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POPULATION DYNAMICS OF THE COLUMBIA SPOTTED FROG (*RANA
LUTEIVENTRIS*): INFERENCE FROM LONG-TERM DEMOGRAPHY

By

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B.A. in Biology, Lewis and Clark College, 2002

Dissertation

presented in partial fulfillment of the requirements
for the degree of

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Population dynamics of the Columbia spotted frog (*Rana luteiventris*): inference from long-term demography

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Worldwide extinctions of amphibians are at the forefront of the biodiversity crisis, with climate change figuring prominently as a potential driver of continued amphibian decline. Changes in both the mean and variability of climate conditions may affect amphibian populations in complex, unpredictable ways. However, few studies have evaluated effects of climate change on individual vital rates and subsequent population dynamics of amphibians. I investigated the population dynamics of a high elevation population of the Columbia spotted frog (*Rana luteiventris*) in relation to climate variation over a ten-year period.

I documented an increase in survival and breeding probability as severity of winter decreased. Therefore, a warming climate with less severe winters is likely to promote population viability in this montane frog population. More generally, amphibians and other ectotherms inhabiting alpine or boreal habitats at or near their thermal ecological limits may benefit from the milder winters provided by a warming climate as long as suitable habitats remain intact.

I then used Bayesian models to demonstrate that changes in mean snowpack had a greater effect on viability than changes in the variance of snowpack. In general, future decreases in mean snowpack increase population viability, and increases in variability have little effect.

Finally, I examined whether heterogeneity in pond hydroperiod on the landscape had the potential to stabilize recruitment and population dynamics. Overall, ponds with different hydroperiods showed contrasting dynamics among years. Variability in recruitment was lowest in the scenario with the greatest pond heterogeneity, suggesting that the presence of a diversity of hydroperiods on the landscape may reduce variability in amphibian recruitment.

Through my research, I have been able to determine relationships between climate variables and vital rates in the Columbia spotted frog, and then use population models to explore how future changes in climate or habitat could affect the viability of this population. These results add to our understanding of how climate variation may influence *Rana luteiventris* dynamics in montane environments, but also provide a demographic backdrop for determining which factors might affect other amphibian populations and species in diverse mountain environments.

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CHAPTER 1

INTRODUCTION AND OVERVIEW

Population ecology seeks to answer fundamental questions about plant and animal populations that can be deceptively difficult to answer, such as: (1) how many individuals are present in a given population or area, (2) are the numbers of individuals increasing or decreasing over time, and (3) what factors are driving changes in population size? Comprehensive field studies, a rich body of ecological theory, and sophisticated statistical analyses are all used to answer these questions. Fundamentally, we seek to determine the mechanisms that govern population dynamics. Among other factors, we study the relative contribution of intrinsic and extrinsic factors to population growth; for example, we frequently examine how weather versus density dependence influence population dynamics (e.g. Coulson et al. 2000, 2001). However, we also address a myriad of other questions in applied ecology and conservation biology. For example, we quantify how many individuals are needed to ensure persistence of a population into the future (Soule 1987), determine the relative impact of stressors or human management strategies on population viability (e.g. Ferreras et al. 2001), compare the efficacy of various management strategies for controlling pest populations (e.g. Shea et al. 2002, Govindarajulu et al. 2005), or determine harvest quotas for species of economic and conservation significance (e.g. Nichols et al. 1995). To achieve these research objectives requires an understanding of the factors influencing population dynamics across various life stages.

The global amphibian decline crisis has presented population ecologists with a new challenge. In the past 25 years, we have witnessed dramatic declines and extinctions of many amphibian species worldwide (Blaustein et al. 1994, Alford and Richards 1999, Houlahan et al. 2000, Wake and Vredenburg 2008). Many of these declines have been documented by abrupt disappearances in populations or species in a given area (Pounds et al. 1997, Lips 1998, 1999). In many cases, we do not have a clear sense of *how* and *why* these populations have declined or disappeared. What were the abundances and dynamics of these populations prior to declines? Efforts to assess how many species are declining worldwide have largely relied on indices of amphibian abundance or presence-

absence data (e.g. Alford and Richards 1999). These analyses can be problematic if indices do not accurately reflect the trends in underlying populations, or if analyses are not conducted over the time scales needed to capture natural variation in dynamics. As such, some biologists have questioned our ability to detect declines in the face of poor data quality and high interannual stochasticity (Pechmann et al. 1991, Pechmann and Wilbur 1994, Marsh 2001, Storfer 2003), and have called for comprehensive, long-term studies to address this issue. Fundamentally, this crisis has highlighted a general lack of natural history and demographic data for most amphibian species, which hampers our understanding of the mechanisms driving amphibian population dynamics.

Part of the challenge is the nature of the stressors affecting amphibians. Proximal stressors like habitat degradation and destruction can readily be attributed to some local declines and extirpations. In contrast, stressors like climate change and the emerging infectious disease *Batrachochytrium dendrobatidis* have more complicated relationships with amphibian decline (Pounds et al. 2006, Lips et al. 2008, Rohr et al. 2008). Climate change has been invoked as a confounding or contributing stressor to the decline or extirpation of amphibian populations, and one that is expected to have increasingly negative effects in the future (reviewed in Carey and Alexander 2003, Corn 2005). However, we have rarely been able to measure relationships between climate variation and vital rates in nature at appropriate time scales that capture a range of climate conditions and the generation time of the species in question.

