From forecasting vulnerabilities to assessing recovery: the utility of demographic models in addressing population declines

by

Amanda Marie Kissel

B.Sc. (Hons.), Colorado State University, 2008

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Name:	**Amanda Marie Kissel**
Degree:	**Doctor of Philosophy**
Title:	**From forecasting vulnerabilities to assessing recovery: the utility of demographic models in addressing population declines**
Examining Committee:	**Chair: Julian Christians** Associate Professor
	Wendy Palen Senior Supervisor Associate Professor
	Bernard Roitberg Supervisor Professor Emeritus
	Purnima Govindarajulu Supervisor Small Mammal and Herpetofauna Specialist British Columbia Ministry of Environment
	Michael Adams Supervisor Supervisory Research Ecologist United States Geological Survey
	John Reynolds Internal Examiner Professor
	Daniel Doak External Examiner Professor Environmental Studies University of Colorado, Boulder
Date Defended/Approved:	April 13, 2017

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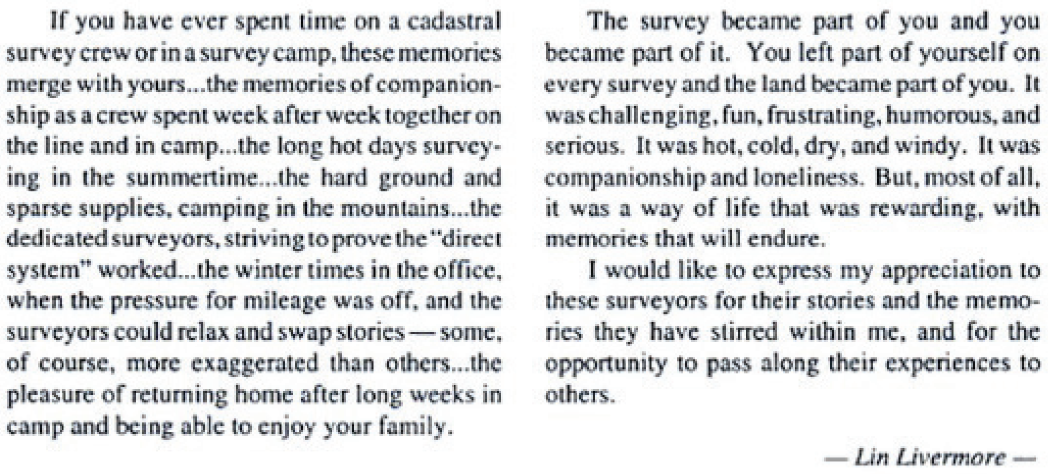
Abstract

Curbing species' decline driven by anthropogenic modifications to natural systems requires a deep understanding of how specific changes to biotic and abiotic processes affect populations. Individual life history stages may differ in their response to such changes, consequently buffering or accelerating population declines. I explore the concept of demographic compensation among life stages using stage-structured demographic models to improve predictions for two conservation challenges; 1) forecasting climate change impacts to amphibian populations in montane ecosystems, and 2) identifying the most effective life history targets for recovering declining amphibian populations. In Chapters 2 and 3, I use demographic data for the Cascades frog (*Rana cascadae*) at northern and southern range boundaries to parameterize stochastic matrix population models under current and future environmental conditions to evaluate how climate change affects population stability. I demonstrate that *R. cascadae* populations at the northern range boundary are stable, but that compounding negative effects of climate on early and late life history stages creates a demographic tipping point by the 2080's. I find that counter to range shift predictions, the population growth rate for the southern population will change little in the face of climate change, and differences in population stability between northern and southern range limits are driven by contrasting responses to climate. Equally important to forecasting population vulnerability, is preventing extinction of declining populations. In Chapter 4, I use demographic models to elucidate recovery potential for declining populations of Oregon spotted frogs (*Rana pretiosa*) by evaluating the effectiveness of population supplementation at multiple life stages. I compare two supplementation strategies, head-starting early life stages and captive breeding, and find captive breeding up to two orders of magnitude more effective at reducing extinction probabilities than head-starting. In Chapter 5, I extend the utility of such models using formal decision analysis to evaluate tradeoffs between the effectiveness of conservation actions and their economic costs. I reveal that the supplementation of wild populations with captive bred larvae results in the largest reduction in extinction risk per dollar invested. In this thesis, I use demographic models to improve our predictions of species' responses to climate change before declines occur, and conversely, advance the quantitative framework for recovering declining populations.

Keywords: **Population ecology; climate change; endangered species; demographic modeling; amphibian decline**

To my grandpa, Lin Livermore, who's stories of surveying the West inspired a passion, and to Annabelle and Carter, who inspire me to continue to work towards understanding and improving their World.



If you have ever spent time on a cadastral survey crew or in a survey camp, these memories merge with yours...the memories of companionship as a crew spent week after week together on the line and in camp...the long hot days surveying in the summertime...the hard ground and sparse supplies, camping in the mountains...the dedicated surveyors, striving to prove the "direct system" worked...the winter times in the office, when the pressure for mileage was off, and the surveyors could relax and swap stories — some, of course, more exaggerated than others...the pleasure of returning home after long weeks in camp and being able to enjoy your family.

The survey became part of you and you became part of it. You left part of yourself on every survey and the land became part of you. It was challenging, fun, frustrating, humorous, and serious. It was hot, cold, dry, and windy. It was companionship and loneliness. But, most of all, it was a way of life that was rewarding, with memories that will endure.

I would like to express my appreciation to these surveyors for their stories and the memories they have stirred within me, and for the opportunity to pass along their experiences to others.

— *Lin Livermore* —

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I am humbled by the large number of incredible people who've helped me along this journey. I would especially like to thank Maureen Ryan, who helped develop much of the framework for my first two chapters, and without who's knowledge of montane wetlands in the Pacific Northwest and extensive network of people to draw on, this project would not have been possible. Your mentorship and advice through the years have also been invaluable. Thank you to the numerous field and lab technicians over the years; Michelle Segal, Morgan Stubbs, Jay Brogan, Monica Pearson, Jill Miners, Hannah Gehrels, Celia Serrano, Katie Goodwin, Noll Steinweg, Mara Healy, Martin Duckhorn, Andrew Boxwell, Griffin Dare, and Chloe Reid. Thank you to all members of the Palen lab, past and present, who have never hesitated to wade into wetlands, climb mountains, and ponder over statistical analyses; Rylee Murray, Pascale Gibeau, Dan Greenberg, Janie Dubman, Viorel Popescu, Sacha O'Regan, Robin Munshaw, Zach Monteith, Gavia Lertzman-Lepofsky, Isabell Eischeid, and Danielle Courcelles, you all kept me going through all the literal and figurative stumbling blocks. Thank you to the Earth to Ocean Research Group for the exchange of ideas and friendship over the years, it has been an amazing experience to be part of such a progressive and intellectually stimulating group.

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Chapter 1. Introduction

The swift emergence of anthropogenic, global-scale ecological problems over the past century such as climate change, habitat loss, and invasive species, have spurred massive scientific efforts to understand the ecology of the systems in which we live. Scientists have engaged in a multi-faceted approach to disentangling the mechanisms of ecosystem stability, ranging from macro-ecological studies to understand global biodiversity hotspots (Myers et al. 2000; Davidson & Dulvy 2017) to theoretical models of ecosystem dynamics (Mangel & Roitberg 1992). In the middle of this spectrum is the field of population ecology, which aims to understand how populations of a species persist within an environment. Using populations as a biological unit to understand ecological systems has been a central tenant of ecology since the early 20th century (Alfred J. Lotka 1925; Volterra 1926; Pearl 1927; Gause 1932), and much of the theory was developed in regards to managing populations for fishing and hunting (Ricker 1954; Leopold 1986). Since then, many scientists have contributed to developing a rich quantitative framework to tease apart the mechanisms of population stability for a wide array of taxa through demographic modeling approaches based on species' life history (Leslie 1945; Lefkovitch 1965; Morris & Doak 2002; Caswell 2006).

Demographic models can play a central role in the conservation of species. Demographic models are commonly used to estimate the magnitude of decline of an already imperiled population (Dennis et al. 1991; Morris et al. 2002; Norris & Mcculloch 2003; Zambrano et al. 2007), or to explore broad patterns of growth and survival for different life history stages across taxa (Heppell et al. 2000; Caswell 2001; Vonesh & De la Cruz 2002; Stahl & Oli 2006a). For example, using stage-structured demographic models, Crouse et al. (1987) overturned a long-standing conservation paradigm for sea turtles, in which managers focused on increasing the survival of hatchlings to stabilize declining populations. By quantitatively assessing survival at multiple life stages, Crouse et al. (1987) found that juvenile mortality contributed the most to population growth, and conservation practices shifted accordingly. Additionally, Govindarajulu et al. (2005) demonstrated that removing larvae and adults from an invasive bullfrog population can lead to an increase in the population growth rates through density dependent release of bullfrog larvae. These examples and others (e.g. Holmes & York 2003; Diller et al. 2016) highlight the importance of including demographic data from multiple life stages in a modeling framework to understand population dynamics.

An important and underutilized aspect of demographic modeling is assessing the capacity for demographic compensation within a population (Doak & Morris 2010; Villellas et al. 2015). To explore the concept of compensatory mechanisms among life stages, I aim to answer two questions that span the spectrum of amphibian conservation challenges; 1) how will the culmination of climate change impacts on different life history stages affect emergent population dynamics of montane amphibians, and 2) can we identify the most efficient targets for recovering species and populations that have declined to near extinction? The effects of climate change on montane amphibians is a timely question that seeks to understand the potential for resilience within the complex life cycle of pond-breeding amphibian populations. Climate change may increase variability in environmental cues for phenological processes such as breeding (Corn 2005; McCaffery et al. 2014), larval metamorphosis (O'Regan et al. 2014), and hibernation (Reading 1998). The synchrony of these processes is particularly important for alpine amphibian populations that experience harsh winter conditions and short growing seasons, and are dependent on annual hydrological patterns for reproductive success (Corn 2005). Understanding how climate change will affect distinct life stages, and in turn influence population equilibrium is necessary for forecasting species' responses to global change.

To address this, in Chapter 2 I combine empirical demographic data for Cascades frogs (*Rana cascadae*) with site-specific estimates of climate data from 1980-2006, and future decades representing the 2080's. I use stage-based demographic models to assess how a warming, drying climate in the Pacific Northwest will affect both the aquatic and terrestrial life stages of *R. cascadae*, and assess whether the effects of climate change at different life stages are compensatory or compounding. In Chapter 3, I compare demographic responses to climate change for *R. cascadae* at its northern and southern range limits to test whether the southern population is more vulnerable to climate change, as would be predicted by recent studies on species range shifts (Parmesan et al. 1999; Thomas et al. 2004; Chen et al. 2011; Sunday et al. 2012).

Equally important to forecasting vulnerabilities of amphibians prior to declines, is preventing extinction of species that are already imperiled. In many cases, reasons for decline are either poorly understood or difficult to reverse, and managers have resorted to population supplementation as a tool to stem population decreases while the ultimate drivers of decline are addressed. Information on how supplementation affects emergent population dynamics and when and where to target supplementation for maximal effect is crucial to success. However, data-driven decision making with regard to supplementation is largely non-existent (but see Sarrazin & Legendre 2000; Hilderbrand 2002; Bretagnolle et al. 2004). Thus, in Chapter 4, I assess whether two forms population supplementation, head-starting wild embryos and captive breeding with reintroduction, can effectively stabilize a declining population of Oregon spotted frogs (*Rana pretiosa*). I simulate supplementation at two distinct life stages, larvae, and post-metamorphic young of the year, and estimate the population growth rate and associated 10-year extinction risk for populations ranging from 50-150 individuals. Finally, in Chapter 5, I incorporate the demographic models developed in Chapter 4 into a formal decision analysis that includes the financial costs associated with recovery programs. I demonstrate that explicitly linking quantitative models of extinction risk with discernable recovery objectives is an underutilized yet important step in broadening our understanding of our ability to recover imperiled species.

With this thesis, I explore two complementary aspects of the amphibian crisis: forecasting population vulnerability and guiding recovery. Using stage-based demographic models, I take a population-level approach to forecasting the effects of climate change on alpine amphibians. Conversely, I use demographic models to elucidate recovery potential for declining amphibian populations by evaluating the effectiveness of reducing extinction risk through supplementation, a tool increasingly used to bolster endangered species. By working through pre and post-decline population dynamics, I expand the set of quantitative tools that can be applied not only to the amphibian crisis, but to a broader scope of taxa facing similar threats in the era of human-induced global change.

Chapter 2.
Evaluating population persistence in the face of climate change for montane amphibians[1]

2.1. Abstract

Anthropogenic climate change presents both challenges and opportunities to the growth, reproduction, and survival of individuals throughout their life cycles. Demographic compensation among life-history stages has the potential to buffer populations from decline, but alternatively, compounding negative effects can lead to accelerated population decline and extinction. It is important to identifying potential drivers of population decline to inform conservation and management decisions in rapidly changing landscapes. In high elevation montane ecosystems of the US Pacific Northwest, temperature, precipitation, and the availability of freshwater are changing simultaneously. As temperatures increase, annual precipitation falls more often as rain rather than snow, resulting in reduced snowpack and earlier snow melt. For species such as amphibians that rely on thermal cues and consistent water sources for specific life history processes, warmer winters can reduce the frequency of critical minimum temperatures and increase the length of summer growing seasons, benefiting post-metamorphic stages, but may also drive higher metabolic costs during winter months resulting in lower survival. Lower snowpack levels also reduce the water storage capacity of watersheds, resulting in wetlands that dry sooner or more frequently, which can create phenological mismatches between minimum larval development times and hydroperiod. For juvenile and adult amphibians, wetlands that dry earlier each summer can reduce the availability of aquatic insect prey and increase overall desiccation risk. To evaluate how these challenges and opportunities affect population stability, we collected demographic data on Cascades frog (*Rana cascadae*) in two landscapes within Olympic National Park in Washington state to parameterize stage-based stochastic matrix population models under current and future (A1B, 2080's) environmental conditions. We estimated how current reproductive effort is distributed across wetlands with different hydroperiods, and predicted the proportion of effort lost

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[1] A version of this chapter is in preparation for publication with W.J. Palen, M.J. Adams and M.E. Ryan

each year due to drying using watershed-specific hydrologic models. We coupled this with a 14-year dataset of *R. cascadae* abundance. We found that by the 2080's larval mortality is predicted to increase by 17% as a result of increased pond drying, and that adult survival will decrease by 6% as both winter length and summer precipitation continue to decline. We predict that currently stable *R. cascadae* populations will decline by the 2080's with a 51% chance of extinction over 20 years, and that contrary to the expectation of demographic compensation, there are multiple compounding negative effects on both early and late life history stages driving this pattern. Our results demonstrate the need to understand the potential for compounding or compensatory effects within different life history stages to exacerbate or buffer the effects of climate change on population stability.

2.2. Introduction

Species' life history strategies, behavioral adaptations, and phenological patterns provide a strong biological basis for predicting responses to climate change (Brodie & Post 2010; Sunday et al. 2014; Williams et al. 2015). To date, many studies focus on specific life stages or the thermal niche of a species to understand responses to climate change (Thomas et al. 2004; Deutsch et al. 2008; Thomas 2010; Sunday et al. 2012), overlooking that vulnerability may increase or decrease depending on important life history traits such as life stage (i.e. larvae vs. adult) and size at maturity. An individual's risk to climate change may be higher at certain life history stages and lower at others, but it is important to understand how these overall effects will 'add-up' across a lifetime and contribute to population level stability (Doak & Morris 2010; van de Pol et al. 2010). Doak and Morris (2010) demonstrated that for two tundra plant species, there are demographic compensation mechanisms within the life history to ameliorate many of the risks posed by climate change. Despite this finding, they conclude that these species can be pushed beyond a tipping point, when compensatory responses are exceeded, and populations decline. Understanding these ecological 'tipping points' is critical to predicting species declines in the face of global change.

High elevation amphibians in particular represent a group for whom climate change may present both challenges and opportunities at different life stages, due to their biphasic life history (Fig. 2.1, Corn 2005; Reading 2006; McCaffery & Maxell 2010;

McCaffery et al. 2012; Cayuela et al. 2016). At the aquatic stage (embryos & larvae) survival depends on ponds that maintain water long enough for individuals to develop and transition to the terrestrial stages. Although ponds are expected to dry sooner under climate change conditions, resulting in increased mortality at the aquatic stage (Matthews et al. 2013; McCaffery et al. 2014; Ryan et al. 2014; Lee et al. 2015), development at aquatic stages is often driven by temperature, and increased pond temperatures may allow larvae to develop at higher rates and escape drying (O'Regan et al 2013, Newman et al. 1998). For terrestrial stages, individuals may spend up to nine months out of the year dormant under several meters of snow, and there is some evidence that milder winters may increase survival at the terrestrial stage (McCaffery and Maxell 2010). However, some studies suggest that if overwintering temperatures are not low enough to sustain dormancy throughout the winter season, this may reduce body condition of post-metamorphic individuals in the spring, ultimately reducing survival (Reading 2006; Williams et al. 2015). Increased temperatures and decreased precipitation may also limit foraging of juveniles and adults during the growing season (Sinervo et al. 2010; Sears et al. 2016; Lertzman-Lepofsky et al. *in prep*), which in turn could affect overwintering survival (Corn 2005) . It is yet unclear if opportunities (faster growth rates, longer growing seasons) at certain stages will act as compensatory mechanisms, offsetting negative responses (phenological disruptions, desiccation, decreased body condition) at others, or if compounding effects have the potential to push populations across ecological tipping points from increasing or stable to decreasing.

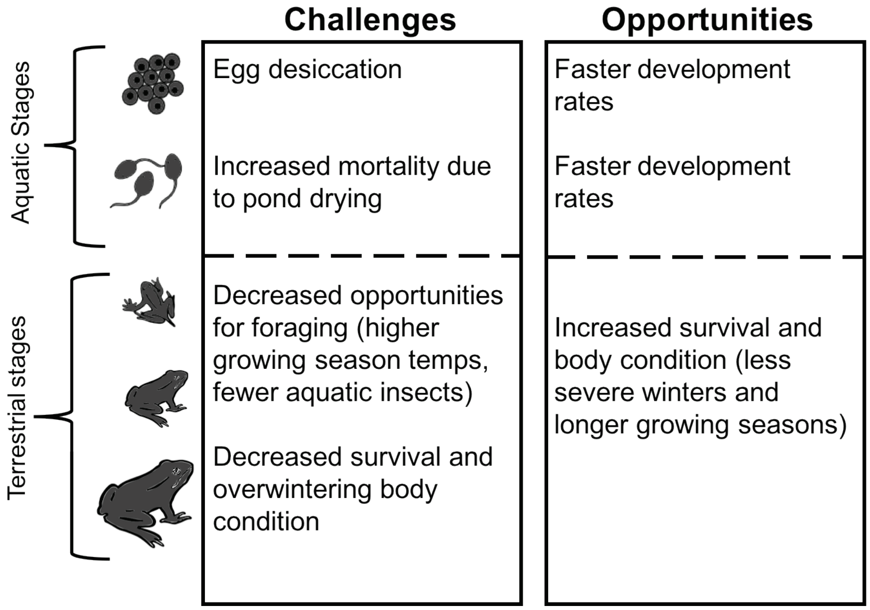

Figure 2.1 Schematic diagram summarizing the challenges and opportunities amphibians may face with climate change, broken down by life stage (aquatic vs. terrestrial).

The Pacific Northwest of North America provides a landscape in which to test the idea of demographic compensation and tipping points in montane amphibians. Increasing temperatures are expected to alter hydrologic patterns, such that more precipitation will fall as rain rather than snow, and less precipitation will fall during the summer months (Hamlet et al. 2007, Hamlet et al. 2005, Mote et al. 2003). These trends are exacerbated at high elevations and may drastically alter the availability of water across the landscape (Mote et al. 2005, Lee et al. 2015). Specifically, snowpack acts as a water storage mechanism for many wetlands, maintaining water levels via sustained snowmelt in the late spring and early summer. This has historically stabilized hydroperiods, and predicted decreases in snowpack and increased evaporation is expected to increase the probability of wetland drying (Lee et al. 2015). These changes in temperature and hydrologic patterns may have a disproportionate effect on amphibians that are uniquely adapted to montane environments (Ryan et al. 2014, Corn 2005, McCaffery & Maxell 2010).

Cascades frogs (*Rana cascadae*) are a montane species, currently classified as stable throughout most of their range (northern California to the Olympic peninsula) with the exception of the southern extent in northern California (Fellers & Drost 1993; Fellers et al. 2007; Garwood & Welsh 2007). Understanding how stable populations of a species respond to a rapidly changing climate at various life stages provides an opportunity to identify potential ecological tipping points (in which the population goes from increasing or stable to decreasing, Doak & Morris 2010; Drake & Griffen 2010) before they occur. To identify important demographic compensation or tipping points, we can explore the vulnerability of each life stage of a species to climate stressors by understanding the sensitivity and exposure to climate change. Sensitivity refers to how each life stage responds to a given climatic threat, and exposure refers to how frequently or how long each stage will be exposed to a threat (Gallopín 2006). We collected multiple years of demographic, phenological, and life history data for a population of *R. cascadae* in Olympic National Park (ONP) in order to identify points of vulnerability or compensation within the species' life history. We coupled empirical data on drying rates of breeding ponds and annual adult survival for the population with current climate data, and used a stage-structured population matrix model to pinpoint potential compensatory or compounding stage-specific response to climate change. Additionally, we modeled the population trajectory (expressed as the stochastic population growth rate and corresponding 20-year extinction probability) under current climate conditions, and predicted climate conditions in the 2080's (A1B climate scenario) to identify potential ecological tipping points for population persistence.

2.3. Methods

2.3.1. Data collection

We combined 15 years of capture-mark-recapture data for adult *R. cascadae* with 3 years of data on the breeding phenology and hydroperiods at 51 wetlands in two landscapes of ONP (Fig. 2.2). From 2013 to 2015, we enumerated breeding effort at each pond during the summer open-water season (May-October), and revisited ponds every two weeks, recording when wholesale larval mortality (i.e. all individuals died) occurred as a result of pond drying before metamorphosis. Each year from 2002 to 2016, we conducted a mark-recapture study in which we surveyed adult and juvenile *R. cascadae* at a sub-set of 13 breeding ponds. We captured frogs by hand, marked them with passive integrated transponder (PIT) tags, and measured, weighed, and released individuals back into the ponds in which they were caught.

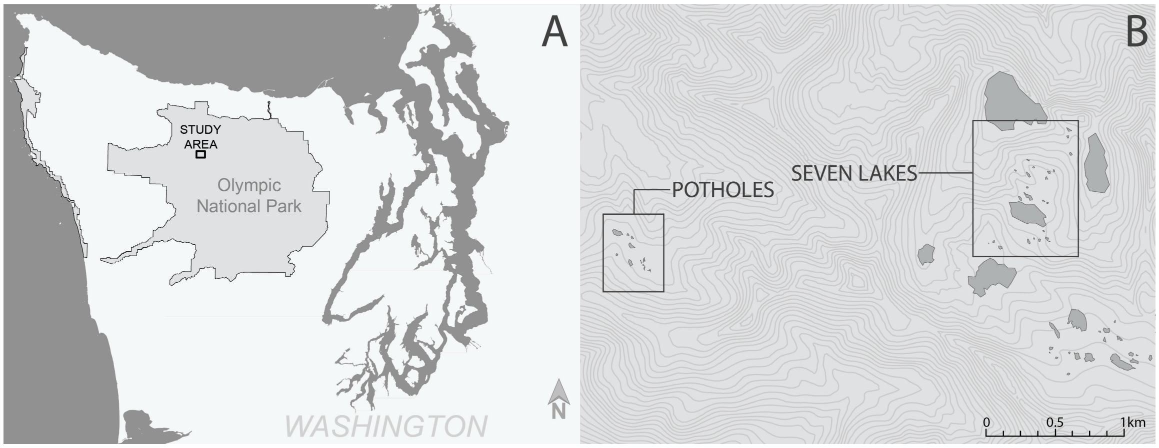

Figure 2.2 **Map of the of the Olympic Peninsula in Washington state (A), and the 7 Lakes Basin and Potholes region of Olympic National Park (B).**

2.3.2. Estimating larval mortality

We estimated mortality to aquatic stage (embryo, larvae) *R. cascadae* resulting from pond-drying for 2 different time periods, ‘current’ (1980-2006), and ‘future’ (2080’s, A1B climate scenario). Estimates of mortality due to pond-drying are separate from background estimates of embryonic and larval survival that result from other stressors such as predation. To estimate current larval mortality due to drying, we coupled data from our breeding surveys with estimates of pond drying from 1980-2006 generated from a variable infiltration capacity (VIC) model implemented for the Columbia Basin Climate Scenarios Project (CBCCSP) and adapted for our study sites (Lee et al. 2015). The VIC model is a macro-scale water balancing hydrologic model which was used to estimate daily wetland water levels for our ponds over the course of 92 years (1916 to 2006). We chose to use VIC estimates from 1980 onwards, as 1980 is often used as a climate benchmark (IPCC 2014). For ponds in which VIC estimates were unavailable (n = 26), we assigned each pond a drying regime of a pond with a VIC projection, based on proximity and observed drying behavior from 2013 to 2015 (Fig. 2.3) and calculated the number of years in which each site dried before metamorphosis could occur.

Additionally, we assigned each pond a hydroperiod class; ephemeral, intermediate, perennial, and permanent. Ephemeral ponds dry in most years and typically hold water for a matter of weeks, intermediate ponds may dry in late summers in dry years, perennial ponds dry only in extreme drought years (but may lose substantial water volume in dry years), and permanent ponds never dry (Lee et al. 2015) (Fig. 2.4). We assigned hydroperiods based on outputs from the VIC models, using the mean minimum water level (mwl) as an index for drying. Ephemeral hydroperiods have an annual mwl of <3%, intermediate 3-33%, perennial >33% and <66%, and permanent >66% (Lee et al. 2015). Oviposition events were fairly similar across our three years of data collection, in which larger, more permanent ponds had more egg masses (Figure A.1). Thus we assumed a mean number of egg masses in each pond based on our three years of data collection in the region, and calculated the additional larval mortality imposed by pond drying for each of the 27 years (1980-2006) for each pond, and an overall mean mortality due to pond drying for the population. We used the inverse of the mortality estimate (i.e. survival) as an additional parameter in our population matrix model (see below), in addition to the background larval mortality during the length of aquatic development. For our estimates of future larval mortality due to pond drying, we repeated this analysis using VIC estimates of the probability of pond drying over the same time period (1980-2006) that have been perturbed to reflect temperature and precipitation patterns for the 2080's under the A1B climate scenario (Lee et al. 2015). VIC models have been generated for three future time periods (2020's, 2040's, and 2080's) for two different climate scenarios; the A1B scenario which represents significant advancements in technology with a balanced energy use that includes fossil fuels (a 'medium' emissions scenario), and the B1 scenario, which reflects significant advancements in greenhouse gas reductions (Hamlet et al. 2010). We chose to use data from the A1B scenario in the 2080's in order to explore how moderate climate change will affect *R. cascadae* in future decades in which warming is likely to have occurred.

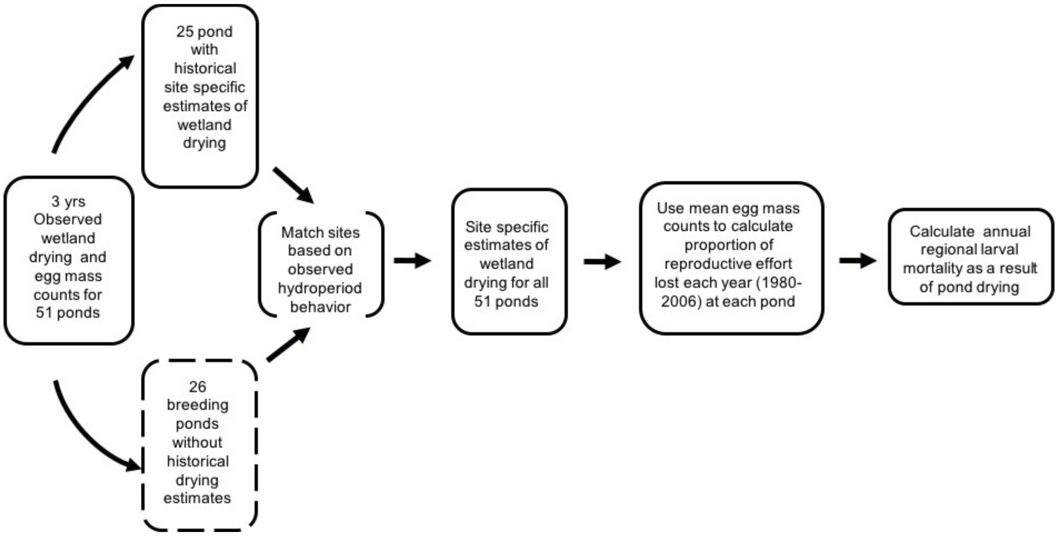

Figure 2.3. **Flow chart describing the way in which we estimated larval mortality using simulated wetland water levels from the VIC model. We paired ponds without VIC simulations to nearby ponds which exhibited similar behavior from 2013 to 2015. We then used the mean number of egg masses across those three years to calculate the proportion of reproductive effort lost in each year from 1980 to 2006, and then again across the same time period perturbed to reflect conditions in the 2080's.**

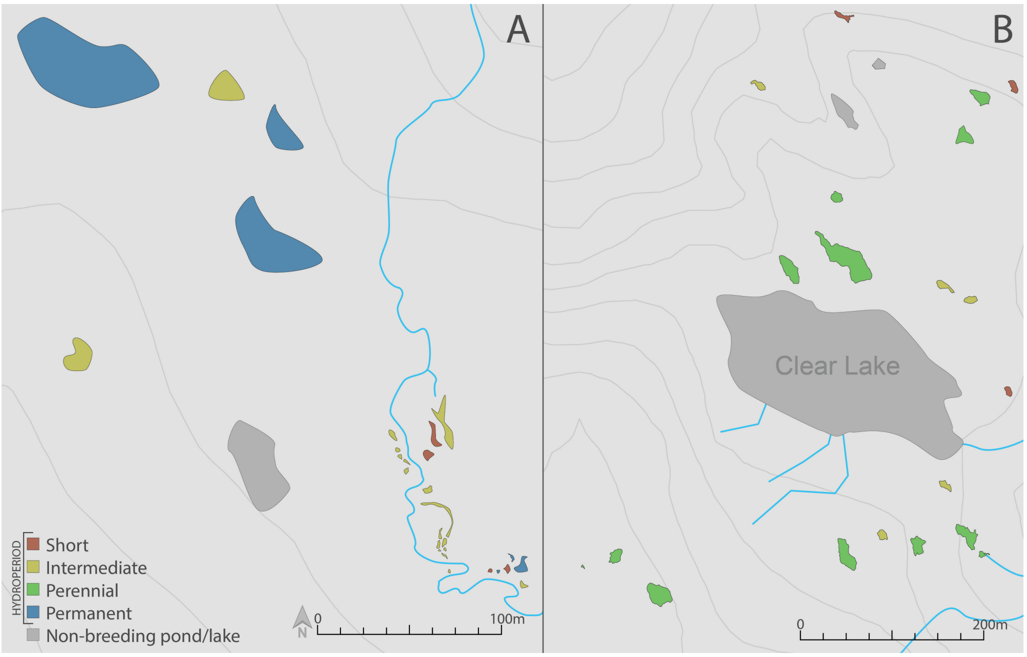

Figure 2.4. **Maps showing the distribution of hydroperiod classes in the Potholes (A) and 7 Lakes (B) regions of Olympic National Park, WA.**

2.3.3. Estimating adult survival

To understand the interplay between climate and adult *R. cascadae* survival, we developed a suite of 13 climate metrics to include as covariates in our mark-recapture analysis (see Table 2.1 for climate metrics and definitions). We collated data for snow water equivalent (SWE, a measure of the amount of water contained in the snowpack) from the nearest SNOTEL station (Waterhole, accessed July 2016) and used temperature and precipitation data from the PRISM dataset (PRISM climate group, accessed July 2016). Finally, we estimated the mean annual Multivariate El Niño Southern Oscillation Index (MEI) from the NOAA Earth Systems Research Laboratory website (www.esrl.noaa.gov/psd/enso/mei/). We included the MEI in our models because strong El Niño years are associated with warmer and drier winters in our system, which in turn could influence adult survival. We calculated each variable on an annual time step, adjusting the year to start on the first day of recorded breeding, and end on the prior to the first recorded breeding in the following year, so that the time scale of the climate variables reflects the ecology of the species. We used a Robust Design framework (Kendall et al. 1995) with a Huggins estimator (Huggins 1989, 1991) to estimate annual adult survival from 2002 to 2016 for female frogs as a function of 1 or 2 climate covariates (see Table A.1 for climate covariate hypotheses) implemented in the package RMark 2.2.0 (Laake 2013) in program R (R Core Team 2017, V3.3.1). Capture and recapture probability varied by sex, year, capture occasion, and mean daily air temperature during the capture occasion. Gamma’ and gamma’’ (temporary emigration parameters) varied by sex, year, and whether data collection occurred before or after breeding began (a proxy for whether females were present in the study area at the time of capture). We used AICc model selection to rank the top models, and averaged models containing 95% of the support (Burnham & Anderson 2002). We then used the model averaged estimates to predict ‘current’ adult survival from 1980 to 2006 (the same time span over which we calculated larval mortality due to pond drying) using temperature, precipitation, and SWE estimates from the VIC model. To predict adult survival in the 2080’s (‘future’ survival), we used the model averaged coefficients from the above model in combination with climate predictions for the 2080’s from the VIC model outputs, holding climate variables for which we do not have future estimates (such as ENSO) at their mean values for the ‘current’ time period.

