

# **The roles of ectotherm physiology and habitat use with changing water availability**

**by  
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B.Sc., Simon Fraser University, 2018

Thesis Submitted in Partial Fulfillment of the  
Requirements for the Degree of  
Master of Science

in the  
Department of Biological Sciences  
Faculty of Science

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Spring 2021

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## **Abstract**

Environmental regimes are shifting with accelerating climate change, putting at risk species whose ecology has been shaped by pre-industrial climates. Both species physiology and habitat associations are central to many predictions of future climate risk. Here I focus on the role of water, both in terms of ectotherm physiology through water loss, and as habitat essential for many amphibian life histories. In Chapter 1, I explore whether amphibian and squamate thermal safety margins are mediated by species' propensity for water loss. In Chapter 2, I combine estimates of species' habitat use and the hydrologic suitability of wetland habitats to predict how drying from climate change may drive future habitat loss in alpine regions of the US Pacific Northwest. This work indicates that water loss has been critical to shaping species' physiology, and that water availability as critical habitat is central to species' persistence across alpine landscapes in the future.

**Keywords:** climate change; water loss; ecophysiology; amphibian; occupancy; hydroperiod

## Acknowledgements

Thank you to everyone who has supported me in getting to this milestone. First, thank you to my supervisor Wendy Palen, for believing in me and investing so much time into my development as a scientist since ever since my undergrad. I hope you enjoyed working with me as much as I did with you. Thank you to my mentor and friend Rylee Murray, who has mentored me through my academic journey and who is the biggest reason I am the scientist I am today. Thank you to my committee members Rebecca McCaffery and Leithen M'Gonigle for all their feedback, expertise and guidance over this abnormal past year.

A special thank you to all the collaborators on this thesis. Thank you to Dan Greenberg for your help with Chapter 1 and helping me dive into species physiology. A big thank you to my former field assistant Alessandra Gentile for her hard work in the summer of 2019. Thank you to Maureen Ryan and Se-Yeun Lee for the foundational work that led to my second chapter, as well as Noll Steinweg and Katie Goodwin for their work early on in this project.

And finally thank you to my family and fields. A special thanks to my partner Braya Quilty, who has lifted me up ever since I started research back in 2016. You've been my biggest supporter and I can only hope I'm able to provide you with that same support as you find your path in your career. Thank you to my family their love and support, and fostering my love of nature and the outdoors ever since I was young. And lastly thank you to both my friends back home and the friends I've made along the way in Earth to Oceans and SFU. You made my masters the unforgettable experience it was so thank you for everything.

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# Chapter 1. The role of dehydration risk in shaping thermal traits of ectotherms<sup>1</sup>

## 1.1. Abstract

Temperature can directly shape demographic fitness in ectotherms, suggesting that there should be strong selection on behaviour to closely track thermal landscapes and regulate body temperatures. However, evaporative water loss also increases exponentially as temperatures rise, and dehydration can independently shape fitness and restrict activity in ectotherms beyond temperature alone. We hypothesized that ectotherm species more vulnerable to dehydration should have larger thermal safety margins—the temperature difference between a species' preferred body temperatures and their physiological temperature limit—to compensate for the joint risk posed by both temperature and water loss. We compiled data from the literature on amphibian and reptile species' thermal safety margin and vulnerability to water loss, quantified as skin resistance to water loss. Consistent with our hypothesis, we found that reptiles on average had 100 times higher skin resistance and 30% smaller thermal safety margins compared to amphibians. The same pattern of higher thermal safety margin with lower skin resistance was also shown within the amphibians, where a 50% decrease in amphibian skin resistance had a 36% higher thermal safety margin. As further evidence of this trade-off between thermal and hydration physiology, we show that species' microhabitat preferences align closely with this pattern: arboreal amphibians have both higher skin resistance and lower thermal safety margins than their more aquatic counterparts. Collectively, these lines of evidence suggest that ectotherm ecophysiological traits appear to coevolve in ways that are critical to species' ecology and may ultimately shape their responses to future global change.

<sup>1</sup> A version of this chapter is in preparation for publication with W.J. Palen, and D. A. Greenberg



## 1.2. Introduction

Prevailing environmental conditions dictate species' microhabitat selection, and are mediated by species' physiological traits and adaptive behaviors. As climate change continues, species are more likely to experience physiological extremes, especially because of shifts in ambient temperature (Gerick et al. 2014, Pacifici et al. 2015, Sinclair et al. 2016, Lertzman-Lepofsky et al. 2020), but also in precipitation, snow cover, and wind (Blennow et al. 2010, Trenberth 2011, Najafi et al. 2017). Many physiological processes are temperature-dependent (Sinclair et al. 2016), and temperatures beyond thermal limits can result in reduced time for foraging, with subsequent costs to growth and reproduction that can reduce fitness and elevate extinction risk (Huey and Berrigan 2001, Sinervo et al. 2010). As a result, temperature is a primary driver of environmental limitation for ectotherms (Sinervo et al. 2010, Gerick et al. 2014). Behavioural thermoregulation, the maintenance of a consistent body temperature through behaviour, can buffer the effects of environmental change (Huey et al. 2012) and allow populations to persist in shifting environments (Adolph 1990, Kearney et al. 2009, Kirchhof et al. 2017), but there is often a limit to this behavioural capacity (Lillywhite et al. 1973, Autumn and De Nardo 1995, Sinervo et al. 2010).

Despite the importance of temperature to ectotherm physiology, ectotherms rarely prefer body temperatures ( $T_b$ ) that would theoretically maximize fitness, i.e. their thermal optimum ( $T_{opt}$ ), and instead often maintain body temperatures well below  $T_{opt}$  or critical thermal maximum ( $CT_{max}$ ) (Martin and Huey 2008). This difference, termed the thermal safety margin ( $TSM$ ), has been defined numerous times (Deutsch et al. 2008, Sunday et al. 2014, Comte and Olden 2017, Pinsky et al. 2019). It can be quantified as the difference between a species' experienced environmental temperature, for example experimentally determined thermal preferences ( $T_{pref}$ ), a measure of selected environmental temperature, and its upper thermal limits, critical thermal maximum ( $CT_{max}$ ) or thermal optimum ( $T_{opt}$ ). Thermal preference is one of many metrics used for environmental temperature, and is measured as the average ambient temperature selected by an organism when exposed to a thermal gradient (Light et al. 1966). Thermal preference is expected to better capture individual thermoregulatory behaviour compared to somewhat coarse estimates of environmental temperature derived from climate data and biophysical models (*sensu* Sunday et al. 2014, Pinsky et al. 2019). This

seemingly paradoxical difference between an individual's preferred temperature and these upper thermal constraints has been attributed to the fact that temperatures are temporally dynamic, that ectotherms are imperfect thermoregulators, and that the costs of exceeding  $T_{opt}$  and approaching  $CT_{max}$  are severe (Huey and Kingsolver 1989). This pattern of existing below  $T_{opt}$  suggests that ectotherms behaviourally thermoregulate at temperatures that balance the trade-off between maximizing performance and minimizing the risk of exceeding  $T_{opt}$  (Martin and Huey 2008). However, environments are also multi-dimensional, and factors in addition to temperature likely influence the behavioural choices organisms make regarding temperature itself.

Water is another major driver of environmental limitation for ectotherms (McCain and Colwell 2011, Sannolo and Carretero 2019), and an organism's hydration state is an important component of fitness alongside temperature (Churchill and Storey 1995, Anderson and Andrade 2017). Dehydration is detrimental to an individual's physiological functions, causing decreased oxygen uptake, limiting the production of ATP, and increasing blood viscosity (Hillman 1980, Gatten 1987, Anderson and Andrade 2017). As a result, in addition to temperature, dehydration negatively influences multiple aspects of individual function and performance (Prest and Pough 1989, Anderson and Andrade 2017). Temperature and water loss are intricately linked: as air temperatures rise the vapour pressure deficit increases exponentially (Anderson 1936, Tracy 1975), which ultimately drives rates of organismal evaporative water loss (Buttemer 1990, Rogowitz et al. 1999). In turn, evaporative water loss actually permits physiological thermoregulation by lowering the organism's body temperature through evaporative cooling (Lillywhite 1970). This implies that water loss and thermal state are correlated axes that must be concurrently managed by individuals and are likely to jointly shape individual behaviour.

Sensitivity to water loss can be quantified using a variety of metrics. Evaporative water loss rates depend directly on the difference in vapor density of an organism and the surrounding air, and this in turn depends on relative humidity and air temperature and an individual's exposed surface area (Tracy 1976, Spotila and Berman 1976, Foley and Spotila 1978, Rubalcaba et al. 2019). Species are able to mediate evaporative water loss through adaptations to increase resistance in the boundary layer between the air and the skin (Spotila and Berman 1976, Young et al. 2005), and this resistance provided by the skin is termed skin resistance ( $R_c$ ). Total evaporative water loss ( $TEWL$ ) consists of both cutaneous water loss ( $CWL$ ), respiratory water loss, and other minor avenues

(e.g. eyes) (Mautz 1982a, Tieleman and Williams 2002), and the contribution of *CWL* to *TEWL* is expected to decline at high levels of  $R_c$ . The composition of *TEWL* from these various sources depends on species' specific adaptations such as  $R_c$  (Mautz 1980, 1982a). However,  $R_c$  may not be a static trait, as individuals'  $R_c$  has shown plasticity in response to environmental cues and can vary intraspecifically along environmental gradients (Riddell et al. 2018, 2019).