To fully confront this conservation issue, we must have a better sense of the population dynamics of amphibians in relation to environmental stochasticity. This is no easy feat, as many species are cryptic or have unobservable life stages. However, some temperate, pond-breeding species can be excellent candidates for this type of study, because of their association with discrete water bodies during part or all of the year. This association makes individuals relatively easy to detect and monitor over successive years. Pond-breeding species are among the best studied amphibians, and we have learned a substantial amount about the influence of environmental conditions (Meyer et al. 1998, Daszak et al. 2005), competitors (Wilbur 1980), predators (Werner 1986), pathogens (Kiesecker et al. 2001), and population density (Newman 1998) on various aspects of their ecology. These studies have typically focused on individual life history stages, such

as the larval stage, or on indices of abundance, such as the female breeding population. More elusive are comprehensive demographic studies that integrate these effects over multiple life stages, and which explore dynamics over enough years to capture the natural variability inherent to pond-breeding amphibians.

In my dissertation, I examined the population dynamics of a high elevation population of the pond-breeding amphibian *Rana luteiventris*. This species is common in western Montana, and inhabits wetlands from valley bottoms to high elevations (Maxell et al. 2003, Werner et al. 2004). Although this species is not declining in Montana, populations on the southern edge of the range are threatened (Reaser and Pilliod 2000), and sister species in Washington and Oregon are facing numerous threats in montane systems. Understanding the natural dynamics of this species in relation to environmental variation informs us about the natural history of this species, helps identify how different environmental stressors may impact the population, and may elucidate key processes important to other populations of the same species or other species inhabiting mountain environments. I examined the relationship between *R. luteiventris* and climate variation in a 10-year demographic study of the species. Current climate models predict a decline in both the extent and duration of snowpack in the Pacific Northwest coincident with an increase in mean temperatures (Stewart et al. 2004, Knowles et al. 2006), and it is of crucial interest to determine how such changes will affect montane amphibians dependent on snowpack for breeding and foraging habitat.

In chapter 2, I examined how *R. luteiventris* vital rates varied in relation to climate variables over the first nine years of the study. I examined a suite of winter and summer climate variables that could be important to amphibian persistence, and found that breeding probability, juvenile and adult survival were best predicted by indices of winter severity including peak snowpack and winter length. When impacts on individual vital rates were combined into a matrix model to examine effects on population growth rate, I found that years with higher peak snowpack and longer winters had lower asymptotic growth rates than years with milder winters. These results suggest that a warming climate could benefit amphibian populations in these high-elevation environments where individuals experience long, harsh winters.

One of our great challenges as ecologists will be to forecast how changes in both the mean and variability of climate conditions will affect populations and species in the future (Clark et al. 2001). Bayesian statistical methods provide a natural framework for forecasting population viability under various climate scenarios (Ellison 2004, Clark 2005). In chapter 3, I further examine the impacts of climate change on this *R. luteiventris* population using Bayesian capture-recapture analysis to estimate vital rates and relate these to variation in snowpack over ten years. I forecasted the effects of changing mean and variance in snowpack on frog population viability using matrix projection models. I found that decreases in mean snowpack increase population viability, and that increases in snowpack variance have little effect on viability. These findings agree with a meta-analysis by Morris et al. (2008), who found that long-lived species (perennial plants and vertebrates) are more resistant to changes in environmental variation than short-lived species (annual plants and insects). My results suggest that focusing on changes in mean conditions may often be sufficient for assessing the impacts of climate on population viability for many amphibians. Finally, my results reiterate that for a species living at the edge of its elevational range and physiological tolerances (Deutsch et al. 2008), a decrease in winter severity as projected by climate models may be beneficial, at least in the short term, and provided suitable habitats remain intact.

While results from chapters 2 and 3 show a relationship between climate variables and juvenile and adult survival rates, most studies on the effect of weather variability on pond-breeding amphibians have examined the impacts of environmental variation on the larval stage and on recruitment potential (e.g. Semlitsch et al. 1996). In chapter 4, I examined recruitment dynamics in this population of *R. luteiventris*. I investigated how different breeding pond types contribute to recruitment on different years, and explored whether heterogeneity in pond hydroperiod on the landscape had the potential to stabilize recruitment and population dynamics. Overall, ponds with different hydroperiods showed contrasting dynamics among years, with ephemeral ponds producing more metamorphs on cool years and permanent ponds producing more metamorphs on hot years. As a result, we never witnessed recruitment failure at the population level, even though most ponds experience at least one year of recruitment failure. Net recruitment and stochastic population growth rate were highest in a hypothetical scenario containing only longer

hydroperiod ephemeral ponds, but variability in recruitment was lowest in the scenario with all ponds. These results suggest that the presence of a diversity of hydroperiods on the landscape may reduce variability in amphibian recruitment.