Table 2.1. Name, abbreviation, and definitions of climate variables included in analysis of adult survival. All climate variables were calculated on an annual time step.

Climate Variable	Abbreviation	Definition
Mean annual temperature (^{o}C)	mt	Annual mean temperature over the course of the breeding year
Mean annual precipitation (mm)	ap	Annual mean precipitation over the course of the breeding year
Maximum snow water equivalent (mm)	mswe	Maximum daily estimate of snow water equivalent
Winter length (days)	wint	Number of days in the breeding year for which swe>0
Summer length (days)	sum	Number of days in the breeding year for which swe=0
Temperature in the warmest quarter (^{o}C)	twq	Mean temperature in the warmest 3 months of the breeding year
Temperature in the coldest quarter (^{o}C)	tcq	Mean temperature in the coldest 3 months of the breeding year
Temperature in the wettest quarter (^{o}C)	twetq	Mean temperature in the wettest 3 months of the breeding year
Temperature in the driest quarter (^{o}C)	tdq	Mean temperature in the 3 driest months of the breeding year
Precipitation in the wettest quarter (mm)	pwq	Mean precipitation in the 3 wettest months of the breeding year
Precipitation in the driest quarter (mm)	pdq	Mean precipitation in the 3 driest months of the breeding year
Precipitation in the coldest quarter	pcq	Mean precipitation in the 3 coldest months of the breeding year
Temperature seasonality	ts	The standard deviation of the mean annual temperature *100 of the breeding year
Mean multivariate El Niño southern oscillation index value	ENSO	mean estimate of the monthly strength of El Niño

2.3.4. Demographic modeling

We modeled the geometric mean stochastic population growth rate (λ_s) and the 20-year extinction risk of adult female *R. cascadae* using an annual stage-based Leslie-matrix model (Fig. 2.5), in which matrix elements were made up of 1 or more lower level vital rates (Morris & Doak 2002). Estimates of vital rate means and variances for larvae and adults incorporated the relationships to specific climate variables described above.

For larvae, we included a vital rate to represent the proportion of larval mortality attributed to pond-drying, by multiplying the background larval survival rate (Palen, unpublished data, Table A.2) by a value randomly drawn from a probability density function characterized by the mean and variance of the proportion of reproductive effort that did not dry from 1980-2006. For adults, we used the mean and variance of predicted annual survival rates from 1980 to 2006, as a function of the model averaged estimates of our top models (see above), to develop a probability density function from which to draw vital rates for the simulation. We used a stochastic model, in which we simulated 500, 20-year runs, pulling vital rates from distributions characterized by the mean and variances of our estimates at each time step (Morris & Doak 2002). Embryonic, larval, and adult vital rates were estimated using empirical data from the 7 Lakes Basin of ONP (Table A.2), and we used estimates of juvenile survival and transition probabilities from previously published Ranid studies (Funk et al. 2005; McCaffery & Maxell 2010), as such data were not available for our study population (Table A.2). We used multiple estimates from the literature to parameterize juvenile survival (n=5), and calculated the mean and variance from the point estimates reported in the studies. Additionally, for the transition rate between juvenile and adult, we used the mean and variance from the annual estimated transition rates for a high elevation population of Columbia spotted frogs (*Rana luteiventris)* from McCaffery & Maxell 2010 (n = 8 years). We parameterized four models based on different climate scenarios to explore whether a demographic tipping point could be crossed in our population as a result of future climate stress. Our first scenario consisted of current larval survival and adult survival; in scenario 2, we modeled future adult survival and current larval drying; for scenario 3, we modeled current adult survival and future larval survival; for the final scenario we incorporated both future larval and adult survival. We chose to run these scenarios to weigh the relative contribution of the larval and adult stages to population growth, as our model does not lend itself to the traditional elasticity analysis for matrix models (Caswell 2001). The majority of our vital rates are pre-reproductive, and Caswell (2001) states that all pre-reproductive survivals are equal.

$$\begin{bmatrix} 0 & 0 & 0 & 0 & F_{14} \\ a_{21} & 0 & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 & 0 \\ 0 & 0 & a_{43} & a_{44} & 0 \\ 0 & 0 & 0 & a_{54} & a_{55} \end{bmatrix} \text{X} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t+1}$$

Vital rate	*aij*	Parameter Equation
Embryo to juvenile$_1$ transition	a_{21}	$\phi_{\text{embryo}} * \phi_{\text{background larvae}} *(1-\text{proportion dried}) *\phi_{\text{YOY}}$
Juvenile$_1$ to Juvenile$_2$ transition	a_{32}	ϕ_{juv1}
Juvenile$_2$ to Juvenile3 transition	a_{43}	ϕ_{juv2}
Juvenile3 to adult transition	a_{54}	$\phi_{\text{juv3}} * p_{\text{adult}}$
Juvenile 3 survival	a_{44}	$\phi_{\text{juv3}} *(1-p_{\text{adult}})$
Adult survival	a_{55}	ϕ_{adult}
Fecundity (Adult)	F_{14}	F_{adult} * sex ratio * ϕ_{adult}

Figure 2.5. Matrix model and vital rate description for *Rana cascadae*.

2.4. Results

2.4.1. Larval mortality

Across a landscape of 51 breeding sites, from 2013-2015 we documented that 9% of egg masses are deposited in ephemeral, 37% in intermediate, 35% in perennial, and 18% in permanent hydroperiod ponds. Based on VIC model predictions of historic drying rates from 1980 to 2016, we estimated that the mean proportion of ponds that dried was 0.91 for ephemeral ponds, 0.44 for intermediate ponds, and 0 for perennial and permanent ponds. Under 2080's climate conditions, the mean proportion of sites that dried remained at 0 for perennial and permanent ponds, however the proportion of ephemeral ponds that dried increased to 1, and the proportion of intermediate ponds increased 1.7-fold, to 0.75 (Table 2.2). Mean annual larval mortality due to pond drying using the VIC models from 1980 to 2006 was 0.25 (sd +/- 0.14), which we translated to a survival rate of 0.75 for our matrix model (Table 2.2, Fig. 2.6a). Larval mortality for our time series perturbed to reflect the 2080's was 0.38 (sd +/- 0.11), or a survival rate of 0.62 (Fig. 2.6b).

Table 2.2. **Distribution of reproductive effort across 4 hydroperiod classes and the proportion of sites that dried historically (1980-2006) and in the 2080's under the A1B climate change scenario.**

Hydroperiod class	n	Proportion of reproductive effort	Proportion dried (current)	Proportion dried (2080's)
ephemeral	13	0.09	0.91	1.00
intermediate	23	0.37	0.45	0.75
perennial	11	0.35	0.00	0.00
permanent	4	0.18	0.00	0.00

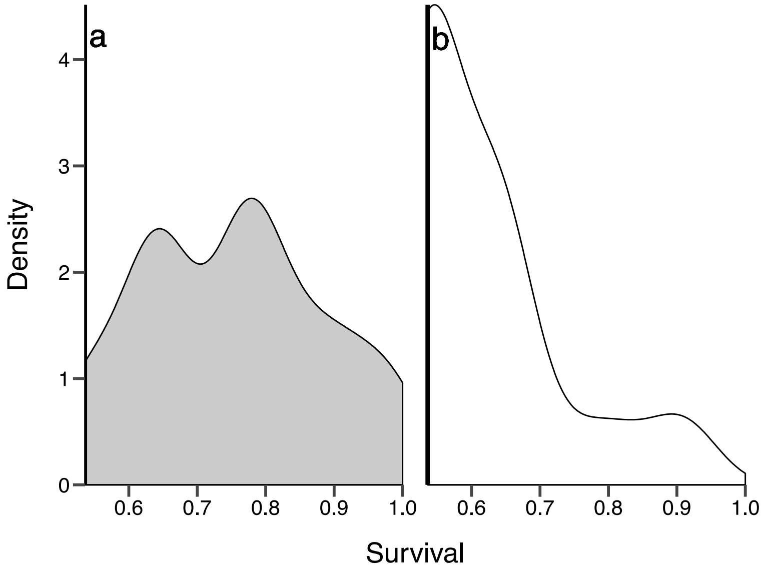

Figure 2.6. **Current (a) and 2080's (b) distribution of the proportion of larvae that 'survived' drying in our matrix model. Mean survival from 1980-2006 current) was 0.75 and mean survival in the 2080's was 0.62, not including background survival rates for larvae.**

2.4.2. Adult survival

We ran models to estimate adult survival using additive combinations of 14 climate variables (Table A.1) resulting in 7105 candidate models, with 23 models containing 95% of the support (Table A.3). In all 23 top models, capture and recapture probability varied by sex, year, and capture occasion, while gamma' and gamma'' varied by sex and time. Adult survival for males was, on average, 7.5% lower than females, however, for the remainder of our study we focus on adult female survival, since our demographic model is female only. We calculated the relative variable importance (RVI) of the climate variables contained in the 23 top models for adult females by summing the AIC weights for each variable and found that precipitation in the driest quarter (pdq) had the highest weight (0.45), followed closely by winter length (0.42). All other climate variables had a RVI of less than 0.25 (Fig. 2.7).

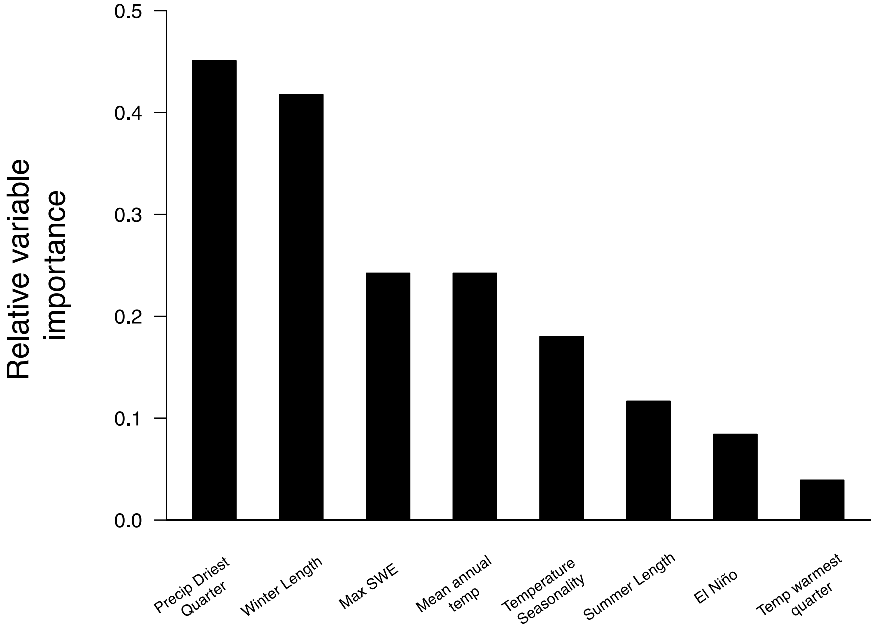

Figure 2.7. **The relative variable importance values of the climate variables that were included in the candidate set of models for adult survival that contained 95% of the weight.**

We calculated model-averaged estimates for all variables holding 95% or less of the weight, and coefficients show that precipitation in the driest quarter (pdq) is positively related to adult female survival, such that a 100mm increase resulted in an 2.2% increase in annual survival (pdq for the current time period ranged from 113mm to 662m per year) (Fig. 2.8a). The relationship between female survival and winter length was positively correlated, such that for every additional 10 days of continuous snow cover, annual survival increased by 1.2% (Fig. 2.8b). Over the course of our ‘current’ time period, winter length varied from 226 to 274 days long. Of the remaining climate variables, maximum SWE, mean annual temperature, summer length, temperature in the warmest quarter, and ENSO had weakly positive relationships with survival, while temperature seasonality had a weakly negative relationship (Fig. A.2).

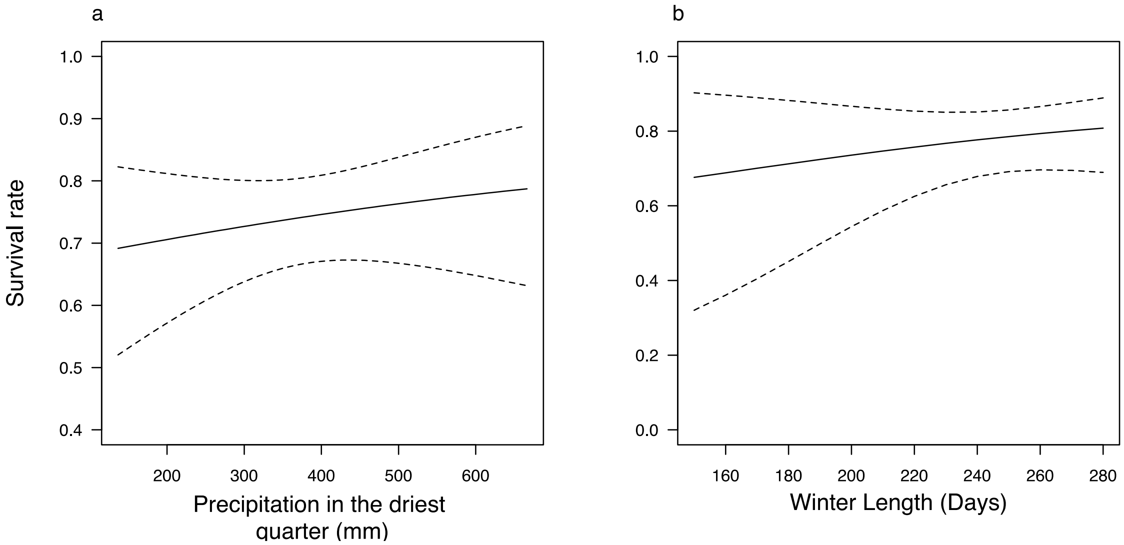

Figure 2.8. **Relationship between adult female survival and a) precipitation in the driest quarter and b) winter length, the two climate variables with the highest RVI in our candidate set. Dashed lines are 95% confidence intervals.**

We used the model-averaged coefficients of the climate variables to predict adult female survival from 1980 to 2006 and found that mean annual survival was 0.79 (sd +/- 0.02), while mean survival over the same time frame (n = 27) perturbed to represent the 2080's (i.e. 'future' survival) dropped to 0.74 (sd +/-0.04), a decrease of 6%.

2.4.3. Demographic modeling

The geometric mean stochastic population growth rate (λ_s) for 'current' larval and adult survival was 1.01 (se +/- 0.003), which decreased to 0.95 (se +/- 0.003) under 2080's climate conditions, predicting a 5% annual decline in population size. Under the scenario in which we modeled current larval mortality and 2080's adult survival, λ_s was 0.97 (se +/- 0.003), and when we modeled 2080's larval mortality and current adult survival, λ_s was 0.99 (sd +/- 0.003) (Fig. 2.9a).

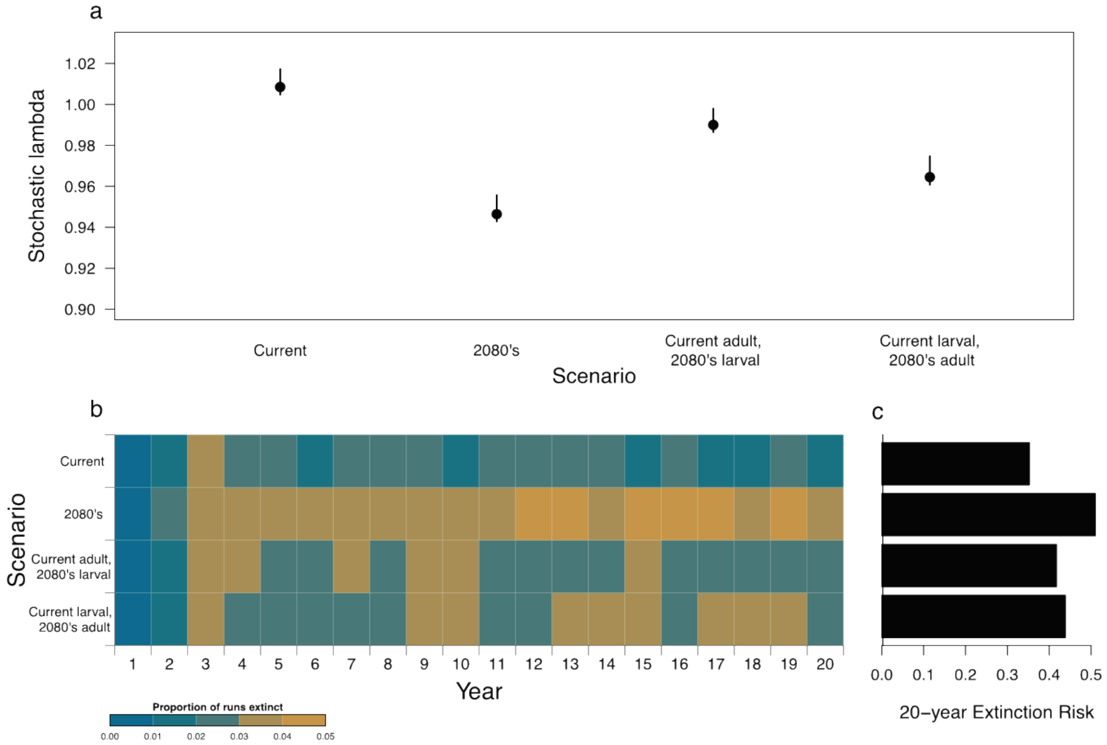

Figure 2.9. **Mean stochastic population growth rate and 95% confidence intervals for each scenario (a), dashed line (λs=1), represents a stable population, points above the line suggests a growing population, while points below the line represent a declining population. Panel b shows the proportion of runs that went extinct in each year for each scenario, and c is the cumulative 20-year extinction risk for each scenario.**

We calculated the 20-year extinction risk for each scenario, and estimate that for the current time period (1980-2006), extinction risk was 35%. In contrast, under 2080's climate conditions, extinction risk increased to 51%, and was 43% and 41% for the remaining two scenarios, respectively (current larval/future adult survival and future larval/current adult survival, Fig. 2.9c). We show that the proportion of runs that went extinct in the last 10 years of the simulation is much higher for the 2080's and, and for the scenario in which we coupled current larval and future adult survival, than for the scenarios in which adult survival is high ('current' and future larval/current adult survival, Fig.2.9b).

2.5. Discussion

We find that under projected 2080's climate conditions, *R. cascadae* may be pushed beyond a demographic tipping point, shifting from a stable population (λ_s =1.01) to one declining at 5% per year (λ_s =0.95) and a 1.4-fold increase in extinction risk, from 35% to 51%. Although the baseline extinction of 35% over 20 years is relatively high, this is can be attributed to the small starting population size of our model (300 breeding females), which reflects estimates of the mean number of egg masses laid from 2013-2015). Despite the small population size, our estimate of λ_s for the current time period reflects field observations of a relatively stable population. The decline in λ_s is driven by a 6% decrease in adult survival and a 17% increase in larval mortality due to pond drying (Fig 2.9a, Table 2.2). However, our analyses demonstrate that the 6% decline in λ_s between the current time period and the 2080's is driven largely by the decrease in adult survival, illustrated by the fact that the scenario in which we simulated current larval mortality with future adult survival, λ_s decreased to 0.96, but when we modeled future larval mortality with current adult survival, λ_s only decreased to 0.99 (a 2% decline in growth rate from 'current' conditions), but growth was still negative. Overall, reduction in adult survival alone results in ~5% decrease in λ_s, the reduction in larval survival alone results in ~2% decrease in λ_s, while additively, reductions in adult and larval survival in the 2080's reduced λ_s by 6%. This suggests that there may be a compensatory response in the aquatic life history stage of *R. cascadae* (i.e. large decreases in survival at this stage do not equate to severe population declines), but that the compensatory effect may be washed out by simultaneous decreases in survival at the terrestrial stage.

The decrease in vital rates (mainly, larval survival due to pond drying and adult survival) is a result of the drier climate and shorter winters expected in the 2080's. Compared to the current period (1980-2006), the proportion of ponds that are expected to dry in our study area in the 2080's increased by 9% and 40% for ephemeral and intermediate ponds respectively (Table 2.2). There is some evidence that developmental rates in amphibians can increase as the aquatic environments warm, compensating for increased drying rates (O'Regan et al.2014), and preliminary data for *R. cascadae* suggest that larvae in ponds with shorter hydroperiods develop faster (Kissel and Palen, unpublished data). However in most cases, drying and wholesale larval mortality occurs well before limb development in larvae (Kissel, personal observation), and thus increased developmental rates are unlikely to be high enough to compensate for increased mortality due to pond drying. Conversely, we did not account for the decrease in larval survival that may occur in years with particularly short growing seasons in which larvae do not have time to metamorphose before ponds freeze. Although we do not have data to explicitly measure how often this occurs, from 1980-2006, only two summers were shorter than 95 days, which is the maximum developmental time of *R. cascadae* larvae estimated by Slater (1939). Thus, it is unlikely that large increases temperature and growing season length will compensate for increased drying rates.

Additionally, we assumed that the proportion of egg masses in each breeding pond is the same each year, but the decrease in larval mortality due to pond drying could be buffered if breeding site fidelity is low (i.e. females breed in different ponds each year). However, for females caught 3 or more times during the study period (2002 to 2015), the mean proportion of captures at the primary pond of capture (i.e. the pond that it was caught the most number of times) was 0.84 (Palen and Adams, unpublished data). Given our observation of high site fidelity, and that over 1/3 of the reproductive effort of *R. cascadae* is deposited in intermediate ponds, these ponds currently act as a ‘source population’ for larvae, but may become a ‘sink’ by 2080’s in lieu of behavioral modifications (i.e. females choosing other ponds to breed in). Our data suggest that there could be some mixing of females between ponds (~26% of the time females were caught in ponds other than their primary pond of capture), and thus if females are able to switch breeding ponds to avoid larval desiccation, this could buffer declines in larval survival due to pond drying.

Despite this seemingly large loss of larval rearing habitat (a 25% reduction in ponds that sustain water through the larval rearing period), we find that predicted decreases in adult survival have a much larger effect on the overall population stability (Fig. 2.9). We hypothesized that shorter winters (and thus longer summers), could ease physiological stress on terrestrial stages via a decrease in winter severity (McCaffery & Maxell 2010, McCaffery et al. 2012), and an increase in growing season length (Corn 2005). However, we found that compared to current estimates, by the 2080’s, mean annual adult female survival is predicted to decrease by 6% (from 0.79 to 0.74), due to shorter winters and drier summers (calculated as cumulative precipitation in the driest quarter). Shorter winters, particularly if the onset of winter is later in the season, may result in a mismatch in phenological patterns, in which food resources are limited at the end of the growing season, but temperatures are not low enough to induce dormancy (Reading 2006; Williams et al. 2015). While longer summers had a weakly positive relationship to adult survival, decreases in pdq (i.e. drier summers) play a more important role in adult survival, and may result in increased risk of desiccation (Sears et al. 2016, Lertzman-Lepofsky et al. *in prep*) and reduced availability of emerging aquatic insects due to pond drying (Winder and Schindler 2004). These individual stressors have the potential to work synergistically (shorter winters coupled with drier summers) to decrease adult survival, which affects λ_s disproportionally in our system.

We leveraged a unique set of demographic and environmental data in combination with future climate projections to forecast the population level effects of climate change on *R. cascadae* at its northern range limit. To date, there are few published studies assessing the response of larval amphibians to a drying landscape (but see Matthews et al. 2013; McCaffery et al. 2014), and our site-specific VIC models allowed us to assess how the distribution of breeding effort across a range of hydroperiod types (exposure) influences larval survival now and in the future. Incorporating this information into a demographic model in turn allowed us to assess the sensitivity of this life stage to this particular stressor, and assess whether reduced survival at this stage due to forecasted changes in the landscape will result in a decrease in the population growth rate.

In addition to the larval stage, we also explored how adult survival, which is shown to have the greatest influence on λ_s for many amphibians (Biek et al. 2002a; Vonesh & De la Cruz 2002; Govindarajulu et al. 2005), is projected to change under 2080's climate conditions. We used 15 years of mark-recapture data in conjunction with observed climate data for the same time period to assess the relationship between a suite of climate hypotheses, and found two key climate variables that influence adult female survival; winter length and precipitation in the driest quarter. In our study, winter length is positively correlated with adult survival, which is counter to other studies that have explored the effects of winter severity on high elevation amphibians (Scherer et al. 2008; McCaffery & Maxell 2010; McCaffery et al. 2012) but in line with others that show that warmer, shorter winters may result in longer periods of time in which individuals are active during times of low food supply (Reading 2006; Church et al. 2007; Williams et al.

2015). To date, few studies have explored how summer precipitation will affect annual adult survival in high elevation amphibians (but see Laurance 1996; Scherer et al. 2008). However, given the critical dependency of most amphibians on aquatic environments, it is intuitive that survival would be positively related to increases in summer precipitation (Corn 2005). Although our study was limited to broad climatic patterns on an annual time scale, this can act as a starting point to further explore the mechanistic underpinnings behind the patterns, which will require detailed studies on the physiology and phenology of the species.

Our dataset allowed us to explore the response of two critical life stages (larval, adult) to a changing climate, however we were unable to assess how climate is directly related to other important life stages, such as metamorphic frogs and juveniles, or how changes in climate patterns may influence breeding behavior. For example, we assumed that the distribution of reproductive effort across a landscape does not change from year to year, an assumption supported by evidence of high site fidelity in our population and many others (Sinsch 1991; Gamble et al. 2007; Palen and Adams, unpublished data), which could have overestimated future larval mortality due to pond drying. However, our observed estimates of larval mortality due to pond drying across the same region from 2013-2015 where much higher (mean of 0.37 compared to estimate of 0.25 from 1980-2006), suggesting the VIC models may underestimate mortality due to pond drying, given that our observed larval mortality rate (from 2013 to 2015) was similar to predicted mortality rates under 2080's conditions (0.38). Although 2013 was an unusually dry summer (PDQ = 136.48mm, compared to the 1980-2006 average of 302.14mm), and the maximum SWE preceding 2015 was unusually low (187.96mm compared to the 1980-2006 average of 1037.45mm). Thus, our estimates of larval mortality due to pond drying are potentially conservative. Our models also did not explicitly consider the effects of desiccation at the embryonic stage, and there is some evidence that even in more permanent ponds, changes in snow melt patterns may cause egg mass stranding, thus increasing mortality at the embryonic stage (Kissel & Palen, unpublished data). However, in our study region in particular, all ponds in which we observed egg mass stranding subsequently dried before metamorphosis occurred, thus this mortality is accounted for in our larval survival parameter. Additionally, we did not have empirical data to estimate how fecundity may be linked to changing climate conditions, and thus our models assume that fecundity is equal for both ‘current’ and ‘2080's’ climate scenarios. However, there is evidence of skipped breeding and reduced fecundity for female amphibians in poor body condition (Reading 2006; Muths et al. 2013), suggesting that we may be overestimating fecundity in the future. Finally, our data for the 2080's does not take into account potential increases in climate variability, which may be an important driver in changing demographic rates (Morris et al. 2008), and thus we may be underestimating the change in survival at both the larval and adult stages.

We used site-specific drying patterns from 1980 to 2006 (the last year in which estimates are available from VIC models) to model the regional mean proportion of reproductive effort lost due to pond drying, and found that it was approximately 0.25. Finally, we relied on estimates of post-metamorphic and juvenile survival from other high elevation *Ranid* species (McCaffery and Baxell 2010, Funk 2005) in our demographic model. Post-metamorphic sub-adults in our system are extremely cryptic and too small in size to mark with PIT tags, thus, we have little data to assess survival at these stages. However, there is evidence that for amphibians, smaller individuals survive at lower rates (Chelgren et al. 2008; McCaffery & Maxell 2010; Matthews et al. 2013), which is reflected in our demographic model. Overall, our models provide a relevant comparison of important demographic rates likely to be influenced by climate change.

We have demonstrated that the effects of climate change at multiple life stages 'add-up' to reduce the population growth rate more than the effects at each stage individually, suggesting that compensatory mechanisms at the larval stage (i.e. increased growth rates) are not strong enough to stabilize the population in the face of large reductions in larval habitat (i.e pond drying) and when adult survival is low. Our findings highlight the importance of collecting demographic data to understand the mechanisms of population stability throughout the life history of a species before declines occur, which can be coupled with climate predictions to identify potential ecological tipping points. The increase in the 20-year extinction risk (~16%, Fig. 2.9c), serves as a "red flag" for conservationists. Although this level of extinction risk may not be expected for several decades, our models effectively forecast a regime shift or an 'ecological surprise' (Paine et al. 1998, Folk et al. 2004), highlighting the need for climate adaptation planning and mitigation measures even for currently stable populations. This is particularly important for species with complex life cycles that often live at the extreme ends of their physiological limits, for which climate change could have opposite effects at different life stages, such as high elevation amphibians (Corn 2005; Sunday et al. 2012). Our analysis reveals that climate change may push *R. cascadae* beyond a critical ecological tipping point, in which a historically stable population is predicted to decline at accelerating rates.

Chapter 3. Contrasting responses to climate reveal unexpected patterns of population vulnerability near the northern and southern range limits of a montane amphibian[2]

3.1. Abstract

Climate change is expected to create biotic conditions conducive to population growth and persistence at the pole-ward end of species' range limits, while abundance and persistence are expected to decline at equator-ward limits. Range shifts have been observed for many species, and predicted for others, but few studies have explicitly incorporated demographic data from multiple populations across a species' range to develop predictions of climate vulnerability. Here, we used stage-based demographic estimates and climate data for two populations of a montane amphibian in the northern hemisphere, Cascades frog (*Rana cascadae*), at the northern (Olympic National Park, WA) and southern (Trinity Alps Wilderness, CA) extent of the species' range to test whether the southern population is more vulnerable to future climate change. We quantified the regional differences in climate conditions, including winter length, growing season length, precipitation patterns, and hydroperiods of breeding ponds, to evaluate which contribute to current regional population dynamics. We estimated how current climate affects aquatic life history stages by quantifying annual larval mortality due to the frequency of pond drying in each population. We estimated annual survival rates of terrestrial stages from long-term population abundance data from each region linked to a suite of climate variables representing hypotheses about the role of temperature, precipitation, snowpack dynamics, and desiccation. We used these relationships to model the stochastic population growth rate (λ_s) of each population for current (1980-2006) and future periods (2080's, A1B emissions scenario), and found that currently, both populations are near stable, with Olympic increasingly slightly ($\lambda_s = 1.01$), and Trinity Alps decreasingly slightly ($\lambda_s =0.98$). The climate drivers of current survival rates in aquatic stages (i.e. changes in precipitation patterns leading to pond drying) were similar, but divergent for terrestrial stages, especially between survival and winter length

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[2] A version of this chapter is in preparation for publication with W.J. Palen, M.J. Adams, M. E. Ryan and J. Garwood

(a top ranked variable in our survival analysis). By the 2080's we predict a slight increase in λ_s for the southern Trinity Alps population (0.99), compared to a sharp decline for the northern Olympic population (λ_s = 0.95). Our results highlight that climate change can influence local landscape processes in ways that lead to unexpected consequences for population stability (i.e. higher vulnerability for populations at the pole-ward range extent) for species with complex life cycles in the face of climate change.

3.2. Introduction

Anthropogenic climate change is affecting species across their distribution, and many studies demonstrate that in the northern hemisphere, populations have generally increased at northern (pole-ward) limits and declined at southern (equator-ward) limits (Parmesan et al. 1999; McCarty 2001; Parmesan & Yohe 2003; Pauli et al. 2007). Climate envelope studies that combine species' thermal physiological limits with distribution-wide patterns of changes in temperature and precipitation also predict contractions in the south and expansions in the north (Root et al. 2003; Thuiller et al. 2005; Sunday et al. 2012). This general pattern can serve as a hypothesis which can be tested by incorporating population specific parameters that are thought to be driven by regional climate, such as survival and reproduction, into models of species persistence to explore whether patterns of vulnerability (i.e. declines in population growth rate, local extirpation) at range limits hold (Doak & Morris 2010; Villellas et al. 2015).

For individual populations, local persistence is thought to be driven by landscape level factors that may be congruent with, or counter to, predictions arising from climate envelope models alone (Doak & Morris 2010; Angert et al. 2011; Sunday et al. 2012). Microclimatic variation in temperature, precipitation, and habitat complexity can be strong drivers of individual success (survival, reproduction), which can scale up to affect population occupancy and persistence (Hereford 2009), and models that incorporate these fine scale data can diverge substantially from predictions based on climate envelope models (Guisan & Thuiller 2005; Buckley et al. 2010; Murray et al. 2015; Villellas et al. 2015). Populations of a species can vary in their exposure to climate attributes such as temperature and the amount and type of precipitation (e.g. snow vs.

rain) across their range; for example, García et al. (2000) suggest that regional patterns in seed production for juniper (*Juniperus communis*) is limited in areas that are colder in the winter or drier in the summer. Angert (2006) proposed that differences in local population growth rates of monkeyflowers (*Mimulus spp.*) were the result of different flooding regimes between low and high elevation populations. Thus, it is critical to incorporate population-level responses to climate into models of species persistence to improve predictions of species-level responses to rapidly changing climate (Doak & Morris 2010; Villellas et al. 2015).

