|---|---|---|---|
| $\psi$(IMP250) | 79.48 | 0.0 | 0.32 | 66.48 | 5 | 0.99 | 0.026 | 0.71 |
| $\psi$(IMP250 + BULLFROG + FISH) | 80.49 | 1.01 | 0.20 | 60.26 | 7 | 1.0 | 0.0012 | 0.71 |
| $\psi$(IMP250 + PONDS1500 + BULLFROG) | 80.49 | 1.01 | 0.20 | 60.26 | 7 | 1.0 | $1.2e^{-4}$ | 0.71 |
| $\psi$(IMP250 + DEPTH) | 82.26 | 2.79 | 0.08 | 65.84 | 6 | 0.99 | 0.024 | 0.71 |
| $\psi$(IMP250 + FISH) | 82.80 | 3.32 | 0.06 | 66.38 | 6 | 0.98 | 0.058 | 0.71 |
| $\psi$(PONDS1500 + BULLFROG) | 83.43 | 3.96 | 0.04 | 67.02 | 6 | 0.93 | 0.11 | 0.74 |
| $\psi$(IMP250 + DEPTH + FISH) | 84.40 | 4.92 | 0.03 | 64.18 | 7 | 0.86 | 0.13 | 0.75 |
| $\psi$(PONDS1500) | 85.04 | 5.56 | 0.02 | 72.04 | 5 | 0.85 | 0.12 | 0.74 |
| $\psi$(PONDS1500 + DEPTH) | 85.69 | 6.21 | 0.01 | 69.26 | 6 | 0.87 | 0.11 | 0.74 |
| $\psi$(PONDS1500 + FISH) | 85.81 | 6.33 | 0.01 | 69.38 | 6 | 0.91 | 0.098 | 0.74 |
| $\psi$(IMP250 + PONDS1500 + FISH) | 86.26 | 6.78 | 0.01 | 66.04 | 7 | 0.86 | 0.14 | 0.74 |
| $\psi$(PONDS1500 + BULLFROG + FISH) | 86.44 | 6.96 | 0.01 | 66.22 | 7 | 0.94 | 0.086 | 0.74 |

| | $w_+$ | Effect |
|---|---|---|
| IMP250 | 0.91 | – |
| BULLFROG | 0.54 | – |

| | | |
|---|---|---|
| FISH | 0.42 | − |
| PONDS1500 | 0.39 | + |
| DEPTH | 0.23 | + |

$AIC_c$ is Akaike's information criterion; $\Delta AIC_c$ is the difference in $AIC_c$ value from the top-ranked model; $w_i$ is Akaike weight; -2L is twice the negative log-likelihood; K is the number of estimated parameters in the model; $\hat{\psi}$ is the estimated proportion of sites occupied (with occupancy covariate set at its mean) and SE($\hat{\psi}$) is the standard error of $\hat{\psi}$; $\hat{p}$ = mean detection probability; IMP250 is percent impervious cover within 250 m; PONDS1500 is number of ponds within 1500 m; $w_+$ is relative variable importance based on the candidate set; Effect is direction of the model averaged coefficient estimate.

### *Calling index*

Impervious cover-250 and road density-500 were collinear and could not be combined in a global model for relative abundance. Impervious cover-250 was retained because of its greater weight during prior model selection. When impervious cover-250 was combined with variables from top predation and connectivity models in a global model and all possible subsets of ≤ 3 covariates were compared, the impervious-250 model remained competitive; however, it was no longer the best model. Three combined models, all of which included impervious cover-250 in combination with predator and/or connectivity covariates, had greater support (Table 3.9). There was considerable model selection uncertainty: the top model received an Akaike weight of 0.20. After summing Akaike weights to determine the relative variable importance of all variables in the candidate set, impervious cover-250 was unequivocally the most important factor influencing *P. regilla* relative abundance ($w_+$= 0.99). Distance to nearest pond was second-most important ($w_+$= 0.62), bullfrogs and fish were of moderate importance, and depth and canopy density were of relatively low importance (Table 3.9).

**Table 3.9** Model selection results for all subsets (max. 3 covariates) of a combined global model for calling index. Only CLMs with ΔAICc < 4 are shown, though weights reflect the entire candidate set.

| Model | AICc | $\Delta AIC_c$ | $w_i$ | LL | K |
|---|---|---|---|---|---|
| IMP250 + NEAR | 63.16 | 0.0 | 0.20 | -25.08 | 6 |
| IMP250 + NEAR + BULLFROG | 63.59 | 0.43 | 0.16 | -23.58 | 7 |
| IMP250 + NEAR + FISH | 63.63 | 0.47 | 0.16 | -23.6 | 7 |
| IMP250 | 64.15 | 0.99 | 0.12 | -27.12 | 5 |
| IMP250 + NEAR + DEPTH | 65.52 | 2.36 | 0.06 | -24.55 | 7 |
| IMP250 + BULLFROG$^A$ | 65.79 | 2.64 | 0.05 | -26.40 | 6 |
| IMP250 + FISH | 65.92 | 2.76 | 0.05 | -26.46 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| IMP250 + NEAR + CANOPY$^A$ | 66.31 | 3.15 | 0.04 | -24.94 | 7 |
| IMP250 + DEPTH | 66.32 | 3.16 | 0.04 | -26.66 | 6 |
| IMP250 + CANOPY | 66.91 | 3.75 | 0.03 | -26.95 | 6 |

| Covariate | $w_+$ | Effect |
|---|---|---|
| IMP250 | 0.99 | – |
| NEAR | 0.62 | – |
| BULLFROG | 0.26 | – |
| FISH | 0.25 | – |
| DEPTH | 0.15 | + |
| CANOPY | 0.11 | – |

$AIC_c$ is Akaike's information criterion corrected for small sample sizes; $\Delta AIC_c$ is the difference in $AIC_c$ value from the top-ranked model; $w_i$ is Akaike weight; LL is the log-likelihood; K is the number of estimated parameters in the model, including thresholds; IMP250 is percent impervious cover within 250 m; NEAR is distance to nearest pond; $w_+$ is relative variable importance; Effect is the direction of the model averaged coefficient estimate; superscript ‘A’ denotes model was ill-defined (condition of the Hessian > 10e4).

## 3.5 Discussion

In this study, I document the use of natural and constructed wetlands in rural and urban areas by chorusing *P. regilla*. Auditory surveys during the peak breeding season detected *P. regilla* at all but one rural pond and at nearly half of urban ponds, demonstrating that the species is persisting in spite of urban and rural development. There was great diversity in the local and landscape-scale habitat characteristics of occupied ponds, even within urban and rural areas, demonstrating that *P. regilla*’s characterization as a habitat generalist extends to urban and rural ecosystems. Surprisingly, *P. regilla* were not detected at waterways, with one exception. I used occupancy and ordinal regression models structured around *a priori* hypotheses to identify whether occupancy and relative abundance at ponds in the developed landscape are driven by a single characteristic or scale, or by multiple characteristics operating at different scales, and what the scales of greatest impact are. The main caveats for this study are that (1) the presence of chorusing males is not evidence of successful breeding or survival of offspring; therefore, further research of other life stages is needed; (2) the identified species-habitat relationships are correlational rather than causal, although known ecological mechanisms explain the observed relationships; (3) there may be other habitat characteristics that are influential that were not considered in this study; and (4) an ability to detect effects and estimate model parameters with a high level of precision are limited by the small sample size. Nevertheless, agreement in the best-supported hypothesis and scale of influence, combined with similarities in the combined model candidate sets and relative variable weights, allows some confidence in the quality of the results of both model frameworks.

### 3.5.1 The terrestrial habitat hypothesis

Among competing hypotheses, terrestrial habitat availability was identified as the most influential factor for both occupancy and relative abundance. The terrestrial habitat characteristic and scale that was best supported by the data was percent impervious cover within 250 metres of a pond. It is increasingly apparent that aquatic-breeding amphibian occurrence and abundance are, in general, influenced more by the quality and availability of terrestrial habitat than by characteristics of their aquatic breeding sites, and it appears that *P. regilla* is no exception. The results of this study echo those of Lehtinen et al. (1999), who found that the influence of urban land use on amphibian species richness in urbanizing ecoregions was so strong that it made all other factors relatively unimportant. Furthermore, in their meta-analysis of the relative effects of wetland amount and terrestrial habitat matrix quality on amphibians, Quesnelle et al. (2015) found that terrestrial habitat was a more important driver of abundance, density and occupancy than wetland amount. Indeed, I found that percent wetland cover at the landscape scale and aquatic habitat characteristics at the local scale received little support in the data relative to impervious cover for both occupancy and relative abundance. It should be noted, before proceeding, that an underlying bias exists among studies that sample aquatic habitats and make inferences about the importance of surrounding terrestrial habitat characteristics: the presence of aquatic habitat is, in itself, a tremendously important influence on site occupancy. Even in the most undisturbed landscapes, frogs may not be present if there is no aquatic habitat to breed in.