Through these analyses, I have been able to determine some of the relationships between climate variables and vital rates in the Columbia spotted frog, and then use population models to explore how future changes in climate or habitat could affect the viability of this population. These results add to our understanding of how climate variation may influence *Rana luteiventris* dynamics in montane environments, but also provide a demographic backdrop for determining which factors might affect other amphibian populations and species in diverse mountain environments. By describing some drivers of amphibian population dynamics over 10 years in one system while exploring factors that may be broadly important for montane amphibians, I have attempted to use the demography of one system to identify general patterns. Bjornstad and Grenfell (2001) may state it best:

For population ecology, the wedding of long-term studies with theory forces scientists to juggle two apparently incompatible aims: to understand any system, we need to appreciate its idiosyncrasies; to encompass broad patterns, we need to extract generalities. The current challenge [...] is this, to simultaneously accommodate and transcend natural history.

Long-term, demographic studies of amphibians in a variety of habitats and ecosystems can help us understand general relationships between environmental variability and population change, determine the impact of variation in different life stages on population dynamics, and decide which populations and species warrant conservation attention.

CHAPTER 2
DECREASED WINTER SEVERITY INCREASES VIABILITY OF A MONTANE
FROG POPULATION

Abstract

Many proximate causes of global amphibian declines have been well documented, but the role that climate change has played and will play in this crisis remains ambiguous for many species. Breeding phenology and disease outbreaks have been associated with warming temperatures, but, to date, few studies have evaluated effects of climate change on individual vital rates and subsequent population dynamics of amphibians. We evaluated relationships between local climate variables, annual survival and fecundity, and population growth rates from a nine-year demographic study of Columbia spotted frogs (*Rana luteiventris*) in the Bitterroot Mountains of Montana, USA. We documented an increase in survival and breeding probability as severity of winter decreased. Therefore, a warming climate with less severe winters is likely to promote population viability in this montane frog population. More generally, amphibians and other ectotherms inhabiting alpine or boreal habitats at or near their thermal ecological limits may benefit from the milder winters provided by a warming climate as long as suitable habitats remain intact. A more thorough understanding of how climate change is expected to benefit or harm amphibian populations at different latitudes and elevations is essential for determining the best strategies to conserve viable populations and allow for gene flow and shifts in geographic range.

Introduction

Amphibian populations are declining around the globe at an alarming rate (Alford and Richards 1999, Houlihan et al. 2000, Stuart et al. 2004), and climate change now figures prominently as a potential interactive driver of some of these declines (Pounds and Crump 1994, Corn 2005, Pounds et al. 2006). A shift to earlier breeding phenology has been documented in a number of species (Beebee 1995, Forchhammer et al. 1998, Reading 1998, Blaustein et al. 2001, Corn 2003), but this shift is not universal across species and has not been tied to population-level consequences. Other work has associated climatic conditions with disease-related declines in the Neotropics (Pounds and Crump 1994, Pounds et al. 2006), yet no mechanisms have been definitively linked to these correlations (Lips et al. 2008, Rohr et al. 2008). Reading et al. (2007) showed a decrease in adult female body condition and survival in a population of common toads (*Bufo bufo*) that corresponded with an increase in average annual temperatures. However, these demographic changes were not explicitly linked to changes in population size over time. Kiesecker et al. (2001) showed that disease, UV-B, and climate change could interact to increase embryo mortality in western toad (*Bufo boreas*) populations, yet these populations have not declined. This increased pre-metamorphic mortality may not be sufficient to cause otherwise increasing populations to decline in the long term. Alternatively, it may be that conditions in short-term or lab-based studies are not always representative of long-term patterns in natural populations. To determine mechanisms of population change, we first need to know which vital rates are affected by changes in climate, and then how these changes affect population dynamics.

The effects of climate change on growth and survival are particularly relevant for amphibian species in high elevation temperate ecosystems, where individuals are exposed to extreme and variable temperatures (e.g. Carey 1978). In these environments, amphibians are active at a wider range of temperatures than closely related species inhabiting lower elevations (Wells 2007). In general, juveniles and adults in high elevation temperate environments must reproduce and acquire resources over much shorter growing seasons than low elevation individuals. Similarly, tadpoles must be able to develop and metamorphose over a short season or survive long cold winters. In these

environments, longer growing seasons due to climate warming may allow more time for adults, juveniles, and tadpoles to grow and acquire resources. Winter severity may decrease, reducing winterkill due to freezing or hypoxia, which can be a major cause of mortality in these systems (Bradford 1983, Tattersall and Boutelier 1997). However, reduced precipitation and a warm environment could result in less water in these high-elevation landscapes, which may negatively impact amphibian species that rely on ephemeral pools for reproduction and foraging. Additionally, amphibian populations and species that are adapted to a colder thermal regime in alpine systems may have physiological constraints that prevent adaptation to an increase in temperature (Bernardo and Spotila 2006). With climate change models for the western United States predicting a reduction in snowpack, as well as increased variability in precipitation levels (MacCracken et al. 2001, Hamlet et al. 2005), understanding the role of these climate variables in the growth and survival of high-elevation populations of amphibians is critical to predicting future impacts of climate change on amphibians.