Ectotherms living at the extreme ends of their thermal tolerances, such as high elevation amphibians, are predicted to be more sensitive to climate change than their low elevation counterparts (Corn 2005), and thus are a model taxonomic group to explore how vulnerability to climate change differs across latitudinal ranges. We quantified how two populations of Cascades frogs (*Rana cascadae*) at the northern and southern extent of their range experience a suite of climate variables at different life stages that are predicted to shift over the coming century. In particular for the Pacific Northwest, it is predicted that temperatures will increase, particularly in summer months, and that precipitation patterns will shift from snow dominated to rain dominated systems (Hamlet et al. 2005; Mote et al. 2005; Lee et al. 2015). Currently, between northern and southern populations there are substantial differences in climate conditions that are hypothesized to influence survival at different amphibian life history stages (Fig. 1). For example, temperature, summer length, and precipitation can affect heat stress and desiccation rates, aquatic habitat availability, and resource availability, while winter snow accumulation and winter length can affect energetic reserves and cold stress (Corn 2005; Scherer et al. 2008; McCaffery & Maxell 2010; McCaffery et al. 2012; Williams et al. 2015; Cayuela et al. 2016). Thus, these two populations provide the opportunity to test the hypothesis that populations at the southern range boundary will have higher vulnerability (i.e. lower population growth rate) to climate change compared to the northern range limit, which in turn can affect range expansion and contraction (Carroll et al. 2015).

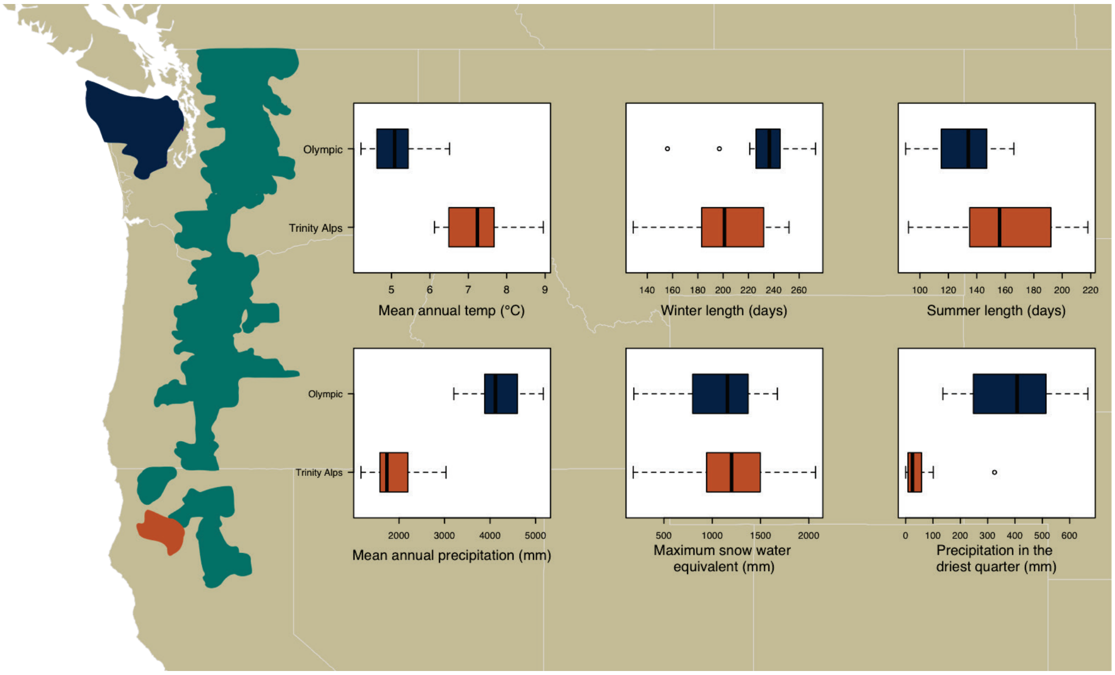

Figure 3.1 ***Rana cascadae*** **range map. We focus on 2 populations at the northern range (Olympic peninsula, purple) and southern range (Trinity Alps Wilderness, orange) and the remainder of the range is shown in green. Population boundaries are exaggerated for visual purpose. Box plots show the range in climate variables that may affect survival of** ***R. cascadae*** **from 2002 to 2016. All climate variables are calculated on an annual time step. DOY = day of the year. Dark blue box plots represent the Olympic population and orange represent the Trinity Alps population.**

We used demographic data collected from two populations of *R. cascadae* (2002 to 2016) to elucidate how two allopatric populations of the same species respond to components of anthropogenic climate change. Specifically, we focused on how breeding patterns and hydrologic stability driven by precipitation patterns in each population interact to affect landscape scale survival at the larval stage, and evaluated the relative importance of a suite of climate variables in driving variation in adult survival. We modeled the stochastic population growth rate and 20-year extinction risk to estimate how these two life stages interact to influence current population stability, and used site-specific predictions of changes in hydrology, temperature, and precipitation in the 2080’s to predict how regional differences in habitat influence population stability at the species' range limits.

3.3. Methods

3.3.1. Study species

Rana cascadae range from northern California to northern Washington (Fig. 3.1), and are listed as Near Threatened by the International Union for the Conservation of Nature (IUCN). Currently, *R. cascadae* are thought to be stable throughout most of their range. However, there have been noted extirpations of populations at the southern end of the range (Fellers & Drost 1993; Fellers et al. 2007), and the species is being considered for listing under the US Endangered Species Act (ecos.fws.gov/ecp0/profile/speciesProfile?spcode=D02E, accessed February 10, 2017) and the California Endangered Species Act (http://fgc.ca.gov/CESA, accessed April 11, 2017). *R. cascadae* are a montane species found above 1,220 meters (m) (Welsh et al. 2006, Fellers et al. 2008), and breed in ponds in the early summer immediately following snowmelt. Embryos hatch in 8-20 days, and larvae typically metamorphose 80-95 days later (Slater 1939). The species takes anywhere between 3 and 5 years to reach maturity (Briggs & Storm 1970, Garwood unpublished data) and individuals can live upwards of 20 years (Palen and Adams, unpublished data). We focused on two populations of *R. cascadae* that have been monitored extensively since the early 2000's; one population in the Seven Lakes Basin of Olympic National Park, Washington (elevation~1200m, distance to ocean = 55 kilometers), and one population in the Echo Lake Basin of the Trinity Alps Wilderness, California (elevation ~ 2100m, distance to ocean = 103 kilometers).

3.3.2. Climate data

To parameterize survival models for terrestrial adults, we used temperature and precipitation data from the PRISM database, which provides climate data interpolated over 4x4km grids from nearby weather stations (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 4 Feb 2004). The PRISM database does not estimate snow water equivalent (SWE), thus we used data from nearby weather stations; Waterhole SNOTEL station for the Olympic population and a combination of Red Rock Mountain, Bonanza King, and Shimmy Lake for the Trinity Alps (missing data required combining data from multiple weather stations) to develop a suite of 14 climate variables that we hypothesized could influence annual survival at different life history stages (Table 2.1, see ‘adult survival’ methods below).

We quantified the change in 13 of the 14 climate drivers for the two populations between now and the 2080’s (future estimates were not available for El Niño), as well as changes in drying regimes of individual breeding ponds, with data from the Variable Infiltration Capacity (VIC) model implemented for the Columbia Basin Climate Scenarios Project (CBCCSP). The VIC model is a macro-scale water balancing hydrologic model used to estimate changes in hydrologic patterns across large spatial and temporal scales, and provides daily estimates of temperature, precipitation, and SWE from 1915-2006, and for the same time series length perturbed to reflect different climate scenarios for the 2040’s and 2080’s (Hamlet et al. 2010, Appendix D). We used data from 1980 to 2006 (the last available year of VIC simulations) to compare ‘current’ climate conditions, to those projected in the 2080’s under the A1B scenario by the VIC models, and used the same time series to predict drying of breeding ponds for the two study regions (see below). The A1B emissions scenario reflects rapid economic growth, rapid and efficient technological advances, and energy use balanced across available sources (IPCC 2004).

3.3.3. Larval mortality data collection and analysis

Northern Population

We categorized all wetlands used by *R. cascadae* for breeding in (n = 51) into one of four hydroperiod types (ephemeral, intermediate, perennial, and permanent) based on the historical drying patterns estimated by the VIC models (Lee et al. 2015). Ephemeral ponds typically hold water for a matter of weeks and dry in most years, intermediate ponds may dry in late summer in dry years, perennial ponds dry only in extreme drought years, and permanent ponds never dry (Lee et al. 2015). We used mean estimates of egg masses from recorded data on the number and distribution of *R. cascadae* egg masses in the Olympic (WA) population from 2013 to 2015 and linked these data with site-specific estimates of drying from 1980-2006 developed with the

Variable Infiltration Capacity (VIC) model (Lee et al. 2015; Kissel et al. 2017, *in prep*). VIC models were available for 26 of the 51 breeding ponds, and for the same time series, perturbed to reflect temperature and precipitation patterns predicted under the AIB climate scenario for the 2080's (Lee et al. 2015). We paired sites without VIC estimates (n = 25) to sites with VIC estimates based on the similarity of empirical observations of pond drying from 2013 to 2015 (see Kissel et al. 2017 *in prep* for details). We used this dataset to calculate a mean population level estimate of larval mortality due to pond drying from 1980-2006, as well as for 2080's conditions (Kissel et al. 2017 *in prep*, see below for matrix model details).

Southern population

There are 50 breeding ponds in the Trinity Alps (CA) population, and we reconstructed whether or not a pond dried on an annual basis from 2003 to 2016 based on detailed hydroperiod surveys across three years (Garwood 2009). VIC data with daily estimates of wetland water level exist for a single large site, Snowmelt pond (representing ~17% of the reproductive effort for the population). We used the relationship between drying patterns estimated from VIC models for Snowmelt pond, observed drying patterns for Snowmelt pond and observed drying for all other breeding ponds, to simulate drying patterns from 1980-2006 for all ponds. We categorized breeding sites into four hydroperiod classes as above (ephemeral, intermediate, perennial, and permanent), and calculated the probability of drying for each hydroperiod class in each year using equation 1.

$$P(Hydroperiod\ class_i\ dries) = \frac{\sum ponds\ dried\ in\ hydroperiod\ class_i}{\sum breeding\ ponds\ in\ hydroperiod\ class_i} \qquad \textit{Equation 3.1}$$

We then used empirical data to calculate the mean probability of drying in years that Snowmelt pond (an intermediate hydroperiod pond) dried (7 out of 13), and conversely the mean probability of drying for each hydroperiod class in years that snowmelt pond did not dry (6 out of 13).

The distribution of egg masses in ponds in each hydroperiod type varied over the course of 13 years (Table B.1). Thus, for each breeding site (n = 50), we calculated the probability of breeding in a year, using equation 2.

$$P(Breeding) = \frac{\sum years\ breeding\ occurred}{n} \qquad \textit{Equation 3.2}$$

Where n=13, the total number of years of the study. For years between 1980-2006 in which the VIC simulation predicted that Snowmelt pond would dry, we estimated whether breeding occurred each year (random draw from a Bernoulli distribution fit to the probability of breeding for each site), and then simulated whether the pond dried (random draw from a Bernoulli distribution fit to the annual probability of drying for the hydroperiod class which the site was assigned in years when Snowmelt pond dried). We repeated this analysis for years in which the VIC model predicted that Snowmelt pond would not dry, drawing from the probability distribution characterized for years in which Snowmelt pond did not dry. Based on these simulated data, we used the mean proportion of the total population reproductive effort in each site to estimate what fraction of reproductive effort was lost from 1980-2006, and repeated this simulation using the VIC model predictions for the 2080's.

3.3.4. Adult survival

There is an ongoing capture-mark-recapture study for both the Olympic and Trinity Alps populations, spanning roughly the same time periods (2002-present for Olympic, and 2003-present for Trinity Alps). For the Olympic population, data collection takes place on three consecutive days during breeding season. For the Trinity Alps, site visits occur throughout the open water (summer) season, and the number of visits to each site varies among years. We used a Robust Design framework implemented in the package RMark V2.2.0 (Laake 2013) in the statistical program R (R Core Team 2017), to predict adult survival for males and females separately for the Olympic population as a function of up to two climate variables (Table 2.1) per model, while *p* (probability of capture), *c* (probability of recapture) varied by year and visit, and gamma' and gamma'' (estimates of temporary emigration) varied by year (see Kissel et al. 2017, *in prep* for details). We analyzed the data from the Trinity Alps population using the same suite of climate variables, removing 4 variables (mean annual temperature, temperature seasonality, maximum snow water equivalent, and summer length) that were strongly correlated to winter length, which ranked highly for the Olympic population. For the Trinity Alps population, we pooled visits by week during the summer (typically June to September), and estimated annual adult survival in a Robust Design framework. Similar to the Olympic population (Kissel et al. 2017 *in prep*), survival estimates varied by sex and a we included a combination up to two additive climate variables, while *p* (probability of capture) and *c* (probability of recapture) varied by year and visit. For the Trinity Alps population, we fixed the population such that no immigration and emigration could occur (gamma''=0 and gamma'=1) (Kendall & Nichols 1995), because models in which these parameters were allowed to vary did not converge. Furthermore, Garwood (2009) found less than one percent of marked frogs dispersed between basins indicating the population closure assumption is reasonably met. Finally, we used AICc to rank alternative survival models, and for parameters occurring in models summing to 95% of the weight, we calculated a relative variable importance value (RVI) and model averaged estimates of each parameter (Burnham & Anderson 2002). We used these model averaged estimates to predict adult survival over the same time period for which we predicted larval mortality due to pond drying (1980-2006), and again for the 2080's (A1B scenario) using climate data from the VIC models.

3.3.5. Demographic modelling

We used a female only 5x5 stage-based Leslie matrix model (Morris and Doak 2002) to estimate the geometric mean stochastic population growth rate (λ_s) and 20-year probability of extinction for both populations. We ran 5,000 iterations of each model, randomly pulling vital rates from a distribution characterized by the mean and variances of each vital rate estimate (see Table B.2 for vital rate means and variances that were equal for both populations). Vital rate distributions for the embryonic, larval, and adult stages were parametrized using the mean and variance from the best estimates of our time series of data (1980-2006 for the current time period and the same time series perturbed to reflect 2080's conditions for the future time period), thus our models included environmental variation but did not include process error (i.e. model uncertainty). For juvenile survival, we calculated the mean and variance from five previously published point estimates of survival from two high elevation populations of Columbia spotted frogs (*Rana luteiventris)* (McCaffery & Maxell et al. 2010; Matthews 2013). Because post-aquatic survival is poorly understood for amphibians (Biek et al. 2002a; Muths et al. 2014), and there is evidence that it is correlated (McCaffery & Maxell 2010), we included a correlation structure for terrestrial stages (metamorph, juveniles, and adults), such that years with high survival for adults resulted in high survival for other terrestrial stages (Morris & Doak 2002). In our models, the populations differ in the time to maturity for females in the Olympic population than the Trinity Alps population; all females in the Trinity Alps are mature after 4 years (Garwood, unpublished data), whereas in the Olympics we suspect that the age at maturity could be between 4 and 5 years (Briggs and Storm 1970), and thus we included a transition rate of 0.54 from 4th year juveniles to adults based on juvenile transition rates estimated for another high elevation amphibian (McCaffery & Maxell 2010, Fig. 3.2). We modeled four scenarios consisting of all combinations of ‘current’ (1980-2006) and future (1980’s) larval and adult survival to weigh the relative contribution of these two vital rates to the population growth rate. Our scenarios consisted of ‘current’ larval mortality due to pond drying and adult survival, ‘current’ larval mortality and 2080’s adult survival, 2080’s larval mortality and ‘current’ adult survival and, both 2080’s larval mortality and adult survival. We chose to model these four combinations rather than a traditional elasticity analysis because larval survival is a pre-reproductive vital rate; Caswell (2001) states that all elasticities of pre-reproductive rates are equal, thus we would be unable to separate elasticity of larval survival from other pre-reproductive rate elasticities. We calculated the sensitivity of λ_s to larval mortality due to pond drying and adult survival using the change in λ_s divided by the change in vital rate ($\Delta\lambda_s/\Delta$ vital rate) between 1) ‘current’ and current larval/2080’s adult survival and 2) ‘current’ and 2080’s larval/current adult survival.

$$\begin{bmatrix} 0 & 0 & 0 & 0 & F_{15} \\ a_{21} & 0 & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 & 0 \\ 0 & 0 & a_{43} & \boldsymbol{a_{44}} & 0 \\ 0 & 0 & 0 & a_{54} & a_{55} \end{bmatrix} \text{X} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t+1}$$

Vital rate	***aij***	**Parameter Equation**
Embryo to juvenile$_1$ transition	a_{21}	$\phi_{\text{embryo}} * \phi_{\text{background arvae}} *(1-\text{proportion dried}) * \phi_{\text{YOY}}$
Juvenile$_1$ to Juvenile$_2$ transition	a_{32}	ϕ_{juv1} l
Juvenile$_2$ to Juvenile3 transition	a_{43}	ϕ_{juv2}
Juvenile3 to adult transition	$\boldsymbol{a_{54}}$	$\boldsymbol{\phi_{\text{juv3}} * p_{\text{adult}}}$
Juvenile 3 survival	a_{44}	$\phi_{\text{juv3}} \boldsymbol{*(1-p_{\text{adult}})}$
Adult survival	a_{55}	ϕ_{adult}
Fecundity (Adult)	F_{15}	$F_{\text{adult}} * \text{sex ratio} * \phi_{\text{adult}}$

Figure 3.2 Matrix model and vital rate description for *Rana cascadae*. Bolded matrix element (a_{44}) represents the additional vital rate for the northern population, in which individual may take an additional year to transition to adults.

3.4. Results

3.4.1. Climate predictions

For both the Olympic and Trinity Alps regions, climate variables associated with temperature (e.g. mean annual temperature, temperature in the warmest quarter) and summer length, are predicted to increase in the 2080's. Mean annual temperature is predicted to be approximately 30% warmer in both populations, and summer length 33% (8.3 weeks) longer for the Olympic region and 27% (8.1 weeks) longer for the Trinity Alps (Fig. 3.3). Changes in precipitation were forecast to be mostly negligible; changes in the amount of annual precipitation were +2% and -4% for Olympic and Trinity Alps, respectively. In contrast, precipitation related climate variables that incorporate the effect of temperature are predicted to change dramatically, where winter length is predicted to decrease by 31% (8.4 weeks) in the Olympics and 35% (8 weeks) in the Trinity Alps due to more winter precipitation falling as rain rather than snow, and maximum snow water equivalent (SWE) is forecast to decrease by over 200% in the Olympics and approximately 150% in the Trinity Alps (Fig. 3.3).

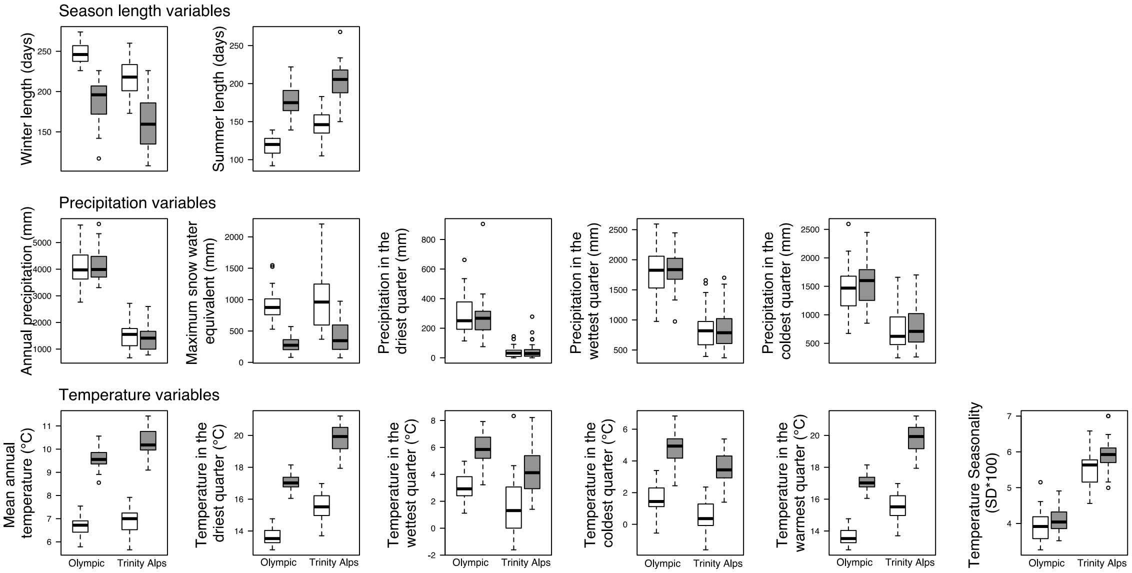

Figure 3.3 **Boxplots comparing the 'current' (1980-2006) and projected 2080's conditions (grey boxes) for each climate variable included in the adult survival analysis. El Nino is not displayed because we did not have climate predictions for this climate variable.**

3.4.2. Larval mortality

The proportion of ponds that dried annually in the 2080's in the ephemeral hydroperiod class increased for the Olympic population from 0.91 (current) to 1 (2080's), and for the Trinity Alps all ephemeral ponds dried both in the current and 2080's time periods. The proportion of intermediate ponds that dried annually increased in the 2080's for both the Olympic (from 0.45 to 0.75) and Trinity Alps regions (from 0.38 to 0.57) (Table 3.1). During the current (1980-2006) period, we estimated that the proportion of larvae lost due to pond drying was similar (0.25 SD+/- 0.14, and 0.22 SD +/- 0.25 for the Olympic and Trinity Alps respectively), which we translated into a mean 'survival' rate of 0.75 and 0.78 (Fig. 3.4a, b), not including background larval survival due to predation etc. (see Table B.2). By the 2080's the proportion of larval mortality due to pond drying increased for both regions by between 7-13% (0.38, SD +/- 0.11 Olympics, 0.32, SD +/-

0.22 Trinity Alps), which translated into a mean survival rate of 0.62 and 0.67 for the Olympic and Trinity Alps populations respectively (Fig. 3.4a,b).

Table 3.1 Distribution of reproductive effort across 4 hydroperiod classes for the two population, where n = the number of ponds in each hydroperiod class. Mean proportion of reproductive effort was measured between 2013 and 2015 for the Olympic population and between 2003 and 2016 for the Trinity Alps population. Proportion dried 'current' is the proportion of ponds that we estimated dried between 1980-2006, and proportion of ponds 2080's = the proportion of ponds that we estimate will dry in the 2080's under the A1B climate scenario.

Hydroperiod class	Population	n	Mean proportion of reproductive effort	Proportion dried (current)	Proportion dried (2080's)
ephemeral	Olympic	13	0.09	0.91	1
	Trinity Alps	6	0.03	1	1
intermediate	Olympic	23	0.37	0.45	0.75
	Trinity Alps	23	0.56	0.38	0.57
perennial	Olympic	11	0.35	0	0
	Trinity Alps	9	0.11	0	0
permanent	Olympic	4	0.18	0	0
	Trinity Alps	12	0.34	0	0

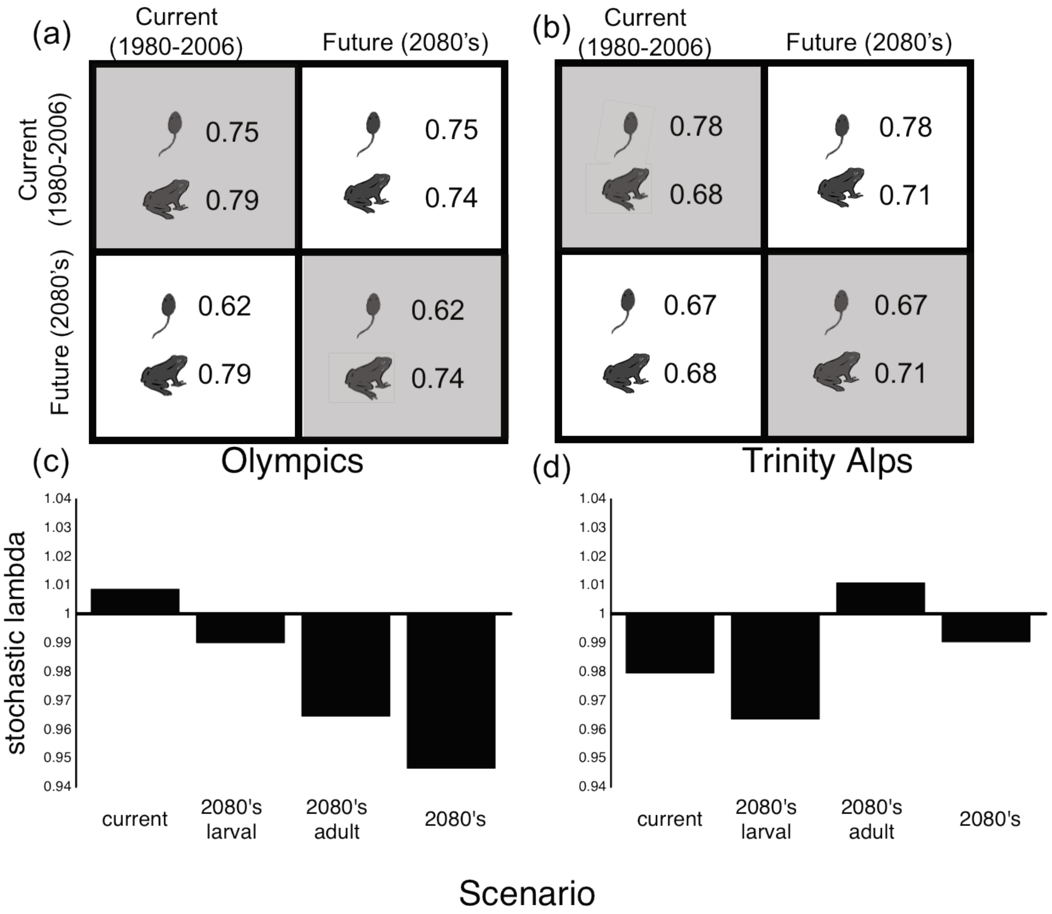

Figure 3.4 **Schematic diagram of matrix model scenarios (a,b) where 'current' represents scenarios in which vital rates were pulled from a distribution in which the mean and variance were described by the 'current' vital rates (estimated from 1980-2006) and 'future' represents scenarios in which vital rates were pulled from a distribution where the mean and variance were described by estimates of the vital rates from the 2080's. Numbers to the right of the symbols are the mean vital rates for the proportion of larvae within a population that did not dry, and adult survival. Left panel represents the northern (Olympic) population and right panel represents the southern (Trinity Alps) population. The top left and bottom right quadrants represent 'current' and 'future' simulations, while the bottom left and top are additional scenarios that we ran to estimate the sensitivity of each vital rate to the population growth rate. Panels c and d are the mean stochastic lambda's estimated for each scenario for the Olympics and Trinity Alps respectively.**

3.4.3. Adult survival

Based on our model-averaged estimates of survival, the predicted mean adult female survival from 1980-2006 was substantially higher for the Olympic population (0.79, sd +/- 0.02) compared to the Trinity Alps (0.68, sd +/- 0.014). In the Olympic population, female survival was on average 7.5% lower than males, and in the Trinity Alps female survival was 4% lower than males. Hereafter, we present only results for females relevant to our demographic models. Under 2080's climate conditions, the mean female survival decreased for the Olympic population to 0.73 (sd +/-0.04), and increased for the Trinity Alps population to 0.71 (sd +/- 0.02) (Figure 4a, b). The top models (those that held 95% of the AICc weight) were slightly different between the populations, in that precipitation in the driest quarter, winter length, temperature seasonality, El Niño, temperature in the driest quarter, temperature in the coldest quarter, and precipitation in the wettest quarter ranked from highest to lowest support for the Trinity Alps population (Fig. 3.5a, Table B.3), while for the Olympic population, precipitation in the driest quarter, winter length, max SWE, temperature seasonality, mean annual temperature, summer length, temperature in the warmest quarter, and El Niño, ranked from highest to lowest support (Fig. 3.5a, Table B.4). Notably, for both populations precipitation in the driest quarter and winter length held the most support (relative variable importance value of 45% for the Olympic population and 33% for Trinity Alps). However increasing precipitation in the driest quarter was weakly positively related to survival for the Trinity Alps population and negatively related to survival for the Olympic population (Fig. 3.5b). Increasing winter length was also negatively related to survival for the Trinity Alps population and positively related to survival for the Olympic population, and the relative importance values for each population were 22% and 41% respectively (Fig. 3.5c).

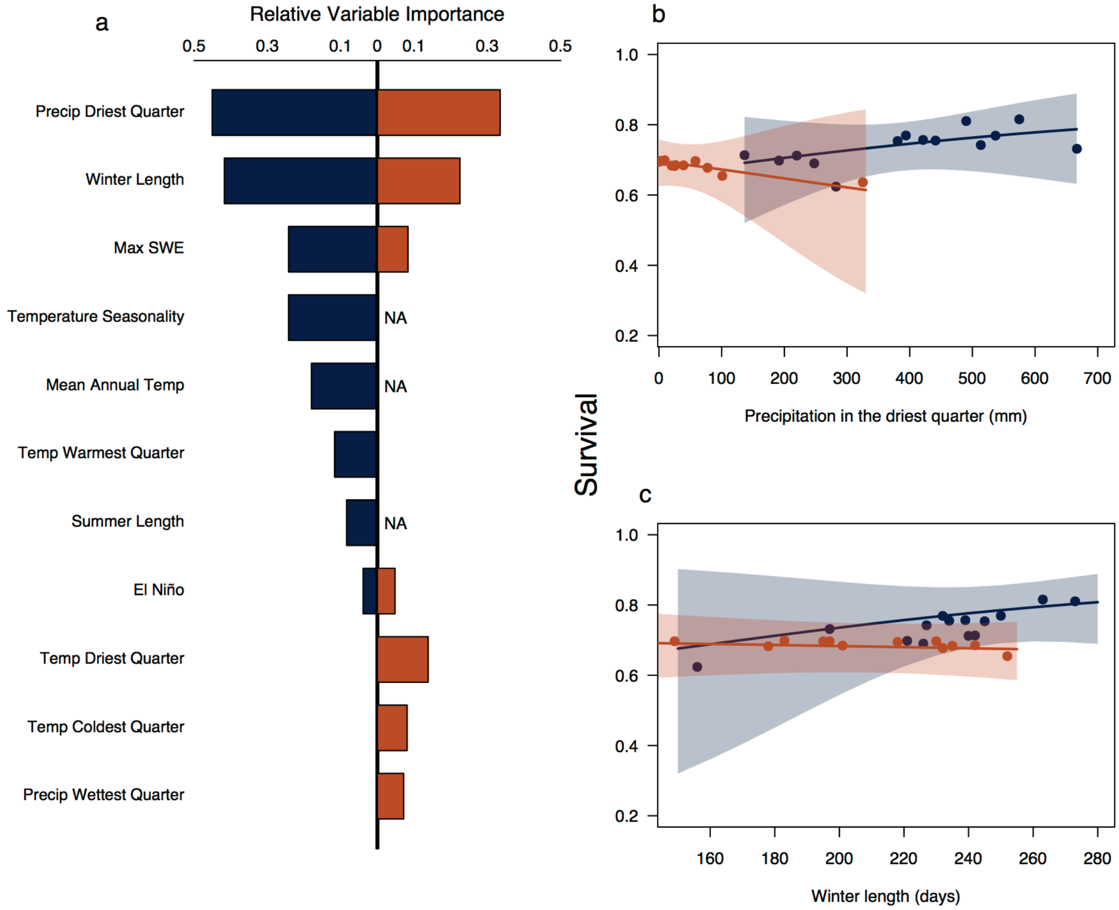

Figure 3.5 Panel a: Relative variable importance (RVI) plot for Olympics (northern, dark blue) population, and Trinity Alps (southern population, orange). 'NA' indicates that variable was not included in survival analysis because it was highly correlated with another variable. Model-averaged estimates of survival for female R. cascadae as a function of precipitation in the driest quarter (b), and winter length (c), the two variables with the highest RVI. Plots show the relationship between observed climate data and survival, estimated over the time period of the respected studies (2002-2016 for Olympics and 2003-2016 for Trinity Alps).