*P. regilla* occupancy and relative abundance showed a strong negative response to impervious cover. This relationship has been observed for other aquatic-breeding amphibians (e.g. Richter & Azous 1995; Knutson et al. 1999; Simon et al. 2009) and there are many explanations for this relationship. Relative to rural and undeveloped wetlands, urban wetlands, which are characterized by higher impervious cover on the surrounding landscape, have been shown to have greater water level fluctuations due to higher surface water flow and lower water retention capabilities due to water level control modifications (Reinelt & Taylor 2001; Kentula et al. 2004). These hydrologic patterns can cause the eggs of aquatic-breeding amphibians to be stranded above water (Reinelt et al. 1998; Hayes et al. 2008), leading to desiccation, mortality and a decline in population abundance. Furthermore, stormwater runoff from roads and other impervious surfaces is well known to carry higher concentrations of pollutants (St-Hilaire et al. 2016), which can contaminate receiving wetlands and create a toxic environment for amphibians. While conductivity at sampled wetlands was likely below the tolerance limits for *P. regilla* (Chambers 2011), I found that conductivity increased as impervious cover increased, such that wetlands in areas of higher impervious cover may have intolerable conductivity levels (Figure 3.2). Additionally, impervious surfaces, such as roads, buildings, and parking lots, limit habitat connectivity by presenting amphibians with barriers to movement and generally high landscape resistance due to risk of desiccation and road mortality.

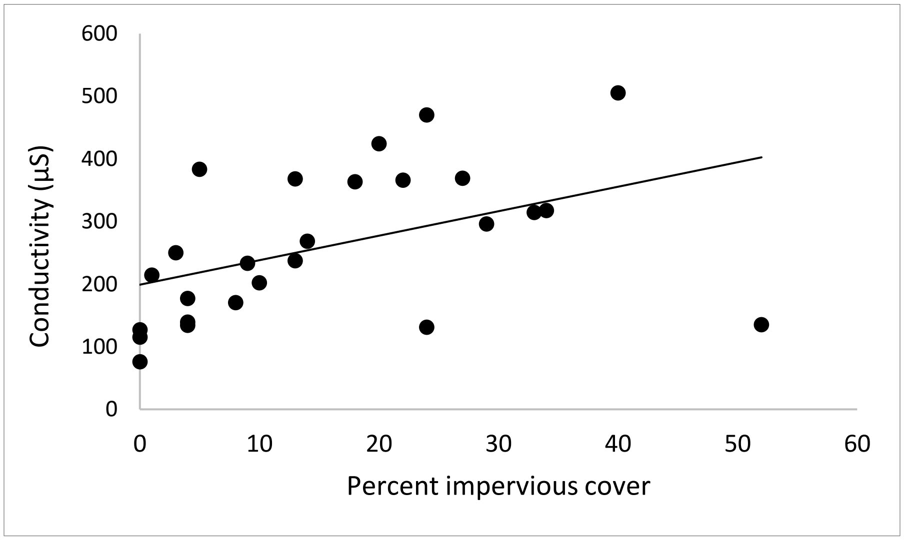

**Figure 3.2** The positive relationship between water conductivity (µS) and impervious surface cover within 250 m of study ponds.

The scale of greatest influence for impervious cover was 250 meters (Table 3.3), suggesting that 250 meters represents the typical home range of *P. regilla*. While no study has investigated *P. regilla* home range size directly, one of the earliest studies of *P. regilla* natural history found that most juveniles that had settled post dispersal remained within 200 metres of their natal pond, while all juveniles recovered were found within 250 metres

(Jameson 1956). Other early researchers incidentally observed adult *P. regilla* hibernating in small holes in the soil on grassy hills approximately 450 metres from a known breeding site (Brattstrom & Warren 1955). To my knowledge, the investigation of *P. regilla* home range size appears to have ended with Schaub and Larsen's 1978 study of the reproductive ecology of *P. regilla*, in which they describe the species as relatively sedentary, tending to remain within 10 metres of the same pond during the breeding season, but capable of moving up to 400 metres. Based on these accounts, it appears as though *P. regilla* home range size is naturally 250-500 metres around a wetland in undisturbed habitats. The importance of impervious cover within 250 metres leads me to speculate that rural and urban development might restrict home range to the lower limit of this range.

In contrast to impervious cover, I detected no influence of tree cover on occupancy or relative abundance. Other researchers have failed to detect anything more than a weak relationship between *P. regilla* and tree/forest cover (Pearl et al. 2005; Guderyahn et al. 2016). In fact, Rorabaugh and Lannoo (2005) suggest that one of the common names of *P. regilla*, “Pacific treefrog,” is a misnomer because the species does not favour trees and is not known to climb to great heights; rather, the species is often found closer to the ground and has been associated with all varieties of low plant growth as well as coarse woody debris, rocks, and animal burrows—anywhere it can find a damp microclimate. Thus, impervious cover is likely so impactful, not because of the aforementioned adverse indirect effects, though these may also be important, but because it is essentially the inverse of habitat cover. As impervious cover increases, there is a direct and proportional decrease in the terrestrial habitats that are thought to support *P. regilla* outside of the breeding season, including naturally occurring shrub, herbaceous vegetation, and grassland cover (Rorabaugh & Lannoo 2005), as well as human-modified ecosystems in cropland, parks, golf courses, cemeteries, and gardens. The latter “hybrid” ecosystems, which may bear differences in community composition from current or historic ecosystems (Hobbs et al. 2009), may still function to provide habitat or food resources for *P. regilla* (Kennedy et al. 2013). These heavily modified habitats have typically been viewed as degraded, though they may bring with them certain advantages, such as a lower abundance of predators. The value of hybrid and completely novel ecosystems for native amphibians is an emerging research area that has great applicability in urbanizing regions (e.g. Pethiyagoda & Manamendra-Arachchi 2012).

### 3.5.2 The habitat connectivity hypothesis

In addition to terrestrial habitat availability, this study is further evidence of the importance of habitat connectivity for *P. regilla*. The habitat connectivity hypothesis considered the influence of aquatic habitat connectivity and isolation (wetland cover, number of ponds, distance to nearest pond) and general habitat fragmentation (road density) on occupancy and relative abundance. While it was not competitive with other hypothesis-based models (Table 3.5 & 3.7), habitat connectivity variables appeared in competing top models when combined with other covariates (Table 3.8 & 3.9). Specifically, the number of ponds within 1500 m was identified as having a moderate influence on *P. regilla* occupancy ($w_+ = 0.39$; Table 3.8), and for relative abundance, distance to the nearest pond was an important factor ($w_+ = 0.62$; Table 3.9).

Road density was identified as one of two important variables relating habitat connectivity to relative abundance (Table 3.6); however, road density could not be considered during *a posteriori* analysis due to its high correlation with impervious cover-250. Relative abundance had a negative response to increasing road density that was most pronounced at the 500 m scale (Figure 3.3). The negative impact of roads on amphibian abundance is well documented (e.g. Fahrig et al. 1995, Lehtinen et al. 1999, Houlahan and Findlay 2003). Roads contribute significantly to amphibian mortality via vehicle collisions (Fahrig et al. 1995, Garrah et al. 2015), and even low-traffic roads may bring about amphibian mortality through contact with exhaust emissions, road salt, oil, and other pollutants (Fahrig et al. 1995; Lefcort et al. 1997; Sanzo & Hecnar 2006). Furthermore, high levels of ambient traffic noise have been shown to significantly mask the breeding calls of *P. regilla*, which are not able to alter the volume, duration or timing of their calls in response to the level of ambient noise at the breeding site (Nelson et al. 2017b). Diminished communication could impede the breeding activities of *P. regilla*, from breeding site orientation to mate selection, with long term consequences for population persistence (Nelson et al. 2017b). This negative relationship with roads may explain the absence of *P. regilla* from ditch sites, the majority of which were located adjacent to roads.