Reptiles and amphibians are two ectotherm clades that generally have divergent sensitivities to dehydration. Reptiles skin is adapted to be impermeable to water loss thanks to scaled skin and multiple layers of  $\alpha$  and  $\beta$  keratin (Lillywhite 2006). Amphibian skin is unscaled and more permeable, containing only limited layers of  $\alpha$  keratin (Lillywhite 2006), but this allows amphibian skin to be relatively permeable to water loss to permit both evaporative cooling (Brattstrom 1979) and cutaneous respiration (Feder and Burggren 1985). This natural contrast between the two clades provides an ideal framework to explore the tradeoffs between thermoregulation and water loss sensitivity. Here, we test the hypothesis that sensitivity to water loss influences ectotherm species' thermoregulatory behaviour, with species more sensitive to water loss, choosing cooler temperatures relative to their thermal maximum compared to more dehydration-resistant species. We test this hypothesis through a compilation of data from studies on amphibian and reptile species' thermal traits and dehydration risk and predicted that the magnitude of thermal safety margin (*TSM*), increases with increased sensitivity to water loss. There is substantial evidence suggesting that species' ecology can shape both  $R_c$  and thermoregulatory traits in ectotherms (Tracy and Christian 2005, Young et al. 2005, Tracy et al. 2010, Li et al. 2017). Among anurans, arboreal species have been found to have the highest  $R_c$ , and conversely, aquatic species generally have very low  $R_c$  values (Young et al. 2005). Therefore, our hypothesis also predicts that *TSM* will be higher in more evaporative microhabitats (drier), and thus we predict that when evaluated by microhabitat, species in wetter microhabitats will have larger *TSMs* and lower dehydration risk compared to those in dryer habitats where higher resistance to water loss should reduce the influence of water loss on thermal preference.

## 1.3. Methods

### 1.3.1. Literature Search

We searched Web of Science (1900 - onwards) and Google Scholar (~1900 – onwards) for existing data on reptile and amphibian thermal and hydration traits (search terms in Table 1.1) to test our hypothesis in a comparative context. For our thermal traits database, we searched the literature for critical thermal maximum ( $CT_{max}$ ), thermal optimum ( $T_{opt}$ ), and thermal preference ( $T_{pref}$ ). While for our water sensitivity database, we collected data on total evaporative water loss TEWL, cutaneous water loss (CWL), and skin resistance ( $R_c$ ).

**Table 1.1 Search terms used to collect data from the literature. Some literature was found via citations and not search terms.**

Topic	Search Terms
Thermal traits	reptile optimal temperature
	reptile temperature
	temperature preference snakes
	temperature preference lizards
	reptile thermal optimum
	reptile thermal breadth
	reptile temperature data
	reptile ctmx
	reptile thermal data
	amphibian optimal temperature
	amphibian optimal temperature
	amphibian temperature
	temperature preference newts
	temperature preference frogs
	amphibian thermal optimum
	amphibian thermal breadth
	amphibian temperature data
	amphibian ctmx
	amphibian thermal data
	Water loss sensitivity traits
skin resistance lizard	
evaporative water loss reptile	
evaporative water loss lizard	
skin resistance lizard	
ewl reptile water	

cutaneous evaporative water loss reptile
amphibian evaporative water loss
skin resistance amphibian
evaporative water loss amphibian
skin resistance amphibian
ewl amphibian water
cutaneous evaporative water loss amphibian
ewl anurans water
cutaneous evaporative water loss frogs
skin resistance frog
evaporative water loss ectotherm
cutaneous evaporative water loss

### 1.3.2. Microhabitat classification

To evaluate whether there are consistent differences in physiological traits by microhabitat, we classified each species with data for either  $TSM$  or  $R_c$  into five broad microhabitat categories (aquatic, semi-aquatic, burrowing, terrestrial, arboreal) using ecological descriptions available from the International Union for Conservation of Nature RedList species assessments (IUCN 2020) and AmphibiaWeb (n.d.). We classified the primary microhabitat for each species based on adult autecology (for criteria see Table 1.2).

**Table 1.2 Descriptions of post-metamorphic microhabitat classification for Squamata and Amphibia using the IUCN Redlist assessment and AmphibiaWeb. Microhabitats are listed from high evaporation to low evaporation habitats.**

Microhabitat	Description
<b>Arboreal</b>	Species thought to spend most of the time off the ground on vegetation (trees, reeds, tall grasses).
<b>Terrestrial</b>	Species that occupy leaf litter or in low-lying vegetation.
<b>Burrowing</b>	Species thought to spend most of their life under rock, downed wood, or underground either in other animals' burrows or its own burrow.
<b>Semi-aquatic</b>	A species thought to be highly associated with an aquatic environment, including the riparian, but not spending most of the time submerged in the water itself.
<b>Aquatic</b>	A species that spends the majority of its post-metamorphosis life in lotic or lentic habitats.

### 1.3.3. Analysis

To explore how thermal safety margin varies with increasing resistance to water loss (higher  $R_c$ ) in Squamata and Amphibia, we fit two ordinary least squares models to both  $TSM$  and  $R_c$  in relation to taxonomic group. Our literature search produced highly unbalanced sample sizes between taxonomic groups for both  $TSM$  and  $R_c$ . To account for the effect of this sample size bias, we took random subsamples from the larger dataset for each trait to match the sample size of the smaller ( $TSM$ : Amphibians,  $n = 16$ ,  $R_c$ : Squamates,  $n = 37$ ) and calculated the difference between the mean of both groups, referred to as the effect size, and repeated the analysis 1000 times, generating a distribution of effect sizes for each trait.

As skin resistance increases, water loss decreases exponentially (Tracy 1976), which may suggest that increasing levels of skin resistance should have diminishing effects on TSM if it influences thermoregulatory behaviour. To model this potential non-linear dependency, we fit an exponential decay curve  $TSM \sim \alpha e^{\beta R_c}$ , where  $\alpha$  and  $\beta$  represent the intercept and the rate of change, respectively,  $R_c$  is skin resistance, and TSM is our thermal safety margin. We used this model to describe the relationship between species' TSM and skin resistance ( $R_c$ ), using the `nls` function in the `nlme` package (Pinheiro et al. 2019). We included interactions between  $R_c$  and taxonomic group, to allow the slope and intercept to vary between Squamates and Amphibians. To account for large differences observed between amphibian and squamate  $R_c$  values, we modelled  $R_c$  on the log scale.

To determine whether  $R_c$  and TSM are inversely linked to microhabitat, we took all species that had either TSM or  $R_c$  and separately modeled each trait in relation to species' microhabitat preferences separately for amphibians and squamates. In order to compare the effects of microhabitat on  $R_c$  and TSM, we centered and standardized the response variables from both sets of models to compute model coefficients in units of standard deviation from the mean. All analysis was done in R v. 4.0 [53].

## 1.4. Results

### 1.4.1. Literature search

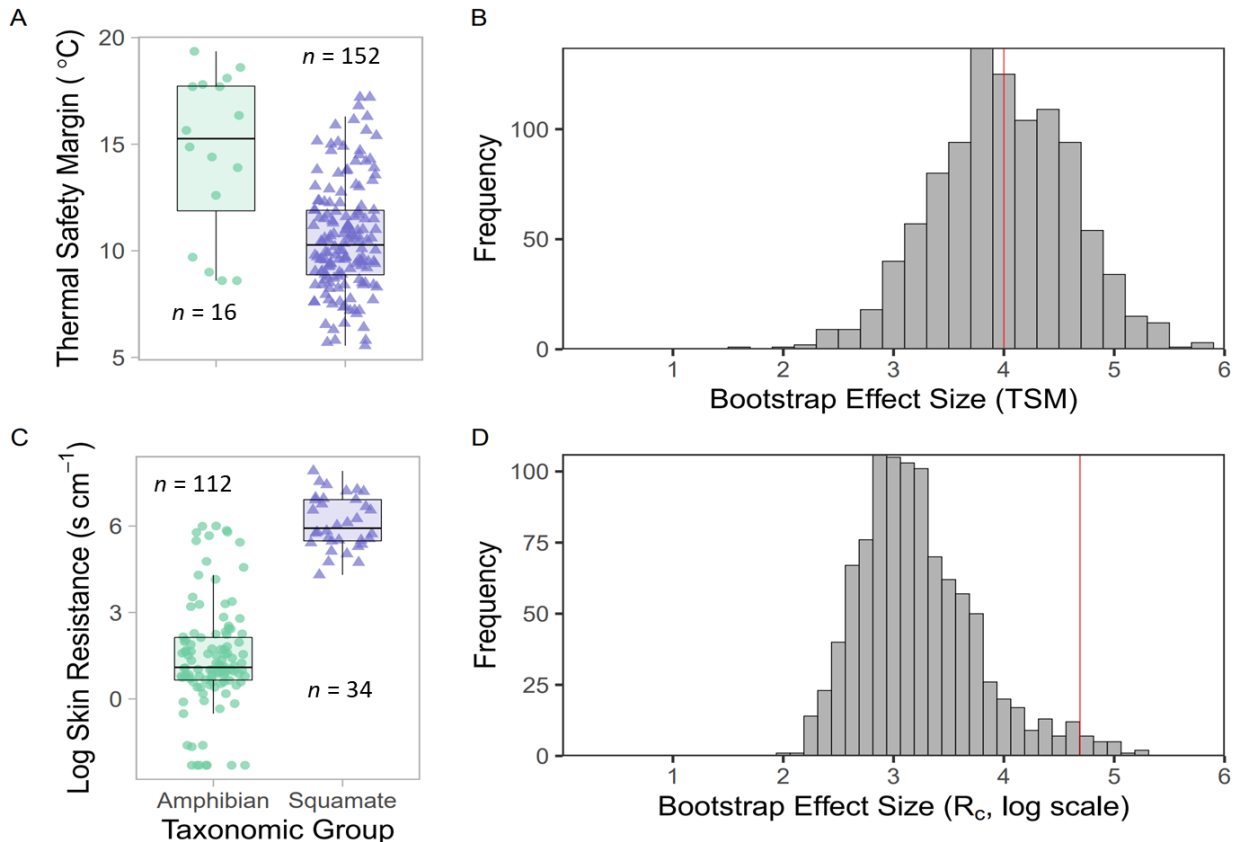
Our literature search produced data for species'  $T_{opt}$  ( $n = 103$  species),  $CT_{max}$  ( $n = 438$  species) and  $T_{pref}$  ( $n = 363$  species). We collated data for  $TEWL$  ( $n = 209$ ),  $CWL$  ( $n = 51$ ), and  $R_c$  ( $n = 392$ ), any of which could have represented water loss sensitivity. In our final database we found that  $T_{pref}$  and  $CT_{max}$ , along with  $R_c$ , had the greatest species coverage for comparative analysis. We remove studies with weak statistical inference (i.e. poor thermal performance curve fit or small sample size), and when species had the same trait estimated multiple times (sex, location, study), we calculated the arithmetic mean values of all estimates ( $CT_{max}$   $n = 7$  species,  $T_{pref}$   $n = 32$  species,  $R_c$   $n = 87$  species). Certain amphibian species form cocoons to reduce evaporative water loss (Shoemaker and Nagy 1977), and we removed these measurements from our analysis.