We evaluated relationships between annual vital rate estimates, estimates of asymptotic population growth rate, and local climate variables in a high elevation population of a temperate pond-breeding frog species, the Columbia spotted frog (*Rana luteiventris*). To evaluate these relationships, we used both mark-recapture and demographic analyses. A longstanding principle of demography is that not all vital rates are equally important for population dynamics. For example, large changes in annual recruitment, which are commonly documented in amphibians, tend to have less impact on population growth rates than relatively small changes in post-metamorphic survival rates (Biek et al. 2002). We examined variation in survival, growth, and recruitment in relation to summer and winter climate variables. We then used matrix models to calculate asymptotic growth rate (λ) for each set of annual vital rates (Leslie 1945, Leftkovich 1965, Caswell 2001) and related λ to these climate variables using linear regression. Our results advance our understanding of how climate change may affect amphibian populations, and have implications for the conservation of other temperate amphibian species occupying alpine and boreal habitats.

We conducted our study in the Little Rock Creek Basin, found in the Selway-Bitterroot Wilderness approximately 16 km south of Hamilton, Montana, USA. This

drainage is composed of two glacial cirques. Our analyses were focused on the upper basin (2200 m), which is delineated by glacial headwalls (Figure 2.1). Although this upper basin contains multiple breeding and foraging sites, they function as one population (Funk et al. 2005). The basin contains requisite habitats for *R. luteiventris* overwintering, breeding, and summer foraging, and is fishless (Figure 2.1). We have not tested for the presence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Bd) in this population, but Bd is widespread in Montana and has been detected in amphibians within a few miles of this watershed (Maxell 2009). However, no mortality events were noted in this watershed, no local or broad-scale declines have been detected for *R. luteiventris* in western Montana during the course of this study (Maxell 2009), and *R. luteiventris* is known to have skin peptides that are highly resistant to Bd (Rollins-Smith et al. 2002). Therefore, we believe that common culprits for amphibian declines at high elevation sites (i.e., introduced fish and disease, Knapp and Matthews 2000, Muths et al. 2003) do not complicate our analyses. We monitored all life stages of *R. luteiventris* from 2000 to 2008 and related these demographic data to climate data collected at a nearby weather station. Climate variables included (1) peak snow-water equivalency (hereafter “SWE”, a common measure of snowpack), (2) winter length, (3) end of winter Julian date (hereafter “last day of winter”), (4) summer length, and (5) growing degree days (see Methods for complete description of climate variables).

Results

Climate variables

During the 9 years of our study SWE ranged from 67-135 cm, winter lengths varied by 41 days, last day of winter varied by 33 days, summer length ranged from 84-120 days, and growing degree days ranged from 431-648 days. There were no trends in any of the climate variables over the study period. The range of SWE falls within the historical range of peak SWE at this station (46 to 171 cm) and average peak SWE for the length of our study is identical to the historical average (101 cm). Therefore, the range and magnitude of variability in climate variables seen in our study captures what has been recorded historically. Winter variables were correlated with each other ($R^2 > 0.62$), as were

summer variables ($R^2=0.66$), but winter variables were not correlated with summer variables.

Relationships between climate and vital rates

Breeding probability was inversely related to the length of the previous winter ($p=0.002$; Figure 2.2). There was no relationship between breeding probability and either of the summer climate variables. There was no relationship between survival to one year of age and any of the winter or summer climate variables.

Survival and transition probabilities depended on winter severity. Capture-recapture data for 4279 individual frogs captured over nine years were analyzed using program MARK (White and Burnham 1999), with climate variables included as group covariates in various combinations. Model selection results for the capture probability models indicated that probability of initial capture (p) and probability of recapture (c) varied both across years and among life stages. Therefore, we used this capture probability structure in all subsequent transition and survival models. Capture probabilities ranged from 4-50%, depending on the year and the life stage. Models with SWE and last day of winter were far better supported than any other candidate models (AIC weight= 0.999, model likelihood=1.0, 93 parameters). In these models, an increase in SWE was associated with a decrease in survival for juvenile and adult stage classes (Figure 2.3). Juvenile frogs showed the strongest relationship with variation in SWE ($\beta=-0.042 \pm 0.005$ SE), but the effect was also significant in adult females ($\beta=-0.037 \pm 0.011$ SE) and adult males ($\beta=-0.051 \pm 0.012$ SE). There was no relationship between SWE and survival for subadult females ($\beta=-0.023 \pm 0.018$ SE).

SWE was inversely related to transition from juvenile to subadult female or male ($\beta=-0.029 \pm 0.007$ SE) and transition from juvenile to adult female ($\beta=-0.081 \pm 0.024$ SE). There was no relationship with transition from subadult to adult female ($\beta=0.015 \pm 0.015$ SE).

Demographic analysis

We used survival and transition parameter estimates from a time-varying capture-recapture model to calculate annual vital rates (Table 2.1) to parameterize female-based,

post-birth pulse Leftkovich matrix models for each year of the study (Figure 2.4). Across these matrices, estimates of λ were higher in years with lower SWE ($p=0.023$; Figure 2.5a), tended to be lower in years with a later last day of winter ($p=0.185$; Figure 2.5b), and were not related to winter length ($p=0.611$).