While I was unable to calculate a statistically significant threshold for maximum road density, *P. regilla* was not detected at ponds where road density exceeded 0.092 m/m$^2$ within 500 metres (Table 3.10).

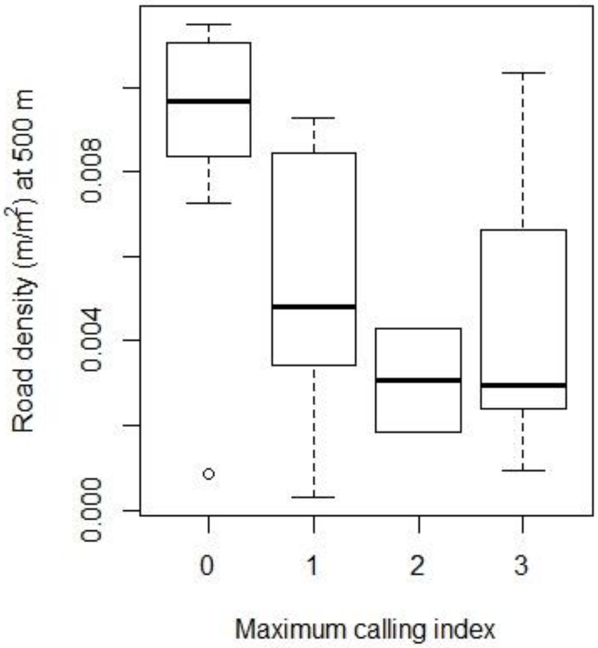

**Figure 3.3** The negative relationship between relative abundance (maximum calling index) and road density within 500 m of a pond. Whiskers represent upper and lower quartiles, the horizontal black line the median, and dots represent outliers.

**Table 3.10** Descriptive statistics of local and landscape variables measured in and around occupied ponds (n=18). Values represent median (range) unless otherwise noted. Note only four of eight landscape scales are displayed.

| | Scale of measurement | | | |
|---|---|---|---|---|
| Variable | **Local** | | | |
| **AREA** | 2807 (63-84266) | | | |
| **DEPTH** | 41.2 (16.4-67.9) | | | |
| **AQVEG** | 33 (6-74) | | | |
| **BULLFROG**$^{A}$ | 12 (67%) | | | |
| **FISH**$^{A}$ | 6 (33%) | | | |
| **NEAR** | 82.5 (6-507) | | | |
| | **50 m** | **150 m** | **500 m** | **1500 m** |
| **%FOR** | 42 (5-73) | 40.5 (8-74) | 43.5 (23-80) | 49 (20-74) |
| **%IMP** | 8 (0-29) | 9.7 (0-24) | 7.5 (0-34) | 8 (3-38) |
| **%WET** | 12.8 (0.9-57.9) | 4.3 (0.2-51.2) | 1.8 (0.1-42) | 2.6 (0.2-14.3) |
| **RD** | 0 (0-0.011) | 0.0050 (0-0.0093) | 0.0036 (2.9e$^{-4}$-0.092) | 0.0038 (0.0021-0.011) |

| | | | | |
|---|---|---|---|---|
| **PONDS** | 1 (1-6) | 3 (1-7) | 15.5 (1-23) | 84.5 (28-133) |

AREA = aquatic footprint (m$^2$); AQVEG = Percent cover emergent/submerged vegetation within 1 m of shore; DEPTH = water depth at 1 m from shore (cm); NEAR = distance to nearest neighbour pond (m); %FOR = percent forest cover; %IMP = percent impervious surface cover; %WET = percent wetland cover; RD = road density (m/m$^2$); PONDS = count of ponds.

[A] Values represent: count of ponds occupied by bullfrogs or fish (percent of occupied ponds with species co-occurrence).

Habitat connectivity is important for persistence of populations that exist in habitat patches that are not big enough to be self-sustaining in the face of demographic and environmental stochasticity or deterministic processes. Many amphibian species are considered, either in theory or from empirical evidence, to exist as metapopulations (Marsh & Trenham 2001; Smith & Green 2005), insomuch as they form local breeding populations in discrete habitat patches (e.g. ponds), all of which are subject to varying risks of extinction, and many of which are not so isolated as to prevent eventual recolonization (Hanski 1997). Furthermore, a species that does not exhibit metapopulation dynamics in undisturbed landscapes may form metapopulations when movements are restricted by habitat loss and fragmentation (Marsh & Trenham 2001). Consistent with the metapopulation concept, the positive relationship between *P. regilla* occupancy and the number of ponds within 1500 metres suggests that *P. regilla* is reliant, to some degree, on occasional dispersal events to maintain local populations, and that the likelihood of occurrence increases as the number of "donor" ponds within a maximum migration distance increases. While *P. regilla* appear to show strong site fidelity and do not tend to make long-distance movements, as previously described, this is not evidence of low vagility. On the contrary, *P. regilla* are capable of moving at least 1900 metres in search of suitable habitat post displacement (Reimchen 1990). Model support for the number of ponds within 1500 metres suggests that this may be the scale at which metapopulation dynamics play out for *P. regilla* in a developed landscape. Focused research on *P. regilla* migration and dispersal in developed landscapes is needed.

Further inferences can be made about *P. regilla* metapopulation structure in the developed landscape based upon the negative relationship between *P. regilla* relative abundance and distance to the nearest pond. In general, maximum calling index (relative abundance) increased as the distance to the nearest pond decreased (Figure 3.4). *P. regilla* were absent from ponds that were located a distance of 300 metres or more from the nearest neighbour pond, whereas the majority of ponds in which a chorus was detected were located less than 200 m from the nearest neighbour pond. This sensitivity to pond isolation at a relatively small scale suggests that *P. regilla* exhibits a metapopulation in which short-distance movements within a patchy core population (e.g. cluster of ponds) are supplemented by occasional long-distance movements to peripheral populations (Hanski 1997). This type of metapopulation structure seems highly plausible for this species, particularly in the context of an urbanizing landscape in which patches of remnant habitat and intense development are irregularly distributed. Regardless of population structure, it would seem that *P. regilla* relative abundance, and therefore persistence, in a developed landscape is linked to the proximity of neighbouring ponds, and that conservation efforts are more likely to be successful where ponds are not isolated from other aquatic habitat by more than 300 metres.

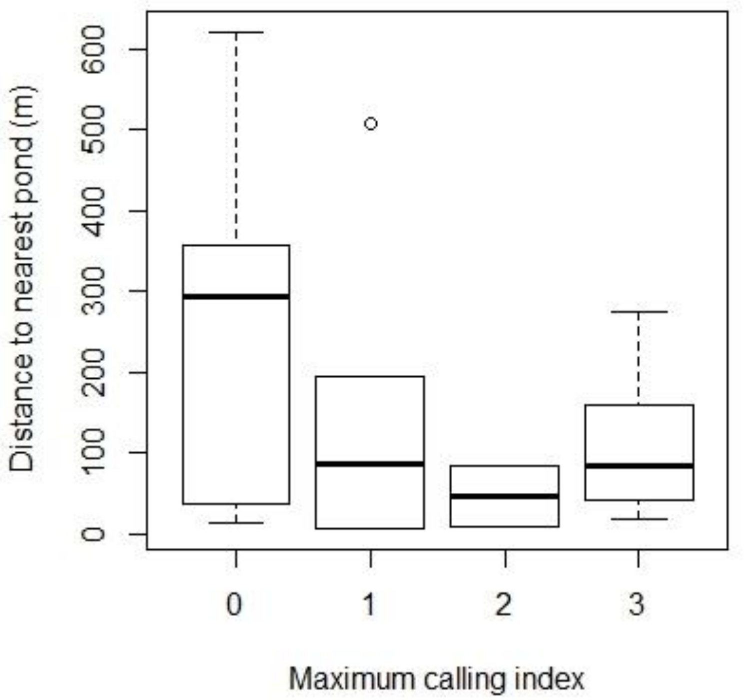

**Figure 3.4** The negative relationship between relative abundance (maximum calling index) and distance to nearest pond. Whiskers represent upper and lower quartiles, the horizontal black line the median, and dots represent outliers.