Our literature search revealed a disparity in data availability along taxonomic lines, with thermoregulatory traits having been studied more for reptiles than amphibians, and the opposite pattern for water loss traits. Specifically, our search resulted in thermal trait data ( $TSM = CT_{max} - T_{pref}$ ) for 16 amphibian and 165 reptile species, skin resistance data ( $R_c$ ) for 118 amphibian and 42 reptile species, and data for both  $TSM$  and  $R_c$  for 7 amphibian and 17 reptile species. The vast majority of reptile species with available data in our dataset were Squamates ( $n = 162$  out of 165), with only 2 Testudines and 1 Crocodylian species with available metrics. Because of the unique evolutionary history of these latter non-avian archosauromorph reptiles (Colston et al. 2020), and very small sample size, subsequent analysis focused solely on comparing Squamates and Amphibians.

### 1.4.2. TSM and Skin Resistance Comparison

We found that the mean Amphibian thermal safety margin (intercept = 14.56, 95% CI = [13.24, 15.88]) was 3.99°C wider than the average Squamate reptile (intercept = 10.57, CI = [10.14, 11.0]; Figure 1.1A). Our model of  $R_c$  in relation to taxonomic group showed, as expected, that Squamate species are generally much more resistant to cutaneous water loss compared to amphibians, with squamates having over four times larger mean  $R_c$  (intercept = 454.1, CI = [258.2, 798.6]) than Amphibians (intercept =

4.18, CI = [3.06, 5.70]; Figure 1.1C). Estimating these effects repeatedly on subsampled datasets, we found that the effect size of  $TSM$  was robust to potential sampling effects (Figure 1.1B), but the true effect size of  $R_c$  might be slightly smaller (Figure 1.1D).



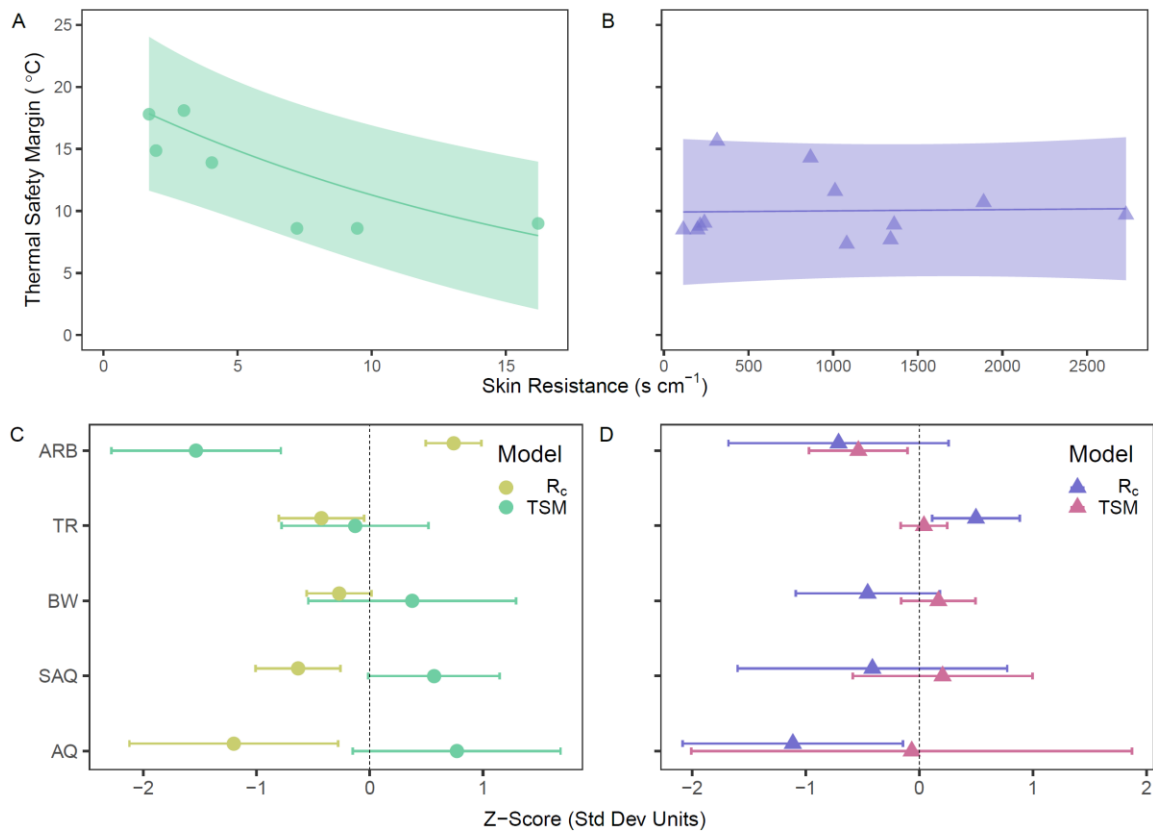
**Figure 1.1** Boxplots showing thermal safety margin (A) and skin resistance (C) for amphibians (green) and squamates (purple). Effect sizes, the difference between Amphibian and Reptile means for  $TSM$  (B) and  $R_c$  (D), generated by 1000 random subsamples of each dataset, balanced between the two taxonomic groups. Red lines indicate the effect size using the full datasets for each trait.

### 1.4.3. Combined TSM Skin Resistance Model

Combining our  $TSM$  and  $R_c$  databases in an exponential decay model, we found that  $TSM$  decreases with skin resistance in amphibians ( $\beta = -0.36$ , CI = [-0.57, -0.14]), corresponding to a 29.5% decrease in  $TSM$  with every  $\log_e$  unit  $R_c$  increase. In



squamates *TSM* increases only slightly with increasing  $R_c$  ( $\beta = 0.0082$ , CI [-0.25, 0.26], Figure 1.2A).



**Figure 1.2 Results for *TSM* vs  $R_c$  model (top) and the microhabitat models (bottom) for both amphibians (left) and squamates (right). A and B show predicted (lines) and observed (points) *TSM* in relation to  $R_c$ , along with 95% confidence intervals. Using the full suite of species with either *TSM* or  $R_c$ , panels C and D show the standardized coefficients for amphibians (C) and squamates (D) for each trait in units of standard deviation from the respective means, along with 95% confidence intervals. Microhabitat abbreviations are Arboreal (ARB), Terrestrial (TR), Burrowing (BW), Semi-aquatic (SAQ), and Aquatic (AQ).**

#### 1.4.4. Microhabitat Models

Comparing each physiological trait (*TSM*,  $R_c$ ), and taxonomic group, by microhabitat, we found that both *TSM* and  $R_c$  varied consistently among species' microhabitats. In four of the five amphibian microhabitat categories,  $R_c$  and *TSM*

standardized effect sizes were inversely related when grouped by microhabitat (Figure 1.2B), meaning that groups with relatively high values in one trait have relatively low values in the other trait. For example, relative to other microhabitats, arboreal amphibians had the smallest  $TSM$  and largest  $R_c$ , and aquatic amphibians had the largest  $TSM$  and smallest  $R_c$  overall (Figure 1.2B). However, in squamates only burrowing and semi-aquatic species displayed this opposing pattern (Figure 1.2D), suggesting that these two physiological traits are less closely linked by ecology in reptiles compared to the stronger trend in amphibians.

## 1.5. Discussion

Collectively the evidence we present here suggests that thermal and hydration physiology have likely coevolved in amphibians, consistent with the theory that a trade-off exists where the benefit of warmer body temperatures is weighed against the cost of accelerated water loss (Tracy and Christian 2005, Rozen-Rechels et al. 2019, 2020a). Amphibians and squamate reptiles show a distinct difference in their thermal physiology and behaviour. When the clades are compared, the desiccation-resistant squamates prefer elevated temperatures closer to their thermal maxima, while desiccation-prone amphibians on average have much larger thermal safety margins (Figure 1.1). Within amphibians, this same pattern is mirrored when comparing species across the spectrum of skin resistance – amphibians that are relatively impervious to water loss have similar thermal safety margins to some reptiles, while more water loss sensitive species have larger thermal safety margins (Figure 1.2). This linkage between thermal and hydration physiology in turn appears to align with species' ecology. Amphibians associated with less evaporative microhabitats (eg. aquatic species) had lower skin resistances and thermoregulated at cooler temperatures relative to their thermal maximum, while the opposite was true for species affiliated with drier microhabitats (eg. arboreal species; Figure 1.2). This trend did not hold for squamates. Overall, while our conclusions are limited by sample size, these results suggest that hydration and thermal physiology in ectotherms are inherently coupled—particularly in amphibians. Further studies on reptile water loss traits and amphibian thermal traits could help future studies expand on our findings.

For squamate reptiles, there was little evidence to suggest that thermal safety margin was influenced by skin resistance (Figure 1.2). These results do not necessarily suggest that water loss is unimportant, as with such high baseline  $R_c$  values in squamates, cutaneous water loss can often be near zero (Mautz 1980). However, water loss can occur through the eyes and respiratory tract, the later contributing 20 to 50% of total evaporative water loss in some species (Mautz 1982b), and the proportion can increase with ambient temperature (Crawford Jr and Kampe 1971). There is emerging evidence for some reptile species that water loss and desiccation risk restrict activity time (Sannolo and Carretero 2019, Rozen-Rechels et al. 2020b, 2020a), impede thermoregulation (Rozen-Rechels et al. 2020a), and can change body temperatures through respiratory cooling (Tattersall et al. 2006). Experiments comparing species' *TEWL* and how this shapes their thermoregulation and thermal traits would help us understand if squamate physiology mirrors our findings in amphibians. Additionally, further experiments that manipulate water availability and monitor individual's thermoregulatory response would clarify this interaction (Rozen-Rechels et al. 2020b, 2020a, Guevara-Molina et al. 2020).