Discussion

Parameters that describe winter severity were negatively correlated with survival, transition, and breeding probabilities in this high-elevation *R. luteiventris* population. These relationships resulted in higher estimated λ in years with earlier ending winters and lower snowpack. Climate change predictions for the Rocky Mountains suggest that snowpack will continue to decrease and snowmelt will occur at an increasingly earlier date (Adam et al. 2009). Because effects of decreased winter severity were uniformly positive, our results indicate that this climate trend will increase population viability of *R. luteiventris* in this mountain system. Researchers have typically assumed that if climate change affects amphibian species, the outcome will be negative: rarely do we allow ourselves to consider that global warming may confer benefits to some species. Contrary to much of what has been discussed in the literature (e.g. Corn 2005, McMenamin et al. 2008, but see Scherer et al. 2008), these results suggest that under certain circumstances, a warming climate may be helpful to some amphibian populations, particularly those that live in harsh conditions at the edge of their thermal tolerances. A reduced winter severity could benefit high and low elevation populations of *R. luteiventris* alike, though failures in recruitment due to drying of breeding habitat may overwhelm positive effects of warmer winters in some populations, especially at lower elevations and latitudes.

There are several reasons that we might expect *R. luteiventris* juvenile and adult survival in these systems to increase with decreased snowpack. At high elevations, this species spends up to eight or nine months overwintering in lakes and permanent ponds, where its metabolism slows considerably. Hypoxic conditions have been shown to be an important source of mortality for overwintering amphibian populations in high elevation systems (Bradford 1983). Winters with above-average precipitation had thicker ice covering on lakes used by mountain yellow-legged frogs (*R. muscosa*) for overwintering,

resulting in an increase in the rate of oxygen depletion (Bradford 1983). Radio-tagged *R. luteiventris* overwintering in low elevation ponds in eastern Oregon all remained in shallow water within 1 m of shore, but they moved to microhabitats with higher water temperatures or dissolved oxygen concentrations (Bull and Hayes 2002). Juvenile frogs in our system may be more likely to overwinter in shallow lakes than adult frogs, because we find them in higher concentrations at these water bodies during summer surveys and they may not be able to locate larger water bodies. Overwintering in shallow waters may expose juveniles to more hypoxic conditions in the winter than adult frogs and likely explains the strong negative associations between SWE and juvenile survival and transition rates.

Years with higher snowpack tended to have snow on the ground for a longer time period and later into the spring. As a result, it is also possible that high winter severity depletes the fat reserves of frogs and leads to greater mortality rates. The later the last day of winter, the longer frogs remain in overwintering sites, and the later insect prey emerge. This delay in foraging and depletion of fat reserves may contribute to the negative relationship between SWE and transition probability to larger age classes, which we observed for juveniles. The depletion of fat reserves may be less important for subadult and adult frogs and may explain why we do not see a relationship between their transition rates and winter severity variables.

In all years of our study, asymptotic estimates of λ were less than one, suggesting a declining population. This agrees with our observation that this population has generally declined over the nine years of the study, from 997 frogs in 2000 to 700 frogs in 2008. A decreasing population growth rate during most years is consistent with population growth patterns measured in other amphibian populations (Pechmann et al. 1991, Semlitsch et al. 1996). However, in contrast to our asymptotic estimates of λ , population size fluctuated considerably among years, with some large increases in population size between years. Therefore, our asymptotic analyses do not capture the range of stochastic fluctuations observed in the field. For example, it may be that population dynamics are partly driven by intermittent pulses of recruitment that were not captured in our nine-year study. As such, we cannot discern whether a warming climate

will actually lead to a viable population in the long term. However, this caveat does not change the result that we observed uniformly positive effects of climate warming.

The results of this study highlight the need for amphibian decline research to focus on environmental variables affecting post-metamorphic survival parameters in addition to those affecting recruitment and larval survival (Biek et al. 2002). While repeated failures in recruitment due to drought may critically affect the persistence of some populations, changes in juvenile and adult survival could have a greater effect on population growth and viability in many amphibian species. Though we saw high annual fluctuations in the number of egg masses laid and successful metamorphs produced in this system (Table 2.1), differences in juvenile and adult survival rates, particularly survival of juvenile frogs, drove the differences we observed in λ across years. In our population, juveniles and adults have greater variance in vital rates among years, as well as higher elasticities in those rates (Table 2.2). Vital rates for *R. luteiventris* juveniles and adults are therefore disproportionately important to the dynamics of this population. Long-term monitoring of amphibian populations has typically focused on variation in recruitment or breeding population size (e.g. Semlitsch et al. 1996). Past research has focused on the effect of weather variability on production of juveniles, which can depend heavily on rainfall in some regions (Daszak et al. 2005). However, it is less clear to what extent this measured variation in annual recruitment affects long-term population dynamics in these systems, because recruitment dynamics are rarely placed in a population-level context (but see Biek et al. 2002, Vonesh and De La Cruz 2002).