3.4.4. Demographic modelling

Under 'current' (1980-2006) conditions the mean stochastic lambda (λ_s) for *R. cascadae* was 1.01 (se +/- 0.004, Fig. 3.7a) for the Olympic population (20-year extinction risk of 0.35, Fig. 3.6) and 0.98 (se +/- 0.004, Fig. 3.7a) for the Trinity Alps population (20-year extinction risk of 0.41, Fig. 3.6). Under future (2080's) conditions, λ_s was 0.95 (se +/- 0.003) and .99 (se +/- 0.004) for the Olympic and Trinity Alps respectively (Fig. 3.7a), and the 20-year probability of extinction increased by 31% for the Olympic population (from 0.35 to 0.51, Fig. 3.6), but only 2% for the Trinity Alps population (from 0.41 to 0.42, Fig. 3.6) between the 'current' and 2080's scenarios (Fig. 3.7b). The mean stochastic lambda for the Olympics decreased from the 'current' growth rate of 1.01 to 0.96 (se +/- 0.004) when we modeled 'current' larval survival and 2080's adult survival, and increased for the Trinity Alps population to 1.01 (se +/- 0.004), with an associated 20-year extinction risk of 0.44 and 0.36 respectively (Fig. 3.4c). Under 2080's larval survival and current adult, λ_s was 0.99 (se+/- 0.003) for the Olympics and 0.97 (se +/- 0.004) for the Trinity Alps, and the associated probability of extinction was 0.42 and 0.48 respectively (Fig. 3.4d). The per unit change in lambda given a per unit change in larval survival rate ($\Delta\lambda_s/\Delta$ vital rate) was 0.14 for the Olympic population and 0.15 for the Trinity Alps, while $\Delta\lambda_s/\Delta$ adult survival was 0.76 for the Olympic and 1.02 for the Trinity Alps (Fig. 3.8).

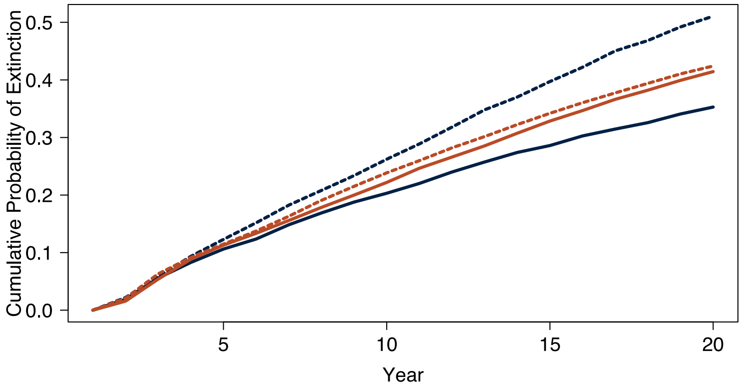

Figure 3.6. **20-year cumulative probability of extinction for 'current (solid lines) and 2080's (dashed lines) scenarios. Dark blue lines represent the Olympic population and orange lines represent the Trinity Alps population.**

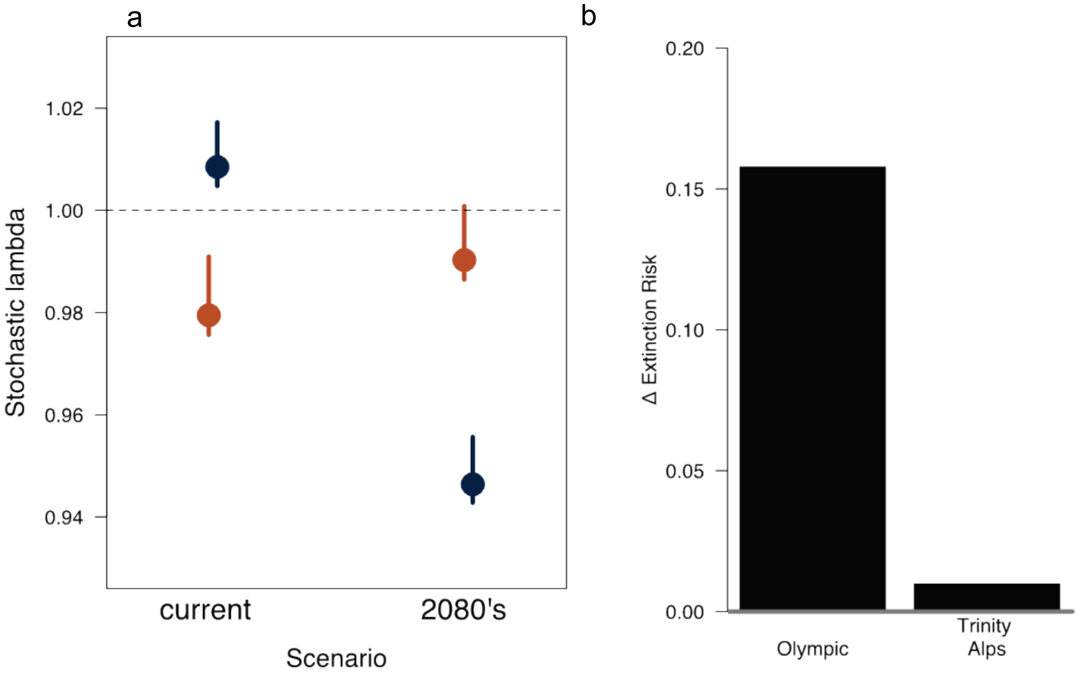

Figure 3.7 Panel a: Stochastic lambda and 95% confidence intervals (calculated from the first 500 runs of the simulation) for the 'current' (1980-2006) and future (2080's) scenarios. Dark blue dots represent the Olympic population and orange represent the Trinity Alps. Panel b: the associated change in extinction risk between 'current' and '2080's' scenarios.

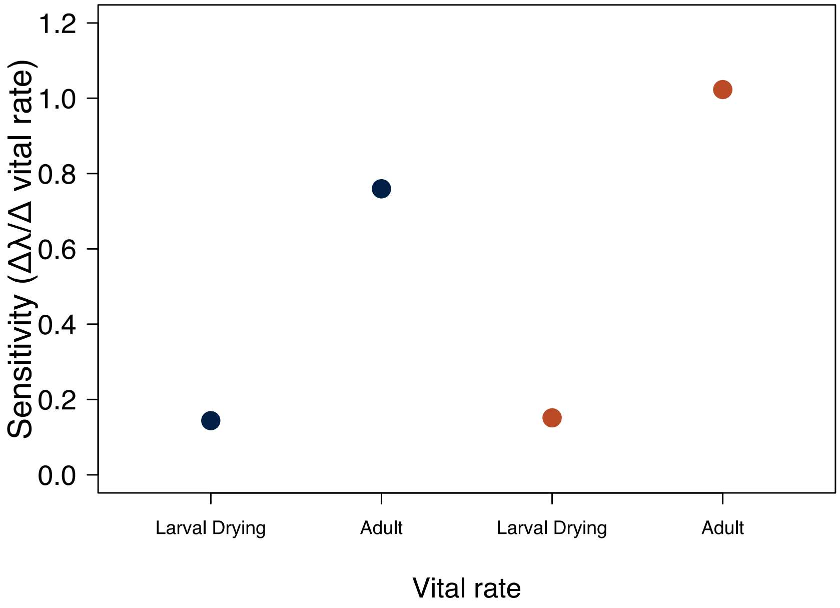

Figure 3.8 **Sensitivity (change in lambda divided by the change in vital rate) between 'current' and 2080's estimates of adult survival and larval mortality due to pond drying. Dark blue dots represent the Olympics and orange dots represent the Trinity Alps.**

3.5. Discussion

Our results demonstrate under 2080's climate conditions, the mean stochastic population growth rate (λ_s) for *R. cascadae* at the northern end of their range (Olympic) is predicted to be well below 1 (5% annual decline), while λ_s for the southern (Trinity Alps) population remains similar (marginal increase from 0.98 to 0.99), suggesting that the northern population of *R. cascadae* is more vulnerable to climate driven extirpation than the southern population. Data from VIC simulations estimate that under 2080's climate conditions (A1B scenario), both regions will be warmer, resulting in shorter winters and reduced snow water equivalent (Fig. 3.3), and that breeding ponds will dry more frequently (Table 3.1). Our analyses predict similar increases in larval mortality due to pond drying (17% and 14% increase for Olympic and Trinity Alps respectively), but divergent estimates of how climate will affect adult survival, in that survival simulated under 2080's climate conditions decreases for the Olympic population (from a mean of 0.79 to 0.74) and increases for the Trinity Alps populations (from a mean of 0.68 to

0.71). When we ‘added up’ the effects of climate on survival at multiple life stages using demographic models, we found that increases in adult survival for the Trinity Alps population more than compensates for the predicted decreases in larval survival, and that the 20-year extinction for the 2080’s was similar to the current extinction risk (0.41 compared to 0.42), but that for the Olympic population, compounding decreases in both larval and adult survival in the 2080’s resulted in a 31% greater extinction risk for the 2080’s (from 0.35 to 0.51, Fig. 3.7).

In both populations, λ_s was more sensitive to changes in adult survival than larval survival, in that large decreases in larval survival due to pond drying (-17% and -14% for Olympic and Trinity Alps respectively) relative to adult survival (-6% and +4% respectively), did not result in larger changes in λ_s. We calculated the sensitivity of lambda ($\Delta\lambda_s/\Delta$ vital rate) for larval mortality due to pond drying and adult survival, and found that sensitivity was similarly low for larval survival (0.14 for the Olympic and 0.15 for the Trinity Alps), and much higher for adult survival (0.76 and 1.02 for Olympic and Trinity Alps respectively, Fig. 3.8). This finding is similar to other amphibian studies that identify adult survival as the primary driver of variation in population growth rate compared to other life history stages (Biek et al. 2002; Vonesh & De la Cruz 2002; Govindarajulu et al. 2005).

The relatively large contribution of adult survival to λ_s highlights the importance of understanding what drives variation in survival at this stage. We found that for both populations, precipitation in the driest quarter and winter length had the highest relative variable importance values for explaining variation in adult survival. However, the effects of precipitation in the driest quarter and winter length were in opposite directions for the two populations; adult survival was weakly negatively related to increases in precipitation in the driest quarter in the Trinity Alps (southern) population and positively related in the Olympic (northern) population, and increasing winter length was negatively correlated to survival in the Trinity Alps and positively related in the Olympic population. Precipitation in the driest quarter is lower and less variable in the Trinity Alps population (Fig. 3.3), which may contribute to the weak relationship we found for the Trinity Alps. Additionally, under 2080’s conditions, our models predict little change in precipitation in the driest quarter for both regions, but larger decreases in SWE, contributing to shorter winters (Figure 3.3). Thus, differences in hydrologic sources of wetlands between the two populations may also partially explain this pattern. The majority of small wetlands used by *R. cascadae* in the Olympic region are fed by snowmelt, and experience large reductions in water volume in particularly dry summers (Lee et al. 2015), increasing the risk of desiccation to frogs and decreasing the availability of aquatic prey. Thus, longer winters (driven largely by snow accumulation coupled with colder temperatures) may play a critical role in sustaining suitable habitat for both aquatic and terrestrial amphibian stages for the northern Olympic population via snowpack runoff in late spring and early summer that acts to stabilize wetland water levels (Ryan et al. 2014; Lee et al. 2015), in turn providing suitable habitat for adults seeking to thermal and hydro-regulate (Mitchell & Bergmann 2016; Sears et al. 2016). In years with shorter winters, summer precipitation (i.e. precipitation in the driest quarter) is likely to be a crucial for maintaining wetland water levels for the Olympics and thus an important driver of survival at both the aquatic and terrestrial stages. However, in the Trinity Alps, many of the small wetlands used by *R. cascadae* are fed by groundwater (J. Garwood, unpublished data), and by comparison, exhibit much more stable water levels even in dry summers, and thus may be less dependent on both precipitation and winter length to provide critical aquatic habitat.

We compared two populations of *R. cascadae* that have been studied over a similar time frame, and used empirical data from each population to estimate how survival at both aquatic and terrestrial stages are driven by local climatic variables as a basis for predicting demographics changes in the 2080's. Although we had comprehensive data sets to estimate survival, we were unable to incorporate other potential sources of climate impacts on demography, such as potential effects on fecundity and body condition (Reading 2006; Muths et al. 2013; Cayuela et al. 2016), density dependent effects, and the effects of climate at sub-adult terrestrial stages. For example, ponds that lose a substantial amount of water but do not dry may concentrate larvae in smaller areas, leading to competition for resources or metamorphosis at smaller body sizes (Newman 1998), which can result in lower juvenile survival (Morey & Reznick 2001). However O'Regan et al. (2014) demonstrated that warming associated with pond drying may increase food resources at the larval stage, negating the effects of earlier metamorphosis on body size. Additionally, the low elasticity at the larval stage suggests that density dependence at the larval stage may be less important for *R. cascadae*. We did not have data to estimate survival and transition probabilities for either population, and used estimates from the published literature to parameterize vital rates at the metamorphic and juvenile stages (Table B.2), thus there is some uncertainty in both survival and age at maturity for both populations. However, our mean estimates of λ_s align with the mean geometric growth from population size estimates generated by our mark recapture models (Fig. B.1), suggesting that the matrix models for both populations approximate population dynamics well. Our study also focused solely on how changes in climate could affect population dynamics, and we did not incorporate disease and invasive predators, which are known threats particularly for the Trinity Alps population (Garwood, unpublished data).

Despite the large amount of data available for both populations, methods of data collection and the types of data available for the two populations differed. For aquatic life history stages, we used pond specific estimates of drying generated by the VIC model to estimate landscape larval mortality due to pond drying for the Olympic population, and linked these data to 3 years (2013 to 2015) of empirical data on the distribution of egg masses within each pond. However, for the Trinity Alps, our estimates of larval mortality due to pond drying rely on reconstructed estimates of pond drying over a 13-year period (from 2003 to 2016). Detailed VIC estimates of drying were only available for one pond (Snowmelt), and thus we calculated probabilities of annual drying for each hydroperiod class in relation to Snowmelt pond from the 13 years of observed data and used these probabilities to simulate hypothetical drying regimes and larval mortality. These estimates are the best available data for larval mortality for the region, and serve as a useful comparison to the Olympic population, but impart some uncertainty to our population results. To estimate adult survival for the Trinity Alps population, we pooled daily capture occasions into weekly visits, and assumed population closure between weeks in order to run a Robust Design model. However movement estimates for this population suggests that it is closed (Garwood 2009), and our estimates for survival overlap with previous estimates for the population (Garwood, unpublished data), lending support to our results. Although the types of data and analyses differed somewhat between the two populations, these are the two best-studied *R. cascadae* populations, and thus the richest source of data available to evaluate our hypotheses. Additionally, our estimates of population growth rate under ‘current’ conditions suggest that both populations are relatively stable, which aligns with >13 years of field surveys for reproductive effort (egg masses) and adult frogs for both populations.

To date, the majority of studies that leverage demographic data to compare survival and growth rates between populations with respect to climate change are for terrestrial plants (Angert et al. 2007; Doak & Morris 2010; see Villellas et al. 2015 for a comprehensive list), and we found only one other study that compares the responses of multiple life stages in more than one population for species with complex life cycles, such as amphibians (Cayuela et al. 2016). Many studies predict contrasting responses to climate change among different amphibian species (McCaffery & Maxell 2010; McCaffery et al. 2012; Matthews et al. 2013; Cayuela et al. 2016; Grant et al. 2016), and here we demonstrate that this may be the case among populations within a single species as well. Our results align with Cayuela et al. 2016, in that they demonstrate opposing responses to several climate variables among populations and between life history stages. However, our analysis goes one step further, in that we use the responses estimated at individual life history stages to predict how populations as a whole will respond to climate change, and in doing so, find there is evidence of demographic compensation at the adult stage in the southern population, but compensation is lacking in the northern population, resulting in a higher sensitivity to climate change. Our results highlight that population-level responses to local climate conditions likely play an important role in predicting vulnerability to climate change, particularly for amphibians, one of the most globally threatened taxa due to threats from disease, habitat loss, and climate change (Stuart et al. 2004; Hoffmann et al. 2010). For example, understanding population level responses of *R. cascadae* to climate may help to disentangle causes for decline throughout much of their southern range, which are unknown but thought to be due to a combination of disease, predation by invasive trout, and pesticide use, all of which may be exacerbated by climate change (Fellers et al. 2007).

Broad-scale analyses of species distributions in the face of climate change may be unable to capture the potential for compensatory or compounding demographic responses within populations or species. Studies that predict higher vulnerability for southern (equator-ward) populations of a species under future climate conditions are generally based on either observed occupancy (i.e. presence/absence of a species across its range), or climate envelope models tied predominately to a single life history stage (Root et al. 2003; Deutsch et al. 2008; Sunday et al. 2012). Here, we demonstrate that linking multiple life-history stages to population growth can lead to unexpected responses to climate change across a species range via demographic compensation that acts to buffer the effects of changing climate, or alternatively compounding effects that lead to demographic tipping points (i.e. population goes from increasing to decreasing). Studies linking life history traits to counterintuitive climate predictions have been demonstrated for some plant species (Angert et al. 2011; Zhu et al. 2012), but here we contribute among the first that leverages empirical life history data at multiple life history stages to mechanistically test for differences between population growth rates at opposite ends of the latitudinal distribution (but see Doak & Morris 2010). The lack of empirical studies on population-level responses to climate change across a species' ranges, combined with our surprising results, suggests that the effect of climate change may be underestimated, particularly for populations at pole-ward range boundaries.

Chapter 4. Quantifying ecological life-support: the biological efficacy of alternative supplementation strategies for imperiled amphibian populations[3]

4.1. Abstract

Global biodiversity loss has prompted diverse efforts to stem or reverse declines for many species. Such efforts are often implemented before the efficacy of alternative management actions are quantified. Here, we used matrix models to compare the effectiveness of two supplementation strategies, head-starting early life stages and captive breeding for reintroduction, at reducing extinction risk of declining amphibians. We used the imperiled Oregon spotted frog (*Rana pretiosa*) as a case study, and find that when supplementation occurs after metamorphosis, captive breeding is more effective at reducing extinction risk than head-starting, but the difference declines with increasing supplementation effort. We also find that captive breeding with release as larvae yields similar reductions in extinction risk, and is two orders of magnitude more effective at reducing extinction probabilities than head-starting the same stage. Our results highlight that even basic demographic data can be leveraged to assess tradeoffs among alternative supplementation strategies.

3

4.2. Introduction

Rates of biodiversity loss over the past century have prompted global concern (Loh et al. 2005; Hoffmann et al. 2010). While some species have declined to extinction (Stuart et al. 2004; Hoffmann et al. 2010), more commonly species exist at lower population densities or in fewer locations. As a consequence, an increasing number of species are conservation reliant, persisting with the aid of continuous management (Scott et al. 2005a). Management tools for such species depend on specific threats, but

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include habitat manipulation, invasive species removal, genetic assurance populations, and population supplementation (Fischer & Lindenmayer 2000; Scott et al. 2005). However, the effectiveness of management strategies are usually poorly understood prior to implementation, especially when knowledge of basic population dynamics and causes of decline are limited. As such, decisions to implement conservation actions to avert extinction often occur despite imperfect or unavailable information (Thorpe & Stanley 2011; Martin et al. 2012).

Unlike addressing habitat limitations or invasive species linked to decline, population supplementation is generally a proximal solution to an ultimate cause of decline, yet can be effective at maintaining populations while underlying mechanisms are better studied (Zippel & Mendelson 2008). Supplementation has been implemented for a wide range of taxa, including birds, mammals, fish, and herpetofauna (Fischer and Lindenmayer 2000), and is attributed to reducing extinction risk of Black-footed Ferret (*Mustela nigripes*) and California condor (*Gymnogyps californianus*) (Woods et al. 2007), among others. However supplementation is highly contested for some species. For example, hatchery raised Pacific salmon (*Oncorhynchus* spp.) often numerically and genetically dominate populations, resulting in reduced productivity and maladaptive changes in feeding or predator-avoidance behavior (Lynch and O'Hely 2001; Araki et al. 2007; Araki et al. 2009).

While using captive-reared individuals to supplement wild populations has the potential for adverse effects, both captive head-start and captive breeding programs are commonly used to counterbalance declines in amphibian populations (Stuart et al. 2004; Gascon et al. 2005; Zippel & Mendelson III 2008). Head-start programs remove individuals from the wild and rear them in captivity during life history stages with suspected low survival in the wild (Dodd Jr & Seigel 1991; Dodd Jr 2005; Adama & Beaucher 2006; Araki et al. 2009) Life history schedules of many amphibians appear to be good candidates for head-starting, as high mortality rates in early life stages present an obvious target for improvement. Similarly, captive breeding programs are also widely employed for endangered amphibians (Gascon et al. 2005; Griffiths & Pavajeau 2008; Zippel & Mendelson III 2008) and use the offspring of captive-reared adults to supplement wild populations. The efficacy of captive breeding to recover amphibians is still under debate (Dodd & Seigel 1991; Seigel & Dodd 2002; Griffiths & Pavajeau 2008), but has been suggested as one of only a few solutions for species experiencing sharp decline (Stuart et al. 2004).

Although resources are commonly devoted to establishing relatively robust supplementation programs, post-release monitoring and quantifying effectiveness at stemming population declines is rare (Dodd & Seigel 1991; Fischer & Lindenmayer 2000). Understanding age structure, growth rate, and population size of focal species before and after supplementation can help increase the success of a program and guide decisions, such as the life stage and quantity of individuals to release (Sarrazin & Legendre 2000; Tenhumberg et al. 2004). To date, few resources exist to both evaluate tradeoffs between supplementation strategies and to determine the level of effort required to effect change in population demographics.

Here we quantitatively compared two forms of population supplementation, head-starting and captive breeding, over a hypothetical 10-year timespan for an imperiled amphibian, *Rana pretiosa*, as a test case. We used field-collected demographic data and population dynamics models to determine how much supplementation would be required to reduce the *R. pretiosa* extinction probability below 20% over 10 years, the threshold criteria for ‘Endangered’ under the International Union for Conservation of Nature (IUCN) guidelines (IUCN 2012). We constructed a series of stochastic matrix models to compare the efficacy of each recovery strategy at reducing the 10-year extinction probability, and evaluated a range of efforts for the two strategies. We additionally explored supplementation scenarios that released animals as larvae or post-metamorphic frogs across a range of wild population sizes (i.e. the degree of imperilment). Finally, we estimated the elasticity of the population growth rate to variation in vital rates of the *R. pretiosa* life cycle to assess whether early life stages are likely to affect population-level dynamics. We present a blueprint for determining what supplementation type and level of effort will elicit the greatest reduction in decadal extinction probabilities. Although based on *R. pretiosa*, we propose that this framework can be modified for other species being considered for population supplementation if a moderate amount of demographic data exist.

4.3. Methods

4.3.1. Study species

Rana pretiosa is an IUCN 'Vulnerable' species, Endangered in Canada, British Columbia (BC), and Washington State, and listed as 'Threatened' under the US Endangered Species Act. The species has been extirpated from up to 90% of its distribution, which ranged between southwestern BC and northern California (Hammerson and Pearl 2004). Three populations (< 500 adults) of *R. pretiosa* persist in Canada, and although lack of genetic data preclude estimates of effective number of breeders (N_b), it has been demonstrated for some *Ranid* species, including one population of *R. pretiosa* in Oregon (Phillipsen et al. 2010) that N_b may be less than total adult population size. Additionally, population isolation and habitat patch size may limit population growth (Pearl & Hayes 2004). To stem declines, both head-start and captive breeding supplementation programs were implemented as part of the federal recovery strategy (Canadian Oregon spotted frog Recovery Team 2012) (details in supplementary information).

4.3.2. Matrix Models

We used stochastic, stage-based matrices with a one-year time interval to model the dynamics of a declining *R. pretiosa* population. We constructed female-only models (Morris and Doak 2002) to simulate, 1) wild population dynamics, 2) wild population with head-start supplementation, and 3) wild population with captive breeding supplementation. We further modeled each strategy with captive individuals reared until A) larvae (free-swimming tadpoles, 1-2 weeks old), or B) post-metamorphic Young-of-Year (YOY) frogs (4-8 weeks post-metamorphosis), resulting in four supplementation scenarios (1. wild, 2A. head-start, larvae, 2B. head-start, YOY, 3A. captive, larvae, 3B. captive, YOY) (Fig. 4.1). We divided the life history of *R. pretiosa* into four annual stages, or matrix elements (a_{ij}, F_{ij}) (Fig. 4.2) made up of one or more vital rates (Caswell 2001) that represent transition probabilities within a single year. Mean estimates of each vital rate were calculated from experiments, surveys, and literature values (see below), and we incorporated stochasticity into our models by using the variances (s^2) around the means for each vital rate (Table C.1). We ran 10,000 iterations of each simulation in

MATLAB (R2012a) to calculate the cumulative 10-year probability of quasi-extinction ($n \leq 20$ adult females, hereto extinction probability) for each scenario. In each forward simulation we began the population at stable-stage distribution, drawing vital rates randomly in each time-step. Finally, we calculated the stochastic growth rate (λ_s) for our wild model to determine the rate of population decline.

Fig. 1

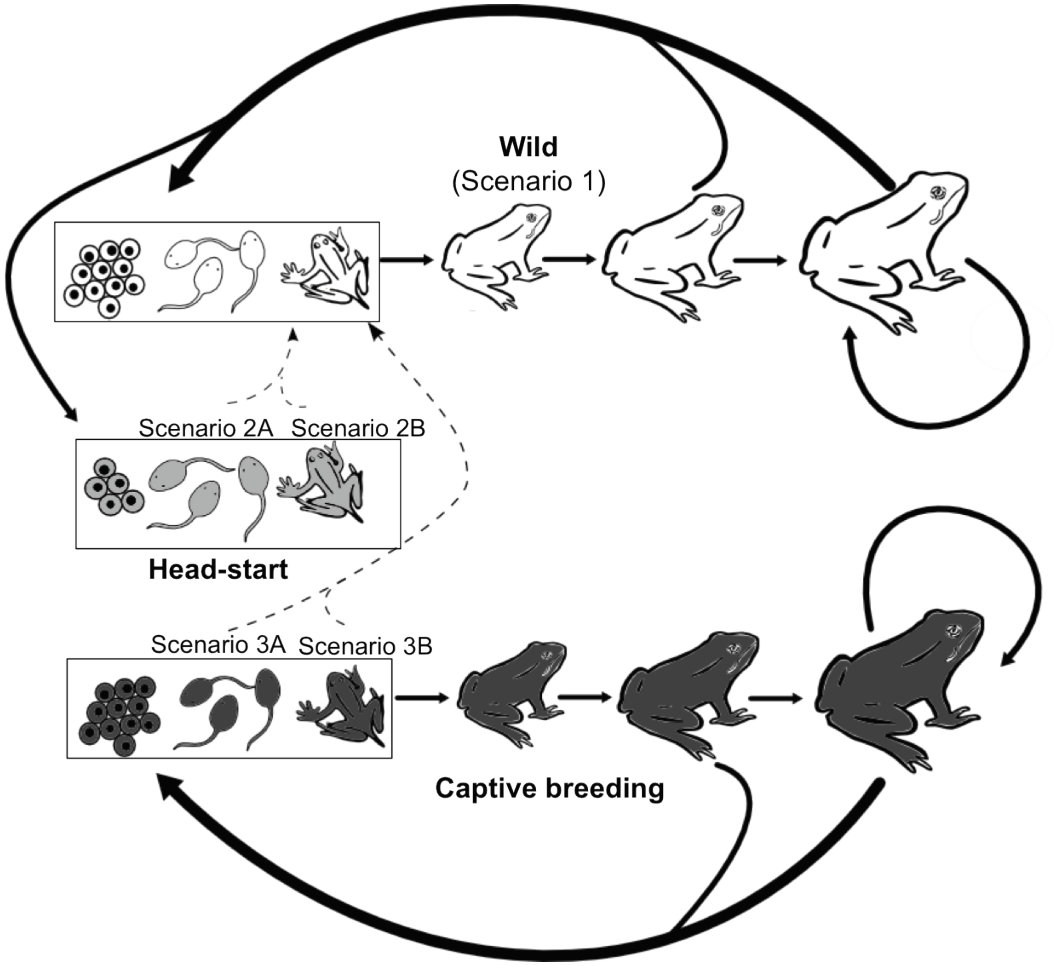

Figure 4.1 **Schematic diagram of the 4-stage Oregon spotted frog matrix models, and alternative supplementation scenarios (dashed lines). Solid arrows represent transition probabilities among stages. The top life-cycle (white frogs) represents the wild population. Stage 1 (in box) includes embryos, larvae, and young of the year (YOY), individuals transition to the next stage after a one-year time step. The arrow going from the adult and juvenile 2 stages back to stage one represents the reproductive contribution (fecundity) of the population. Under head-start scenarios (2A, 2B), a portion of the reproduction is removed from the wild and raised in captivity, represented by the arrow leading from the fecundity of wild individuals to light gray individuals, with release into wild at either the larval (Scenario 2A) or YOY (Scenario 2B) stage. Finally, the dark gray population shown at the bottom represents an independently regulated captive breeding population from which individuals are released into the wild at either the larval (Scenario 3A) or YOY (Scenario 3B) stage.**

$$\begin{pmatrix} 0 & 0 & F_{13} & F_{14} \\ a_{21} & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 \\ 0 & 0 & a_{43} & a_{44} \end{pmatrix} \text{X} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_{t+1}$$

Transition rate	*aij*	Parameter Equation
Wild (Scenario 1)		
Embryo to juvenile$_1$	a_{21}	$\phi_{\text{embryo}} * \phi_{\text{larvae}} * \phi_{\text{YOY}}$
Juvenile$_1$ to Juvenile$_2$	a_{32}	ϕ_{juv1}
Juvenile$_2$ to Adult	a_{43}	ϕ_{juv2}
Adult	a_{44}	ϕ_{adult}
Fecundity (Adult)	F_{14}	$\text{F}_{\text{adult}} * \text{sex ratio} * \phi_{\text{adult}}$
Fecundity (Juvenile$_2$)	F_{13}	$\text{F}_{\text{juv2}} * \text{sex ratio} * \phi_{\text{juv2}} * \text{Pr}_{\text{breed}}$
Head-start		
Scenario 2A	a_{21}	$((\phi_{\text{hsembryo}} * \text{P}_{\text{HS}})+(\phi_{\text{embryo}} * (1-\text{P}_{\text{HS}})))*\phi_{\text{larvae}} * \phi_{\text{YOY}}$
Scenario 2B	a_{21}	$(((\phi_{\text{hsembryo}} * \phi_{\text{hlsarvae}}) * \text{P}_{\text{HS}})+((\phi_{\text{embryo}} * \phi_{\text{larvae}}) * (1-\text{P}_{\text{HS}})))*\phi_{\text{YOY}}$
Captive breeding		
Scenario 3A	a_{21}	$((\phi_{\text{embryo}} * \phi_{\text{larvae}})+(((\text{F}_{\text{CB stage1}} * n_{\text{4CB}} * \text{Pr}_{\text{breed}} * \text{sex ratio})-\text{HB}) * \phi_{\text{CBembryo}} * \phi_{\text{larvae}})/n_{\text{w1}}) * \phi_{\text{YOY}}$
Scenario 3B	a_{21}	$((\phi_{\text{embryo}} * \phi_{\text{larvae}})+(((\text{F}_{\text{CB stage1}} * n_{\text{4CB}} * \text{Pr}_{\text{breed}} * \text{sex ratio})-\text{HB}) * \phi_{\text{CBembryo}} * \phi_{\text{Cbarvae}})/n_{\text{w1}}) * \phi_{\text{YOY}}$

Figure 4.2 Matrix model structure and vital rate definitions, where n_i is the number of individuals in stage *i* at time t, F_{ij} represents per capita fecundity, a_{ij} is the transition rate from one stage to the next and is made up of component vital rates shown in the *Parameter Equation* column. ϕ represents survival, YOY = young of the year, Pr_{breed} is the probability of a second year juvenile breeding, HS=head-start, P_{HS} is the proportion of the population removed from the wild for head-starting, CB=captive breeding, HB=the number of individuals held back to maintain the captive population, W= wild population.

We varied the degree of effort for each supplementation strategy based on practices with *R. pretiosa* head-start and captive breeding facilities in Canada (Table 4.1) (Canadian Oregon Spotted Frog Recovery Team 2012). For head-start scenarios, we varied the proportion of annual breeding effort removed from the wild from 5% to 30%, in increments of 5%. For captive breeding scenarios, we varied the number of breeding females in captivity from 10 to 60 in increments of 10. We tracked the cumulative number of YOY added to the population for each scenario (see supporting information for details). To compare efficacy across scenarios and effort, we calculated the decrease in extinction probability (ΔE) when compared to the un-supplemented wild population ($\Delta E = E_{wild} - E_{\text{scenario}},$ herein effectiveness) for one example of low, medium, and high levels of effort for each scenario (Table 4.1).

Table 4.1 Comparison of effort for head-start (% wild reproduction removed to captivity) and captive breeding (number of captive breeding females) scenarios.

Effort	% Head-started	No. of Captive breeding Females
Low*	5	10
Low	10	20
Medium*	15	30
Medium	20	40
High	25	50
High*	30	60

4.3.3. Demographic rates

We modeled survival (ϕ), fecundity (*F*), and transition probabilities between stages (*Pr*) (Fig. 4.2) primarily from our field studies of *R. pretiosa* in BC, with additional rates derived from published literature (Table C.1). Field studies consisted of an *in situ* larval enclosure experiment in 2011 to estimate larval survival, and a capture-mark-recapture study of adults in 2010 and 2011 to estimate adult female survival (see Supplementary Information for details). We derived head-start and captive breeding vital rates from observations from captive facilities in BC (A. Gielens and D. Thoney, *unpublished data*) (Table C.1). Differences among the four supplementation scenarios were modeled within matrix element a_{21} (Fig. 4.2), which is composed of three lower level vital rates making up the first year of life (embryonic, larval, and post-metamorphic stages). For head-start models (Scenario 2A, 2B), we added vital rates for captive survival ($\phi_{HSembryo}$, $\phi_{HSlarvae}$), and for captive-breeding models (Scenario 3A, 3B), we generated embryos from a fixed captive population that survived in captivity at rates independent of those in the wild ($\phi_{CBembryo}$, $\phi_{CBlarvae}$), and held back a small subset of embryos each year to maintain the captive population (Fig. 4.2, Table C.1).