The results of our microhabitat analysis are consistent with the idea that species' ecophysiological traits have coevolved as complexes that are shaped in part by microhabitat. Microhabitat affiliations have been suggested to exert distinct, and consistent, selection pressures on morphology and performance in anurans, resulting in species sharing these niches showing remarkable convergence in form and function even across separate continents and highly divergent clades (Buttimer et al. 2020). A similar process of convergent evolution in physiology appears likely as well, given the consistent abiotic conditions of certain microhabitats across ecosystems (Bohlman et al. 1995, Scheffers et al. 2014). Future work could compare both water loss sensitivity and thermal traits of species that have different microhabitat associations within the same site, as well as species sharing microhabitat affiliations from different evolutionary arenas or climatic zones. Targeted comparative studies of this nature can help us understand how these trait complexes have evolved within and across clades in response to common and divergent environments.

Much of the interest in these ecophysiological traits ultimately centers around how species may fare under a changing climate. The question then becomes: can these species adapt to the pace of climate change physiologically, or will behavioral adaptation

be required to cope with a climate that will outpace the rate of evolution (Huey et al. 2003)? Evidence suggests that tropical ectotherms are at a greater risk to climate change thanks to lower acclimatization potential, and overall, smaller thermal safety margins (Tewksbury et al. 2008, Deutsch et al. 2008; but see Gerick et al. 2014). Further, thermal limits appear unlikely to evolve quickly enough to adapt to climate change (Bennett et al. 2021, Bodensteiner et al. n.d.). Incorporating the interdependency of thermal and hydration states is likely to considerably improve accuracy for predicting how ectotherms may respond to climate change with mechanistic models (Kearney et al. 2018, Lertzman-Lepofsky et al. 2020), and failing to incorporate species' water loss limits, in addition to thermal limits, has been shown to underestimate climate change vulnerability in amphibians by up to 50% (Lertzman-Lepofsky et al. 2020). Our findings support the growing evidence (Tracy and Christian 2005, Rozen-Rechels et al. 2020b, 2020a, Guevara-Molina et al. 2020) that ectotherm hydration and thermal physiology are closely inter-related ecophysiological axes that should be jointly considered in species' ecology and climate change vulnerability.

## **Chapter 2. Bayesian occupancy estimates of subalpine amphibian breeding habitat use and climate driven hydrologic loss<sup>2</sup>**

### **2.1. Abstract**

Environmental regimes are shifting with accelerating climate change, putting at risk species and ecosystems shaped by the climate of the pre-industrial era. Many recent assessments of species vulnerability to climate change have focused on using individual traits, such as thermal sensitivity, to predict population-level responses. However, many species rely on ephemeral habitats that may be especially sensitive to changing climate, and their disappearance in the future may limit species persistence in landscapes in ways not captured by species physiology alone. Here we forecasted the loss of subalpine wetlands as breeding habitat for three amphibian species in the US Pacific Northwest, *Ambystoma gracile*, *A. macrodactylum*, and *Rana cascadae*. We combined historic and modern wetland surveys ( $n = 519$  sites) to build single-season Bayesian occupancy models of current breeding habitat use. We combined these results with existing hydrological models to predict the loss of suitable breeding habitats by the 2080s due to increased wetland drying (drying interval < minimum development time). We found that occupancy of wetlands used for reproduction by each species differed, but was predicted by elevation and site-level characteristics (elevation, % shallows, % wooded, and emergent vegetation), and that detection varied primarily by air temperature and visit depth. Of those wetlands predicted to be currently used for reproduction by each species ( $\psi > 0.5$ ), we estimate that 45% (*R. cascadae*, 79), 53% (*A. macrodactylum*, 384 days), and 51% (*A. gracile*, 414 days) will be unsuitable for the aquatic life history requirements of each species by the 2080s (A1B emissions scenario). Overall, we find that, independent of the myriad individual impacts of climate on amphibians, the rapid drying of montane wetlands could severely limit the persistence of these species in the Pacific Northwest.

<sup>2</sup> A version of this chapter is in preparation for publication with W.J. Palen, S.Y. Lee, M.E. Ryan, and L.K. M'Gonigle

## 2.2. Introduction

The threat of accelerating climate change as a driver of extinction has motivated conservation scientists to predict species' response to future changes. Climate change is already causing local extinctions of birds, reptiles, amphibians, and mammals (Sinervo et al. 2010, Stewart et al. 2017, Campos-Cerqueira and Aide 2017, Freeman et al. 2018). Many studies have focused on relating species-level traits to individual survival, with the intention of inferring population vulnerability or changes to species ranges. With temperature acting as a primary axis of environmental change, thermal physiological traits, such as thermal limits ( $CT_{max}$ ,  $CT_{min}$ ) or thermal tolerance to warming, are among the most common metrics used for assessing climate vulnerability (Logan et al. 2013, Gerick et al. 2014, Khaliq et al. 2014, Mitchell et al. 2018, Pinsky et al. 2019, May et al. 2019). Additionally, habitat suitability may be altered, or specific habitats lost as a result of changing climates. Changing habitat suitability is often presented as a confounding factor for predicting climate change impacts (Travis 2003, Pyke 2004, Mantyka-pringle et al. 2012, Segan et al. 2016), but climate change can also directly lead to habitat loss, such as sea level rise in coastal areas or a forest becoming increasingly dry (Nally et al. 2009). Many species with complex life histories require specific habitats for short periods or individual life stages that may also be sensitive to environmental change (McMenamin et al. 2008, Stenson and Hammill 2014, Purves 2015, Wauchope et al. 2017). This is particularly true for biphasic species such as many amphibians, whose successful breeding and rearing relies on the availability of aquatic habitats (e.g. wetlands) that persist longer than the minimum development period for aquatic life stages.

The persistence of wetland ecosystems is threatened by climate change, primarily through shifts in hydrological patterns due to shallow water depths and relatively small sizes (Kundzewicz et al. 2007, Johnson et al. 2010). Montane wetlands in particular are some of the most threatened ecosystems globally by climate change (Burkett and Kusler 2000). In mountains of the US Pacific Northwest, snowmelt is a key driver of the region's hydrology (Hamlet et al. 2005, Stewart et al. 2005), and climate change is markedly reducing snowpack levels and accelerating the timing of spring snowmelt (Lee et al. 2015, Najafi et al. 2017). As a consequence, wetland hydroperiods are shortening and becoming less permanent (Burkett and Kusler 2000, Elsner et al. 2010, Lee et al. 2015), threatening amphibians and other aquatic biota that depend on

wetlands. Hydroperiod is an important predictor of amphibian community composition and diversity (Pechmann et al. 1989, Snodgrass et al. 2000), acting as a filter that limits which amphibian species can successfully complete the aquatic stages of their life cycle based on the interval between drying events and the species' minimum development time before metamorphosis (Pechmann et al. 1989, Wellborn et al. 1996, Ryan et al. 2014).

Accurately estimating wetland hydroperiods can require years of monitoring, but recent coarse-scale hydrological variable infiltration capacity (VIC) models have been implemented in the Western United States (Littell et al. 2014), making it possible to predict hydroperiods with only limited empirical observations (Lee et al. 2015). VIC models have already been successfully applied in a variety of ecological settings (Falke et al. 2013, Pilliod et al. 2015, Sofaer et al. 2016, Kissel et al. 2019). We can now use historical climate records, and future climate scenarios, paired with VIC models and empirical site data, to make site-level historic and future hydroperiod predictions. Such hydroperiod estimates can be combined with independent estimates of breeding site occupancy to estimate both the number of sites historically suitable for breeding and forecast the suitability of breeding sites in the future.

Monitoring of wetland-breeding amphibian species can be logistically and quantitatively challenging because adults may only be present for short periods, such as during breeding, and egg or larval stages can be behaviourally or physically cryptic and difficult to detect. Historically, wetland amphibian habitat use was assessed using single visit presence-absence surveys (Corn 1990), but such methods are unable to distinguish between true absence and non-detection of the species. Occupancy models (MacKenzie et al. 2002) provide an analytical solution to imperfect detection by using repeat visit presence-absence surveys to estimate differences in the probability of detecting particular species or life stages. Because of the ability to account for imperfect detection of species, occupancy models are now a common tool for assessing amphibian wetland use (Hossack and Corn 2007, Gorman et al. 2009, Scherer et al. 2012, Sievers et al. 2019). The benefits of occupancy models are heightened when species are difficult to detect and false-absences are likely.

Here we estimate one impact of accelerating climate change for a suite of wetland-breeding amphibians by estimating current breeding habitat, combined with

predictions of shortening hydroperiods in those wetlands under future warming scenarios. We hypothesize that species with longer aquatic life histories will be more threatened by shortening hydroperiods compared to species with shorter aquatic life stages. We constructed single season-Bayesian occupancy models for each of three common subalpine amphibian species, Cascade frog (*Rana cascadae*), Northwestern salamander (*Ambystoma gracile*), and Long-toed salamander (*Ambystoma macrodactylum*), to estimate current breeding habitat use in 519 wetlands within watersheds of Mount Rainier and Olympic National Parks. We combined three datasets as the basis for our occupancy models to expand the geographic coverage of the study. Occupancy models serve as a bridge between the three datasets from different time periods and allow us to predict probability of breeding as a function of several habitat characteristics in each wetland during a broadly inclusive period of current habitat use (2001-2019). We used predictions of the frequency of wetland drying from Lee et al. (2015) for a subset of our study sites and predicted drying frequency for the remaining wetlands using site-level data from the occupancy datasets. Combining estimates of breeding occupancy with historical and future hydroperiod, we predicted the number of wetlands suitable for breeding in each time period to assess how climate change may restrict breeding habitat availability for each amphibian species in the future.