Although there was variation in annual recruitment, we never witnessed complete failures in recruitment, even in the driest years. Every year, individuals breed in both ephemeral and permanent water bodies. On cool and wet years, most successful recruitment comes from ephemeral ponds, which persist throughout the growing season, while tadpoles from colder permanent ponds do not have enough time to reach metamorphosis. However, in hot, dry years the majority of recruitment comes from permanent ponds, because ephemeral ponds dry up before animals are able to successfully metamorphose. Therefore, it may be that frogs in our study system have the ability to compensate recruitment in dry years through the diversity of breeding sites available across this glacial basin. The presence of a diversity of unimpacted breeding

sites in these types of systems may be important for amphibian populations to persist in the face of climate change. In high-elevation systems where amphibians are negatively impacted by introduced fish (e.g. Knapp and Matthews 2000), reduction of hydroperiod in ephemeral, fishless breeding sites may be much more important to species persistence. Because this system is fishless, amphibians are able to breed and forage in a greater diversity of habitats than in areas where fish and other predators restrict populations to ephemeral ponds and wetlands.

Our analyses suggest that for amphibians and other ectotherms living at temperatures below their physiological optima, such as those found at high elevations or latitudes, global warming may have neutral or positive impacts, at least under some climate change scenarios (Deutsch et al. 2008). However, outcomes will surely depend on how quickly and to what extent the climate changes. It is possible that changes in temperature and precipitation may only have benefits to a certain point, after which habitat will be negatively affected, possibly by changing community structure or reducing heterogeneity of breeding sites. At the extreme, if ongoing climate change eventually makes high elevation and latitude sites unsuitable, species may have no other refugia to move to (Wake and Vredenburg 2008). Both the positive and negative impacts of climate change on species will need to be reassessed as climate change progresses to determine whether such a tipping point will be reached.

We have shown how individual amphibian vital rates and asymptotic population growth rates vary with summer and winter climate variables in a high elevation population of the Columbia spotted frog. These results unambiguously demonstrate that earlier ending winters with lower snowpack in this system lead to higher survival rates, higher probabilities of breeding, and higher population viability. Most research on amphibian declines assumes that climate change will have negative impacts on already vulnerable species, yet we show that this may not be the case for alpine and boreal amphibian populations currently persisting in harsh environments. This provides a unique perspective to the role of climate change in amphibian declines in temperate ecosystems. Previous shifts in climate have had dramatic effects on the distribution, genetics, and ecology of numerous temperate amphibian species (Vieites et al. 2007, Funk et al. 2008, Goebel et al. 2009). The impacts of ongoing climate change will vary across the globe,

and this is likely to increase the viability of some species while being detrimental to others. In order to best conserve viable populations, promote gene flow, and allow for shifts in geographic range in the face of climate change, developing a more comprehensive understanding of how climate change is expected to benefit or harm amphibian populations at different latitudes and elevations is imperative. Ultimately, research that simultaneously evaluates the effects of climate change on multiple vital rates is key to disentangling which population processes may be affected by a warming climate.

Methods

Population surveys

We collected demographic data from 2000-2008. We conducted systematic searches for egg masses in late spring. We searched all shallow water environments for egg masses over several weeks and recorded counts of egg masses at each water body. We calculated multi-year estimates and variances in clutch size for *R. luteiventris* at most of the breeding ponds using volumetric displacement (Morris and Tanner 1969, Corn and Livo 1989, Werner et al. 1999). During the egg mass surveys, we also measured the snout-vent length of females present at the breeding site to determine the range of size of breeding females. These data were used to distinguish breeding adult females from subadult females in our demographic analyses.

We used a robust design capture-mark-recapture method to monitor juvenile and adult frogs (Pollock 1982). For this method, we captured animals for multiple consecutive secondary sessions (days) within the primary sampling period (year). Across the secondary sessions, we assumed that the population was closed to immigration, emigration, births, and deaths. This closure allowed population size, corrected for capture probability, to be estimated. Between primary sessions, the population was open to gains and losses, and survival was estimated using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). We monitored three female life stages; juveniles were frogs that were too young to be sexed, subadults were frogs that were larger than the size at which secondary sex characteristics of males were present but smaller than the smallest

documented breeding female, and adults were frogs large enough to breed. During each primary sampling period, we systematically surveyed all the ponds and lake shores in the basin each year and captured animals by hand or net. We individually marked animals by clipping unique combinations of toes using an alphanumeric coding system (Waichman 1992) and weighed and measured snout-vent length. We also recorded the general location of all new and recaptured animals at each session.

Climate data

Climate data were from the Twin Lakes SNOTEL site (<http://www.wcc.nrcs.usda.gov/snow>), located 18 km northwest of the upper Little Rock Creek basin at 1950 m elevation. This SNOTEL site is located within the same mountain range, and has similar aspect and elevation to our study area. We used data on SWE and temperature as annual covariates. SWE is the depth of water that would theoretically result if one were to melt the entire snowpack instantaneously, and is commonly used as a measure of snowpack (e.g. Hamlet et al. 2005). We used the peak SWE value recorded for each year in our analyses. We calculated the end of winter Julian date as the last day that SWE was recorded in the spring. Then we calculated the number of consecutive days with snow on the ground (winter length) and the number of consecutive days without snow on the ground (summer length). Finally, we calculated the cumulative number of days throughout the summer that the temperature was above 10 degrees C (www.ipm.ucdavis.edu/WEATHER/ddconcepts.html), which represented growing degree-days. The value of 10 degrees C was used as a relative physiological zero for the species, temperatures below which we would not expect to see growth. Though it is unlikely that this temperature is the true physiological zero, which is unknown, this cutoff allows for comparison of relative growing season length across years. We used winter length, last day of winter, and SWE data as indices of local winter severity, and used growing degree days and summer length as indices of summer intensity.