4.3.4. Wild Population Size

Extinction probability for a wild population is a function of population size and rate of decline. For our wild model, we explored how extinction probability changed with the degree of imperilment by running models with population sizes ranging from 50 to 300 breeding females. This range of population sizes reflects observed spatio-temporal variation in population size for *R. pretiosa*, and includes population sizes for which urgent conservation actions, including supplementation, are generally warranted (Caughley 1994). We limited our evaluation of the effectiveness of supplementation to population sizes that resulted in a 10-year extinction probability >20% which roughly corresponds to the IUCN criteria for 'Endangered'. Under IUCN criteria, a population is considered 'Endangered' if extinction risk is greater than 20% over 20 years, or 5 generations, which would be equal to 25 years for *R. pretiosa* , (Hammerson & Pearl 2004; IUCN 2012).

4.3.5. Elasticity Analysis

We calculated deterministic elasticity values, which give the proportional change in lambda given a proportional change in a vital rate, as a relative ranking of vital rate contributions to population dynamics using mean values of the wild population matrix. Declining populations often experience variation in multiple vital rates simultaneously, and such changes violate the basic assumptions of deterministic elasticity analysis (Caswell 2001). To account for the possibility of multiple changing vital rates, we also conducted a simulation-based elasticity analysis in which 10,000 random matrices were constructed with vital rates drawn at random from uniform distributions between minimum and maximum values (2.5 and 97.5 quantiles of the probability density functions for each vital rate, Table C.5) and calculated mean deterministic elasticities across the simulations (*sensu* Wisdom et al. 2000).

4.4. Results

4.4.1. Matrix Models

Without supplementation, our wild *R. pretiosa* model (Scenario 1) predicts a stochastic growth rate (λ_s) of 0.86, equivalent to a 14% annual rate of decline, and a 10-year extinction probability between 3% and 92% at initial population sizes of 300 and 50 adult females respectively (Fig. 4.3). Only wild populations of ≤150 breeding females had an extinction probability >20%, coinciding with IUCN criteria for Endangered listing and warranting consideration for supplementation. We found that supplementation can strongly reduce extinction probability, but the degree of reduction varied with supplementation type, stage at release, effort, and initial population size (Fig. 4.4). Head-start models with release at the larval stage (Scenario 2A) reduced extinction risk below 50% in 12 out of 18 cases we ran (when effort was ≥5% of eggs removed from the wild and populations were ≥100), but were ineffective at reducing extinction risk for smaller populations (Fig. 4.4a). In contrast, head-start models with release at the YOY stage (Scenario 2B) reduced extinction risk below 50% in 16 out of 18 cases, and large populations (≥100), required only 5% of wild eggs be removed to captivity and raised to YOY stage. For small populations, ≥15% effort (i.e. 15% of wild eggs removed to captivity) was required to reduce extinction risk below 50% under Scenario 2B. Captive breeding models with release at the larval stage (Scenario 3A) were more effective than Scenario 2A at reducing extinction probability, and comparable to Scenario 2B (16/18 cases resulted in <50% extinction risk) (Fig. 4.3c); breeding ≥30 captive females and releasing as larvae reduced extinction risk to <50% for a population of 50 individuals, whereas breeding 10 captive females was enough to reduce extinction below this threshold for populations >50. Captive breeding models with release as YOY (Scenario 3B) were most effective at reducing extinction probability (<50% extinction in 17/18 cases), dropping below 50% at an effort of 20 breeding females for a population size of 50 individuals, and at a minimum effort for population sizes ≥100 (Fig. 4.3d).

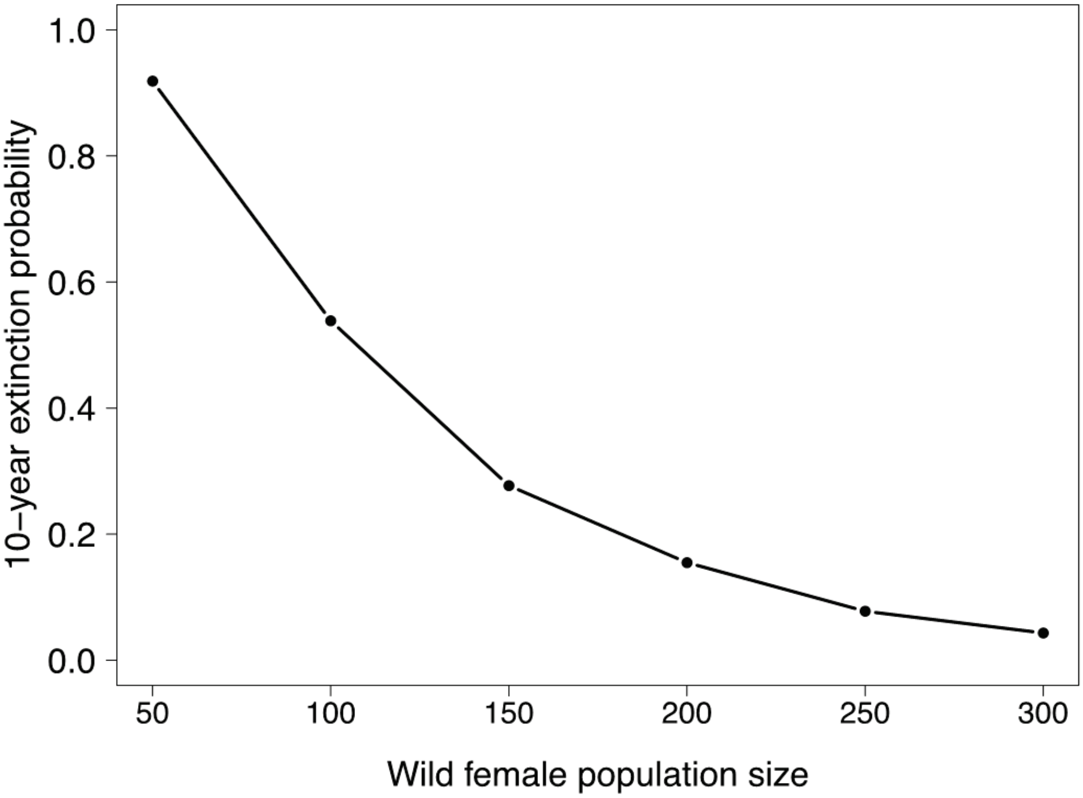

Figure 4.3 **Ten-year cumulative extinction probability for *R. pretiosa* with no supplementation as a function of initial wild population size (number of adult females).**

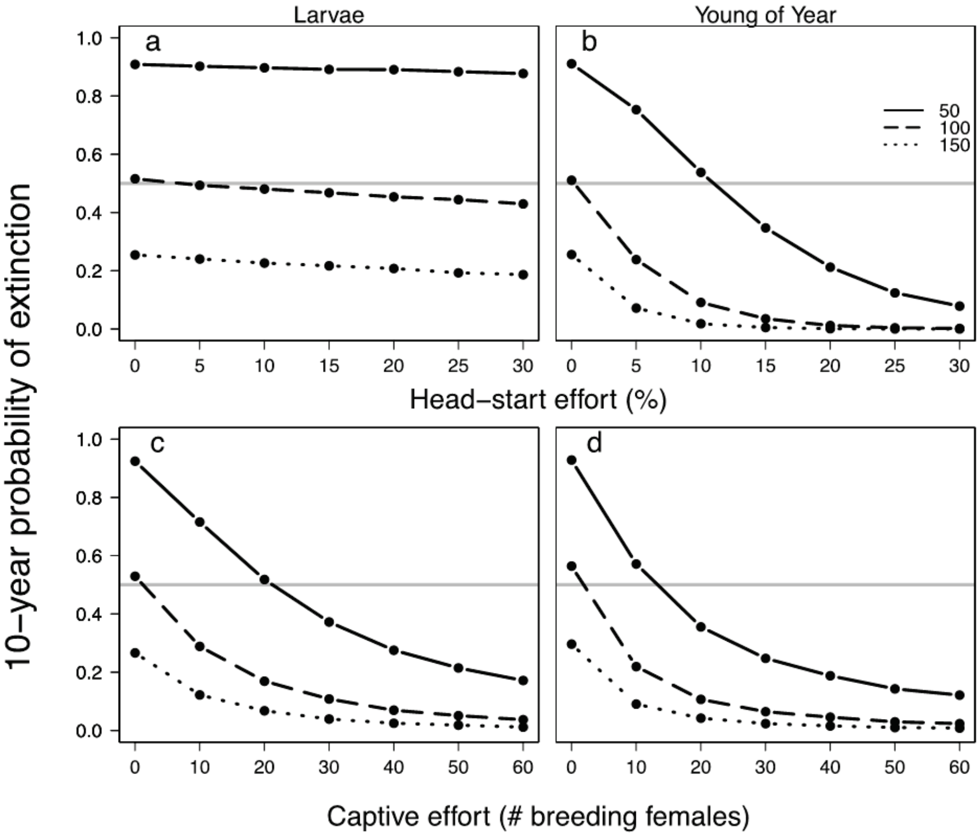

Figure 4.4 **The 10-year extinction probability for a range of efforts (x-axis) for, (a) Scenario 2A, head-start and larval release, (b) head-start and release as YOY (2B), (c) captive breeding, larval release (3A), and (d) captive breeding and YOY release (3B). Lines depict initial wild population sizes (50, 100, 150). Note an effort of zero corresponds to no supplementation (Scenario 1). The gray line shows 50% extinction risk (Critically Endangered threshold).**

Effective strategies are those that maximize reduction in extinction risk over 10 years. We calculated the decrease in extinction probability relative to the un-supplemented wild population (effectiveness) for a subset of our scenarios (lowest, medium, and highest, Table 1) and found that captive breeding models maximized effectiveness with one exception (high effort, release as YOY) (Fig. 4.5). When reintroduction occurred at the larval stage, captive breeding scenarios were 23 to 33 times more effective than head-start scenarios. When individuals were released as YOY, captive breeding and head-start scenarios were virtually identical, except at low effort when captive breeding was 2.1x more effective.

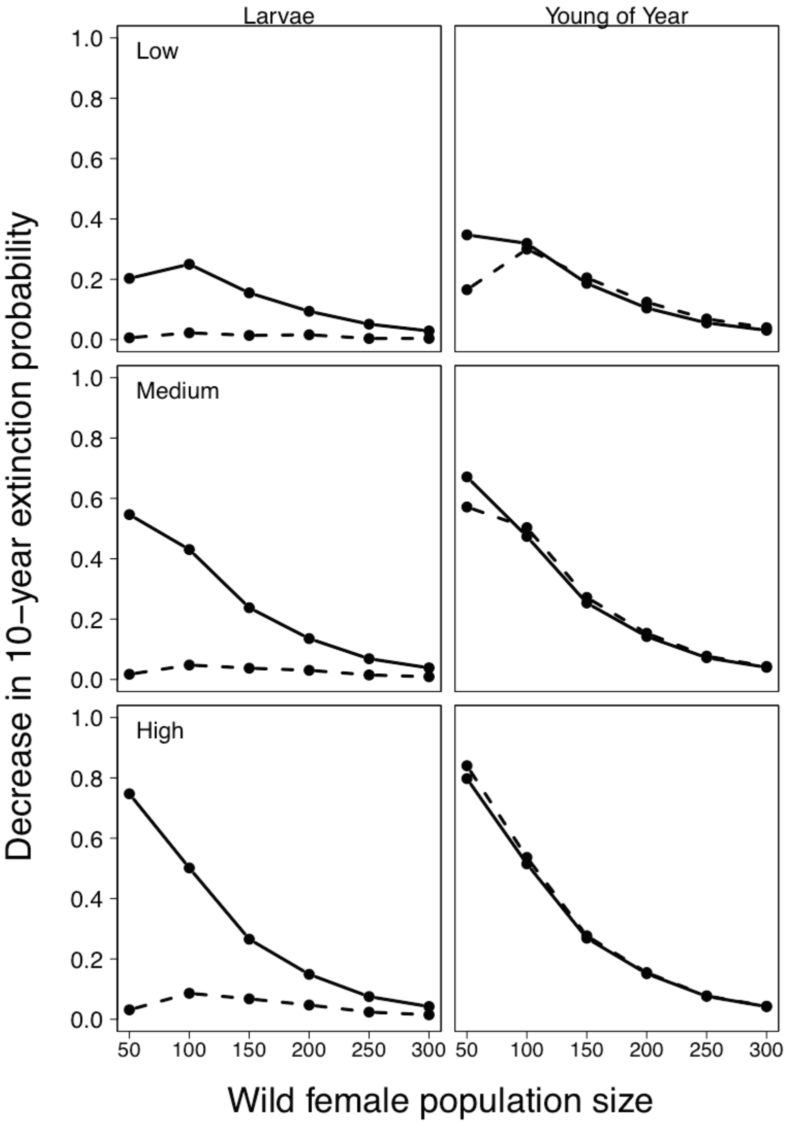

Figure 4.5 **The decrease in the 10-year extinction probability under a given supplementation strategy for a low, medium, and high level of effort across a range of initial wild population sizes (number of adult females). Left panels depict supplementation with release at the larval stage, and right panels release at the YOY stage. Solid lines indicate captive breeding and dashed lines indicate head-starting.**

4.4.2. Elasticity Analysis

The elasticity analysis revealed that vital rates contributed unequally to population growth. The most elastic parameter was adult survival for both the deterministic and simulated elasticity analysis. Larval and metamorphic elasticity ranked among the second most elastic parameters, ahead of adult and juvenile fecundity (Fig. 4.6A). Our simulation-based elasticity results were highly correlated with the deterministic elasticity for all stages ($\text{Elasticty}_{\text{sim}} = 1.098 \cdot \text{Elasticty}_{\text{det}}$, $r^2 = 0.99$) (Fig. 4.6).

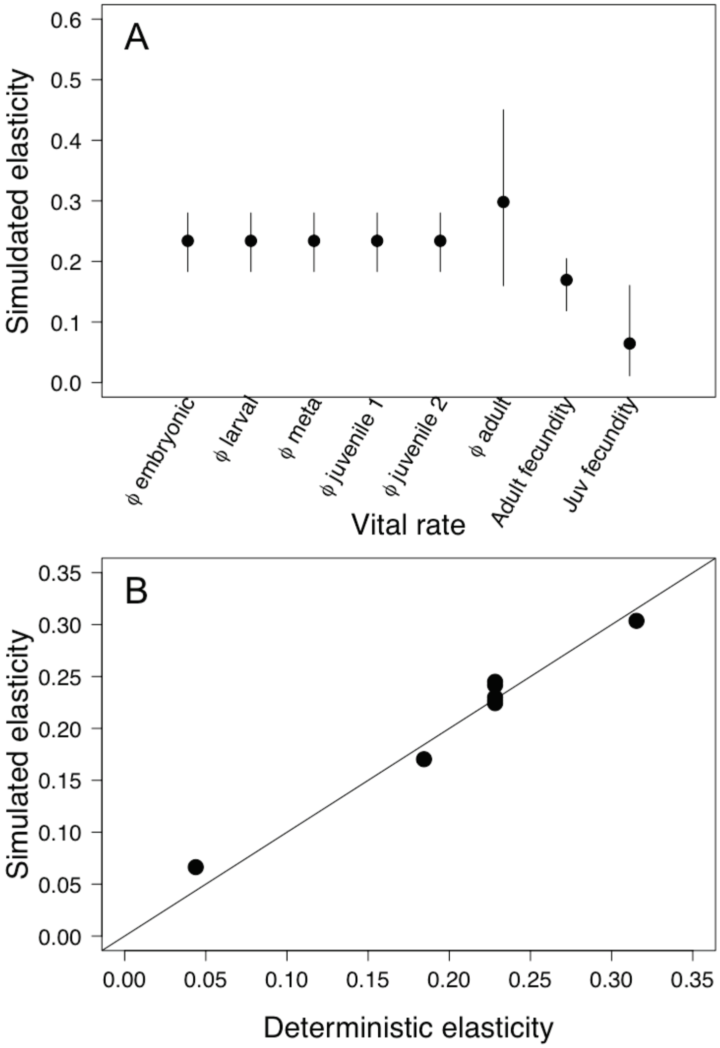

Figure 4.6 **Simulated mean elasticity values and 95% confidence intervals for wild *R. pretiosa* population vital rates (top panel, A). Correlation between the deterministic and simulated elasticity values of the component vital rates for *R. pretiosa* ($\text{Elasticty}_{\text{sim}} = 1.098 \cdot \text{Elasticty}_{\text{det}}$, $r^2 = 0.9912$) (bottom panel, B).**

4.5. Discussion

Our analysis demonstrates the tradeoffs among supplementation strategies for a declining amphibian, and that effectiveness depends on when supplementation is initiated during a decline. When our simulated wild population was small (≤100), extinction probability (0.53-0.92) met the criteria of 'Endangered' by the IUCN (> 20% extinction probability in 20 years or 3 generations, IUCN 2012). In contrast, our head-start and captive breeding scenarios illustrate pathways to reduce extinction probabilities below this threshold. We found that supplementation under all scenarios was most effective when the population was initially ≤ 100 individuals (Fig. 4.4). These findings, if more general, imply that supplementation at the levels of effort we explored is likely to be most effective at very small population sizes, when the high degree of imperilment demands consideration of 'last resort' options.

Although we have illustrated pathways to reduce extinction risk below IUCN 'Endangered' for imperiled amphibian populations, we also present a framework for identifying supplementation scenarios that maximize reduction in extinction probability while minimizing conservation effort. When we compared the reduction in 10-year extinction probabilities between a simulated wild population and our four supplementation strategies, we found lower levels of captive breeding effort reduced extinction risk more effectively than a head-start program, and that captive breeding and release as larvae can reduce extinction risk almost as effectively as release at the YOY stage (Fig. 4.5). This suggests that captive breeding may help buffer a wide range of demographic and population-level variability. Because captive breeding and release occurs independently of fluctuations in wild populations, this strategy allows managers to consistently add individuals to the wild population (Fig. C.1).

Developing tools and metrics to evaluate conservation strategies to decrease extinction risk are critical for imperiled populations. Stage-based demographic models provide a unique opportunity to couple the complexities of species' life histories with quantitative models to identify life-stages with the highest potential to affect population dynamics (Crouse et al. 1987a; Sæther & Bakke 2000). Later life-stages have been demonstrated to contribute more to overall population growth rates than early stages in mammals (Biek et al. 2002; Vonesh & De la Cruz 2002; Govindarajulu et al. 2005)). Yet our analysis suggests that despite lower elasticity for early life-stages, with large enough efforts, population level improvements are possible through early life-stage supplementation. Given that affecting survival at later life stages often requires elucidating and treating specific causes of low survival, it is important to know that targeting alternative stages can positively impact emergent population dynamics.

Our modeling approach assumes no genetic cost to the population, and that individuals from captivity survive at rates equal to that of their wild counterparts following release. There is some evidence that releasing captive bred individuals can result in a fitness reduction for other taxa (Lynch & O'Hely 2001; Araki et al. 2007, 2009), and that captive rearing wild individuals for release can negatively affect growth (Adama and Beaucher 2006). Although questions regarding the utility of supplementation remain for most species, there are few other options available when management is required to maintain critically imperiled populations (Stuart et al. 2005; Scott et al. 2010). Setting aside assumptions that captive breeding and rearing have negligible effects on survival and fitness in the wild, another conservation reality is the financial cost of recovery. Keeping individuals in captivity is expensive (Dodd 2005) and costs likely constrain recovery options. A holistic approach to decision-making which incorporates both the biological and financial realities of recovery is therefore necessary to determine the best way to increase population numbers.

Here we have shown that it is possible to improve the quantitative basis for decisions regarding alternative recovery actions when basic demographic data are available. The framework we used with *R. pretiosa* provides an example of the biological tradeoffs that exist among alternative supplementation strategies. Such tools are not commonly available to conservation decision-makers, but we argue that adapting models for other species is relatively straightforward and can be used to guide management decisions. For species with limited data, a similar, but deterministic approach can be used to make relative comparisons of management options. Although supplementation alone is unlikely to sustain a population in the long term (but see Scott et al. 2005), we have shown that it has the potential to be an effective tool to reduce short-term (10-year) extinction probability while ultimate causes for decline are better understood.

Chapter 5. A decision-theory approach to cost effective population supplementation for imperiled species[4]

5.1. Abstract

Despite decades of managing endangered species, few have been successfully recovered. One option to reduce this gap is to use decision analysis to weigh alternative recovery actions. Using decision analysis, we evaluated tradeoffs between conservation actions to reduce extinction risk and financial cost for the imperiled Oregon spotted frog (*Rana pretiosa*). We simulated population supplementation via captive breeding or head-starting wild embryos, and releasing offspring into the wild as larvae or young of the year. We ranked the biological efficacy of recovery actions to reduce the 10-year extinction risk below 10% while minimizing financial costs, and explored how rankings varied with respect to the extinction risk target, the size of the endangered population, and the reproductive output of the captive population. Our top-ranked pathway was to supplement the population with captive bred larvae, which resulted in a 3% reduction in extinction risk for every $100,000 spent. In general, supplementing with captive bred larvae resulted in the biggest reduction in extinction risk per dollar invested. Our results demonstrate that increasing spending does not always result in a proportional reduction in extinction risk. These results link quantitative and applied conservation by considering the biological and economic efficacy to recover endangered species.

5.2. . Introduction:

The US Endangered Species Act (ESA) and Canadian Species at Risk Act (SARA) mandate that recovery strategies be developed for endangered and threatened species. Of the 1,872 species or populations listed under the ESA or SARA, two thirds (1,393) have formal recovery plans (Fig. 5.1). Despite this large-scale effort, relatively few listed species have been sufficiently recovered as to be removed or down-listed from either the ESA or SARA. Of the 61 species delisted from the ESA, only half (32 species) have been delisted because they have met recovery goals, 10 species have been removed due to extinction, and the remainder as a result of updated information (e.g.

taxonomic revisions) (https://ecos.fws.gov/tess_public/reports/delisting-report accessed 7 December, 2015), while only 3 species under SARA have been delisted because they were recovered (Favaro et al. 2014). The challenge of recovering species often stems from uncertainty in the causes of decline, mitigating or circumventing the drivers of decline, and having sufficient resources to meaningfully address these problems at the often large spatial and temporal scales required for species recovery.

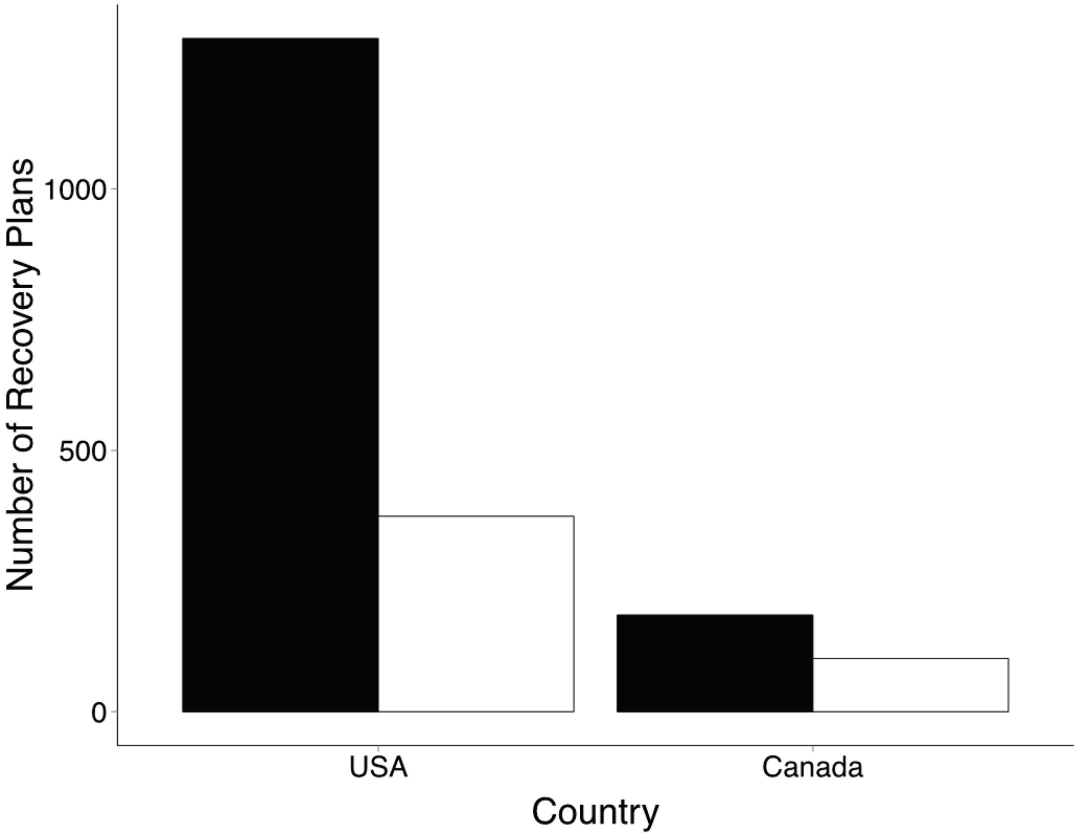

Figure 5.1 The number species listed under the Endangered Species Act (USA) and Species at Risk Act (Canada) with written recovery plans. Black bars indicated endangered species and white bars indicate threatened species.

Recovery decisions for endangered species are often made quickly and with limited data with which to inform recovery objectives (Martin et al., 2012; Gerber and Hatch 2002). However, reviews of ESA recovery plans found that plans with a higher number of clear quantitative recovery goals (i.e. target population sizes, number of populations, etc.) are associated with improving species status (Gerber and Hatch 2002; Boor 2014), suggesting that leveraging even limited data to inform species recovery is useful. Others have also suggested steps to improve science-based decision making that are applicable across taxa, including specifying quantitative requirements for species recovery and recovery timelines, as well as identifying the number of populations or the spatial extent to which recovery measures apply (P. Possingham et al. 1993; Scott et al. 1995; Boersma et al. 2001; Gerber & Schultz 2001; Clark et al. 2002; Waples et al. 2013; Himes Boor 2014), but such standards have yet to be adopted in a way that improves planning (Boor 2014, Doak et al. 2015, Troyer and Gerber 2015). For instance, recent updates to the US Fish and Wildlife Service and National Marine Fisheries Service failed to make any quantitative criteria or standards mandatory (Troyer and Gerber 2015).

Integrating quantitative measures into recovery planning can be challenging due to lack of data for rare species, uncertainties in recovery costs, and sociopolitical factors (Scott et al. 1995; Restani & Marzluff 2002). One way to leverage limited data in support of choices between alternative recovery actions is to apply decision theory, which provides a logical structure for complex problems (Kenney and Raiffa 1976; Morgan and Henrion 1990; Peterman and Anderson 1999). While most natural resource management decisions are ultimately made based on more than scientific data (e.g. economic, social, cultural, political factors), decision analysis can provide clear support to these decision-making processes by identifying and ranking options that meet stated objectives and provide quantitative information regarding trade-offs among alternative actions. A decision analysis can help to streamline decision-making processes that often involve multiple pathways to achieve an objective, and an array of different stakeholders, sometimes with competing objectives (Peterman & Anderson 1999). The steps of a decision analysis include; 1) explicitly stating the objectives or targets, 2) outlining alternative pathways to achieve the targets, 3) identifying uncertainties or unknowns in the data (referred to as ‘uncertain states of nature’) and explicitly incorporating them into the analysis, 4) using a quantitative model to determine the outcomes of each potential pathway, 5) determining the ‘optimal’ decision by ranking the outcomes with respect to the objectives, and 6) performing sensitivity analyses on key parameters in the model to determine the robustness of the ‘optimal’ decision (Peterman & Anderson 1999). Acknowledging uncertainty in the process by assigning probabilities to each identified uncertain state of nature (step 3), and performing sensitivity analyses on critical parameters (i.e. targets or key model assumptions , step 6), decreases the likelihood of choosing an ineffective recovery option by increasing the quantitative basis of the decision making process.

Decision analysis models have been applied to numerous conservation problems, such as invasive species management (Maguire 2004; Buhle et al. 2012), designing ecological reserves (Possingham et al. 2000), and endangered species planning (Drechsler 2000; Pestes et al. 2008). Several studies highlight the utility of decision analysis for endangered species management (P. Possingham et al. 1993; Drechsler et al. 1998; VanderWerf et al. 2006; Southwell et al. 2008; Moore et al. 2010), and it can be a valuable tool for quantifying tradeoffs between the biological efficacy and economic cost of a suite of alternative recovery strategies (Engeman et al. 2002; Fairburn et al. 2004; Martínez-Abraín et al. 2011; Converse et al. 2013; Canessa et al. 2014; Rose et al. 2015).

A fundamental assumption of most recovery efforts is that increased spending will result in improvements in species status (Miller et al. 2002; Male & Bean 2005; Kerkvliet & Langpap 2007). However, it has been demonstrated for marine turtles that there can be a three-fold difference in the benefit-cost ratio between alternative predator removal strategies (Engeman et al. 2002), and for the kokako, an endangered bird in New Zealand, that an increase in spending for predator control does not always lead to an increase in the number of breeding pairs (Fairburn et al. 2004). These examples highlight the need to explore tradeoffs between the cost of management actions, and the resulting net benefit to the population or species. Weighting a recovery option by its associated cost in a decision analysis framework may help identify pathways to recovery that are easier to achieve given both financial and biological constraints, and ensure that limited funds are not allocated to recovery options that are unlikely to succeed.

Here, we use decision analysis in a novel way by incorporating both the biological efficacy and monetary cost of recovery to quantitatively assess alternative population supplementation strategies, captive breeding or head-starting wild embryos, and to explore the return on investment for each potential management action. Captive breeding and head-starting are two commonly proposed population supplementation tools for critically endangered populations particularly for amphibians which are at higher risk of extinction than many other vertebrate taxa (Stuart et al. 2004; Hoffmann et al. 2010). Captive breeding and release involves establishing a population in captivity, in which individuals mate and produce offspring that are subsequently released into a separate wild population. Head-starting and release typically involves removing individuals from the wild at an early life stage (embryos or larvae) and raising individuals in captivity through sensitive life stages before re-releasing into a wild population. Although both options include rearing individuals in captivity for a period of time, the relative genetic and demographic consequences, as well as the economic tradeoffs between captive-breeding and head-starting are largely unknown (Griffiths and Pavajeau, 2008). In general, the effectiveness of population supplementation, regardless of method, has been difficult to assess (Dodd Jr & Seigel 1991; Griffiths & Pavajeau 2008), and thus is often reserved for when other threat mitigation strategies (e.g. habitat degradation, competition with invasive species) are not feasible (Zippel and Mendelson 2008). We identified 24 alternative supplementation strategies using either eggs from captive females (captive breeding) or wild collected eggs (head-starting), which we compared to no supplementation (for a total of 25 alternative scenarios), to aid the recovery of a critically endangered population of Oregon spotted frogs (*Rana pretiosa*). Using empirical data and an existing population demographic model (Kissel et al. 2014) we evaluated the biological efficacy of each of the 25 alternative strategies (henceforth recovery pathways) and conducted a decision analysis from the perspective of conservation managers with a baseline recovery target of reducing the 10-year extinction risk below 10% while minimizing cost. We calculated the cost of each alternative recovery pathway and used stochastic population viability analysis to estimate the reduction in extinction risk over 10 years of continuous implementation of each pathway. We explored uncertainties in the top ranked scenario with sensitivity analyses by relaxing model assumptions and recovery targets, which allowed us to assess the robustness of the top-ranked recovery pathway under non-static conditions. We found that decision analysis is a feasible, intuitive method for improving the quantitative basis for ranking alternative recovery actions, and can be a useful lens through which to balance tradeoffs between costs and endangered species management.

5.3. Methods

5.3.1. Study species

Oregon spotted frogs (*Rana pretiosa*) are categorized as 'Vulnerable' under the International Union for Conservation of Nature (IUCN), and federally listed as 'Threatened' under the U.S. ESA and Canada's SARA. The species historically ranged between northern California and southwestern British Columbia (BC), but has been extirpated from more than 90% of its distribution (Hammerson & Pearl 2004). In BC, there are five extant populations of *R. pretiosa*, each of which are estimated to have fewer than 250 breeding females by the Canadian Oregon spotted frog Recovery Team (COSFRT, unpublished data). Head-start and captive breeding supplementation programs were implemented for the BC populations in 2008 and 2010 respectively as part of a federal recovery strategy to address declines (Kissel et al. 2014).