## **2.3. Methods**

### **2.3.1. Study Species & Survey Methods**

Subalpine areas of the Cascade and Olympic mountain ranges are home to a suite of wetland-breeding amphibian species including the Red-legged frog (*Rana aurora*), Columbia spotted frog (*Rana luteiventris*) Western toad (*Anaxyrus boreas*), Rough skinned newt (*Taricha granulosa*), Pacific chorus frog (*Pseudacris regilla*), Cascades frog (*Rana cascadae*), Northwestern salamander (*Ambystoma gracile*), and Long-toed salamander (*Ambystoma macrodactylum*) (Nussbaum et al. 1983). Of these species, Cascade frogs are the only species that specializes in montane areas, with the remaining species ranges extending down to sea-level (Nussbaum et al. 1983).

Amphibian surveys took place at wetlands in Mount Rainier National Park (Figure 2.1B) and Olympic National Park (Figure 2.1C) at wetlands ranging between 900 – 2050 meters in elevation, and with a maximum depth between 0.1 to 18 meters. We



conducted visual encounter amphibian surveys according to standard methods, where one observer wades through shallow water and with another following on shore, noting the presence and identity of any amphibian seen (Olson et al. 1997). We restricted our analysis of these survey data to include only observations of eggs and larvae, as they indicate the occurrence of breeding in each wetland. Survey records included enough observations to reliably estimate the probability of occupancy for *R. cascadae*, *A. gracile*, and *A. macrodactylum*.

The three focal species have a diverse set of aquatic life history requirements at subalpine elevations (900 – 2050m). *A. gracile* breeds in more permanent wetlands, compared to *A. macrodactylum* (Hoffman et al. 2003), and requires 2-3 years to complete development to metamorphosis at subalpine elevations (Snyder 1956, Eagleson 1976). The life history of *A. macrodactylum* is more flexible with metamorphosis occurring 80-90 days after hatching in more ephemeral sites, or after two or more years in larger and more permanent sites (Kezer and Farner 1955, Anderson 1967, Howard and Wallace 1985). In contrast, *R. cascadae* require only a single season for development, and typically metamorphose in late summer (Nussbaum et al. 1983, Garwood and Welsh 2007).

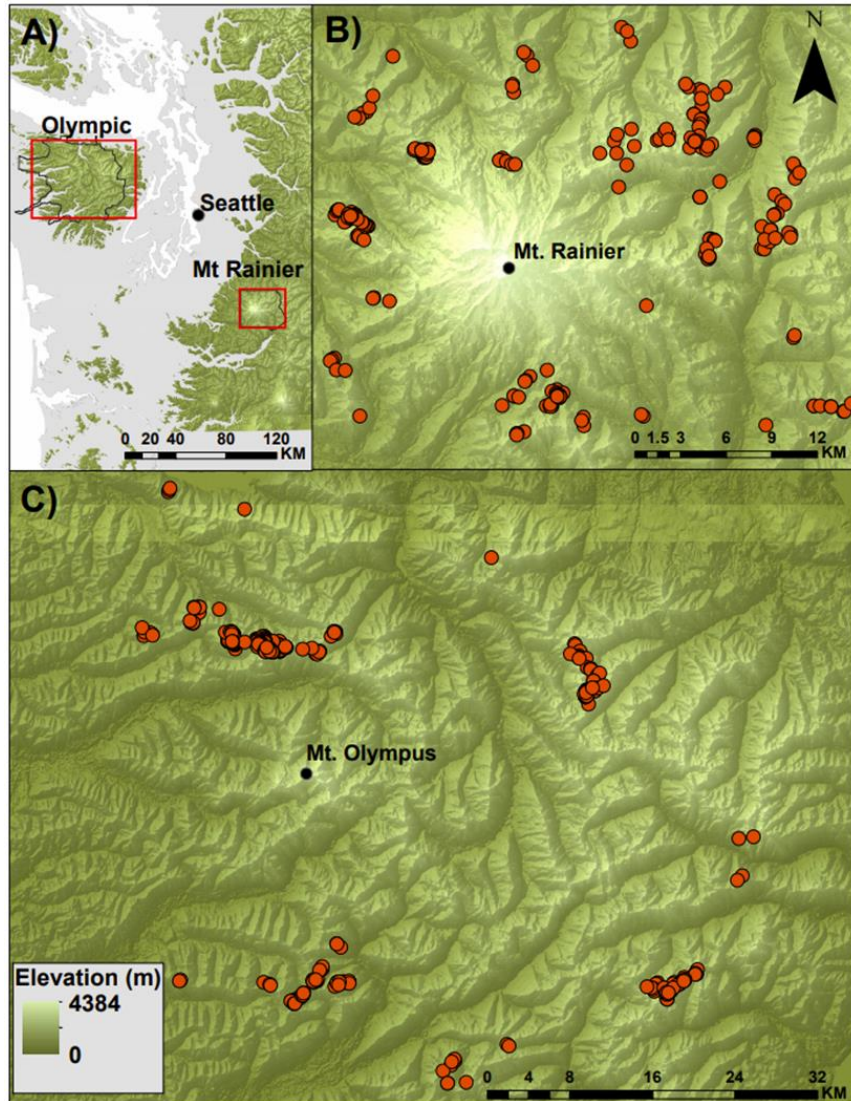


Figure 2.1. Map of the study region (topography > 500m elevation) (A), and inset maps indicating survey locations (red) in Mount Rainier (B), and Olympic (C) National parks.

### 2.3.2. Datasets

The Amphibian Research and Monitoring Initiative (ARMI) began in 2000, with a goal of monitoring amphibian populations across the lands of the U.S. Department of the Interior (Muths et al. 2005). We used monitoring data from this effort, including 93 sites in Olympic National Park and 105 sites in Mount Rainier National Park. Our core dataset was collected during summer of 2012 and 2013, where we conducted repeat-visit visual

encounter amphibian surveys at 31 sites in Mt. Rainier and 106 sites in Olympic. Sites were visited 1-6 times (mean = 2.96) in total over the two summers. We extended these surveys in 2019 and used the same survey protocols to conduct single-visit surveys at additional wetlands in both parks ( $n = 115$  sites in Olympic,  $n = 67$  sites in Mt. Rainier). Across all three datasets, our analysis included 315 sites (525 visits) in Olympic and 186 sites (265 visits) in Mt. Rainier (Table 2.1). During each visit, surveyors recorded depth (m), date, sky (clear or cloudy), and wind speed (calm or windy), all of which varied by visit, and at the site level maximum depth (m), percent shallows (percent area less than 50cm deep), percent emergent (percent surface area with emergent vegetation), and elevation (m) (Table 2.2). We estimated percent wooded, the percent of site perimeter that was forested, using satellite imagery from Google Earth (Google Earth 2021).

**Table 2.1. Occupancy database details including, the number of sites surveyed, number of visits made for sites in Olympic and Mount Rainier national parks. The total number of unique sites are reported in the bottom row.**

Database	Number of sites		Number of visits		Average visits per site	
	Olympic	Mt. Rainier	Olympic	Mt. Rainier	Olympic	Mt. Rainier
2012-2013 Surveys	105	32	287	118	3.28	4.43
2019 Surveys	115	72	115	72	1	1
2001-2004 ARMI Surveys	103	128	155	135	2.03	1.39
<b>Total of all databases</b>	<b>305</b>	<b>214</b>	<b>557</b>	<b>318</b>	<b>2.49</b>	<b>2.45</b>

**Table 2.2. Parameters included in the detection ( $\rho$ ) and occupancy ( $\psi$ ) models.**

Parameter	Data type	Explanation
Visit depth ( $\rho$ )	Continuous*	Maximum depth (m) of the pond during visit
Air temperature ( $\rho$ )	Continuous	Air temperature during visit ( $^{\circ}\text{C}$ )
Wind ( $\rho$ )	Categorical	Calm (1) or windy (0)
Sky ( $\rho$ )	Categorical	Sunny (1) or cloudy (0)
Julian day ( $\rho$ )	Continuous	Julian day of year
Percent shallows ( $\psi$ )	Continuous	Percent wetland area <50cm deep
Percent wooded ( $\psi$ )	Continuous	Percent of wetland perimeter covered by trees, estimated using satellite imagery
Max depth ( $\psi$ )	Continuous	Maximum water depth (m)
Percent emergent vegetation ( $\psi$ )	Continuous	Percent of wetland area with emergent vegetation

<b>Elevation (<math>\psi</math>)</b>	Continuous	Elevation (m) of the site
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\*Note: Maximum depth recorded in the ARMI dataset was recorded as categorical (<1m, 1-2m, >2m) and was converted to continuous values for each category (0.5m, 1.5m, 2.5m).

### 2.3.3. Occupancy Analysis

We used a Bayesian framework to construct hierarchical occupancy models (Royle and Kéry 2007, MacKenzie et al. 2017) for the three focal species. Bayesian occupancy models were chosen because they can more readily estimate parameters in situations where a frequentist models might struggle (MacKenzie et al. 2017). For each species we combined survey data from all three datasets into a single-season occupancy model (MacKenzie et al. 2017) to estimate current breeding occupancy ( $\psi$ , circa 2001 - 2019). We included Julian day, visit depth, sky, air temperature and wind in the detection model, and max depth, elevation, percent emergent vegetation, percent shallows, and percent wooded in the detection model (Table 2.1). For each species, we estimated detection (1) as follows:

$$(1) \text{logit}(p_{ij}) = \beta_0 + \beta_1 * air_{ij} + \beta_2 * depth_{ij} + \beta_3 * sky_{ij} + \beta_4 * wind_{ij} + \beta_5 * jday_{ij}$$

and occupancy (2) as follows:

$$(2) \text{logit}(\psi_i) = \alpha_0 + \alpha_1 * \%shallows_i + \alpha_2 * \%wooded_i + \alpha_3 * elevation_i + \alpha_4 * \%emergent_i + \alpha_5 * max\ depth_i$$

where  $i$  is the  $i^{\text{th}}$  site and  $j$  is the  $j^{\text{th}}$  visit.