### 3.5.3 The non-native predators hypothesis

The predation pressure by non-native predators hypothesis received little or no support at all modeling stages. Bullfrog-only and fish-only models received less support than the null model for occupancy (Table 3.4), so it is not surprising that the predation pressure hypothesis was not supported when compared with other hypotheses for occupancy (Table 3.5). The presence of bullfrogs and/or fish also did not explain relative abundance (Table 3.7). However, bullfrog and non-native fish variables appeared with considerable Akaike weight in competing models during *a posteriori* analysis (Table 3.8 & 3.9). Thus, my research does not add clarity to the question of whether bullfrogs, non-native fish, or a combination of bullfrogs and non-native fish pose a serious threat to native amphibians.

There is ample evidence that bullfrogs compete with, and predate on, native amphibians (Ehrlich 1979; Werner et al. 1995; Kiesecker & Blaustein 1997; Pearl et al. 2004), but after decades of research on the threat posed by bullfrog invasions, their impact on the survival rates and long-term persistence of native amphibians remains unclear. For example, Moyle (1973), Fisher and Shaffer (1996) and many others have associated bullfrog invasions with native amphibian declines, but when relationships were investigated under field conditions or in an experimental setting, direct negative effects on pond occupancy and survival rates were not detected or only weakly detected (Adams 1999, Govindarajulu 2004, Pearl et al. 2005 though see Kiesecker et al. 2001). It has been suggested that non-native fish pose a greater threat to native amphibians than bullfrogs (Hayes & Jennings 1986; Monello & Wright 1999; Adams 2000; Pearl et al. 2005; Rowe & Garcia 2014). This may be due to a lack of evolved fish predator avoidance traits because of low habitat overlap between tadpoles and native fish, greater vulnerability to non-native fish predation during embryonic and larval life stages, or a matter of likelihood given the large number of non-native fish species that have been introduced (Hayes & Jennings 1986). Alternatively, there is some indication that the combination of bullfrogs and non-native fish exerts the greatest pressure on native amphibian populations, as multiple facilitative interactions have been observed between non-native fish and bullfrogs (Kiesecker & Blaustein 1998; Adams et al. 2003).

My observations suggest that the presence of predators is not deterring habitat use and there is little evidence to suggest that non-native predators are limiting abundance: *P.*

*regilla* were more commonly found in ponds with bullfrogs than without, and were found in five of eight ponds in which fish were detected. Furthermore maximum calling index was more commonly 2 or 3 in ponds in which *P. regilla* co-occurred with bullfrogs, non-native fish, or both types predator. Nevertheless, the moderate negative impact of non-native predators on occupancy and relative abundance, as indicated in the combined models (Table 3.8 & 3.9), can be mitigated against with the restoration and creation of temporary wetlands that have a hydroperiod sufficient to support native tadpoles to metamorphosis but which does not support the permanent water requirements of bullfrogs and fish (Snodgrass et al. 2000; Govindarajulu 2004; Pearl et al. 2005).

### 3.5.4 The aquatic habitat hypothesis

The top aquatic habitat model for both occupancy and relative abundance was a depth-only model that indicated a positive relationship: the deeper the littoral zone, the higher the probability of occupancy and the greater the calling index. However, during *a posteriori* analysis littoral depth did not appear in top models and was of low importance relative to other variables ($w_+$= 0.23 and 0.15 for occupancy and relative abundance, respectively). The response of aquatic-breeding amphibians to water depth has been shown to be species-specific (e.g. Licht 1969, Hamer et al. 2012, Guderyahn et al. 2016). *P. regilla* egg masses are commonly found at depths less than 10 cm (Rorabaugh & Lannoo 2005). Shallow water warms more rapidly, and warmer temperatures can be beneficial because they speed embryo development (Licht 1971). Deeper water is more resistant to extreme water level fluctuations and provides a greater range of temperatures along the water column for tadpoles to thermoregulate (Dupré & Petranka 1985). Deeper water may also provide a refuge for tadpoles from adult bullfrogs (Kiesecker & Blaustein 1998). Thus, the positive relationship with littoral depth may be the result of greater microhabitat diversity. Another explanation for the positive relationship with water depth is the relationship between water depth and hydroperiod: deeper ponds recede and dry more slowly than shallow ponds. The period of *P. regilla* larval development overlaps with the dry season on southern Vancouver Island and populations are unlikely to persist at ponds that dry before larva complete metamorphosis; therefore, deeper ponds may be beneficial in this region. Guderyahn et al. (2016) also report a positive relationship between *P. regilla* and water depth, but note a threshold water depth of 60 cm, above which the relationship transitioned from positive to negative; it is possible that this threshold was not detected in this study due to the small sample, within which depth ranged from 15-68 cm.

Models revealed a weak positive relationship between occupancy and aquatic vegetation and a weak negative relationship with canopy density. The weakness of these relationships was unexpected because *P. regilla* are typically associated with open wetlands with abundant aquatic vegetation. It is probable that failure to detect a stronger response to these variables is the result of the small sample size. Many other researchers have found a positive relationship between amphibian presence, abundance, or diversity and aquatic vegetation cover (e.g. Pearl et al. 2005, Hamer and Parris 2011, Holzer 2014), attributing the relationship to the provision of structures for oviposition, grazing habitat for tadpoles, or protective cover for all life stages, among other qualities. Likewise, a number of studies have found a strong negative relationship between anurans and canopy cover (Werner et al. 2007; Skelly et al. 2014). More exposed sites tend to be warmer, speeding embryo development, and have higher primary productivity which increases resource availability and quality for tadpoles (Werner et al. 2007). On the other hand, the observed relationships for these aquatic habitat variables may reflect *P. regilla*'s tolerance of a range of UV light conditions (Ovaska et al. 1997; Blaustein et al. 2003) and their ability to oviposit on floating structures as well as the wetland bottom (Rorabaugh & Lannoo 2005). Again, due to the small sample size, I was unable to identify thresholds for minimum aquatic vegetation cover and maximum canopy density. More research in this area, including specific plant species associations, would benefit breeding habitat design.

### 3.5.5 Detectability

Among top models of detection probability (constant $\psi$), mean detection probability ranged from 0.68-0.75 (Table 3.1), which is in agreement with my initial detection probability estimate of 0.7 (Appendix F). The considerable model selection uncertainty regarding detection factors suggests that *P. regilla* detectability is not strongly influenced by any of the sampling covariates measured, nor by pond area and the presence of non-native predators (Table 3.1). Nevertheless, *P. regilla* detection was positively, albeit weakly, related to minutes since sunset and negatively related to bullfrog presence, anthropogenic disturbance, and relative humidity. The former three relationships can be readily explained. *P. regilla* move towards ponds and begin to call around sunset (Allan 1973); this chorus may continue well into the morning (past 0200 hours) (Nelson et al. 2017). It is therefore reasonable to expect that the chorus (and therefore detectability) will increase in intensity with minutes since sunset as individuals are drawn to the wetland and this increased density increases the number of interactions and related vocalizations (Allan 1973; Brenowitz 1989). Anthropogenic noise may directly impede call detection by masking calls of distant or few individuals or by supressing calling behaviour. Given the audibility of *P. regilla* calls (Brenowitz 1989), it is more likely that *P. regilla* call less in the presence of the anthropogenic activity associated with the noise disturbance (e.g. vibrations from traffic on roads, predator cues from barking dogs, etc.). Interestingly, anthropogenic noise and time since sunset were only very weakly correlated ($r_s = -0.17$). Finally, it is possible that *P. regilla* alter their calling behaviour in the presence of American bullfrogs, and may cease calling altogether depending on bullfrog density: Brattstrom and Warren (1955) observed that *P. regilla* would call in the presence of American bullfrogs but not within 4 feet. This interaction, which would have serious implications for *P. regilla* persistence in the face of bullfrog range expansions and population explosions, can be further investigated experimentally or through field observations at sites where the two species are known to co-occur.