We tested for relationships among all climate variables over the nine years of the study using principal components analysis. The first two axes explained 89% of the variance. Axis 1 (56% of variance) was correlated with winter severity ($r > 0.85$ for all winter variables; $r < 0.53$ for all summer variables). Axis 2 (33% of variance) was

correlated with summer variables ($r > 0.75$ for all summer variables; $r < 0.40$ for all winter variables). Therefore, we can clearly distinguish winter from summer variables, but cannot statistically separate individual winter or summer variables. However, we chose to analyze all variables individually in order to discuss hypothetical mechanisms associated with each variable.

Breeding probability and pre-juvenile analysis

We estimated breeding probability as the number of egg masses deposited each year divided by the number of adult females that year (closed population estimate from the mark-recapture data). We estimated survival from eggs to one year for each year by dividing the number of one year-old frogs by the number of eggs laid the previous spring (average number of eggs per mass multiplied by the number of egg masses deposited). We used an average of 812 eggs/mass (assumed to be equivalent to 406 female embryos given a 1:1 sex ratio) from our clutch size estimates for all years of the analysis. To estimate the number of one year-old frogs, we isolated the capture histories for all animals 34 mm snout-vent length and smaller each year and then calculated the abundance of those animals using Huggins closed population models in program MARK (White and Burnham 1999).

We used weighted linear regressions to examine the dependence of breeding probability and first year survival on the five climate variables described above. Additionally, we examined relationships between number of egg masses deposited and climate variables.

Post-metamorph analysis

We analyzed capture data of juveniles, subadults, and adults in program MARK using closed robust design, multi-state mark-recapture models (Hestbeck et al. 1991, White et al. 2006). The “states” in our models were frog life stages: juvenile, subadult female, adult female, and adult male frogs. These models provided parameter estimates and variances for age- and sex-specific survival, transition rates between life stages, and population size for each year (Kendall 1998, Morris and Doak 2002). Survival, transitions, and the covariates were our primary parameters of interest, but we first

evaluated models of capture probability (p) and recapture probability given initial capture (c) to avoid bias and imprecision in the survival estimates (Lebreton et al. 1992). We evaluated the following capture probability models: (1) p and c were constant across years but varied among age classes, (2) p and c varied across years but did not vary among age classes, (3) p and c varied across years and differed between juvenile and adult age classes, but not within adult age classes, and (4) p and c varied across years and among all age classes. For these models, survival and transition rates were held constant.

We modeled age-specific survival and transition probabilities to examine their variation in relation to snowpack, winter length, end of winter, summer length, and growing degree-days. First, we examined how each of these variables related to survival in each age class individually. Then, we examined whether additive models containing multiple climate variables improved the fit. For each model structure, we estimated models where (1) the effect of covariates was the same for each age class and (2) the effect of covariates was different for each age class, resulting in a total of 16 basic models (Table 2.3). Once we tested these models, we also examined two additional models where (1) male survival was equal to female survival and (2) all adult age classes had the same survival. For these models, we kept transition probabilities constant. Once we had modeled survival, we examined how climate variables affected growth using the structure from the best survival model. We examined the same suite of variables for growth as we did for survival. In addition to the 16 models described above, we estimated models where probability of transitioning from juvenile to subadult was equal to transitioning to male (Table 2.3). We evaluated all models for relative support and ranked them using Akaike's Information Criterion (AICc) (Akaike 1973, Burnham and Anderson 2002).

Demographic analysis

We determined the demographic consequences of changes in climate variables on the population growth rate using matrix models. We constructed female-based post-birth pulse stage-structured matrix models using the average vital rates estimated for each year (Table 2.1, Figure 2.4). Survival and transition parameters came from the best time-dependent model ranked using AICc. We tested four time-dependent models where

survival varied by both year and life stage: (1) survival varies in the same way for each life stage in each year; (2) juvenile survival varies differently from subadult, male, and female survival, which vary in the same way each year; (3) male and female survival vary in the same way, but both juvenile and subadult survival vary differently in each year; and (4) all life stages varied differently from each other in each year. The best model varied transitions for each life stage and year, but transition probability from juvenile to subadult was equal to that for juvenile to male. Capture and recapture probabilities varied by year and life stage for all models. Other vital rates were calculated as described above. For each year, we calculated asymptotic λ , the rate at which a population would increase if vital rates remained constant over time. This metric represents an integrative measure of population performance. We then used linear regression of the asymptotic lambda values for each year against values of climate variables for each year to see if this integrative metric showed similar patterns to individual vital rates.