We used R v. 4.0 (R Core Team 2019) and JAGS (Plummer 2003) to implement the models using the R package *run.jags* (Denwood 2016). We standardized all continuous parameters (Table 2.1) and assigned vague uniform priors ( $N[0, 0.01]$ ). For each species we generated three MCMC chains of 1,000,000 iterations each from the posterior distribution of model parameters, removing the first 1000 iterations as a burn-in. These samples were thinned by keeping every 100<sup>th</sup> sample. Convergence was assessed by the calculation of Gelman-Rubin statistics ( $\hat{R} = 1.01$ ; Brooks and Gelman 1998) and by visually assessing the trace and density plots of the posterior distributions.

### 2.3.4. Drying Probability Estimates

Macro-scale hydrological models called Variable Infiltration Capacity (VIC) models (Liang et al. 1994) have been implemented for the Pacific Northwest (PNW) and California at a roughly 1/16<sup>th</sup> degree resolution (Littell et al. 2014). Using inputs including temperature, precipitation, wind, vapor pressure, net incoming longwave and shortwave radiation, and air pressure from historic climate records or simulated future data under different climate scenarios, VIC models can simulate daily water balance variables including soil moisture, runoff, and evapotranspiration (Lee et al. 2015). Additional methodological detail on the VIC model formulation and extension are provided in Lee et al. (2015), Elsner et al. (2010), Hamlet et al. (2013), and Tohver et al. (2014). Briefly, Lee et al. (2015) used repeated depth observations of wetland water depth collected during the summer and fall of 2012, paired with daily VIC model outputs, to construct site-specific linear regressions. Site-specific regressions were combined with either hindcasted or forecasted daily VIC outputs to predict daily water levels over a 91-year period under historic (1915-2006) conditions and perturbed to future (2080s) conditions under the A1B emissions scenario (Hamlet et al. 2013). We used the historic and future outputs to compute the average number of days in the snow-free season (June 12<sup>th</sup> to October 31<sup>st</sup>; 141 days) between site drying events over 91 years for each time period at each site, hereby referred to as the site's average drying recurrence interval. This interval could span only months, multiple years, or all 12831 days of the simulation if no drying occurs.

Lee et al. (2015) was able to collect consecutive water depths within a water year at 74 of our study sites (Olympic  $n = 50$ , Mt. Rainier  $n = 34$ ), and reported 1/16<sup>th</sup> degree resolution predictions of drying frequency (total years dried out of 91 years) across both parks for both historical and 2080s conditions. To extend predictions of drying recurrence interval at our remaining study sites we predicted historic and future average drying recurrence interval using a linear model for each time period. We trained the models using the empirical data from the original 74 wetland sites, and predicted average drying recurrence interval as a function of site-level habitat data from our occupancy surveys (maximum depth, elevation, percent emergent vegetation, percent wooded), as well as the course VIC prediction of drying frequency reported in Lee et al. (2015). We removed 32 sites that never dried in both time periods and, for the remaining 41 sites, log-transformed the response variable to avoid overdispersion in the model. For

each time period (historic, future), we compared all possible combinations of the global model (32 models) using Akaike's Information Criterion (Burnham and Anderson 1998) and the model selection package in MuMIn (Barton 2019). For both time periods (historic, future) the best-fit model had low support (historic  $w = 0.18$ , future  $w = 0.11$ ), so we created a model average of candidate models within two  $\Delta AIC$  units of the best-fit model (Burnham and Anderson 1998). We found that of the 74 sites in the empirical dataset, those with a maximum depth greater than 1.5 meters ( $n = 87$ ) did not dry during either historic or future conditions. As a result, we limited our model predictions to sites with a maximum depth less than 1.5m and assumed that all other sites never dried during either time period.

### **2.3.5. Classifying historic and future breeding sites**

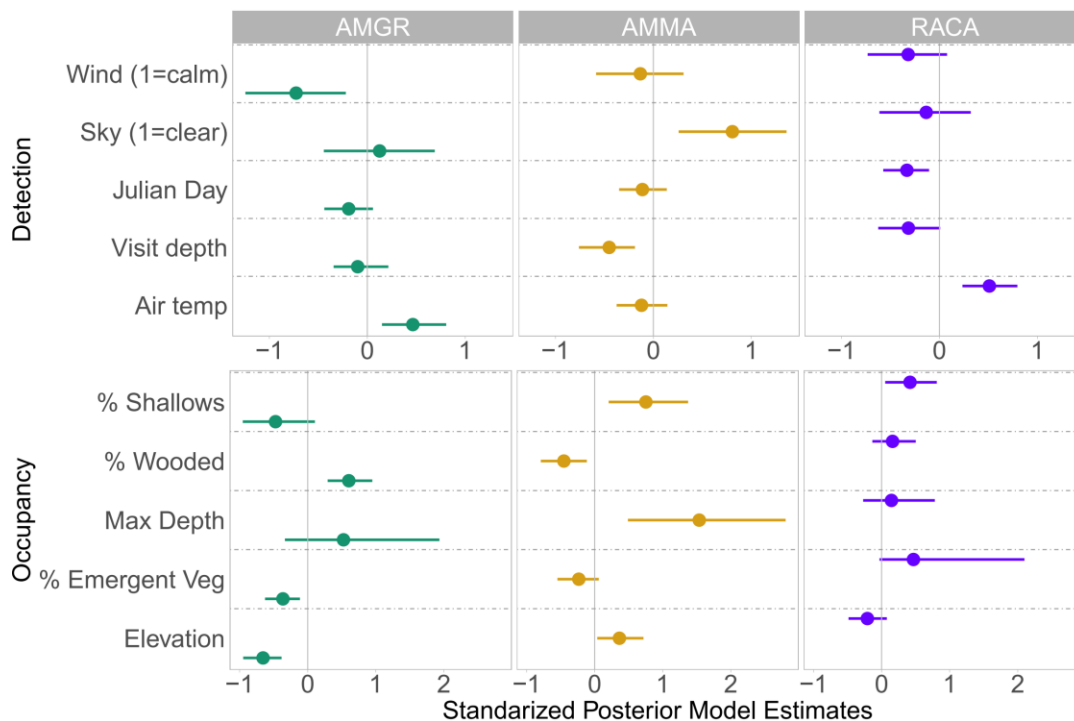
To assess how more frequent wetland drying in the future may reduce the availability of suitable breeding wetlands for our three focal species, we calculated the number of sites that met two independent criteria; (1) the species'  $\psi$  estimate under current conditions (2001-2019) was greater than 0.50 (referred to as used breeding sites), and (2) if the site's predicted mean drying interval was longer than the minimum development time required for the aquatic stages of each species (referred to as suitable breeding sites, see below), repeated for both historical and 2080s simulated hydroperiod. We also evaluated the sensitivity of our conclusions to the threshold of  $\psi$  used to determine breeding sites by varying the threshold by  $\pm 0.20$  and recalculating the percent of sites lost.

Based on information from the literature, we assigned minimum aquatic development times as 414 days for *A. gracile*, 384 days for *A. macrodactylum*, and 79 days for *R. cascadae*. We used June 12<sup>th</sup> as the average day breeding began based on data from Olympic National Park (Lertzman-Lepofsky, pers comm). We evaluated the sensitivity of our results to each species' minimum aquatic development time by varying the number of days by  $\pm 30$  and recalculating the percent of suitable breeding sites lost.

## 2.4. Results

### 2.4.1. Occupancy models

During the surveys of 519 sites, *A. gracile* were detected in 270 sites, *A. macrodactylum* in 148 sites, and *R. cascadae* in 327 sites. Our models predict that mean probability of detection varied among the three species, where *A. macrodactylum* had the lowest mean detection of 0.46 (95% CRI: 0.39, 0.55), *R. cascadae* had a mean detection of 0.72 (95% CRI: 0.65, 0.78), and *A. gracile* had the highest mean detection at 0.78 (CRI: 0.71, 0.85). We found the effects of covariates on detection probability varied by species. Detection of *A. macrodactylum* was positively related to clear sky conditions ( $\beta = 0.56$ ) and negatively associated with calm wind conditions ( $\beta = -0.73$ ), while both *A. gracile* ( $\beta = 0.58$ ) and *R. cascadae* ( $\beta = 0.50$ ) detection was positively related to higher air temperatures. Lastly, *R. cascadae* was negatively related to visit depth ( $\beta = -0.21$ ) and Julian day ( $\beta = -0.33$ ) (Figure 2.2).



**Figure 2.2.** Standardized posterior means (points) and 95% Bayesian credible intervals of the posterior distributions for detection (top panels) and occupancy (bottom panels) parameters for *A. gracile* (AMGR, left), *A. macrodactylum* (AMMA, center), and *R. cascadae* (RACA, right).

The overall probability of occurrence varied among the three species, with *R. cascadae* having the highest  $\psi$  (0.65, 95% CRI: 0.59, 0.71), followed by *A. gracile* (0.51, 95% CRI: 0.46, 0.57), and *A. macrodactylum* (0.48, 95% CRI: 0.38, 0.59). For the covariates of  $\psi$ , we found that percent shallows positively influenced *R. cascadae*  $\psi$  ( $\beta = 0.35$ ) and decreased  $\psi$  for *A. gracile* ( $\beta = -0.50$ ). Percent wooded increased  $\psi$  for *A. gracile* ( $\beta = 0.52$ ), while percent emergent was associated with lower  $\psi$  ( $\beta = -0.32$ ). *A. macrodactylum*  $\psi$  was positively associated with deeper maximum depths ( $\beta = 1.54$ ). Finally, elevation was associated with increased  $\psi$  for *A. macrodactylum* ( $\beta = 0.40$ ), and decreased  $\psi$  for *A. gracile* ( $\beta = -0.58$ ) (Figure 2.2).