The negative effect of relative humidity on *P. regilla* detectability is surprising and defies explanation. Relative humidity is defined by the National Oceanic and Atmospheric Administration as “[the] ratio, expressed in percent, of the amount of atmospheric moisture present relative to the amount that would be present if the air were saturated. Since the latter amount is dependent on temperature, relative humidity is a function of both moisture content and temperature” (NOAA n.d.). The cooler the air, the lower its moisture capacity and saturation point and the higher the relative humidity. Thus, relative humidity will generally increase through the night and early morning as temperatures cool, and decline sharply after sunrise as temperatures rise and moisture evaporates. The temporal pattern of relative humidity is similar to that of *P. regilla* calling activity, leading one to expect a positive effect of relative humidity within the species’ temperature tolerance. Steelman and Dorcas (2010) and Cui et al. (2011) also detected a negative relationship between anuran calling activity and relative humidity, which was contrary to their expectation that higher relative humidity would imply greater surface moisture availability, which would correlate with higher calling activity. Neither group of researchers was able to suggest a biological mechanism for the negative relationship, whereas a positive relationship between anuran calling activity and relative humidity has been explained by a reduced risk of desiccation and improved call transmission (sound travels better through humid air than dry; Oseen and Wassersug 2002). Therefore, it is possible that the relationship I identified is a product of the small sample size and would disappear or change with a greater sample size.

This study has provided future researchers with an initial detection probability estimate for study design and identified factors that may influence detectability for *P. regilla*. The top model estimate ($\hat{p} = 0.71$) was similar to that of the constant detection probability model ($p = 0.75$). The latter model had some support in the data ($\Delta AIC_c < 4$), indicating that even in a developed landscape, and provided survey conditions meet NAAMP protocol criteria, *P. regilla* are readily detected.

### 3.5.6 The absence of *Pseudacris regilla* from waterways

The most surprising outcome of this study was the absence of *P. regilla* from all waterway sites. *P. regilla* are well known to breed in slow-flowing streams and ditches (Rorabaugh & Lannoo 2005) and this habitat use is not limited to undisturbed landscapes: Riley et al. (2005) observed *P. regilla* tadpoles in all streams surveyed in the Los Angeles area. It is possible that the large proportion of non-detections are a consequence of inhospitable local characteristics arising by chance. As previously described, waterway sites were significantly shallower and shadier, which may partly explain the absence of *P. regilla*. The absence of *P. regilla* from waterways may also be another response to the many impacts of impervious cover. Waterways, particularly roadside ditches, in urbanizing watersheds are known to receive high concentrations of pollutants transported by overland flow of stormwater (Barrett et al. 2010; St-Hilaire et al. 2016). Urban and rural waterways are also known to have a greater frequency and magnitude of high water flow, which can flush amphibian larvae out of suitable habitat (Barrett et al. 2010). Additionally, stream benthic invertebrate biomass has been shown to decline with increasing impervious cover at scales ranging from the riparian buffer (tens or hundreds of metres) to the sub-basin (kilometres), indicating that waterways in urbanizing watersheds are in poor biological condition (Morley & Karr 2002). While water depth and flow were not monitored throughout the study, given the significance of impervious cover in models of pond occupancy and abundance, I believe that the most plausible explanations for the absence of *P. regilla* from waterways are rooted in the flashy response of the system to impervious cover, particularly in regions that experience high rainfall.

### 3.5.7 Conclusion

A primary implication of the negative relationship between impervious cover and *P. regilla* occurrence and relative abundance is that densification of urban areas and development of rural areas will need to be managed with caution if the "flagship" amphibian of urbanizing western North America is to persist. Thoughtful and innovative approaches to densification and development that retain existing vegetation wherever possible, limit impervious surface cover to 20% within 250 m of frog ponds, and incorporate herbaceous and shrub vegetation (the closest approximation of natural habitat) in place of lawns should ensure that *P. regilla* populations will have sufficient terrestrial habitat to compliment breeding habitat.

Metapopulation dynamics can be supported by maintaining structural connectivity and enhancing matrix permeability, including strategically-placed riparian corridors and road underpasses. My results suggest that the number of ponds on the landscape at a scale of 1500 m and the proximity of nearest neighbour ponds are important positive factors for pond occupancy and relative abundance, respectively. When selecting sites for breeding habitat restoration or construction, managers should consider placing ponds within 200 m of other suitable ponds to increase population resilience while maintaining a number of ponds at a scale of 1500 m for metapopulation resilience. In urbanizing regions in which a large proportion of the landscape is privately owned, one of the greatest challenges to amphibian conservation efforts will be coordinated management and landowner cooperation.

A number of within-pond management considerations can be inferred from my results. Within-pond conservation priorities should shift from bullfrog population control, which is costly and, under certain circumstances, ineffective (Govindarajulu et al. 2005;

Adams & Pearl 2007), to ongoing monitoring of bullfrog and native frog population numbers where the species co-occur. In addition, created ponds could be designed to be temporary (with a hydroperiod sufficiently long to support *P. regilla* offspring to metamorphosis) so as to exclude fish and bullfrog larvae. Pond restoration or creation designs should include a wide depth gradient within the littoral zone. Aquatic vegetation should be maintained with a minimum of 20% coverage.

This study provides support for municipalities planning or implementing aquatic-breeding amphibian habitat restoration and creation initiatives. Although urban and rural development has led to habitat loss and fragmentation, to date *P. regilla* has been able to persist in relict natural habitats as well as novel ones. However, status quo urbanization, including densification of existing urban areas and expansion into rural surroundings, will likely result in the extirpation of *P. regilla* from human population centres due to increased impervious cover and resultant habitat loss and fragmentation. This would be a missed opportunity to enhance regional biodiversity and sustainability. Aquatic breeding amphibians are an important component of the food web, both as predators and prey, supporting the flow of nutrients between aquatic and terrestrial environments and helping to control insect populations (Wells 2010; Bishop et al. 2014). Due to their physiology and complex habitat requirements, amphibians are vulnerable to many environmental stressors and pollutants, making them a good indicator of ecosystem health (U.S. EPA 2002, Blaustein et al. 2003, but see Kerby et al. 2010). Amphibians are also excellent wildlife “ambassadors;” the presence of this non-threatening, brightly-coloured frog and its breeding chorus (recognizable as the classic Hollywood jungle scene’s ambient noise) can be used to address the growing disconnect between urban children and nature (Louv 2008). For urbanizing regions, such as southwestern British Columbia, I suggest that there currently exists a window of opportunity to conserve identified habitat and create new habitat for *P. regilla* using the suitability criteria identified by this, and other, studies.

# Chapter 4 Conclusion

Aquatic and terrestrial ecosystems around the world are becoming increasingly modified by human activity (Vitousek et al. 1997). In the midst of the amphibian biodiversity crisis (Stuart et al. 2004), the urgency to understand the severity and scope of the impacts of these changes on amphibians has never been greater. Over the past three decades, the number of studies published on amphibian conservation has increased steadily, with the proportion of conservation papers published on amphibians more than doubling between 1990 and 2010 alone (Ficetola 2015). We now have a better understanding of the potential underlying, in some cases synergistic, causes of decline as well as improved research and analytical methods for observing and interpreting species-specific responses (Ficetola 2015). Having identified habitat loss and fragmentation due to development as a primary driver of amphibian declines (Cushman 2006), and responses to development as species-specific (Hamer & McDonnell 2008), we are currently in a phase of research in which we are prioritizing species for surveys of distribution and abundance, observational and experimental studies of habitat use and movement in developed landscapes, and analysis of responses to development along an urbanization gradient. For species whose ecology and behaviour are not yet fully documented, urban ecological studies may also prove valuable for management within undeveloped landscapes, such as protected areas.

In this thesis, I address some of these research areas for two native frog species whose ranges overlap heavily with urbanization in northwestern North America. I investigate species-habitat relationships for the northern red-legged frog and Pacific chorus frog, two species with different apparent disturbance tolerances, habitat associations, and justifications for conservation. I investigate relationships across aquatic and terrestrial habitats and between multiple spatial scales within the developed landscape. For *R. aurora*, I observe similarities between occupied wetlands that suggest a sensitivity to adjacent forest patch size and proximity, the presence of road barriers, and the proportion of tree cover within the landscape matrix at all biologically relevant scales. *P. regilla*, on the other hand, was more strongly impacted by the proportion of impervious cover at the scale of (what may be) its home range than any other terrestrial or aquatic habitat characteristic. My research adds to a small but growing body of literature on the urban ecology of *R. aurora* and *P. regilla* (Richter & Azous 1995; Pearl et al. 2005; Riley et al. 2005; Mathias

2008; Holcomb 2012; Holzer 2014; Rowe & Garcia 2014; Guderyahn et al. 2016; Grand et al. 2017), which can be used both to inform site-level habitat suitability assessments and towards developing a regional conservation strategy that integrates and harnesses urban ecosystems.