5.3.2. *Decision analysis*

Our baseline management target was to reduce the 10-year extinction risk of an imperiled *R. pretiosa* population (n=100 breeding females) to below 10% and minimize the financial cost of recovery. We chose a 10-year time horizon to coincide with the stated recovery objectives in the BC Oregon spotted frog recovery plan (COSFRT 2012), and a 10% extinction risk threshold as it is consistent with the IUCN quantitative criteria for 'Endangered' (20% over 20 years or 3 generations-25 years for *R. pretiosa*, IUCN 2012). We used a stage-based stochastic matrix model (developed in Kissel et al. 2014, see supplemental materials, Fig. D1) to estimate the consequences of management pathways that would result in 25 potential 'outcomes', which we defined as the combination of 10-year extinction risk for the wild *R. pretiosa* population, and financial cost of the pathway. We developed a decision tree to demonstrate each pathway (Fig. 5.2), which consisted of decisions for four separate management actions; 1) the decision to supplement or not, 2) the decision to head-start or captive breed, 3) the decision to release individuals as larvae (2-4 week-old tadpoles) or young of the year (YOY, recently metamorphosed frogs), and 4.) a decision regarding the 'level of effort' at which to head-start or captive breed (Table 5.1, supplemental materials). Transition probabilities from one life stage to the next, called vital rates (see Kissel et al. 2014, Fig. D1), were modeled as uncertain states of nature in the decision analysis (Fig. 5.2), and we randomly pulled individual vital rates (e.g.; survival, fecundity) from probability distributions representing the range in values estimated from empirical data to parameterize our matrix model (see Kissel et al. 2014). We used these quantitative models to calculate the 10-year *R. pretiosa* extinction risk based on λ_s, generated by running 10,000 simulations of separate models for head-starting and captive breeding at each of the 6 levels of effort, resulting in a model for each of the 24 pathways. Our final pathway consisted of an additional matrix model that did not include any form of supplementation (and thus had a recover cost of $0). Finally, we quantified the cost of each pathway (See below), and ranked the pathways according to our objectives; reduce extinction risk below 10% and minimize cost.

Table 5.1 Categorization scheme of the level of effort for Head-starting and captive breeding.

Effort	% Head-started†	No. of Captive-breeding Females‡
Minimum	5	10
Low	10	20
Medium	15	30
Medium-high	20	40
High	25	50
Maximum	30	60

† Percentage of the wild population removed for head-starting

‡ The number of captive females bred to produce individuals that will be released into the wild population.

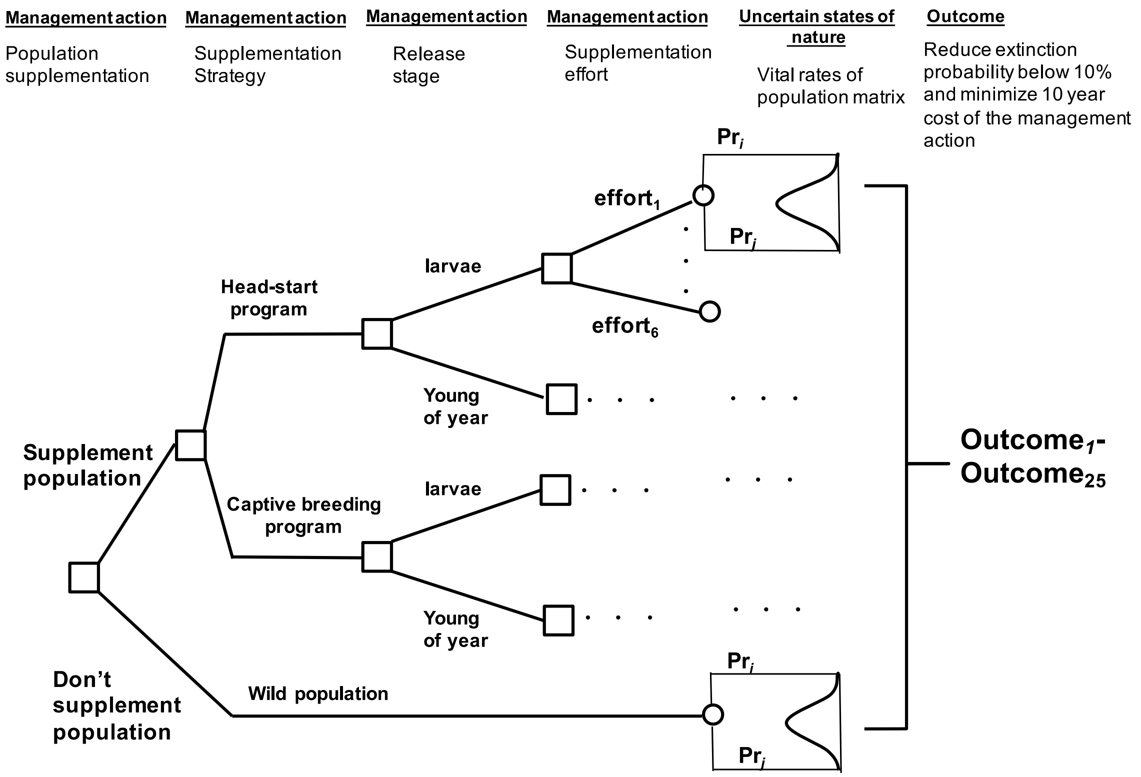

Figure 5.2 **Decision tree for *R. pretiosa* supplementation strategies. Square nodes represent decisions while circles represent uncertain states of nature. Similar branches that are not shown are indicated by the sequence of three dots. *Pr* represents the probability of a given vital rate being drawn from a beta distribution for the matrix model simulation.**

The final step in our decision analysis was to explore the robustness of our supplementation pathway rankings with three separate sensitivity analyses (i.e. explored changes to our baseline scenario) to determine if the optimal pathway changes. We considered a shift in management objectives by varying thresholds of acceptable extinction risk over 10 years to reflect variation in intrinsic social and economic constraints in setting recovery targets, and changes in the size of the wild population (number of adult females is either greater or less than 100) to acknowledge uncertainty in estimates of wild population sizes affecting extinction risk. Our final sensitivity analysis was to explore variation in the reproductive output for captive females as it has been widely documented that breeding amphibians in captivity is difficult for most species, and even when successful, often results in lower rates of reproduction or lower offspring viability compared to wild individuals (Kouba et al. 2009; Trudeau et al. 2010; Kiik et al. 2013; Muths et al. 2014; Penfold et al. 2014).

To reflect changes in recovery targets compared to the baseline scenario (reduce 10-year extinction risk below 10% and minimize cost), we assessed three additional scenarios; reduce extinction risk below 50% over 10 years (the IUCN criteria for 'Critically Endangered', IUCN 2013) and minimize cost, reduce extinction risk below 25% over 10 years and minimize cost, or minimize 10-year extinction risk regardless of cost, which would represent the ideal recovery scenario if funds were unlimited. To explore uncertainty in measuring abundance for critically small populations (baseline = 100 females), we varied the size of the population between 50 and 150 adult females in increments of ten, representing a range of populations in which extinction risk warrants supplementation (Caughley 1994, Kissel et al. 2014). Finally, we assessed sensitivity in the optimal pathway to changes in the annual reproductive output of captive females (baseline = 100% captive breeding each year), by exploring whether the optimal decision would shift if only 90%, 75%, or 50% of the females in captivity successfully bred each year. We compared the benefit-cost ratios of the 'optimal' decisions from our baseline analysis and sensitivity analyses as an additional metric to explore tradeoffs in the reduction in extinction risk per conservation dollar spent.

5.3.3. Head-start program costs

We estimated the cost of the head-starting program using actual operational and capital costs from *R. pretiosa* recovery efforts in BC (2008 and 2009) at the Greater Vancouver Zoo, where ~5% of the population is brought in each year, reared to metamorphosis and released as YOY (Table D.1 and D.2). We divided costs into capital (one time) and recurring and included 'in-kind' costs such as husbandry infrastructure and labor not directly supported through recovery funds. For scenarios outside of current *R. pretiosa* recovery efforts (> 5% of the population removed for head-starting), we predicted costs as a linear function of the level of 'effort' and the starting population size to provide a relative comparison, assuming that cost efficiencies gained with increasing the program size were equal among supplementation programs (head-starting and captive breeding), with the exception of capital expenditure for enclosures needed to house individuals (see supplemental materials for details).

5.3.4. Captive breeding program costs

Costs for captive breeding were based on 2013 estimates from an ongoing *R. pretiosa* captive breeding program at the Vancouver Aquarium where ~ 20 females are bred and offspring are released as larvae 2-4 weeks post hatching to the wild population (Table S3). As with the head-start program, we included ‘in-kind’ costs and scaled costs linearly with effort, estimating costs for a range of effort from 10 to 60 adult females in captivity. For scenarios in which individuals were released as young of the year (YOY) frogs, we assumed the additional costs associated with the post-hatching period would be equal to head-starting and releasing as YOY (Table D.1), as estimated above. For example, at a captive-breeding effort of 20 females, our model predicts that approximately 18,200 tadpoles would be produced annually. Raising 18,200 tadpoles to metamorphosis would require 182 tanks to house individuals. This scenario would also require similar recurring costs as the head-start program, thus the total cost of captive breeding with release as YOY was calculated as the sum of the capital and 10-year recurring costs of captive breeding, plus the cost of head-staring the resulting number of tadpoles until they reached metamorphosis.

5.3.5. Results

The top ranked pathway (i.e. ‘optimal decision’) for the baseline scenario (reduce 10-year extinction risk below 10% and minimize costs for a wild population of 100 breeding females), was captive breeding, with release to the wild population as larvae, and to do so at a ‘medium-high’ effort (Fig. 5.3a). This translates to breeding 40 females each year and releasing offspring as larvae into the wild population. The total cost for this strategy was $1.49 million over 10 years, with a 46% reduction of the 10-year extinction risk (from 53% without supplementation, to 7%), which equates to a benefit-cost ratio of a 3% reduction in extinction risk for every $100,000 spent (Fig. 5.4). There was no reduction in extinction risk for the pathway in which supplementation did not occur, and thus we use this pathway to compare the reduction in extinction risk for the 24 other pathways.

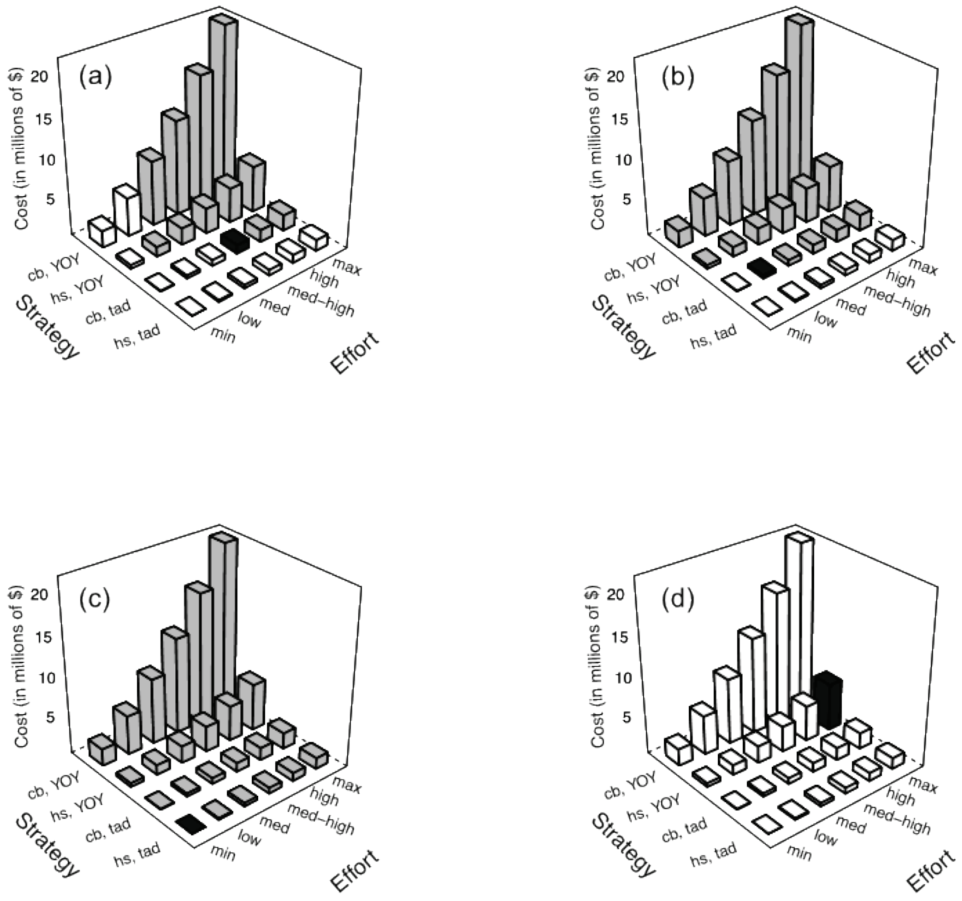

Figure 5.3 **The outcomes for decision analysis for a wild population of 100 females in which the management target is to reduce extinction risk below 10% and minimize cost (a). Light grey bars indicate pathways which meet the extinction risk criteria. The black bar indicates the optimal recovery strategy. Panels c-d show a sensitivity analysis in which we adjust the management target to reducing extinction risk below 25% (b) and 50% (c) while minimizing cost. Panel d is a management target in which we chose to maximize reduction in extinction probability while minimizing cost, thus there is only one scenario which meets both the extinction criteria and cost criteria, highlighted in black. “cb” = captive breed, “hs” = head-starting, “YOY” represents release back into the wild at the young of year stage, and “tad” = release back into the wild at the larval stage.**

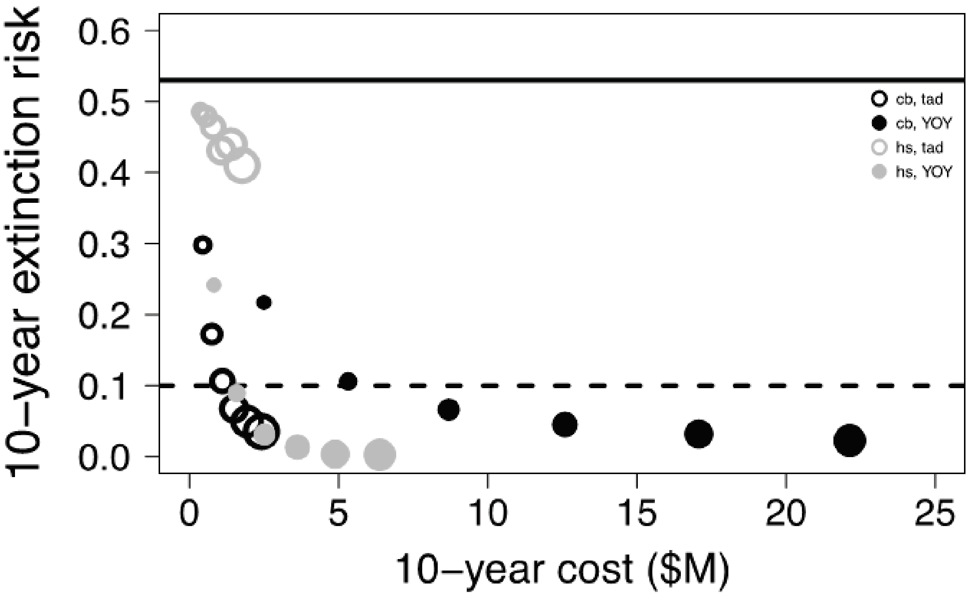

Figure 5.4 **The 10-year extinction risk as a function of recovery dollars invested for each supplementation scenario. Open circles represent release as larvae (tad) while filled circles represent release as young of the year (YOY). Captive breeding scenarios are represented by black points while head-starting are in grey. The size of the point represents the level of 'effort', ranging from a minimum effort (head-start 5% of the wild population or captive breed 10 females) to maximum effort (head-start 30% of the population or captive breed 60 females). The solid black line is the extinction risk without supplementation and the dashed line represents our baseline recovery target of reducing extinction risk below 10%.**

When we explored the robustness of the top-ranked pathway for the baseline scenario to different management objectives, we found that the optimal decision was highly sensitive to the recovery target (10-year extinction risk). When we eased the recovery target to equal 25% extinction risk over 10 years (as opposed to the baseline 10%), the optimal decision was still to captive breed and release as tadpoles, but required only a low level of effort (breed and release offspring from 20 captive females as opposed to 40), with a total cost of $750,000 over 10 years (Fig. 5.3b). This strategy reduced extinction risk by 36% (from 53% to 17%) and equated to a benefit-cost ratio of 4.8% reduction in extinction risk for every $100,000 spent (Fig. 5.4). When the recovery target was eased further to a 50% chance of extinction in 10 years while also minimizing costs, the top-ranked pathway shifted to head-starting wild collected eggs with release as tadpoles at a minimum effort, which reduced extinction from 53% to 48.5%, with 10-year total cost equal to $370,000 (1.2% reduction in extinction risk for every $100,000 spent) (Fig. 5.3c, Fig. 5.4). When we minimized the 10-year extinction risk regardless of cost, the optimal decision shifted to head-starting wild eggs and re-introducing them into the population as YOY using maximum effort (equivalent to removing 30% of the reproductive effort from the wild each year) (Fig. 5.3d). However, this strategy only reduced extinction risk by 0.8% for every $100,000 invested (Fig. 5.4) and would require 482 tanks over the course of 10 years to raise larvae to metamorphosis and a total of $6.38 million.

When we simulated a range of hypothetical starting wild population sizes from 50-150, the resulting optimal scenarios required greater effort as the population size declined (Fig. 5.5a & b) because the background extinction risk increases as population size decreases. At population sizes <70 wild females, the optimal strategy was to head-start wild eggs, and release as young of year at a maximum effort, and the total 10-year cost ranged between $3.02 million and $3.29 (for a population size of 50 and 60 respectively) (Fig. 5.5c). However, if the population size was 70 or above, the optimal strategy was always to captive breed and release as tadpoles at decreasing levels of effort as the starting population increased (Fig. 5.5d). Regardless of wild population size, we found that head-starting and release as tadpoles was never an optimal recovery action.

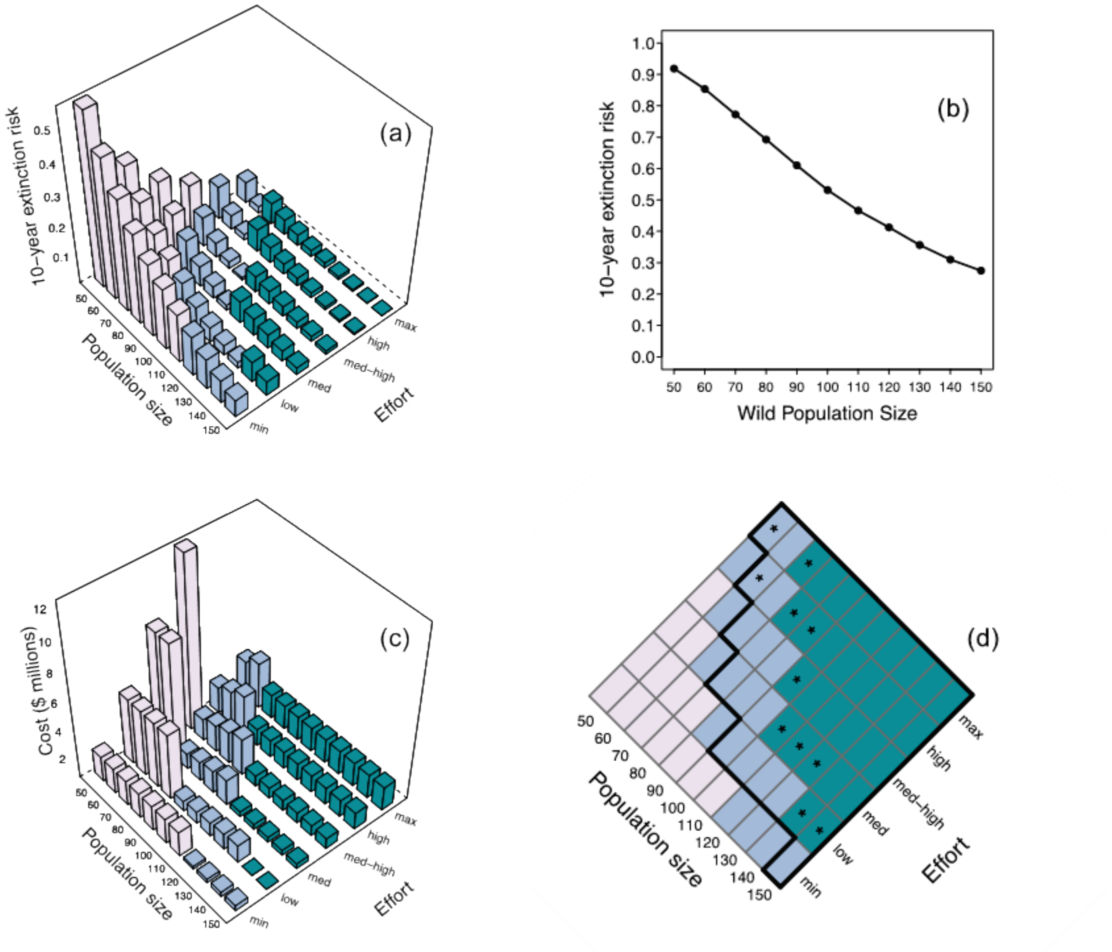

Figure 5.5 **A sensitivity analysis with respect to starting wild population size. For each population size (ranging from 50 to 150), we show the supplementation pathway that minimizes the 10-year extinction risk for a given level of effort (a) and the initial extinction risk at each starting population size for comparison (b). Panel c shows the costs associated with each level of effort. Panel d is a bird's eye view of panel a, and the stars indicate the top-ranked pathway for each population size. The bold black line outlines pathways in which 10-year extinction risk is reduced below 10%. For example, if the wild population is 50 breeding females, the top-ranked pathway is to head-start and release as YOY at a maximum effort. Bars are shaded by release strategy. Grey bars are captive breeding and release as YOY, blue bars are head-starting and release as YOY, and green bars are captive breeding and release as tadpoles.**

We also explored how assumptions regarding the reproductive output of the captive population affected the optimal decision. We found that with a 10% reduction in reproductive output each year (i.e. 90% of females successfully reproduce) (Fig. 5.6a), the optimal decision switched to head-starting and release as YOY at a low effort for a wild population size of 100 breeding females. For scenarios in which only 75% and 50% of successfully produce offspring, the optimal decision was also to head-start and release as YOY at a low level of effort (Fig. 5.6b & c respectively), which corresponds to head-starting 10% of eggs in the wild population each year for 10-years.

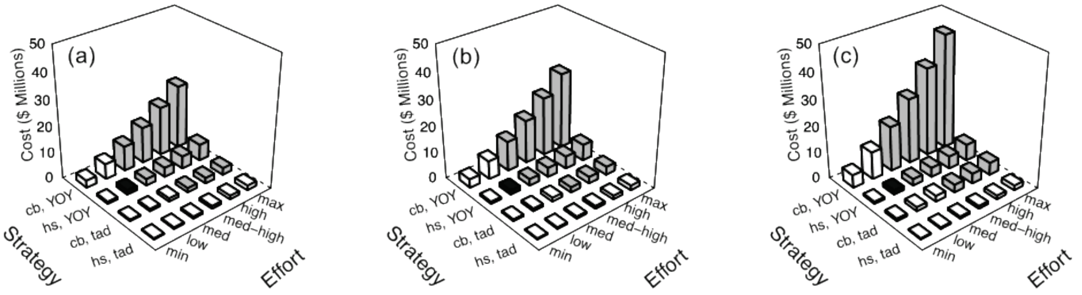

Figure 5.6 **Sensitivity analysis with respect to the number of females that breed in captivity. These panels represent (a) a situation in which only 90% of the females kept in captivity produce viable offspring (i.e. need to keep 11 females in captivity to meet the minimum "effort" of 10 breeding females), (b) 75% of females produce viable offspring, and (c) 50% of females produce viable offspring. Grey bars indicate the pathways which reduce extinction risk below 10%, while black bars indicate the optimal decision. Note the change in the z axis (cost) from Fig. 2. "cb" = captive breed, "hs" = head-starting, "YOY" represents release back into the wild at the young of year stage, and "tad" = release back into the wild at the larval stage.**

5.3.6. Discussion

We combined biological and economic aspects of species recovery into a decision framework to estimate the optimal strategy for reducing extinction risk for a highly imperiled population of *R. pretiosa*. Our approach of weighing tradeoffs between conservation actions and their costs highlights that a seemingly beneficial recovery option with respect to the biology of a species, may not be optimal once monetary resources, often the deciding factor in implementing conservation measures, are considered. The top-ranked recovery pathway depended on the specific management target, but in general, captive breeding achieved our baseline recovery target more often than head-starting, with 8 of 10 population sizes resulting in captive breeding and release as larvae (Fig. 5.5). Only at the two lowest population sizes we considered (50 and 60 breeding females) was head-starting the top-ranked pathway. Similarly, we found that the optimal recovery pathway, captive breeding and release as larvae, was the same whether the recovery target was to reduce extinction risk below 10% (baseline scenario) or 25%, though achieving the latter target could be done more cost-effectively (3% reduction and 4.8% reduction for $100,000 spent respectively). However, when the recovery goal was relaxed to extinction risk below 50%, the optimal pathway switched to head-start and release as tadpoles, and although it was the least expensive pathway ($370,000 total cost), the benefit-cost ratio was low (only 1.2% reduction in extinction risk per $100,000 spent). When we removed the consideration of cost all together, and prioritized simply minimizing the 10-year extinction risk, the optimal recovery pathway was to head-start and release as YOY, and resulted in a benefit-cost ratio of only 0.8% reduction in extinction risk per $100,000, but reduced overall extinction risk to below 1% over 10 years. These results demonstrate a non-linear relationship between the financial costs of recovery actions and their biological efficacy (Fig. 5.4).

The decoupling between the amount of money spent on recovery actions and their biological effectiveness highlights the utility of adopting a decision analysis framework, as it can help identify non-intuitive pathways to recovery. Kissel et al. (2014) compared the biological efficacy of head-staring and captive breeding without considering costs, and demonstrated that head-starting 15% of the wild egg masses and releasing as YOY reduced the 10-year extinction risk to a similar level as captive breeding 40 females and releasing as larvae (3% and 6% probability of extinction respectively). By incorporating costs into our decision analysis, we show that captive breeding 40 females (assuming a 1:1 ratio of females to reproductive output in captivity) is a more economically viable option than head-starting 15% of the population by a difference of more than 1 million dollars. Overall, our analysis demonstrates that although head-starting and release as YOY reduces extinction risk to levels similar to captive breeding and release as larvae, the tradeoff in monetary costs of recovery is typically lower for captive breeding and release as larvae (Fig. 5.4), and thus drives the rank order of the pathways in our analysis.

We simulated using early life stages (larvae and YOY) to supplement a wild population, effectively bolstering survival at these stages. Yet for many species, including *R. pretiosa*, adult survival has been shown to have the greatest influence (e.g. sensitivity or elasticity) on population stability (Crouse et al. 1987; Biek et al. 2002; Vonesh & De la Cruz 2002; Stahl & Oli 2006b), suggesting that greater biological efficacy could be achieved by targeting adults. However, recovery actions aimed at improving adult survival for amphibians are rare (Biek et al. 2002), as there are often logistical challenges, or actions require long-term commitments and large monetary investments that exceed the resources of most conservation organizations and many government agencies. Here, we demonstrate that targeting life-stages with lower demographic sensitivity can be effective at reducing the extinction risk of populations using several forms of population supplementation.

Our decision analysis framework included elements that are already commonly recommended for recovery planning, such as population viability analyses (PVAs) and recovery actions including population supplementation. Although PVAs have been criticized as data-hungry models (Coulson et al. 2001), we argue that they are useful tools for making relative comparisons of conservation pathways, even when data are limited. We extended the use of PVAs to quantify the potential for recovery with respect to two common conservation actions employed for amphibians and other vertebrates, captive breeding and head-starting with release into the wild (Fischer & Lindenmayer 2000b; Zippel & Mendelson III 2008; Muths et al. 2014; Harding et al. 2015). The effectiveness of supplementation to bolster populations over longer management time-horizons (>10 years) is largely unknown (Griffiths and Pavajeau 2008). In particular, artificial selection imposed by captive breeding and rearing can dramatically reduce population fitness (Araki et al. 2007), and many species in captivity fail to produce offspring at the same rate as their wild counterparts (Kouba et al. 2009; Trudeau et al. 2010; Kiik et al. 2013; Muths et al. 2014; Penfold et al. 2014). Such observations encourage caution in adopting captive breeding, but despite this uncertainty, supplementation is increasingly proposed for many species, amphibians in particular

(Stuart et al. 2004). We argue that quantifying the tradeoffs between alternative supplementation approaches, while explicitly incorporating uncertainty, is a useful step in recovery planning given the frequency with which such actions are employed for species conservation. For example, we demonstrated that accounting for the diminished reproductive output of adult females in captivity resulted in a re-ranking of our recovery pathways, but that our conservation target could still be reached (Fig. 5.6).

This case study represents a dire conservation problem in which population supplementation is one of few options currently available to reduce extinction risk (Caughley 1994). Our models suggest that large decreases in extinction risk over a 10-year time horizon are possible. Although we simulated continuous supplementation for 10 years, a timescale considered relevant for conservation actions (Semlitsch 2002; SSC Re-introduction Speacialist Group 2012), in our baseline scenario only half of the pathways achieved or surpassed the goal of minimizing extinction risk below 10% (Fig. 3a). This along with other assessments of recovery plans that show improved species status with longer time since listing (Boersma et al. 2001; Male & Bean 2005) suggests that 10 years may actually be an artificially short management time horizon for conservation measures to be effective. We also emphasize that unless the ultimate causes of decline in wild populations are addressed, population supplementation is likely to be but short-term life-support for species that otherwise will become reliant on continuous conservation action (Scott et al. 2005, 2010).

Managing a population for recovery is often a non-linear process in which management targets can change through time. Decision analysis provides a flexible framework to evaluate multiple management targets simultaneously with imperfect information as an iterative process (Peterman & Anderson 1999). Through explicitly incorporating uncertainty at multiple levels (uncertain states of nature in the model, observer uncertainty, and recovery target uncertainty), decision analysis provides a roadmap of options for decision-makers and managers that can increase the probability of success (Converse et al. 2013). However, decision analysis is highly dependent on both the management targets and the alternative pathways included in the analysis (Peterman and Anderson 1999; Converse et al. 2013). For example, we found that the top-ranked pathway when cost was unlimited was to head-start wild collected eggs and release individuals as YOY (Fig. 5.3a). However, this finding likely reflects the different pathways we chose to include in our analysis. Had we chosen to include a wider range of ‘effort’ for both head-starting and captive breeding, it is likely that the rank order would change. Additionally, our 10-year timeframe only allows us to compare a snapshot of costs, and had we chose to frame our recovery target differently (for example exploring the number of years it took to reduce extinction risk below a threshold), our rankings may have changed.

Although decision analysis can clarify options and identify the optimal management action based on input criteria, it is still ultimately a tool for decision-makers, who must determine if the top-ranked action produced by the model is the right action for the problem at hand, once the uncertainty in the process, data, and social and political factors have been considered. Despite these limitations, we argue that decision analysis is an under-used tool for endangered species recovery, and could improve the quantitative basis for recovery planning (*sensu* Boor et al 2013, Gerber and Hatch 2002, Boersma et al. 2001). By leveraging even relatively modest data regarding species at risk and the costs associated with recovery options, those tasked with endangered species recovery can adapt this framework as a means to streamline the complexities related to species recovery for a range of conservation problems, from population supplementation, to habitat management, to threat eradication, while also exploring important nonlinearities in the benefits and costs of alternative recovery actions.

Chapter 6. General Discussion

Understanding the trajectory of individual populations in the face of anthropogenic threats is key to preventing widespread loss of populations and species that maintain functional ecosystems. Climate change can act synergistically with other threats, including habitat loss, pollutants, invasive species, and disease, and may pose a threat to even the most pristine and protected ecosystems. Thus, it is likely that mitigation and heavy-handed management of biological systems worldwide (Scott et al. 2005, 2010) will play an increasing role in conservation for decades to come. In this thesis, I demonstrate how demographic data spanning the life history of a species can be leveraged both pre- and post population declines to assess how anthropogenic threats will affect populations and conversely, how they can be mitigated.

In Chapter 2, I combine empirical data with quantitative modeling to assess the effects of climate change on *R. cascadae*, a high elevation specialist. *R. cascadae* are pond-breeding amphibians endemic to the Pacific Northwest, where climate change predictions suggest a shift from snow dominated to rain dominated watershed, and an overall increase in temperatures (Hamlet et al. 2005; Mote et al. 2005; Lee et al. 2015). I demonstrate that although individuals are currently exposed to harsh winters (i.e. freezing temperatures and long winters), the increasing temperatures and decreasing winter length associated with future climate are likely to reduce the population growth rate below replacement. I use site-specific hydrologic climate models and field observations to explore how reduced aquatic habitat for amphibians will affect mortality rates at the aquatic stage, which previously has only been done via theoretical simulations or with limited (<4 years) empirical data (Matthews et al. 2013; McCaffery et al. 2014). My analysis reveals that currently, approximately 25% of the reproductive effort of *R. cascadae* is lost due to pond drying, but under 2080's A1B climate conditions, this could increase to up to nearly 40%. I then use 15 years of data on over 950 individually marked frogs to explore the relationship between annual survival and a suite of 14 climate variables hypothesized to influence survival. Using an information theoretic approach (AICc, Burnham and Anderson 2002) to weigh the relative support of these climate variables, I find support for five climate variables, including temperature in the driest quarter and winter length. Counter to other montane amphibian studies

(Scherer et al. 2008; McCaffery & Maxell 2010; McCaffery et al. 2012), I find that adult survival is positively correlated to longer winters, suggesting that predicted declines in snowpack may decrease survival for *R. cascadae*. Few studies have demonstrated the effects of precipitation outside the winter season on amphibians (but see Laurance 1996; Scherer et al. 2008), but my analysis suggests that precipitation in the driest quarter (typically July-September) is important for amphibian survival at the terrestrial stage.