### 2.4.2. Drying Frequency

We used site-specific predictions of average drying recurrence interval ( $n = 74$  sites; Lee et al. 2015) to train a predictive model for extrapolating hydroperiod to our remaining 445 sites. After competing all possible combinations of the global models for both time periods we found the top-ranked models by AIC for historic and future predictions had  $R^2$  values of 0.33 and 0.23, respectively. For both time periods the top models contained maximum depth and VIC grid prediction (Table 2.3 and 2.4). Both the historical and future predictive model averages contained all five variables.

**Table 2.3. AIC model selection results for generalized linear models of historic (1915-2006) drying recurrence interval from 41 sites in Mount Rainer and Olympic national park, including the models within 2 delta AIC, the global model, and intercept-only model. “dry.hist” is the drying frequency for an intermediate wetland under historical conditions for each VIC grid cell as reported by Lee et al. (2015).**

Model variables	df	logLik	$\Delta AIC_c$	w
Max Depth + Elevation + % Emergent + dry.hist	6	-37.25	0.00	0.18
Max Depth + Elevation + dry.hist	5	-38.88	1.25	0.10
Max Depth + % Emergent + dry.hist	4	-36.99	1.50	0.09
Max Depth + Elevation + % Emergent + dry.hist + % Wooded	7	-39.02	1.55	0.08
Max Depth + Elevation + % Emergent	5	-37.25	1.62	0.08
Intercept-only	2	-44.80	8.4	0



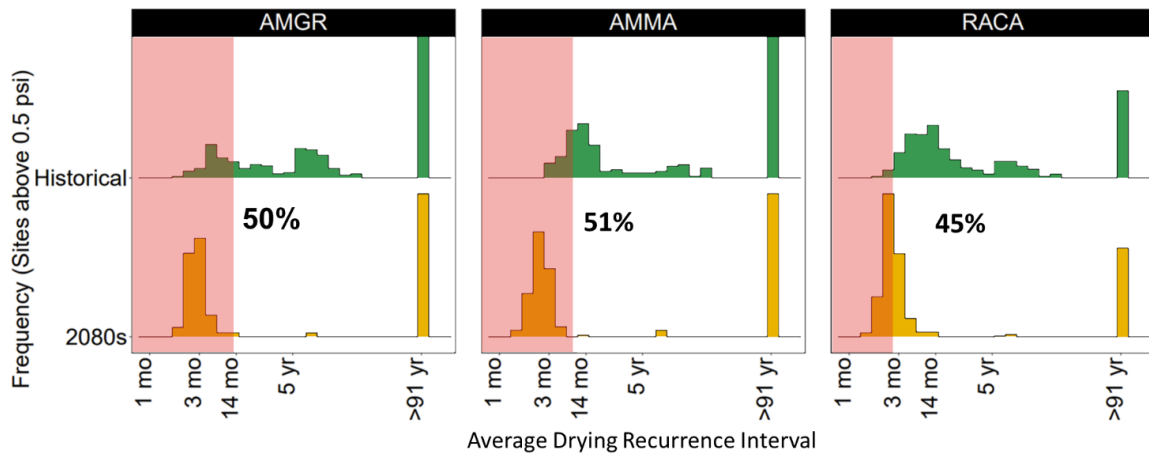
**Table 2.4. AIC model selection results for generalized linear models of future (2080s) drying recurrence interval in 41 wetlands from Mount Rainer and Olympic national parks, including all models within 2 delta AIC units, the global model, and an intercept-only model. “dry.fut” is the drying frequency for an intermediate wetland under 2080s conditions for each VIC grid cell as reported by Lee et al. (2015).**

Model variables	df	logLik	$\Delta AIC_c$	w
Max Depth + dry.fut + % Emergent	5	-16.35	0.00	0.109
dry.fut + Max Depth	4	-17.39	0.06	0.106
dry.fut	3	-18.44	0.16	0.101
% Emergent + dry.fut	4	-17.55	0.39	0.090
Max Depth + Elevation + dry.fut	5	-17.01	1.31	0.057
Max Depth + Elevation + % Emergent + dry.fut	6	-16.18	1.66	0.048
Elevation + dry.fut	4	-18.24	1.78	0.045
Max Depth + % Emergent + dry.fut + % Wooded	6	-16.35	2.00	0.040
Max Depth + Elevation + % Emergent + dry.fut + % Wooded	5	-16.18	3.65	0.02
Intercept-only	2	-21.69	4.67	0.01

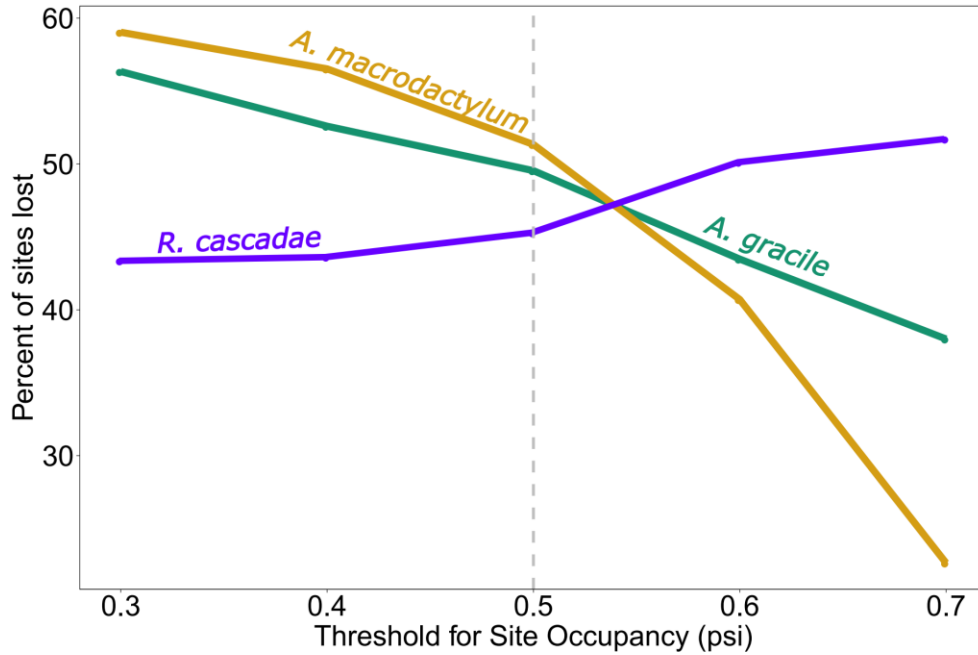
### 2.4.3. Historic and future suitable breeding sites

For each species we combined estimates of site occupancy ( $\psi > 0.5$ ) with historic (1915-2006) and future (2080's) drying intervals to determine the number of suitable breeding sites for our species of interest. Based on our criteria, we estimated that 220 sites support *A. gracile* breeding historically (1915-2006), and we predict based on changing hydrology that 110 of those sites (50%) will be unsuitable for breeding by the 2080's. Similarly, we estimate that of the 194 sites support *A. macrodactylum* breeding historically, 103 of those sites (53%) will be unsuitable by the 2080's. Lastly, we estimate that 486 of sites surveyed support *R. cascadae* are historically suitable for breeding, and that 220 (45%) will be unsuitable as drying frequency increases in the 2080's (Figure 2.3). We found that for *A. macrodactylum* our conclusions did depend on the value of  $\psi$  used, ranging from 60% of suitable sites lost with a threshold of 0.30  $\psi$ , or 23% with a threshold of 0.70  $\psi$ . The results for both *R. cascadae* or *A. gracile* were relatively insensitive to assumptions about  $\psi$ , with the percent of sites lost remaining relatively unchanged regardless of the  $\psi$  value (Figure 2.4). When we evaluated how our results varied based on different minimum aquatic development times, we found that *R. cascadae* could avoid suitable breeding habitat loss if metamorphosis could occur in

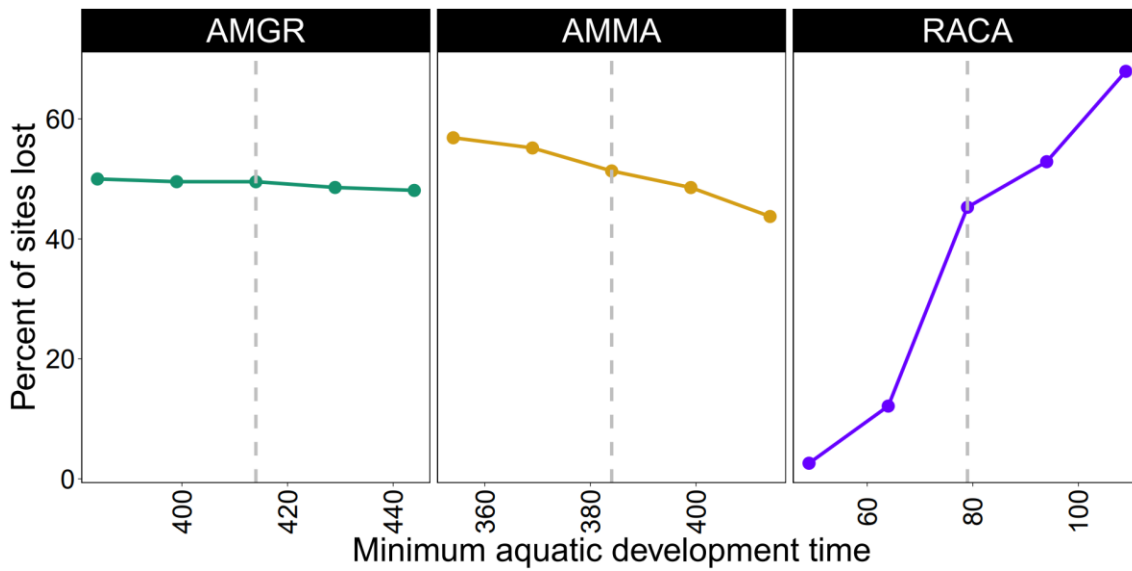
only 50 days. The remaining two species' results remained relatively unchanged regardless of aquatic development time (Figure 2.5).