## 4.1 Management implications

This study is further evidence of the use of both urban and constructed wetlands by *R. aurora* and *P. regilla*, which is indication that urban habitat restoration and wetland creation efforts may be successful when local and landscape habitat suitability criteria are met. While further research to confirm species-habitat relationships and isolate the biological mechanisms underlying responses to landscape scale factors would be beneficial, my findings provide biologically defensible criteria to inform management strategies in the interim. I make the following general recommendations for conserving, restoring, and creating suitable breeding habitat for *R. aurora* and *P. regilla* in urbanizing regions:

(1) Around the breeding habitat of *R. aurora* and other forest-associated amphibians, maintain large patches of remnant forest (patches with core forest free of edge effects may be sufficiently large) and expand smaller patches where possible.

(2) Prioritize wetland restoration and creation for locations surrounded by less than 20% impervious cover and greater than 50% forest cover to address the terrestrial habitat requirements of both *P. regilla* and *R. aurora*, which together may represent the spectrum of amphibian responses to urbanization.

(3) Within a management zone of 2 km around occupied wetlands, efforts should be made to support migration and dispersal movements of both species. Connectivity between identified *R. aurora* breeding habitat and neighbouring forest patches should be enhanced. In the medium term, this can be achieved with the installation of road underpasses or the closure of roads during migration periods; in the long term, connectivity can be enhanced by establishing forested corridors.

(4) Discourage the use of impervious materials for new development and replace impervious with pervious materials whenever possible. Similarly, encourage

landscaping with native grasses, forbs, and shrubs in place of lawns to increase foraging habitat for *P. regilla*.

(5) Continue to monitor the impacts of both American bullfrogs and non-native fish on native amphibians, which are complex, synergistic, and may be related to structural characteristics of aquatic habitat (Kiesecker & Blaustein 1997, 1998; Kiesecker et al. 2001; Govindarajulu 2004; Pearl et al. 2005).

(6) Maintain and enhance aquatic vegetation cover in breeding and rearing habitat.

(7) Monitor water levels to assess impacts on egg masses and mitigate fluctuations due to stormwater runoff where possible.

(8) Coordinate management efforts among private landowners and municipal governments. A regional or provincial government-led program that registers created and constructed ponds and oversees monitoring efforts could help achieve this.

## 4.2 Applications

There are a number of practical applications for my findings. Foremost among these is the creation of habitat suitability maps to identify wetlands in the developed landscape where the focal species may occur. Many wetlands in urban and rural areas are constructed for purposes other than the provision of wildlife habitat. In this region, these include ornamental ponds on golf courses and in private gardens, reservoirs for agriculture, stormwater treatment ponds, and roadside ditches. These wetlands may attract breeding amphibians but because they are not managed for wildlife they may inadvertently become ecological traps. For example, golf course ponds may accumulate high concentrations of pesticides and fungicides and stormwater treatment ponds are intended to process pollutants (Metcalfe et al. 2008; Snodgrass et al. 2008), yet both wetland types may have features of natural wetlands that appear attractive to amphibians (Hale et al. 2015). Indeed, amphibians have been documented using a number of constructed, unintended habitats (e.g. Hamer et al. 2012, Saarikivi et al. 2013, Homyack et al. 2016), and I detected *P. regilla* in three of three active agricultural reservoirs and four of four golf course ponds surveyed. The long term persistence of these populations will depend, in part, on awareness of their existence by the private landowners and efforts to mitigate negative impacts. Thus, urban and rural land managers ought to have a responsibility to manage aquatic elements of the built environment to ensure that they are contributing to, rather than counteracting, amphibian conservation. Managers can use the criteria I identify in this thesis to locate areas of the landscape that have a high likelihood of amphibian occurrence and in doing so prioritize presence-absence surveys, landowner outreach, and within-wetland remediation or enhancement activities where occupancy is confirmed.

Identified habitat suitability criteria can also aid managers in locating or assessing the suitability of candidate sites for proactive wetland creation or restoration. Several municipalities in this region have taken an interest in restoring and creating wetlands for the dual purpose of increasing biodiversity and providing ecosystem services (e.g. City of Portland 2009, Schaefer and Miles 2013, Golds 2016), and provincial and state governments have established general guidelines for such projects (Stevens & Vanbianchi 1993; Devroy et al. 2000; Cox & Cullington 2009). My findings can increase the specificity of existing development guidelines as they pertain to habitat for *R. aurora* and *P. regilla*. Location of the most suitable candidate sites at landscape scales will increase the likelihood of colonization and persistence of these species at the local scale. Similarly, landscape-scale suitability criteria can be used to prioritize sites for restoration or enhancement to reduce inter-pond isolation, which may improve population and metapopulation resilience. Whether a wetland has been designed for amphibians or not, the risk of forming an ecological trap is inherent among restored and created wetlands because there may be a mismatch between perceived and actual habitat suitability (Hale et al. 2015); therefore, long term monitoring is essential.

## 4.3 Future research

In his 2006 review of the state-of-the-knowledge of amphibian research in developed landscapes, Cushman suggests that “conservation strategies would benefit by moving from generalizations to species and process specific recommendations and by moving from site-specific actions to implementing conservation plans at multiple scales across broad landscapes” (231). Similarly, Scheffers and Paszkowski (2012) called for a shift towards studies that do more than simply “document negative associations between urbanization and amphibians” without definitively identifying “mechanisms that link predictive urban metrics and response variables such as abundance or species richness" (134). By identifying factors to which *P. regilla* and *R. aurora* respond most strongly, and the scales of importance for these factors, I lay the groundwork for such studies.

Within the constraints of a small sample size, I identify percent impervious cover within 250 metres of a breeding site as the most influential driver of *P. regilla* occurrence and relative abundance, and add support to the findings of others that forest/tree cover is an important determinant of *R. aurora* wetland occupancy. I also suggest thresholds for these variables based on my data and a literature review. The next step is to understand how the spatial distribution of terrestrial habitat resources influences the species' distribution and abundance in order to better reflect the manner in which the species use the landscape. I also make inferences about *P. regilla* home range size and dispersal ability based on the scale of greatest impact for associated variables. Future studies using mark-recapture or telemetry would yield more reliable information for dispersal distances and home range size, and have the added value of providing information on landscape resistance of different cover types, habitat selection, and survival rates (Cushman 2006). It is important to note that distribution patterns do not necessarily reflect habitat suitability: remnant habitats that are becoming increasingly degraded or isolated may be population sinks, with the species headed towards extirpation. Long-term studies that quantify abundance, reproductive effort, or juvenile survival over time will give an improved picture of habitat suitability for these species. The ultimate assessment of long-term persistence in the developed landscape will be a genetic study to determine functional connectivity among breeding ponds despite habitat loss and fragmentation.

Further research could also be directed at how best to implement the findings of studies like this through policy and public engagement. Nowhere is local and regional conservation more complex than in urban and rural areas, where many competing priorities must be weighed, private landowners act independently and for different purposes, habitat may cross jurisdictional boundaries, and management actions are driven as much by socioeconomic and cultural factors as by science-based policy (Aronson et al. 2017). Foremost among these challenges is the coordination of private landowners (e.g. households, small businesses) to avoid the "tyranny of small decisions," whereby the cumulative effects of decisions made on a small scale or at the individual level amount to unproductive or undesirable ecological outcomes (Odum 1982). For example, maximizing habitat heterogeneity within a public park or private garden may seem ecologically beneficial, but if widely adopted this management strategy may amount to habitat patches that are too small and too isolated to be useful to many species at a landscape scale. Rather, developing the tools to harness private lands to achieve larger-scale outcomes, such as replacing lawns and unnecessary impervious surfaces with native plant gardens on properties near ponds occupied by *P. regilla*, or planting trees in adjacent yards to create corridors across the landscape for *R. aurora*, is a much-needed area of research. Another research direction involves understanding and addressing public perceptions of wildlife and wildlands. For example, there may be resistance to habitat restoration and creation initiatives from people who have an irrational fear of amphibians or their predators, or who harbour misconceptions about the relationship between wetlands and mosquitos. Understanding public perceptions will help predict the level of cooperation with management efforts and target outreach and education activities. Finally, provincial, regional, and municipal conservation and development policies and guidelines should be analyzed to identify weaknesses in species and habitat protection measures that are unique to urban and rural areas, as well as opportunities to integrate the species-specific habitat criteria identified in this study and others.