When I add up the effects of climate change on both the aquatic and terrestrial stages through demographic modeling, I find evidence for compounding negative effects on population growth. I model population growth rate under current (1980-2006) and future (2080's) climate conditions, and find that currently, the population is stable or slightly increasing ($\lambda_s = 1.01$), but that under theoretical 2080's climate conditions, the population is pushed beyond a demographic tipping point and into decline ($\lambda_s = 0.95$). This chapter is one of the first to forecast the effects of climate change on vertebrate populations (Villellas et al. 2015).

In Chapter 3, I compare demographic rates of two populations of *R. cascadae* at the northern and southern range limits, and find that contrary to expectations, the northern population is more vulnerable than the southern population to climate change. I compare climate driven changes in larval mortality and adult survival from Chapter 2 (northern range limit), to a population at the southern range limit. My analysis reveals that although there are similar decreases in larval survival for both populations in the 2080's, adult survival increases as winter length decreases in the Trinity Alps, compensating for the increased mortality levels at the aquatic stage. Overall, the population growth rate increases marginally for the southern population in the 2080's (from $\lambda_s = 0.98$ to 0.99), while λ_s for the northern population decreases by 7%. This chapter provides the first range-wide assessment of demographic compensation for an amphibian species, and runs counter to the current paradigm that species are more vulnerable to climate change at the southern end of their range (Parmesan et al. 1999; Parmesan 2006; Chen et al. 2011; Sunday et al. 2012; Carroll et al. 2015). Thus, my results demonstrate the need to incorporate population-level responses to climate in modeling species' response to climate change (*sensu* Doak & Morris 2010; Villellas et al. 2015).

In Chapters 4 and 5, I focus on targeting specific life stages for reducing extinction risk of an imperiled amphibian, *R. pretiosa*. In Chapter 4, I establish that reducing the 10-year extinction risk of a population is possible through continued supplementation at either the larval or post-metamorphic young of the year (YOY) stage, but that effectiveness varies depending on the size of the population to be supplemented, the method of supplementation (head-starting or captive breeding), and the number of individuals released into the wild population. In general, I find that captive breeding and release at the larval stage is more effective than head-starting and release at the larval stage, and yields similar reductions in extinction risk to supplementation at the YOY stage for either supplementation strategy. In Chapter 5, I feed this model into a formal decision analysis that factors in the economic constraints of conservation actions, quantifying the costs of each supplementation strategy at increasing levels of effort, and assess the tradeoffs with biological recovery targets. I find that supplementing a population with captive bred larvae provides the largest reduction in extinction risk per dollar invested, but that counterintuitively, increasing spending does not always lead to proportional reductions in extinction risk. With these results, I highlight the importance of assessing both the biological capacity and economic efficacy of alternative recovery strategies.

For both *R. cascadae* and *R. pretiosa*, adult survival is the life stage that contributes the most to population growth. This result falls in line with many other studies across taxa (Heppell et al. 2000; Vonesh & De la Cruz 2002; Stahl & Oli 2006a), however I demonstrate that changes in the demographic structure of a population at life stages with lower sensitivity can still impact a population in important ways. In Chapters 2 and 3, I find that decreases in larval survival can reduce the population growth rate of *R. cascadae*, and in fact for the northern population, a 17% reduction in larval survival due to pond drying, could reduce the population growth rate by 2%, enough to tip the population from increasing to declining ($\lambda_s<1$). For the southern population, I find that reductions in larval survival have a larger effect on population stability than the northern population (a 14% decrease in larval survival results in an 11% decrease in λ_s), in part because adult survival is generally lower. Additionally, in chapter 4, I demonstrate that targeting life stages with lower elasticity (larvae, YOY) for recovery actions can compensate for low adult survival, suggesting that overall, life stages with lower sensitivity may be important for mitigating declines.

The demographic models I construct in Chapters 2-4 focus on relative comparisons of survival of early (larval) and late (adult) life stages. While data for these stages is comprehensive and empirically based, survival rates for juvenile amphibians are rare (Biek et al. 2002; Muths et al. 2014). I rely on estimates of juvenile survival for closely related Ranids in my thesis, and although other studies demonstrate that survival is correlated at the terrestrial stage for Ranids (Chelgren et al. 2008; McCaffery & Maxell 2010), reducing uncertainty in juvenile survival will continue to improve predictions of population dynamics. This is particularly important in the context of supplementation at early life history stages, in which there is some evidence of deleterious effects from captivity post-release for other species (Lynch & O'Hely 2001; Araki et al. 2007; Muths et al. 2014).

In general, preventing global biodiversity loss will be a multi-faceted, rigorous scientific undertaking. Populations are often the biological unit at which conservation actions are applied (Hutchings & Reynolds 2004; Scott et al. 2005, 2010), and thus population ecology will play an important role in this prevention. Quantitative tools to forecast threats to population stability, such as results from Chapters 2 and 3, can be used to inform conservation efforts for montane amphibians. For example, removing invasive trout in montane landscapes, which are known to exclude amphibians from more permanent ponds (Knapp et al. 2001; Ryan et al. 2014), can increase access to aquatic larval rearing habitat, and increase access to aquatic habitat during dry portions of the year for terrestrial stages. On the opposite end of the conservation spectrum, quantitative decision-making for populations in decline, which I demonstrate in Chapters 4 and 5, will allow conservation ecologists to maximize limited conservation funds to reduce extinction of imperiled species. Thus, with this thesis, I demonstrate how we can improve our predictions of species' responses to anthropogenic threats, and conversely, advance the quantitative framework for recovering declining populations.

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Appendix A. Supporting material for Chapter 2.

Table A.1 **Climate Hypothesis for adult survival. (Following page)**

Climate Variable	Formula	Hypothesis
Winter Length	S~b0 + b1*Wint	Winter length may negatively affect adult survival if it is too long and individuals do not have enough resources to withstand the long winter.
Summer Length	S~b0 + b1*Sum	Generally, longer summers will have a positive effect on adult survival, as they will have a longer growing season in which to gather resources and gain mass to withstand the winter
Maximum Snow Water Equivalent	S~b0 + b1*MaxSWE	Increasing maximum snow water equivalent is negatively correlated with adult survival
Annual mean temperature	S~b0 + b1*Annual MT	Higher mean annual temperature will increase adult survival because individuals spend much of the year below their thermal optima (Sunday et al. paper)
El Niño (MEI)	S~b0 + b1*MEI	Strong el Niño years will have a negative effect on survival because they tend to be drier in the summer. Strong la Niña years will also have a negative effect because they will result in longer winters
Mean Precipitation in the Driest Quarter (PDQ)	S~b0 + b1*PDQ	Increased precipitation in the driest quarter will have positive effect on adult survival because it will increase access to wetland habitats and decrease desiccation risk.
Temperature Seasonality	S~b0 + b1*TS	Temperature seasonality is a measure of the variation in temperature across the year. We hypothesize that a lower variation will result in increased adult survival because individuals will have to spend less time thermoregulating (whether basking or seeking shade/water) and thus, more time feeding or mating.
Mean Temperature in the Warmest Quarter	S~b0 + b1*TWQ	Lower temperatures in the warmest quarter will increase adult survival because individuals will be at lower risk of desiccation and heat stress.
Mean Temperature in the Driest Quarter	S~b0 + b1*TDQ	Lower temperatures in the warmest quarter will increase adult survival because individuals will be at lower risk of desiccation and heat stress.

Mean Temperature in the Coldest Quarter	S~b0 + b1*TCQ	Increased temperatures in the coldest quarter will increase adult survival, as there will be less risk of freezing.
Cumulative Precipitation in the Wettest Quarter	S~b0 + b1*PWQ	Increased precipitation in the wettest quarter will have a positive effect on adult survival because it will maintain hydrologic stability in wetland habitat, which will in turn increase access to water and reduce desiccation risk.
Summer length + winter length	S~b0 + b1*Wint + b2*Sum	Longer summer + winter length (year length) will decrease survival of adults because in general, the longer the ‘year’ the higher the probability of death is.
Max SWE + summer length	S~b0 + b1*MaxSWE + b2*Sum	Increasing maximum snow water equivalent is negatively correlated with adult survival and increasing summer length is positively correlated, thus we hypothesize the two combined will have a cancelling effect on annual survival
Winter length + Mean Precipitation in the Driest Quarter	S~b0 + b1*Wint + b2*PDQ	Increased winter length and increased precipitation of the driest quarter will have a cancelling effect on adult survival because we hypothesize that increasing winter length will decrease adult survival and increased precipitation in the driest quarter will decrease adult survival.
Max SWE + Mean Precipitation in the Driest Quarter	S~b0 + b1*MaxSWE + b2*PDQ	Increased max SWE and increased precipitation of the driest quarter will have a cancelling effect on adult survival because we hypothesized that Max SWE will decrease adult survival and increased precipitation in the driest quarter will decrease adult survival.
Summer Length + Mean Precipitation in the Driest Quarter	S~b0 + b1*Sum + b2*PDQ	Increased summer length and increase precip in the driest quarter will have a positive effect on adult survival because they will have more time to gain resources, and will have to spend less time behaviorally regulating water loss with increased precipitation.
Temperature Seasonality and Mean Precipitation in the Driest Quarter	S~b0 + b1*TS+ b2*PDQ	A decrease in TS and an increase in PDQ will have a positive effect on adult survival because adults will spend less time behaviorally regulating temperature and water loss, and thus can spend more time foraging and mating.

El Niño + Maximum SWE	S~b0 + b1*MEI+ b2*MaxSWE	A strong El Niño year and higher max swe will have a neutral effect on adult survival because increased max swe in strong el Niño years may result in increased availability of wetland habitats during dry summers, which provide opportunities for adults to behaviorally regulate water loss.
Max SWE + Temperature Seasonality	S~b0 + b1*MaxSWE+ b2*TS	Increased max swe and decreased variation in seasonal temperatures will have a cancelling effect on adult survival because we predict that max swe will have a negative effect on survival whereas decreased variation in seasonal temps will have a positive effect.
Max SWE + Mean Annual Temperature	S~b0 + b1*MaxSWE+ b2*MT	Increased max swe and increased mean annual temperature will have a cancelling effect on adult survival because the negative effects of increased swe will cancel out the positive effects of increased mean annual temperature.
Winter Length + El Niño	S~b0 + b1*Wint + b2*MEI	Increased winter length and strong El Niño years will have a strong negative effect on adult survival, given that individuals will have to hibernate longer, and there will be fewer resources and drier summers in strong el Niño years.
Winter Length + Mean Annual Temperature	S~b0 + b1*Wint + b2*MT	Increased winter length and increased mean annual temperature will have a neutral effect on adult survival because the negative effects of increased winter length will cancel out the positive effects of increased mean annual temperature.
Winter Length and Temperature in the Warmest Quarter	S~b0 + b1*Wint + b2*TWQ	increased winter length and increased temperature in the warmest quarter will have a strong negative effect on adult survival because individuals will have to spend more time hibernating and thermoregulating rather than foraging, which will in turn negatively impact body condition and survival.
Winter Length + Temperature Seasonality	S~b0 + b1*Wint + b2*TS	Increased winter length and a decrease in variation of seasonal temperatures will have a cancelling effect on adult survival.

Annual Mean Temp + Temperature Seasonality	S~b0 + b1*MT + b2*TS	An increase in mean annual temperature and a decrease in the variation of seasonal temperatures will have a positive effect on adult survival, given that individuals would likely have to spend less time thermoregulating, leaving more time for foraging.
Summer Length + Mean Annual Temperature	S~b0 + b1*Sum + b2*MT	An increase in summer length and an increase in mean annual temperature will have a net positive impact on adult survival because there will be a longer window for foraging and less time spent thermoregulating.
Summer Length and El Niño	S~b0 + b1*Sum + b2*MEI	Increased summer length and strong El Niño years will have a net neutral effect on adult survival.

Table A.2 Vital rate means and (variance reported in parentheses) for the ‘current’ and ‘2080’s’ time period. Vital rates that change between the two time periods are bolded.

stage	Current	2080's
embryonic	0.92 (0.01)	0.92 (0.01)
larval	0. 09 (0.12)	0. 09 (0.12)
proportion of larvae that did not dry	0.75 (0.019)	0.62 (0.013)
juvenile	0.49 (0.59)	0.49 (0.59)
Transition to adult	0.54 (0.027)	0.54 (0.027)
adult	0.81 (0.001)	0.74 (0.002)
fecundity	311.31 (10420.43)	311.31 (10420.43)

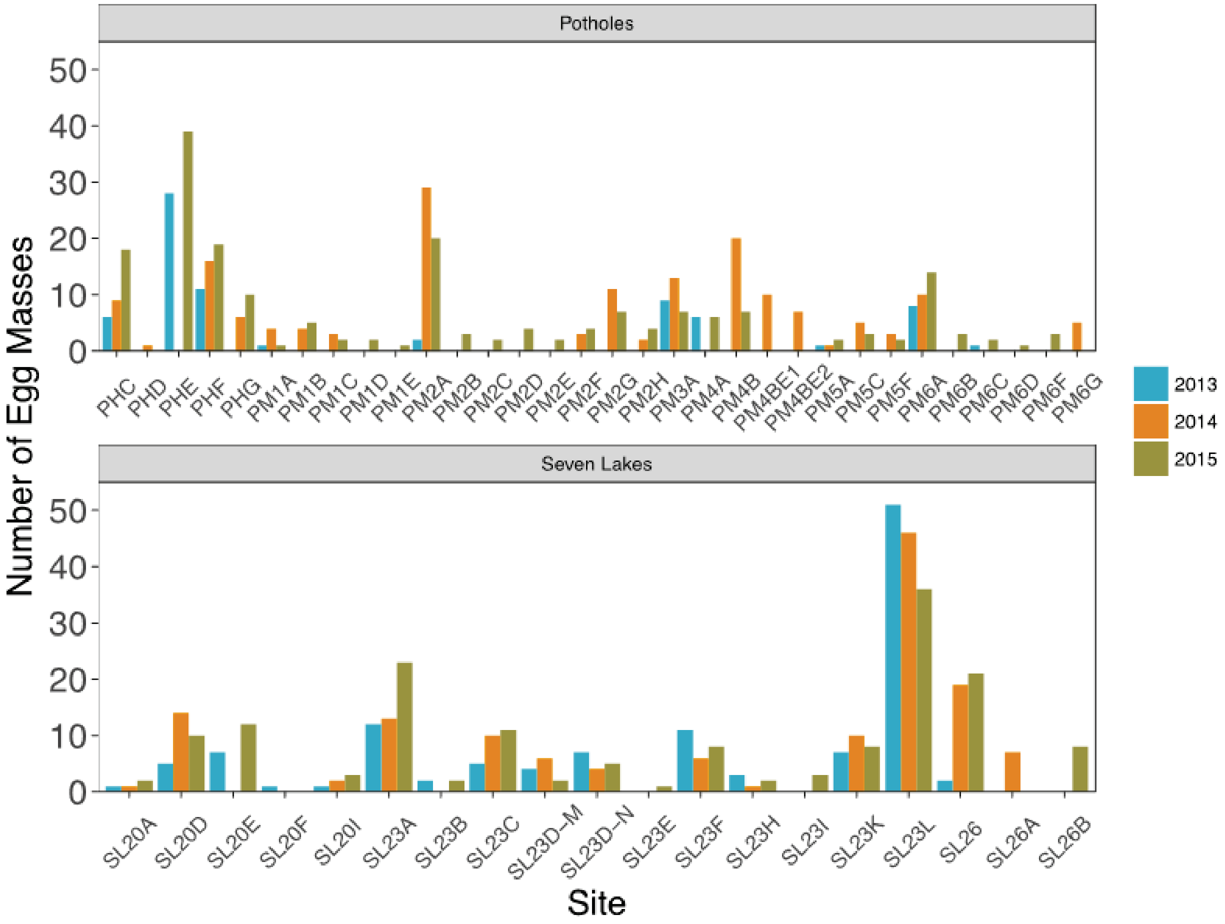

Figure A.1 Number of egg masses laid in each pond from 2013 to 2015. Top panel shows the Potholes regions and bottom pannel shows the Seven Lakes Basin.

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Table A.3. AIC table for Robust Design mark recapture analysis

Model	# Par	AICc	ΔAICc	*weight*	Deviance	Cumulative Weight
S(~wint + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11242.57	0	*0.09*	11103.59	0.09
S(~mswe + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11242.7	0.13	*0.08*	11103.72	0.17
S(~wint + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11242.79	0.22	*0.08*	11105.9	0.25
S(~pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11242.89	0.32	*0.07*	11106	0.32
S(~ts + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11243.08	0.51	*0.07*	11104.1	0.39
S(~wint * pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	69	11243.38	0.81	*0.06*	11102.31	0.45
S(~pdq * sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11243.51	0.94	*0.06*	11104.53	0.51
S(~mswe + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11243.93	1.36	*0.04*	11107.04	0.55
S(~wint + mt + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.04	1.47	*0.04*	11105.06	0.59
S(~wint + enso + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.35	1.79	*0.04*	11105.38	0.63
S(~wint + twq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.42	1.85	*0.03*	11105.44	0.66
S(~wint + ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.45	1.88	*0.03*	11105.47	0.7
S(~sum + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.52	1.95	*0.03*	11105.54	0.73
S(~sum + wint + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.73	2.16	*0.03*	11105.75	0.76
S(~wint * sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.87	2.31	*0.03*	11105.89	0.79
S(~ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11245.12	2.55	*0.02*	11108.23	0.81
S(~enso + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11245.24	2.67	*0.02*	11108.35	0.84
S(~mswe + ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.45	2.88	*0.02*	11106.47	0.86
S(~mswe + mt + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.67	3.1	*0.02*	11106.69	0.88
S(~mswe * sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.87	3.3	*0.02*	11106.89	0.89
S(~mswe + sum + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.89	3.32	*0.02*	11106.91	0.91
S(~enso + mswe + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11246	3.43	*0.02*	11107.02	0.93
S(~sum + ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11246.47	3.91	*0.01*	11107.5	0.94
S(~sum + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11246.64	4.07	*0.01*	11109.75	0.95

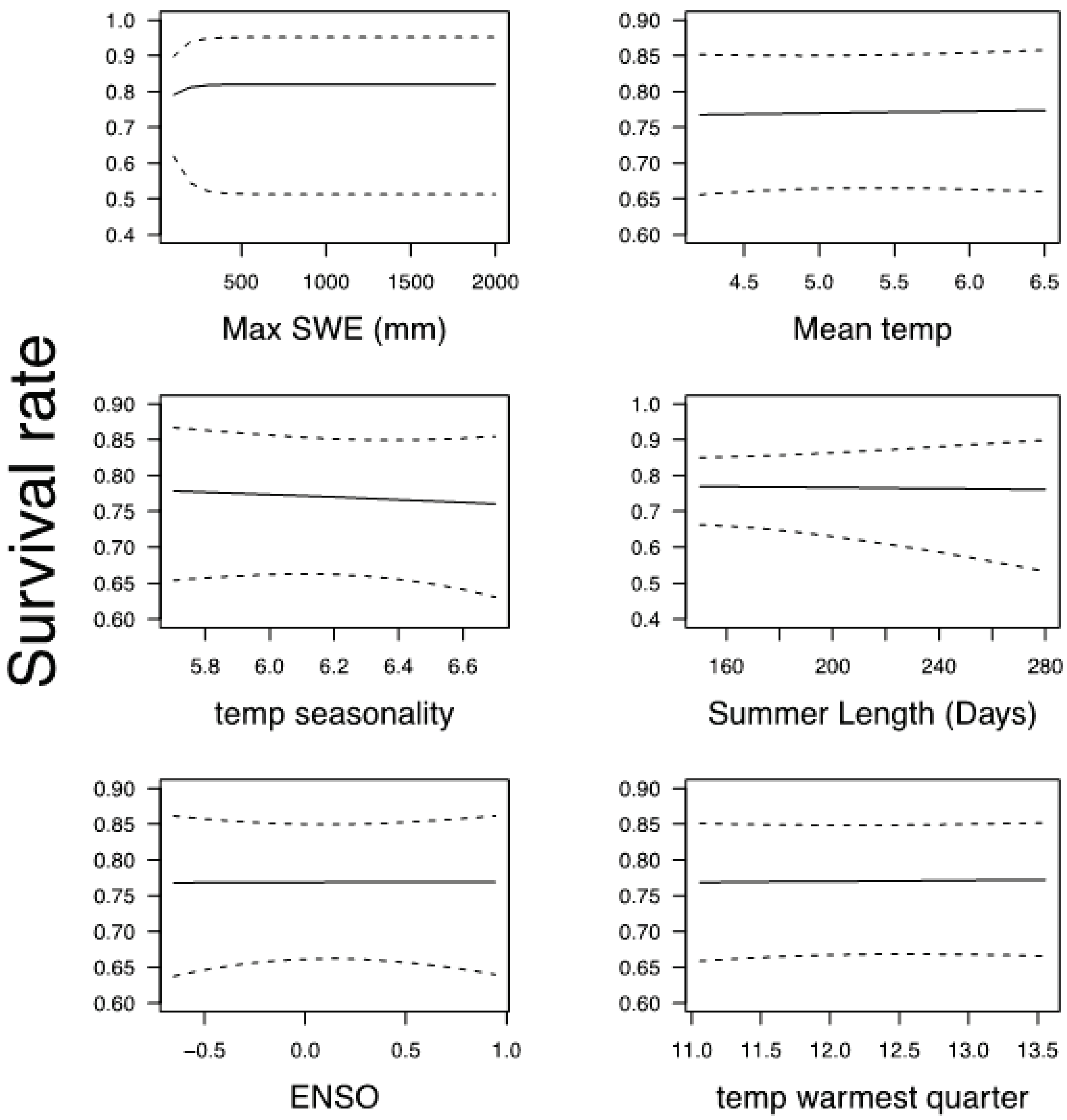

Figure A.2. **Relationship between adult survival and climate variables with a summed AIC (relative variable importance) of .25 or less. Dashed lines represent 95% confidence intervals.**

Appendix B. Supporting Information for Chapter 3

VIC model details

We used data from Variable infiltration capacity (VIC) models implemented over Washington and California at a spatial scale 1/16th degree resolution (Hamlet et al. 2010). We selected the VIC cell that corresponded with our study population to model the effects of climate. Each VIC cell database contains modeled daily estimates of 16 climate variables related to climate and hydrology (Hamlet et al. 2010), of which we used estimates of temperature, precipitation, and snow water equivalent (SWE) to model adult survival. We checked that climate estimates for each cell were representative of observed climate data, by comparing temperature, precipitation, and SWE values for years in which our studies overlapped with VIC projections (2002 to 2006 for Olympics and 2002 to 2010 for Trinity Alps). VIC estimates for SWE for both sites were underestimates, and thus we substituted SWE values from the nearest VIC cell SWE estimates (16km from the Olympic site and roughly 10km for Trinity Alps). The VIC models overestimated temperature by approximately 1.75°C for the Olympics and 1.86°C for the Trinity Alps, thus we corrected for the warm bias by subtracting these values from daily estimates of temperature for both the 'current' (1980-2006) and future (2080's) VIC datasets.

We used pond-specific estimates of daily wetland water levels from VIC models for 25 breeding ponds in the Olympic population, and 1 breeding pond in the Trinity Alps to estimate the proportion of ponds that dried annually from 1980-2006. Lee et al. (2015) used empirical estimates of water levels to fit regression models over a >90 year time series for each pond and the mean R^2 for all wetlands was >0.8, suggesting that the models performed relatively well at capturing wetland water levels. These models were then used to forecast daily wetland water levels for the 2080’s using climate data from downscaled global circulation models (Hamlet et al. 2010).

Table B.1 Number of years that breeding was observed in each site in the Trinity Alps (following page).

Site	hydroperiod class	# year s breeding observed
DPM8	ephemeral	4
DPM9	ephemeral	1
PTH7	ephemeral	2
RMM4	ephemeral	1
RMM5	ephemeral	1
UVM4	ephemeral	2
CAS2	intermediate	9
CAS3	intermediate	1
CAS4	intermediate	1
CAS5	intermediate	2
CAS6	intermediate	3
CLM1	intermediate	1
DPM2	intermediate	9
EDN1	intermediate	4
GSP1	intermediate	11
GSP2	intermediate	12
MOS1	intermediate	6
MOS2	intermediate	4
MVM1	intermediate	6
MVM2	intermediate	7
MVM4	intermediate	6
PTH5	intermediate	1
RMM1	intermediate	11
RMM2	intermediate	10
SMP1	intermediate	14
UVM1	intermediate	14
UVM2	intermediate	10
UVM3	intermediate	1
UVM5	intermediate	1
CAS1	perenial	10
DMP1	perenial	1
DPM1	perenial	14
DPM10	perenial	6
DPM7	perenial	4
EVM1	perenial	3
MVM3	perenial	4

PTH8	perenial	1
PTH9	perenial	1
DPM11	permanent	1
DPM3	permanent	12
DPM4	permanent	7
DPM5	permanent	3
DPM6	permanent	14
ECH1	permanent	14
PTH1	permanent	12
PTH2	permanent	10
PTH3	permanent	10
PTH4	permanent	10
PTH6	permanent	1
RMM3	permanent	4

Table B.2 Mean and variance of vital rates used to construct probability distributions for matrix modeling. For these vital rates, we used the same estimates for both populations, and vital rates did not change between 'current' and 2080's scenarios. For juvenile survival, we used the mean value from multiple estimates of survival from the two studies.

Vital Rate	mean	variance	Data Source
embryonic	0.92	0.01	Palen, unpublished data
larval	0. 09	0.12	Palen, unpublished data
juvenile	0.49	0.59	Funk et al. 2005, McCaffery and Maxell 2010
juvenile transition probability	0.54	0.027	McCaffery and Maxell 2010
fecundity	311.31	10420.43	Kissel, unpublished data

Table B.3 AICc tables for adult survival analysis for Olympic Population

Model	# Par	AICc	ΔAICc	weight	Deviance	Cumulative Weight
S(~wint + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11242.57	0	0.09	11103.59	0.09
S(~mswe + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11242.7	0.13	0.08	11103.72	0.17
S(~wint + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11242.79	0.22	0.08	11105.9	0.25
S(~pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11242.89	0.32	0.07	11106	0.32
S(~ts + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11243.08	0.51	0.07	11104.1	0.39
S(~wint * pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	69	11243.38	0.81	0.06	11102.31	0.45
S(~pdq * sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11243.51	0.94	0.06	11104.53	0.51
S(~mswe + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11243.93	1.36	0.04	11107.04	0.55
S(~wint + mt + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.04	1.47	0.04	11105.06	0.59
S(~wint + enso + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.35	1.79	0.04	11105.38	0.63
S(~wint + twq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.42	1.85	0.03	11105.44	0.66
S(~wint + ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.45	1.88	0.03	11105.47	0.7
S(~sum + pdq + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.52	1.95	0.03	11105.54	0.73
S(~sum + wint + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.73	2.16	0.03	11105.75	0.76
S(~wint * sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11244.87	2.31	0.03	11105.89	0.79
S(~ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11245.12	2.55	0.02	11108.23	0.81
S(~enso + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11245.24	2.67	0.02	11108.35	0.84

S(~mswe + ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.45	2.88	0.02	11106.47	0.86
S(~mswe + mt + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.67	3.1	0.02	11106.69	0.88
S(~mswe * sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.87	3.3	0.02	11106.89	0.89
S(~mswe + sum + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11245.89	3.32	0.02	11106.91	0.91
S(~enso + mswe + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11246	3.43	0.02	11107.02	0.93
S(~sum + ts + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	68	11246.47	3.91	0.01	11107.5	0.94
S(~sum + sex)Gamma''(~time + sex)Gamma'(~time + sex)p(~time + session + sex)c(~time + session + sex)	67	11246.64	4.07	0.01	11109.75	0.95

Table B.4. AICc table for the Trinity Alps adult survival analysis.

Model	Par	AICc	ΔAICc	Weight	Deviance	Cumulative Weight
S(~1 + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	65	14572.35	0	0.13	15474.69	0.13
S(~pdq * sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14572.76	0.41	0.11	14434.93	0.24
S(~tdq * sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14573.1	0.75	0.09	14435.27	0.33
S(~pdq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14573.21	0.86	0.09	14437.5	0.42
S(~wint + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14573.91	1.57	0.06	14438.2	0.48
S(~wint + pdq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14574.21	1.86	0.05	14436.38	0.53
S(~wint * pdq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	68	14574.22	1.87	0.05	14434.27	0.59
S(~enso + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14574.25	1.91	0.05	14438.54	0.64
S(~tcq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14574.35	2	0.05	14438.63	0.69
S(~pwetq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14574.39	2.04	0.05	14438.67	0.74
S(~mswe + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14574.44	2.09	0.05	14438.72	0.78
S(~tdq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	66	14574.44	2.1	0.05	14438.73	0.83

S(~mswe + pdq + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14575.08	2.73	0.03	14437.25	0.86
S(~wint + enso + sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14575.21	2.87	0.03	14437.38	0.9
S(~wint * sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14575.54	3.2	0.03	14437.71	0.92
S(~tcq * sex)Gamma''(~1)Gamma'(~1)p(~time + session + sex)c(~time + session + sex)	67	14575.9	3.56	0.02	14438.07	0.95

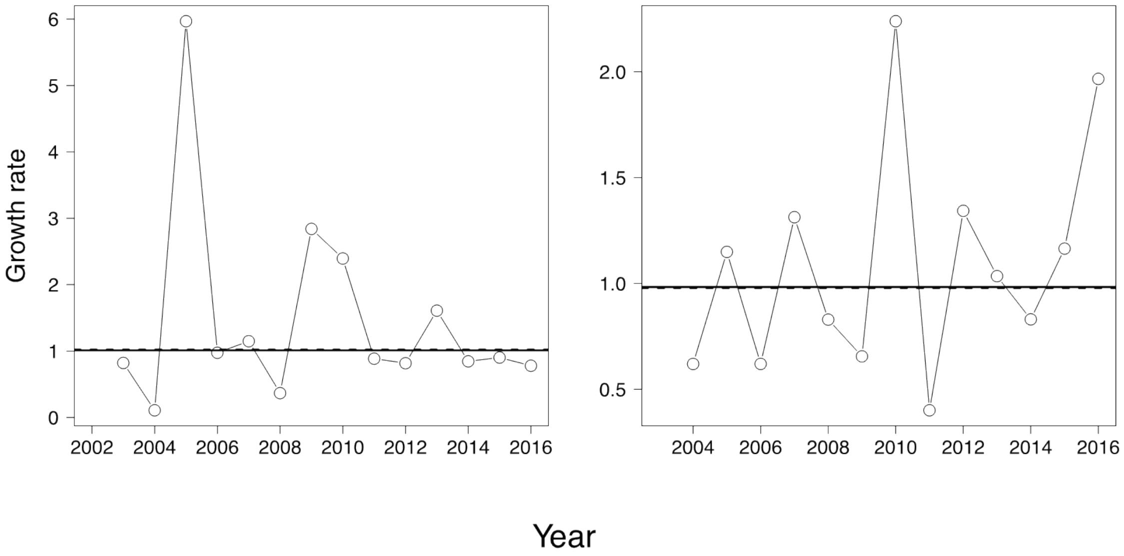

Fig. B.1 Annual population growth rates generated from model averaged estimates of population size from mark recapture models for the Olympic population (left) and Trinity Alps population (right). Dashed line indicates the mean geometric growth rate calculated from model averaged estimates of population size, and solid line indicates the mean λ_s from the 'current' matrix model scenario (1980-2006).

Appendix C. Supporting information for Chapter 4

Supplementation Programs

Two forms of population supplementation have been used in an attempt to recover *Rana pretiosa* populations in British Columbia. Head-starting programs remove a proportion of the embryos from wild populations (<10% of annual reproduction), raise the animals in captivity past metamorphosis, and return them to the wild the same year as they were collected as Young-of-Year (YOY). The head-start program has been conducted at various levels of effort since 2004. In the captive breeding program, eggs are collected from the wild and the animals are retained in captivity until the animals reach sexual maturity two or three years after collection, at which time they are induced to breed either naturally or by hormonal induction. These eggs laid in captivity are returned to the wild populations either as hatchlings (free-swimming tadpoles with fully resorbed yolk sacs) or as YOY (4-8 weeks post-metamorphosis). *R. pretiosa* grown to adulthood from wild collected eggs bred for the first time in captivity in 2009, and these captive-bred animals have been released primarily as hatchling larvae, but a small number have been raised in captivity and released as YOY similar to the age of release of the head-started animals.