**Figure 2.3** Frequency histograms of sites with 0.50 or greater occupancy for each species, *A. gracile* (AMGR, left), *A. macrodactylum* (AMMA, center), and *R. cascadae* (RACA, right), as a function of the average drying interval (log<sub>10</sub> scale) during historical (1916-2006, green) and future time periods (2080's, yellow). Areas shaded in pink indicate drying intervals shorter than required for successful metamorphosis in an average year for each species (AMGR = 14 months, AMMA = 13 months, RACA = 3 months), and the percent reduction in suitable sites for each species is shown on the bottom portion of the panels.



**Figure 2.4** Sensitivity in the estimates of the percent of sites classified as unsuitable for successful reproduction in the 2080's for each species based on variation in the  $\psi$  threshold used to determine habitat use.



**Figure 2.5** Sensitivity of the estimates of the percent of sites classified as unsuitable for successful reproduction in the 2080's for each species based on variation in the minimum aquatic development time. Grey dashed lines represent the development time used.

## 2.5. Discussion

Occupancy models allowed us to robustly estimate current habitat use, and combined with existing predictions of future hydrologic change, estimate changes in habitat suitability with climate change. Here we found between 46 and 53% of current breeding habitat for three montane amphibian species of the Pacific Northwest is projected to become unsuitable due to drier hydrological conditions by the 2080s. These results emerge from estimates of species occupancy for reproductive life stages in 519 surveyed wetlands, combined with existing hydrological models that predict historic and future drying frequency (Figure 2.3). The drivers of the probability of occupancy in our occupancy models aligns with the known breeding ecology of the three species (Figure 2.2). *R. cascadae* is known to deposit eggs in the shallow margins of wetlands (Briggs 1987), often within emergent vegetation (Garwood and Welsh 2007; *pers obs*). Similarly, a study of the reproductive ecology of *A. gracile* and *A. macrodactylum* found in Mount Rainier that *A. gracile* were associated with wetlands that are more forested, and lower in elevation, compared to *A. macrodactylum*, which bred in sites in more open meadows, at higher elevations, and greater amounts of emergent vegetation (Hoffman et al. 2003).

While our occupancy models estimate the probability of occurrence of reproductive life stages, this probability does not always equate to habitat that is suitable for reproductive success. We found that all three species historically use habitats that on average dry too frequently for the successful completion of their aquatic life stage (Figure 2.3). This aligns with observations of amphibians still breeding in wetlands that end up drying too quickly for larval metamorphosis (Berven 1990, McMenamin et al. 2008, Kissel et al. 2019). When we compare historical to future habitat suitability, the predicted loss of *A. macrodactylum* breeding habitats likely emerges from a relatively slow larval development rate compared to *R. cascadae*, combined with a generalist habit of breeding in wetlands with a range of hydroperiods (Kezer and Farner 1955, Hoffman et al. 2003). Contrary to our hypothesis, *A. gracile* might be slightly more buffered from the negative effects of increased wetland drying by their reliance on permanent wetlands (Hoffman et al. 2003), despite having long development requirements. In contrast, *R. cascadae* develop rapidly as larvae, but breed in many intermediate hydroperiod wetlands that are predicted to experience a dramatic increase in drying (Lee et al. 2015).

Given considerable variation observed in the larval development period of many amphibian species, we evaluated the sensitivity of our conclusions to assumptions about larval development rates. For *A. macrodactylum* we found that the estimated loss of suitable habitats is relatively insensitive even when we assume a much shorter minimum development time (110 days; 50% loss), which has been documented in high elevation populations towards the southern end of the species range (Kezer and Farner 1955). We also estimated the sensitivity of our conclusions to changes in development time for *R. cascadae* and *A. gracile*, and out of the three species, *R. cascadae* was the most sensitive, with 0% loss of current habitats if metamorphosis could occur 30 days earlier (Figure 2.5). However, observations from Northern California suggest this rate of development is rare and only during exceptionally early breeding years (Garwood and Welsh 2007). In contrast, *A. gracile* are relatively insensitive to assumptions about minimum development times (Figure 2.5). We also assessed the sensitivity of our conclusions to assumptions about the threshold of  $\psi$  used to determine the number of occupied breeding sites. If we select sites using higher or lower value of  $\psi$ , we find that our predictions for *R. cascadae* vary by less than 5%, however if we use a  $\psi$  threshold of 0.70, predictions for *A. macrodactylum* and *A. gracile* are reduced to 23% and 38%, respectively (Figure 2.4). The pattern of diminishing losses of suitable breeding habitat with a higher  $\psi$  threshold in the *Ambystoma* species suggests that higher  $\psi$  sites are more permanent overall, while the opposite is true for *R. cascadae*. This is likely due to the aquatic life histories of the species, *R. cascadae* requiring less permanent sites than the remaining two species.

We acknowledge that our conclusions emerge from uncertainty in each component of our analysis. We used occupancy model outputs to identify current (2001-2019) breeding sites as the basis for predicting habitat suitability under current as well as future (2080s) conditions. We did so with the assumption that most site-level variables included in the model (elevation, percent shallows, max depth, percent wooded) are relatively stable, and may remain similar by the 2080s. However, some other variables (emergent vegetation) may be more likely to change in response to increased drying frequency. For example this might increase habitats for species that prefer emergent vegetation and decrease habitat for others. Another source of uncertainty includes how species development time may shift with changing climate. Larval development times can vary depending on site characteristics, larvae grow faster

and metamorphose earlier with higher food availability (Licht 1992) and water temperature (Anderson 1967, Brown 1976, Howard and Wallace 1985), and can metamorphose at smaller sizes with accelerated pond drying (Kezer and Farner 1955, O'Regan et al. 2014). However field observations and models confirm that amphibian larvae are often unable to develop fast enough to escape drying wetlands (Berven 1990, McMenamin et al. 2008, Kissel et al. 2019), suggesting that faster larval development is unlikely to buffer against shortening hydroperiods in the future. In addition, there is high uncertainty associated with the estimates of drying recurrence intervals for a majority of our study sites. While 74 of our study sites have empirically-based estimates of drying frequency from Lee et al. (2015), we predicted historic and future drying recurrence intervals for 445 sites using only coarse scale estimates from Lee et al. (2015), and our models explain only a modest amount of variation in the data (historic  $R^2 = 0.33$ , future  $R^2 = 0.22$ ). However, we expect that hydroperiod estimates from Lee et al. (2015) are conservative with regard to future climate (CMIP 3 based predictions), as updated climate models predict warmer air temperatures in the western United States (Wright et al. 2016). Warmer temperatures are expected to exacerbate the general loss of moisture sources such as snowpack and amplify summer drought conditions, suggesting that even with considerable uncertainty in hydrological predictions, our ecological predictions are expected to be conservative with regard to wetland suitability.

While breeding and rearing wetlands are only required during the aquatic life stages (embryo, larvae) for each of our study species, their disappearance could affect population persistence. Breeding habitat loss has been linked to population-level consequences across a range of avifauna (Sutherland 1996, Purves 2015, Taylor and Stutchbury 2016). Here the projected loss of half of currently used breeding sites by the 2080s for all three of our focal species suggests that population persistence in these landscapes is highly uncertain. Population-level impacts might be negated if species are able to track the decline in habitat suitability as climate change progresses, and shift breeding effort to more climate-resilient sites at higher densities. However, our occupancy models predict that all three species currently breed in some sites that historically dry too frequently to complete their aquatic life stage (Figure 2.3), suggesting that with some frequency these species may continue to breed in habitats that are unsuitable. Additionally, even if species are able to many amphibian larvae exhibit density dependent survival (Walls 1998) and growth (Newman 1998), in that higher

densities of larvae may decrease survival and growth, and can even decline at very high densities (Hels 2002). This suggests that population-level impacts are likely with accelerating climate change. While the two *Ambystoma* species are also found at lower elevations, populations in subalpine areas are often clustered across the landscape (Figure 2.1), and may act as metapopulations (Hanski 1998, Marsh and Trenham 2001). As breeding habitat is lost within amphibian metapopulations, connectivity often decreases, reducing overall metapopulation viability (Hanski 1998). Providing spatially connected refugia from stressors (e.g.; disease, predators) has been shown to allow amphibian metapopulations to persist (Heard et al. 2015). Restoring historic access to breeding habitat might also provide climate refugia, as widely introduced non-native trout often exclude amphibians through predation (Ryan et al. 2014, Pilliod et al. 2015, Polocavia et al. 2019). Most (95%) montane lakes in the western United States have been stocked with non-native trout for recreation (Bahls 1992). but when removed, subsequent lake surveys have shown amphibian populations are frequently able to recolonize (Hoffman et al. 2003, Knapp et al. 2007, Larson et al. 2017). As described by Ryan et al. (2014), fish removal could provide managers with a tool to counteract the climate-driven loss of many smaller breeding wetlands that we describe here.

Increasingly predictions of species vulnerability to climate change is based on individual physiological limits, such as critical thermal maxima ( $CT_{max}$ ) or critical levels of dehydration ( $EWL_{crit}$ ). In particular, montane amphibians in the Pacific Northwest are predicted to experience heightened risk from climate change due to increased rates of evaporative water loss acting synergistically with higher temperatures (Lertzman-Lepofsky et al. 2020). Here we find that the potential loss of suitable breeding wetlands may create an additional, and previously unexamined, constraint on amphibian populations and their persistence in the region. While our analysis does not allow for an explicit comparison with climate impacts predicted from individual physiological limits (Huey et al. 2009, Gerick et al. 2014, Khaliq et al. 2014, Kissel et al. 2019, May et al. 2019, Lertzman-Lepofsky et al. 2020), the potential exists that the persistence of breeding habitats may be as sensitive to climate as these more commonly used individual measures.

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