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# Appendix A
# Optimal sampling design calculations for *R. aurora*

**Table A.1** Pre-study estimates of probability of occupancy ($\psi$), according to site type and landscape context.

| **Type** | **Origin** | **Context** | **Estimated $\psi$** | **Justification** |
|---|---|---|---|---|
| Waterway | Natural (stream) | Urban | <0.1 | Suboptimal terrestrial habitat, highest water flow, low aquatic vegetation |
| Waterway | Constructed (ditch) | Urban | <0.1 | Suboptimal terrestrial habitat, water quality, shallow |
| Pond | Natural | Urban | <0.1 | Suboptimal terrestrial habitat |
| Pond | Constructed | Urban | <0.1 | Suboptimal terrestrial habitat |
| Waterway | Constructed (ditch) | Rural | 0.1 | Water quality, shallow |
| Waterway | Natural (stream) | Rural | 0.1 | Highest water flow, low aquatic vegetation |
| Pond | Natural | Rural | 0.2 | Suboptimal terrestrial habitat |
| Pond | Constructed | Rural | 0.1 | Suboptimal terrestrial habitat, low canopy cover |
| **Average** | | | **0.1** | |

**Table A.2** Pre-study estimates of probability of detection ($p$), according to site type and landscape context.

| **Type** | **Origin** | **Context** | **Estimated $p$** | **Justification** |
|---|---|---|---|---|
| Waterway | Natural (stream) | Urban | 0.3 | Moderate streamflow noise, shallow at times (hydrophone range) |
| Waterway | Constructed (ditch) | Urban | 0.2 | Considerable anthropogenic noise, shallow at times (hydrophone range) |
| Pond | Natural | Urban | 0.7 | Aquatic vegetation density, area, depth |
| Pond | Constructed | Urban | 0.7 | Aquatic vegetation density, area, depth |
| Waterway | Natural (stream) | Rural | 0.3 | Considerable streamflow noise, shallow at times (hydrophone range) |
| Waterway | Constructed (ditch) | Rural | 0.2 | Moderate anthropogenic noise, shallow at times (hydrophone range) |
| Pond | Natural | Rural | 0.7 | Aquatic vegetation density, area, depth |
| Pond | Constructed | Rural | 0.7 | Aquatic vegetation density, area, depth |
| **Average** | | | **0.5** | |

# Appendix B
# Level of uncertainty metrics for *R. aurora* occupancy study based on initial estimates and sample size[5]

**Table B.1** Metrics for specifying the level of uncertainty for *R. aurora* occupancy and detection probability based on initial number of sites and estimates of occupancy and detection probability.

| **Estimate Type** | $\psi$ | $p$ | $p^*$ | $\mathrm{Var}(\hat{\psi})$ | **SE** | **Coeff. Var.** | **Optimal K** |
|---|---|---|---|---|---|---|---|
| Streams | 0.1 | 0.3 | 0.66 | 0.0044 | 0.067 | 0.67 | 5 |
| Ditches | 0.1 | 0.2 | 0.49 | 0.010 | 0.10 | 1.0 | 7 |
| Most ponds | 0.1 | 0.7 | 0.66 | 0.0017 | 0.041 | 0.41 | 2 |
| Rural natural ponds | 0.2 | 0.7 | 0.97 | 0.0030 | 0.055 | 0.27 | 2 |
| Averaged | 0.1 | 0.5 | 0.88 | 0.0021 | 0.045 | 0.45 | 3 |

### $p^*$: Probability of detecting *R. aurora* at least once

$$p^* = 1 - (1-p)^K$$

*Where*
$p$ = Detection probability
$K$ = Number of repeat surveys (3)

### $\mathrm{Var}(\hat{\psi})$: Variance

$$\mathrm{Var}(\hat{\psi}) = \frac{\psi}{s}\left[(1-\psi) + \left(\frac{1-(1-(1-p)^K)}{(1-(1-p)^K) - Kp(1-p)^{K-1}}\right)\right]$$

*Where*
$\psi$ = Occupancy probability
$s$ = Number of sites (56)

### $\sqrt{\mathrm{Var}(\hat{\psi})}$: Standard error

### $\sqrt{\mathrm{Var}(\hat{\psi})}/\psi$: Coefficient of variation

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[5] Equations from MacKenzie et al. (2006)

# Appendix C
# Comparison chart for visual estimation of emergent/submerged aquatic vegetation cover

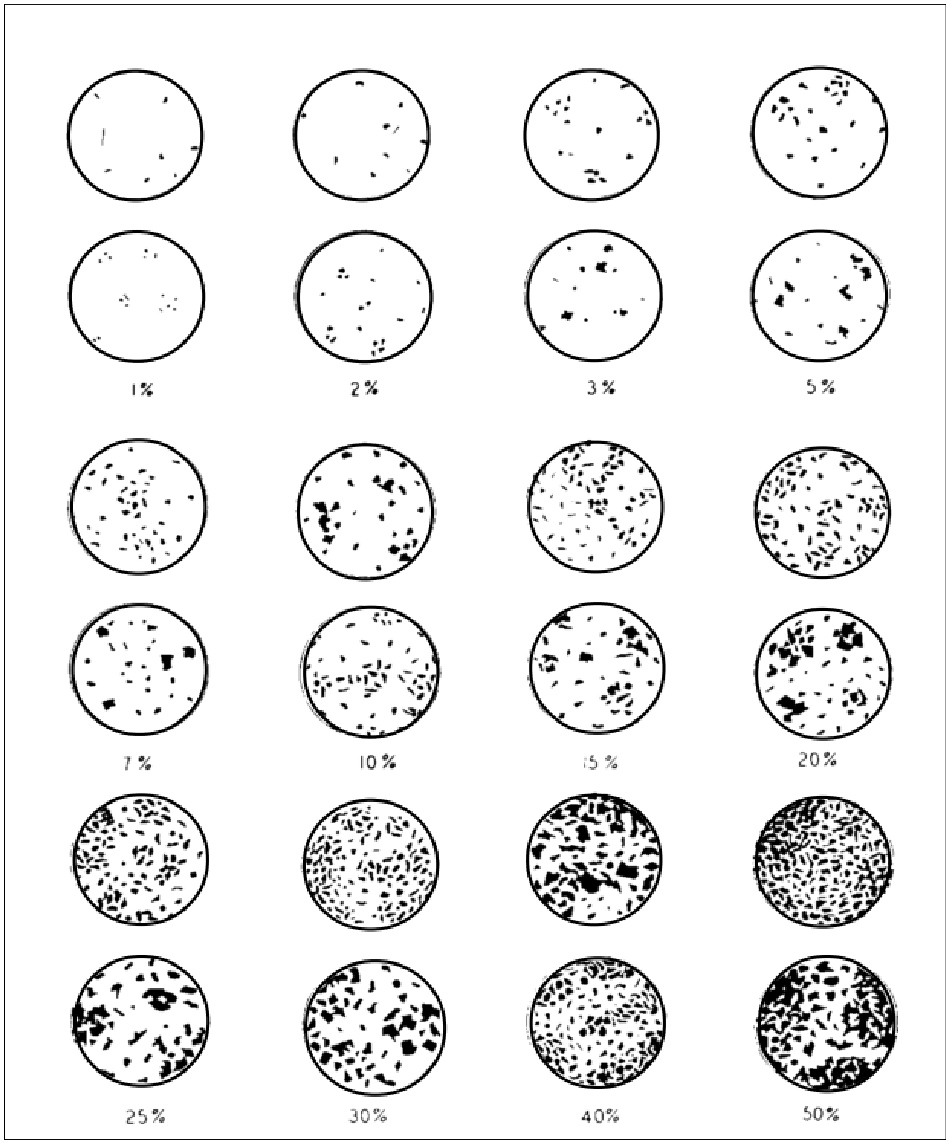

**Figure C.1** Comparison chart for visual estimation of emergent/submerged aquatic vegetation cover. Source: B.C. MELP & B.C. MF (1998: 9)