Larval Survival Estimation

We placed tadpoles in 400 litre floating enclosures inoculated with natural substrate and vegetation at one of two densities; 30 tadpoles (0.075 tadpoles/litre) or 60 tadpoles (0.15 tadpoles/litre). We used a paired study design with six replicates at two sites in which each low density enclosure was coupled with a high density enclosure to control for environmental effects in different regions of the wetlands. Pairs of enclosures were placed anywhere from five meters to 150 meters apart depending on water depth at the beginning of the experiment. Enclosures had a solid bottom with flow through sides constructed of fiberglass window screening (mesh size = 18x4) and an open top. Each pair of enclosures was covered with deer fencing (mesh size = 2x2 inches) to keep avian predators out. Enclosures were designed to float as water level changed to maintain a relatively constant depth throughout the study. To stock the enclosures, we enclosed five egg masses at each site and upon hatching (Gosner stage 22 through 25), randomly assigned tadpoles from each egg mass to an enclosure. Extra tadpoles were released back into their natal wetlands. Upon metamorphosis (all appendages emerged, tail length ≤ 10mm), we removed individuals from the enclosures and measured snout-urostyle length (SUL), right shank length, and mass of each individual, gave each a mark using Visual Implant Elastomer (VIE) dye to denote the experimental treatment (high or low density), and released the metamorph into the wetland.

At the end of the study (all tadpoles metamorphosed), we destructively sampled each enclosure to get estimates of vegetation biomass, invertebrate biomass, and a measure of predator abundance. We dried the vegetation in each enclosure for 48 hours in a drying oven at 60°C and used dry biomass as a proxy for resource availability in our analysis. We enumerated and weighed the number of invertebrate predators collected during destructive sampling and calculated invertebrate predator biomass to include in our models.

Mark Recapture

In 2010 and 2011 we conducted a mark recapture study of adults during the breeding season at two breeding locations (Maria Slough and Morris Valley, District of Kent, British Columbia). We placed passive minnow traps throughout the wetland and around historic oviposition sites to catch frogs. Each trap was checked once every 24 hours so that no frogs were kept in traps for longer than 24 hours. A capture occasion was defined as a period of time in which we caught at least six individuals. The number of capture occasions varied by site and year (2010 Maria Slough n = 8, Morris Valley n=11; 2011 Maria n=18, Morris n=22) and generally began just before the first egg mass was laid and continued until after all egg masses were laid. We gave each individual caught in a trap a Passive Integrated Transponder (PIT) tag, recorded sex, mass, SUL, and right shank length and released the animal back into the wetland near the trap in which it was caught.

Cumulative additional YOY

We compared the performance of each head-start and captive breeding scenario by tracking the cumulative number of YOY added to the wild population over 10 years. Since head-start models are based on bringing a proportion of wild reproduction (fecundity) into captivity each year, the number of YOY added over 10-yr scales with the initial wild population size. In contrast, the number of YOY added to the population from captive breeding scenarios is solely a function of the number of females in captivity and not the wild population size, thus the number added is constant for each starting wild population size considered.

Data analysis and results

Larval survival

We ran generalized linear models (glm) with a binomial distribution and logit link to test for differences in tadpole survival between the two treatments (high and low density) and to explore the effects of vegetation biomass, predator biomass, and an interaction between vegetation and predator biomass on larval survival. We ran 10 *a priori* models for each site and ranked models using Quasi-Akaike Information Criterion corrected for small sample size (QAICc). We used QAICc because our data were over-dispersed.

Mean larval survival at Maria slough was 0.47 (SD± 0.28) . The model with the most support (53% of the QAICc weight) was the intercept only model (Table S2). There was one other model with moderate support (ΔQAICc <2) which was predator biomass. For Morris Valley mean larval survival was 0.12 (SD ± 0.07) and the glm model with the most support was again the intercept only model (63% of the weight). No other model had a ΔQAICc less than 2 (Table S3). We chose to use the lower of these two values (0.12) in our matrix analysis to create a hypothetically declining population of *R. pretiosa* in which to demonstrate the utility of supplementation.

Mark recapture

We used closed capture-recapture robust design models in program MARK (White and Burnham 1999) to estimate apparent survival (ϕ) at Maria Slough and Morris Valley. Closed capture-recapture models are comprised of parameters that estimate probability of detection (p_i is the probability of initial capture on occasion i, and c_i is the probability of recapture on occasion i), apparent survival (ϕ) and population size ($\hat{N}$). We estimated these parameters for males and females separately at Morris, however data limitations in 2011 precluded separate estimates of ϕ for males and females at Maria. We tested 4 hypotheses for detection probability (p): 1. p constant within year (null model, p(.)), 2. p varies by capture occasion p(t), 3. p varies by initial capture and recapture (p≠c), and 4. initial capture (p) and recapture(c), vary by time (p(t)≠c(t)). We allowed p, c, and ϕ to vary by year for both sites. We used AICc to rank models (Burnham and Anderson 2002). See Table S3 for results.

Cumulative additional YOY

For each of the four supplementation scenarios, we calculated the cumulative number of YOY added to the population after 10 years of supplementation (Fig. S1) to explore how “effort” as defined in our study compared across supplementation scenarios. In general, release at the YOY stage added more YOY to the population after 10 years than release at the larval stage. Scenario 3A added more YOY than Scenario 2A, and Scenario 2B added more YOY than Scenario 3B only when the initial population size was greater than 100 individuals. There was huge variation in number of additional YOY for scenario 2B (head-start, YOY release), which depended on the initial population size. For Scenario 2A (head-start, larvae) (Fig. S1a), the number of YOY added to the population ranged from 28 (low effort, small population size) to 5110 (high effort, large population size). For scenario 2B (head-start, YOY) these numbers increased to between 2,173 and 107,048 for low and high effort respectively (Fig. S1b). For Scenario 3A (captive breeding, larvae), at minimum effort (10 captive breeding females) 3,205 YOY were added to the population, and at maximum effort (60 captive breeding females), 19,343 YOY were added (Fig. S1c). Finally, under Scenario 3B (captive breeding, YOY) the minimum and maximum number of YOY added were 7,049 and 42,321 respectively (Fig. S1d).

Estimation of metamorph (YOY) and juvenile survival rates

We used the mean estimate of small (<53mm SUL) female survival (0.23) from Chelgren et al. 2008 as estimates of juvenile survival for our *R. pretiosa* matrix models. To date, there are no published estimates of YOY survival for *R. pretiosa*, and we were unable to estimate this rate in our field studies. As a proxy for metamorph survival, we scaled the annual estimate of small female survival (<53mm SUL) from Chelgren et al. (2008) to 36 weeks, the mean number of weeks that individuals spend as metamorphs (A. Kissel *unpublished data*).

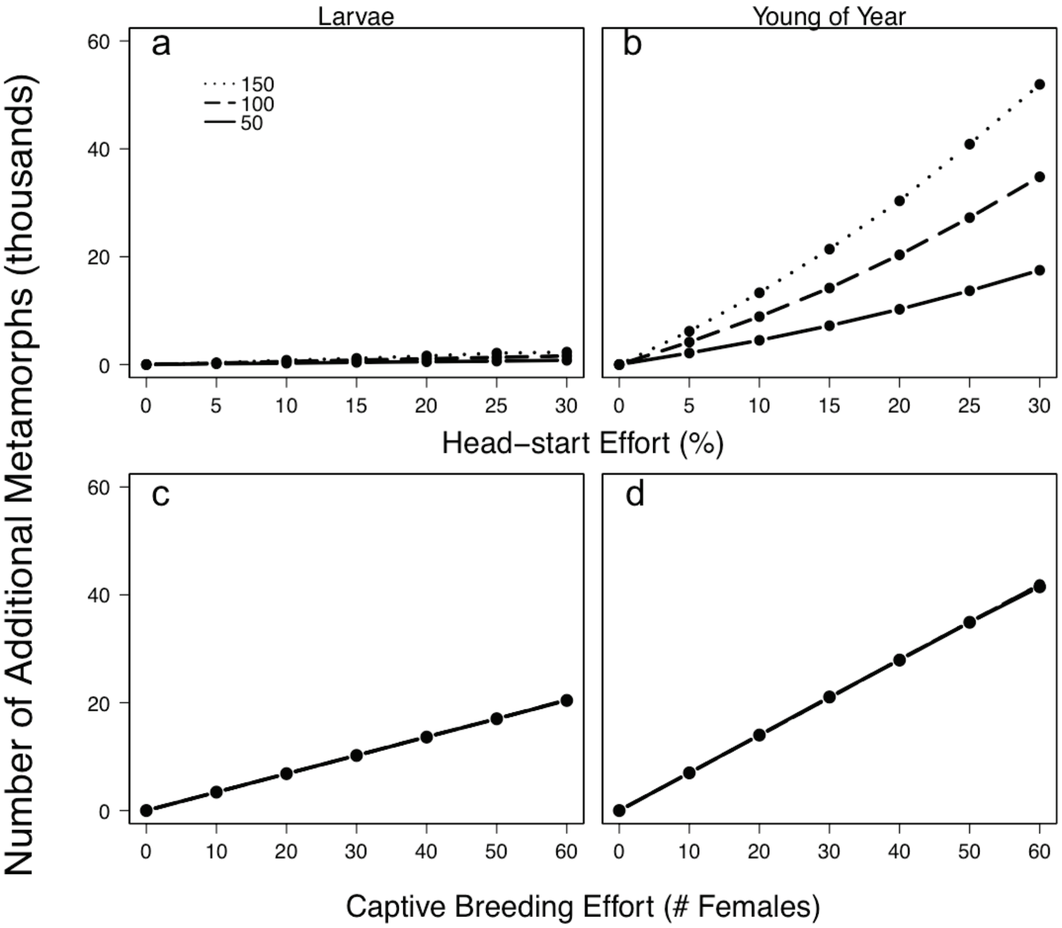

Figure D.1. Cumulative number of YOY produced by supplementation scenario over 10-years. Head-start supplementation (top panels) scales with the initial size of the wild population (dashed lines), and captive breeding supplementation (bottom panels) is fixed based on effort (single solid line). Left panels depict release as larvae, right panels release as YOY.

Table C.1. Mean estimates, variances, and sources for each vital rate used in the matrices. Notes: ϕ = survival rate, F = fecundity, $\mathrm{Pr}_{\text{breed}}$ = probability of breeding, HS = head-start, CB = captive breeding, CBW = captive breeding + wild survival as larvae spend some time in captivity before release in this scenario.

Vital Rate	Mean	Variance	N	Source
Wild				
ϕ_{embryo}	0.78	0.032	10	Literature and this study
ϕ_{larvae}	0.12	0.002	12	This study
$\phi_{\text{metamorph}}$	0.36	0.003	3	Chelgren et al. 2008
ϕ_{juv1}	0.23	0.002	3	Chelgren et al. 2008
ϕ_{juv2}	0.23	0.002	3	Chelgren et al. 2008
ϕ_{adult}	0.36	0.0096	-	This study
F_{adult}	832	71694.29	7	Literature and This study
F_{juv}	520	76117.42	12	D. Thoney unpublished data
$\mathrm{Pr}_{\text{breed}}$	0.27	-	1	D. Thoney unpublished data
Head-start				
ϕ_{embryoHS}	0.92	0.003	10	Geilens 2008 and 2009
ϕ_{larvaeHS}	0.49	0.052	13	Geilens 2008, 2009 and Hawkes 2009
Captive breeding				
ϕ_{embryoCB}	0.32	0.08	15	D. Thoney unpublished data
$\phi_{\text{larvaeCBW}}$	0.24	0.012	12	This study
F_{CB}	607	99071.43	22	D. Thoney unpublished data

Table C.2 Generalized linear models for larval survival at Maria Slough ranked according to QAICC where df= degrees of freedom, logLik = log likelihood, and w = weight

Model	df	logLik	$QAIC_C$	$\Delta QAIC_C$	w
Intercept only	1	-105.06	16.66	0	0.53
Predator biomass	2	-89.43	18.64	1.98	0.2
Density	2	-96.85	19.44	2.78	0.13
Vegetation Biomass	2	-104.95	20.31	3.66	0.09
Density + Predator biomass	3	-88.2	23.22	6.56	0.02
Predator biomass + Vegetation biomass	3	-89.18	23.33	6.67	0.02
Density + Vegetation biomass	3	-96.59	24.13	7.47	0.01
Density+Predator biomass+Vegetation biomass	4	-87.89	29.47	12.82	0
Predator biomass+Vegetation biomass+Predator biomass:Vegetation biomass	4	-88.77	29.57	12.91	0
Density+predator biomass+Vegetation biomass +Predator biomass: Vegetation biomass	5	-87.47	38.23	21.57	0

Table C.3 **Generalized linear models for larval survival at Morris Valley ranked according to $\mathbf{QAIC_C}$ where df= degrees of freedom, logLik = log likelihood, and w = weight.**

Model	df	logLik	QAICc	ΔQAICc	w
Intercept Only	1	-28.65	32.37	0	0.63
Density	2	-28.12	35.54	3.17	0.13
Vegetation biomass	2	-28.54	35.93	3.56	0.11
Predator biomass	2	-28.61	36	3.63	0.1
Denisty+Predator biomass	3	-28.08	40.21	7.85	0.01
Density+Vegetation biomass	3	-28.09	40.22	7.85	0.01
Predator biomass+Vegetation biomass	3	-28.45	40.56	8.19	0.01
Predator biomass + Vegetation biomass + Predator biomass:Vegetation biomass	4	-26.24	44.76	12.4	0
Denisty+ Predator biomass +Vegetation biomass	4	-28	46.42	14.06	0
Density+Predator biomass +Vegetation biomass + Predator biomass:Vegetation biomass	5	-25.96	53.3	20.93	0

Table C.4 Annual adult survival estimates for *R. pretiosa*. SE is the standarderror of the estimate.

Site	Survival	SE
Maria Slough	0.36	0.10
Morris Valley	0.52 (male)	0.07
Morris Valley	0.68 (female)	0.20

Table C.5. Mean, minimum, and maximum vital rate values used for simulated elasticity analysis.

Vital Rate	Mean	Minimum	Maximum
ϕ Embryonic	0.78	0.38	0.99
ϕ Larval	0.12	0.03	0.26
ϕ Metamorph	0.36	0.26	0.47
ϕ Juvenile 1	0.23	0.15	0.32
ϕ Juvenile 2	0.23	0.15	0.32
ϕ Adult	0.36	0.18	0.56
Adult fecundity	832	445	1169
Juv fecundity	520	192	1552

Appendix D. Supplemental material for Chapter 5

Matrix Models

We used a stochastic, stage-based matrix models with a 1-year time interval to model the 10-year extinction risk of our 25 supplementation scenarios (see ‘methods’ in Kissel et al. 2014 for details). The models were post-breeding, female only matrices in which we divided the life history of *R. pretiosa* into 4 stages (i.e. matrix elements, which can be made up of one or more vital rates). We used these models to calculate a stochastic population growth rate (λ_s) and a 10-year probability of extinction (Caswell 2001; Kissel et al. 2014).

Head-start and captive breeding effort

For head-start scenarios, effort is defined as the percentage of reproduction removed from the wild and raised in captivity annually, whereas captive breeding effort is quantified as the number of breeding females in captivity, assuming each female lays one egg mass. For example, a ‘minimum’ effort for head-starting (removing 5% of the reproductive effort from the wild) for a population size of 100 is equivalent to bringing five egg masses into captivity in the first year of supplementation, and this number will increase or decrease in subsequent years depending on the population growth rate. This is in contrast to captive breeding, where a ‘minimum’ effort is static (10 egg masses from 10 females) because the population size in captivity does not change over time.

Tank Cost

The costs of tanks were calculated as a step function based on the optimal rearing density (0.15 tadpoles/liter) for *R. pretiosa* in captivity (A. Gielens, unpublished data), in which an additional tank was added for every 100 additional tadpoles above the initial baseline scenario of head-starting 5% of the reproductive effort of 100 females. Thus, we scaled the number of tanks needed by the predicted λ_s for scenarios in which $\lambda_s > 1$, and calculated the maximum number of tanks needed over the course of 10 years using equation 1.

$$total\ tanks = \frac{N_{hs1} * \lambda^9}{100} \qquad \text{(D1)}$$

Where N_{hs1} is the number of tadpoles collected from the wild population for head-starting in year one of the program.

$$\begin{bmatrix} 0 & 0 & F_{13} & F_{14} \\ a_{21} & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 \\ 0 & 0 & a_{43} & a_{44} \end{bmatrix} \text{X} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}_{t+1}$$

Transition rate	***aij***	**Parameter Equation**
Wild		
Embryo to juvenile$_1$	a_{21}	$\phi_{\text{embryo}} * \phi_{\text{larvae}} * \phi_{\text{YOY}}$
Juvenile$_1$ to Juvenile$_2$	a_{32}	ϕ_{juv1}
Juvenile$_2$ to Adult	a_{43}	ϕ_{juv2}
Adult	a_{44}	ϕ_{adult}
Fecundity (Adult)	F_{14}	$F_{\text{adult}} * \text{sex ratio} * \phi_{\text{adult}}$
Fecundity (Juvenile$_2$)	F_{13}	$F_{\text{juv2}} * \text{sex ratio} * \phi_{\text{juv2}} * \text{Pr}_{\text{breed}}$
Head-start		
Release as larvae	a_{21}	$((\phi_{\text{HSembryo}} * P_{\text{HS}}) + (\phi_{\text{embryo}} * (1-P_{\text{HS}}))) * \phi_{\text{larvae}} * \phi_{\text{YOY}}$
Release as YOY	a_{21}	$(((\phi_{\text{HSembryo}} * \phi_{\text{HSlarvae}}) * P_{\text{HS}}) + ((\phi_{\text{embryo}} * \phi_{\text{larvae}}) * (1-P_{\text{HS}}))) * \phi_{\text{YOY}}$
Captive breeding		
Release as larvae	a_{21}	$((\phi_{\text{embryo}} * \phi_{\text{larvae}}) + (((F_{\text{CB stage1}} * n_{4\text{CB}} * \text{Pr}_{\text{breed}} * \text{sex ratio}) - \text{HB}) * \phi_{\text{CBembryo}} * \phi_{\text{larvae}}) / n_{\text{w1}}) * \phi_{\text{YOY}}$
Release as YOY	a_{21}	$((\phi_{\text{embryo}} * \phi_{\text{larvae}}) + (((F_{\text{CB stage1}} * n_{4\text{CB}} * \text{Pr}_{\text{breed}} * \text{sex ratio}) - \text{HB}) * \phi_{\text{CBembryo}} * \phi_{\text{CBarvae}}) / n_{\text{w1}}) * \phi_{\text{YOY}}$

Figure D.1. Matrix model structure and vital rate definitions, where n_i is the number of individuals in stage *i* at time t, F_{ij} =per capita fecundity, a_{ij} is the transition rate between stages and can be made up of component vital rates shown in the *Parameter Equation* column. ϕ =survival, YOY = young of the year, Pr_{breed} is the probability of a second year juvenile breeding, HS=head-start, P_{HS} is the proportion of the population removed from the wild for head-starting, CB=captive breeding, HB=the number of individuals held back to maintain the captive population, W= wild population.

Table D.1. **Cost breakdown for head-start and release as YOY scenario. Costs are based on the 2013 *R. pretiosa* head-start program at the Greater Vancouver Zoo and include a post-release monitoring program. Costs are based on housing 100 larvae per tank (following page).**

Husbandry/post-ease monitoring	Cost Type	Category	Description	Units	Units/year	Cost/unit	Total Cost
Husbandry	Capital	set-up	filtration system	1	1	$1,000.00	$1,000.00
Husbandry	Capital	set-up	shed	1	1	$3,500.00	$3,500.00
Husbandry	Capital	set-up	zoo space	12	1	$1,500.00	$18,000.00
Husbandry	Capital	set-up	lighting	2	1	$30.00	$60.00
Husbandry	Capital	set-up	nets	40	1	$5.00	$200.00
Husbandry	Capital	set-up	buckets	40	1	$7.00	$280.00
Husbandry	Capital	set-up	tanks	40	1	$250.00	$10,000.00
Husbandry	Recurring	food	lettuce	2	1	$17.00	$34.00
Husbandry	Recurring	food	bloodworms	187	1	$2.00	$374.00
Husbandry	Recurring	food	crickets	112	1	$15.00	$1,680.00
Husbandry	Recurring	vet	Animal Health Care Submissions	1	1	$500.00	$500.00
Husbandry	Recurring	maintenance	water changes	20	24	$0.69	$331.20
Husbandry	Recurring	maintenance	disinfectant	1	1	$10.00	$10.00
Husbandry	Recurring	maintenance	water quality testing	1	24	$62.50	$1,500.00
Husbandry	Recurring	maintenance	disease testing	1	40	$25.00	$1,000.00
Husbandry	Recurring	maintenance	energy costs	1	1	$1,250.00	$1,250.00
Husbandry	Recurring	maintenance	plugs for tanks	1	1	$20.00	$20.00
Husbandry	Recurring	maintenance	lids for tanks	1	2	$100.00	$200.00
Husbandry	Recurring	maintenance	buckets	2	1	$7.00	$14.00
Husbandry	Recurring	maintenance	nets	10	1	$5.00	$50.00
Husbandry	Recurring	labour	project planning	20	12	$35.00	$8,400.00
Husbandry	Recurring	labour	lead husbandry technician	960	1	$26.04	$24,998.40
Husbandry	Recurring	labour	field tech-egg collection	40	2	$8.75	$700.00

Husbandry	Recurring	labour	mileage-egg collection/meta release	1	7	$100.00	$700.00
Husbandry	Recurring	equipment	waders, buckets, etc. -egg collection	1	1	$100.00	$100.00
Husbandry	Recurring	equipment	VIE dye/needles	1	1	$400.00	$400.00
Husbandry	Recurring	administration	13% of tech wages	1	1	$3,340.79	$3,340.79
Monitoring	Capital	Equipment	minnow traps	120	1	$11.19	$1,342.80
Monitoring	Capital	Equipment	GPS	1	1	$249.00	$249.00
Monitoring	Capital	Equipment	PIT tag reader	1	1	$585.00	$585.00
Monitoring	Capital	Equipment	Sein nets	12	1	$21.00	$252.00
Monitoring	Recurring	Labour	2 field techs at 18.00 an hour for 4 weeks	320	2	$18.00	$11,520.00
Monitoring	Recurring	Labour	employee benefits	1	2	$921.60	$1,843.20
Monitoring	Recurring	mileage	mileage to release sites	30	20	$0.50	$300.00
Monitoring	Recurring	accommodation	Field tech housing	1	1	$500.00	$500.00
Monitoring	Recurring	per diem food	2 field techs, 30 a day for 20 days	20	2	$30.00	$1,200.00
Monitoring	Recurring	Administration	13% of project cost	1	1	$1,997.22	$1,997.22
Monitoring	Recurring	Equipment	PIT tags	250	1	$4.00	$1,000.00
Monitoring	Recurring	Equipment	datasheets	1	1	$100.00	$100.00
Monitoring	Recurring	Equipment	waders	4	1	$120.00	$480.00

Table D.2. Cost breakdown for head-start and release as tadpole scenario including a post-release monitoring program. Costs are based on 2013 estimates from Greater Vancouver Zoo head-start program, and reflect head-starting 5% of the wild population in that year (following page.

Husbandry/post-release monitoring	Cost Type	Category	Description	Units	Units/year	Cost/unit	Total Cost
Husbandry	Capital	set-up	filtration system	1	1	$1,000.00	$1,000.00
Husbandry	Capital	set-up	shed	1	1	$3,500.00	$3,500.00
Husbandry	Capital	set-up	zoo space	12	1	$1,500.00	$18,000.00
Husbandry	Capital	set-up	lighting	2	1	$30.00	$60.00
Husbandry	Capital	set-up	nets	40	1	$5.00	$200.00
Husbandry	Capital	set-up	buckets	40	1	$7.00	$280.00
Husbandry	Capital	set-up	tanks	14	1	$250.00	$3,500.00
Husbandry	Capital	set-up	2 pack ziploc medium rectangle containers	1	21	$3.49	$73.29
Husbandry	Recurring	vet	Animal Health Care Submissions	1	1	$500.00	$500.00
Husbandry	Recurring	maintenance	disinfectant	1	1	$10.00	$10.00
Husbandry	Recurring	maintenance	water quality testing	1	24	$62.50	$1,500.00
Husbandry	Recurring	maintenance	buckets	2	1	$7.00	$14.00
Husbandry	Recurring	maintenance	nets	10	1	$5.00	$50.00
Husbandry	Recurring	labour	project planning	5	3	$35.00	$525.00
Husbandry	Recurring	labour	lead husbandry technician	960	0.25	$26.04	$6,249.60
Husbandry	Recurring	labour	field tech-egg collection	40	2	$8.75	$700.00
Husbandry	Recurring	labour	mileage-egg collection/meta release	1	7	$100.00	$700.00
Husbandry	Recurring	equipment	waders, buckets, etc. -egg collection	1	1	$100.00	$100.00
Husbandry	Recurring	administration	13% of tech wages	1	1	$880.70	$880.70
Monitoring	Capital	Equipment	minnow traps	120	1	$11.19	$1,342.80
Monitoring	Capital	Equipment	GPS	1	1	$249.00	$249.00
Monitoring	Capital	Equipment	PIT tag reader	1	1	$585.00	$585.00
Monitoring	Capital	Equipment	Sein nets	12	1	$21.00	$252.00

Monitoring	Recurring	Labour	2 field techs at 18.00 an hour for 4 weeks	320	2	$18.00	$11,520.00
Monitoring	Recurring	Labour	employee benefits	1	2	$921.60	$1,843.20
Monitoring	Recurring	mileage	mileage to release sites	30	20	$0.50	$300.00
Monitoring	Recurring	accommodation	Field tech housing	1	1	$500.00	$500.00
Monitoring	Recurring	per diem food	2 field techs, 30 a day for 20 days	20	2	$30.00	$1,200.00
Monitoring	Recurring	Administration	13% of project cost	1	1	$1,997.22	$1,997.22
Monitoring	Recurring	Equipment	PIT tags	250	1	$4.00	$1,000.00
Monitoring	Recurring	Equipment	datasheets	1	1	$100.00	$100.00
Monitoring	Recurring	Equipment	waders	4	1	$120.00	$480.00

Table S3. Cost breakdown for captive breeding and release as tadpole scenario. Costs are based on the Vancouver Aquarium's 2013 captive breeding program, in which they housed 23 females and 39 males and include a post-release monitoring program.

Husbandry/ post-release monitoring	Cost Type	Category	Description	Units	Units/year	Cost/unit	Total Cost
Husbandry	Capital	set-up	greenhouse 8 X 12, curved, twin wall greenhouse, Pacific Model	2	1	$5,023.00	$10,046.00
Husbandry	Capital	set-up	PVC sink 1 per greenhouse	2	1	$48.00	$96.00
Husbandry	Capital	set-up	plumbing (supply, sewer, heat tape)	2	1	$80.00	$160.00
Husbandry	Capital	set-up	electrical (supply, outlets and hook-ups)	2	1	$2,500.00	$5,000.00
Husbandry	Capital	set-up	light fixtures (3/GH)	6	1	$80.00	$480.00
Husbandry	Capital	set-up	light fluorescent tubes (2/fixture)	12	1	$5.00	$60.00
Husbandry	Capital	set-up	shade paint	2	1	$55.00	$110.00
Husbandry	Capital	set-up	pest proofing screening fans and vents	2	1	$110.00	$220.00
Husbandry	Capital	set-up	Thermometer (1/GH)	2	1	$54.00	$108.00
Husbandry	Capital	set-up	UV bulb fixtures 6/GH	12	1	$32.00	$384.00
Husbandry	Capital	set-up	Shelving units I/GH	2	1	$60.00	$120.00
Husbandry	Capital	set-up	tanks, 40 gallon, 8/GH	16	1	$114.00	$1,824.00
Husbandry	Capital	set-up	tanks, 25 gallon, 20/GH	40	1	$63.00	$2,520.00
Husbandry	Capital	set-up	tanks, small pall pens 4/GH	8	1	$3.50	$28.00

Husbandry	Capital	set-up	tanks, large pal pens 4 per GH	8	1	$8.50	$68.00
Husbandry	Capital	set-up	tanks, wide pal pens 1 pack of 6 per GH	2	1	$12.00	$24.00
Husbandry	Capital	set-up	aquarium stands, 6/GH	12	1	$136.00	$1,632.00
Husbandry	Capital	set-up	aquarium lids, 28/GH	56	1	$60.00	$3,360.00
Husbandry	Capital	set-up	Cleaning system tubing(1/greenhouse)	2	1	$60.00	$120.00
Husbandry	Capital	set-up	Fake plants(1/greenhouse)	2	1	$60.00	$120.00
Husbandry	Capital	Life support systems	25-gallon aquarium (sump), glass (6/GH)	12	1	$63.00	$756.00
Husbandry	Capital	Life support systems	Magnetic Drive 700GPH Pump (6/GH)	12	1	$89.75	$1,077.00
Husbandry	Capital	Life support systems	bio-filter with media (6 x ~200/GH)	12	1	$14.00	$168.00
Husbandry	Capital	Life support systems	PVC piping/fittings(6/greenhouse)	12	1	$65.00	$780.00
Husbandry	Capital	Life support systems	Water Chiller (1/10th HP) (6/GH)	12	1	$409.00	$4,908.00
Husbandry	Capital	Life support systems	Aquarium Thermometer (11201) (6/GH)	12	1	$1.10	$13.20
Husbandry	Capital	Life support systems	800W Titanium Heater (6/GH)	12	1	$46.55	$558.60
Husbandry	Capital	Life support systems	Heater Controller (6/GH)	12	1	$133.11	$1,597.32
Husbandry	Recurring	equipment	filter media - floss	1	1	$40.00	$40.00
Husbandry	Recurring	food	algae paste	1	1	$60.00	$60.00
Husbandry	Recurring	food	crickets	1	53	$32.40	$1,717.20

Husbandry	Recurring	food	flakes	1	1	$40.00	$40.00
Husbandry	Recurring	food	earthworms	1	12	$60.00	$720.00
Husbandry	Recurring	maintenance	water- based on ~600 gallons/wk 150-200% water change	104	1	$2.47	$257.30
Husbandry	Recurring	maintenance	electrical power first 1350 kwh	1350	1	$0.07	$91.80
Husbandry	Recurring	maintenance	electrical power-remaining	33650	1	$0.10	$3,428.94
Husbandry	Recurring	equipment	Virkon	2	1	$60.00	$120.00
Husbandry	Recurring	equipment	gloves	1	1	$376.32	$376.32
Husbandry	Recurring	food	Bloodworms	1	1	$90.00	$90.00
Husbandry	Recurring	food	Repashy Calcium Plus supplement	1	1	$60.00	$60.00
Husbandry	Recurring	equipment	Hibitane	1	1	$60.00	$60.00
Husbandry	Recurring	equipment	Doodlebug Pads	1	1	$30.00	$30.00
Husbandry	Recurring	maintenance	Water Quality Reagents/Sticks	1	1	$3,200.00	$3,200.00
Husbandry	Recurring	equipment	Paper Towel	1	1	$120.00	$120.00
Husbandry	Recurring	equipment	Light Bulbs	1	1	$576.00	$576.00
Husbandry	Recurring	vet	Veterinary Supplies	1	1	$3,000.00	$3,000.00
Husbandry	Recurring	equipment	Aquarium Nets	1	1	$12.00	$12.00
Husbandry	Recurring	equipment	Garbage bags	1	1	$100.00	$100.00

Husbandry	Recurring	labour	Husbandry staff	1	1	$25,350.00	$25,350.00
Husbandry	Recurring	labour	Curator	1	1	$2,400.00	$2,400.00
Husbandry	Recurring	labour	Director	1	1	$1,300.00	$1,300.00
Husbandry	Recurring	labour	Engineering	1	1	$1,500.00	$1,500.00
Husbandry	Recurring	labour	Carpentry	1	1	$570.00	$570.00
Husbandry	Recurring	labour	water quality	1	1	$5,600.00	$5,600.00
Husbandry	Recurring	labour	Veterinary	1	1	$2,000.00	$2,000.00
Husbandry	Recurring	vet	Animal Health Cetnre submissions	1	1	$1,607.00	$1,607.00
Husbandry	Recurring	vet	courier costs for AHC submissions	1	1	$2,755.00	$2,755.00
Husbandry	Recurring	vet	surgery materials	1	1	$90.00	$90.00
Husbandry	Recurring	vet	treatment chemicals	1	1	$300.00	$300.00
Monitoring	Recurring	Release	Vehicle and gas to and from sites	1	1	$100.00	$100.00
Monitoring	Capital	Equipment	minnow traps	120	1	$11.19	$1,342.80
Monitoring	Capital	Equipment	GPS	1	1	$249.00	$249.00
Monitoring	Capital	Equipment	PIT tag reader	1	1	$585.00	$585.00
Monitoring	Capital	Equipment	Sein nets	12	1	$21.00	$252.00
Monitoring	recurring	Labour	2 field techs at 18.00 an hour for 4 weeks	320	2	$18.00	$11,520.00
Monitoring	recurring	Labour	employee benefits	1	2	$921.60	$1,843.20

Monitoring	recurring	mileage	mileage to release sites	30	20	$0.50	$300.00
Monitoring	recurring	accommodation	Field tech housing	1	1	$500.00	$500.00
Monitoring	recurring	per diem food	2 field techs, 30 a day for 20 days	20	2	$30.00	$1,200.00
Monitoring	recurring	Administration	13% of project cost	1	1	$1,997.22	$1,997.22
Monitoring	recurring	Equipment	PIT tags	250	1	$4.00	$1,000.00
Monitoring	recurring	Equipment	datasheets	1	1	$100.00	$100.00
Monitoring	recurring	Equipment	waders	4	1	$120.00	$480.00