# Appendix D
# Ordinal sampling covariate codes[6]

**Table D.1** Ordinal sampling covariates and associated code descriptions.

| Variable / code | Description |
|---|---|
| **Wind Speed** | |
| 0 | Calm (<1.6 km/hr) |
| 1 | Slight (1.6-4.8 km/hr) |
| 2 | Light breeze (4.9-11.3 km/hr) |
| 3 | Gentle breeze (11.4-19.3 km/hr) |
| **Cloud Cover** | |
| 0 | Clear or few clouds |
| 1 | Partly cloudy (scattered or variable) |
| 2 | Overcast |
| **Precipitation** | |
| 0 | None |
| 1 | Drizzle |
| 2 | Steady light rain |
| 3 | Showers affecting hearing ability (pause or discontinue surveys) |
| **Moon brightness** | |
| 0 | No moon or overcast |
| 1 | Quarter moon unobstructed or later phase mostly obstructed |
| 2 | Half-moon unobstructed or later phase partly obstructed |
| 3 | Three-quarter moon unobstructed or later phase slightly obstructed |
| 4 | Full moon, unobstructed |
| **Anthropogenic disturbance** | |
| 0 | No appreciable effect |
| 1 | Slightly affecting sampling (distant traffic or a single car passing) |
| 2 | Moderately affecting sampling (nearby traffic or 2-5 cars passing) |
| 3 | Seriously affecting sampling |

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[6] Wind speed, cloud cover, and anthropogenic disturbance codes adapted from Weir and Mossman (2005)

# Appendix E
# Summary statistics for waterway sites

**Table E.1** Local variables measured in 100-metre transects of 26 waterways (streams and ditches) in urban and rural Saanich, BC. Bold values indicate significantly different from ponds ($p<0.05$).

| Variable | Median | Range |
|---|---|---|
| Width (cm) | 6.3 | 0.4-248 |
| Distance to tree cover (m) | 3.2 | 0-51.5 |
| Canopy density (%) | **81.37** | **0-100** |
| Aquatic veg. cover (%) | 22 | 2-57 |
| Water depth (cm) | **10.8** | **3-80.2** |
| Shore slope (°) | 34 | 0.7-80 |
| Nitrate concentration | 0 | 0-8.8 |
| Nitrite concentration | 0 | 0-0 |
| pH | 7.9 | 6.8-8.8 |
| Conductivity (µS) | **346** | **150-804** |
| Hydroperiod (seasonal/permanent) | 12/14 | |
| American bullfrog* | 2 | |

*Count of sites at which American bullfrogs were incidentally observed

# Appendix F
# Sample and survey number calculations for *P. regilla*

**Table F.1** Pre-study estimates of probability of occupancy ($\psi$), according to site type and landscape context.

| **Type** | **Origin** | **Context** | **Estimated $\psi$** | **Justification** |
|---|---|---|---|---|
| Waterway | Natural (stream) | Urban | 0.3 | Context, highest water flow, low aquatic vegetation |
| Waterway | Constructed (ditch) | Urban | 0.2 | Context, water quality, shallow |
| Pond | Natural | Urban | 0.4 | Context |
| Pond | Constructed | Urban | 0.4 | Context |
| Waterway | Constructed (ditch) | Rural | 0.3 | Water quality, shallow |
| Waterway | Natural (stream) | Rural | 0.4 | Highest water flow, low aquatic vegetation |
| Pond | Natural | Rural | 0.8 | Natural range of occupancy variability |
| Pond | Constructed | Rural | 0.8 | Natural range of occupancy variability |
| | | **Average** | **0.5** | |

**Table F.2** Pre-study estimates of probability of detection ($p$), according to site type and landscape context.

| **Type** | **Origin** | **Context** | **Estimated $p$** | **Justification** |
|---|---|---|---|---|
| Waterway | Natural (stream) | Urban | 0.6 | Moderate streamflow noise |
| Waterway | Constructed (ditch) | Urban | 0.5 | Frequent anthropogenic noise |
| Pond | Natural | Urban | 0.8 | Intermittent calling |
| Pond | Constructed | Urban | 0.8 | Intermittent calling |
| Waterway | Natural (stream) | Rural | 0.5 | High streamflow noise |
| Waterway | Constructed (ditch) | Rural | 0.6 | Periodic anthropogenic noise |
| Pond | Natural | Rural | 0.8 | Intermittent calling |
| Pond | Constructed | Rural | 0.8 | Intermittent calling |
| | | **Average** | **0.7** | |

# Appendix G
# Level of uncertainty metrics for *P. regilla* occupancy study based on initial estimates and sample size[7]

**Table G.1** Metrics for specifying the level of uncertainty for *P. regilla* occupancy and detection probability based on initial number of sites and estimates of occupancy and detection probability.

| **Estimate Type** | $\boldsymbol{\psi}$ | $\boldsymbol{p}$ | $\boldsymbol{p^*}$ | $\mathbf{Var}(\hat{\boldsymbol{\psi}})$ | **SE** | **Coeff. Var.** |
|---|---|---|---|---|---|---|
| Averaged | 0.5 | 0.7 | 0.97 | 0.0048 | 0.069 | 0.14 |
| Minimum | 0.2 | 0.5 | 0.88 | 0.0038 | 0.061 | 0.31 |
| Maximum | 0.8 | 0.8 | 0.99 | 0.0030 | 0.055 | 0.068 |

$\boldsymbol{p^*}$**: Probability of detecting *P. regilla* at least once**

$$p^* = 1 - (1-p)^K$$

*Where*
$p$ = Detection probability
$K$ = Number of repeat surveys (3)

$\mathbf{Var}(\hat{\boldsymbol{\psi}})$**: Variance**

$$\mathrm{Var}(\hat{\psi}) = \frac{\psi}{s}\left[(1-\psi) + \left(\frac{1-(1-(1-p)^K)}{(1-(1-p)^K) - Kp(1-p)^{K-1}}\right)\right]$$

*Where*
$\psi$ = Occupancy probability
$s$ = Number of sites (56)

$\sqrt{\mathbf{Var}(\hat{\boldsymbol{\psi}})}$**: Standard error**

$\sqrt{\mathbf{Var}(\hat{\boldsymbol{\psi}})}/\boldsymbol{\psi}$**: Coefficient of variation**

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[7] Equations from MacKenzie et al. (2006)

# Appendix H
# Correlation matrix for modeled covariates

**Table H.1** Correlation coefficients for modeled covariates. Bold font indicates that the covariate pair is highly correlated and should not be included in the same model.

| | CANOPY | AQVEG | DEPTH | BULL | FISH | NEAR | RD 500 | PONDS 1500 | WET 2000 | TREE 500 | IMP 250 | TREE 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AREA | −0.15 | 0.16 | −0.24 | 0.19 | 0.46 | −0.16 | −0.29 | 0.24 | 0.02 | 0.21 | −0.34 | 0.33 |
| CANOPY | - | −0.41 | −0.05 | −0.14 | 0.13 | 0.09 | 0.16 | 0.05 | 0.22 | 0.21 | 0.00 | 0.04 |
| AQVEG | | - | 0.10 | 0.31 | −0.11 | −0.14 | −0.21 | 0.16 | 0.08 | −0.02 | −0.10 | 0.07 |
| DEPTH | | | - | −0.04 | 0.16 | 0.04 | −0.36 | 0.33 | 0.41 | 0.10 | −0.21 | 0.30 |
| BULL | | | | - | 0.19 | −0.24 | −0.54 | 0.44 | 0.26 | 0.34 | −0.45 | **0.56** |
| FISH | | | | | - | 0.10 | −0.41 | 0.21 | 0.16 | 0.29 | −0.17 | 0.35 |
| NEAR | | | | | | - | 0.29 | −0.44 | −0.28 | −0.07 | 0.24 | -0.33 |
| RD500 | | | | | | | - | **−0.70** | −0.45 | −0.54 | **0.80** | **−0.60** |
| PONDS1500 | | | | | | | | - | 0.53 | **0.59** | **−0.69** | **0.78** |
| WET2000 | | | | | | | | | - | 0.45 | −0.40 | 0.48 |
| TREE500 | | | | | | | | | | - | **−0.74** | **0.68** |
| IMP250 | | | | | | | | | | | - | **−0.58** |