Table 2.1. Annual vital rate estimates (± 1 SE) for *R. luteiventris* and peak SWE for each winter. Vital rates were estimated using a time-dependent model where survival and transition rates differed by life stage and year.

Year	SWE (cm)	Annual Vital Rate Estimates								
		Breeding Probability (P_b)	Survival from egg to one year (S_0)	Juvenile Survival (S_j)	Subadult Survival (S_s)	Male Survival (S_m)	Female Survival (S_f)	Transition from Juvenile to Subadult or Male (P_{js} or P_{jm})	Transition from Juvenile to Female (P_{jf})	Transition from Subadult to Female (P_{sf})
2000-2001	67	-	0.0089	0.70 (0.02)	0.33 (0.16)	0.76 (0.03)	0.67 (0.04)	0.28 (0.01)	0.043 (0.01)	0.64 (0.04)
2001-2002	118	0.427	0.0081	0.38 (0.02)	0.65 (0.06)	0.77 (0.03)	0.67 (0.04)	0.36 (0.01)	0.061 (0.01)	0.72 (0.03)
2002-2003	117	0.557	0.0006	0.40 (0.02)	0.96 (0.12)	0.73 (0.03)	0.63 (0.03)	0.13 (0.02)	0.016 (0.003)	0.39 (0.04)
2003-2004	97	0.703	0.0032	0.61 (0.04)	0.56 (0.11)	0.72 (0.03)	0.62 (0.04)	0.29 (0.02)	0.044 (0.01)	0.64 (0.04)
2004-2005	68	0.631	0.0089	0.51 (0.03)	0.71 (0.09)	0.79 (0.05)	0.70 (0.06)	0.15 (0.02)	0.020 (0.004)	0.44 (0.05)
2005-2006	125	0.640	0.0013	0.13 (0.01)	0.61 (0.09)	0.47 (0.05)	0.36 (0.04)	0.21 (0.03)	0.030 (0.01)	0.55 (0.05)
2006-2007	89	0.568	0.0022	0.42 (0.06)	0.83 (0.16)	0.61 (0.06)	0.50 (0.07)	0.30 (0.04)	0.047 (0.01)	0.66 (0.05)
2007-2008	135	0.587	0.0094	0.25 (0.04)	0.36 (0.08)	0.44 (0.05)	0.34 (0.05)	0.06 (0.02)	0.0078 (0.003)	0.24 (0.07)

Table 2.2. Vital rate mean, variance, and elasticity values across the nine years of our study.

Vital Rate	Mean value	Relative variance	Elasticity
Breeding probability (P_b)	0.587	<i>0.0265</i>	<i>0.146</i>
Survival from egg to one year (S_0)	0.00533	<i>0.00279</i>	<i>0.146</i>
Juvenile survival (S_j)	0.426	0.123	0.248
Subadult survival (S_s)	0.625	0.127	0.203
Female survival (S_f)	0.561	0.0678	0.403
Transition from Juvenile to Subadult (P_{js})	0.223	0.0513	0.0962
Transition from Juvenile to Female (P_{jf})	0.034	0.00926	0.0154
Transition from Subadult to Female (P_{sf})	0.534	0.0973	0.0393

Vital rates for juvenile and adult survival and transition probabilities were corrected for sampling variation using White's variance discounting method (White 2000, Morris and Doak 2002). The relative variance is the corrected variance across years, standardized across the ranges of all vital rates (relative variance = corrected variance / (mean vital rate * (1-mean vital rate))). The elasticity of each vital rate represents the proportional effect of changes in each vital rate on population growth rate. Vital rates for juvenile and adult survival have higher variance and elasticities (bold) than pre-juvenile vital rates (italicized). Therefore, changes in juvenile and adult vital rates have a greater effect on the population growth rate *and* are more likely to change than changes in breeding probability or survival to age one.

The low variability that we see in pre-juvenile survival is contrary to most demographic studies carried out on individual ponds, which show pre-juvenile survival to be highly variable. If we were to examine variability at the individual pond level, we would see higher variance at each pond. However, the low variability across ponds (i.e. at the population level) and relative constancy across the landscape help illustrate the importance of heterogeneity in pond hydroperiod of breeding ponds. Eggs laid in permanent waters do well in low snow years and those laid in ephemeral waters do well in high snow years.

Table 2.3. Model structures for assessing how climate variables relate to survival and growth parameters. For all models, we let p and c vary by both age class and time. We first estimated survival probabilities, keeping growth probabilities constant, and then estimated growth probabilities using the best model from the survival analysis. For transition models, we examined scenarios where all transitions were different and where probability of juvenile to male transition was equal to juvenile to subadult transition.

Winter variables	Summer variables
Stage+(SWE)	Stage+(summer length)
Stage+(end of winter)	Stage+(growing degree days)
Stage +(winter length)	Stage+(summer length+growing degree days)
Stage +(SWE +winter length)	Stage*(summer length)
Stage +(SWE +end of winter)	Stage*(growing degree days)
Stage*(SWE)	Stage*(summer length+growing degree days)
Stage*(end of winter)	
Stage*(winter length)	
Stage*(SWE +winter length)	
Stage*(SWE +end of winter)	

Figure legends

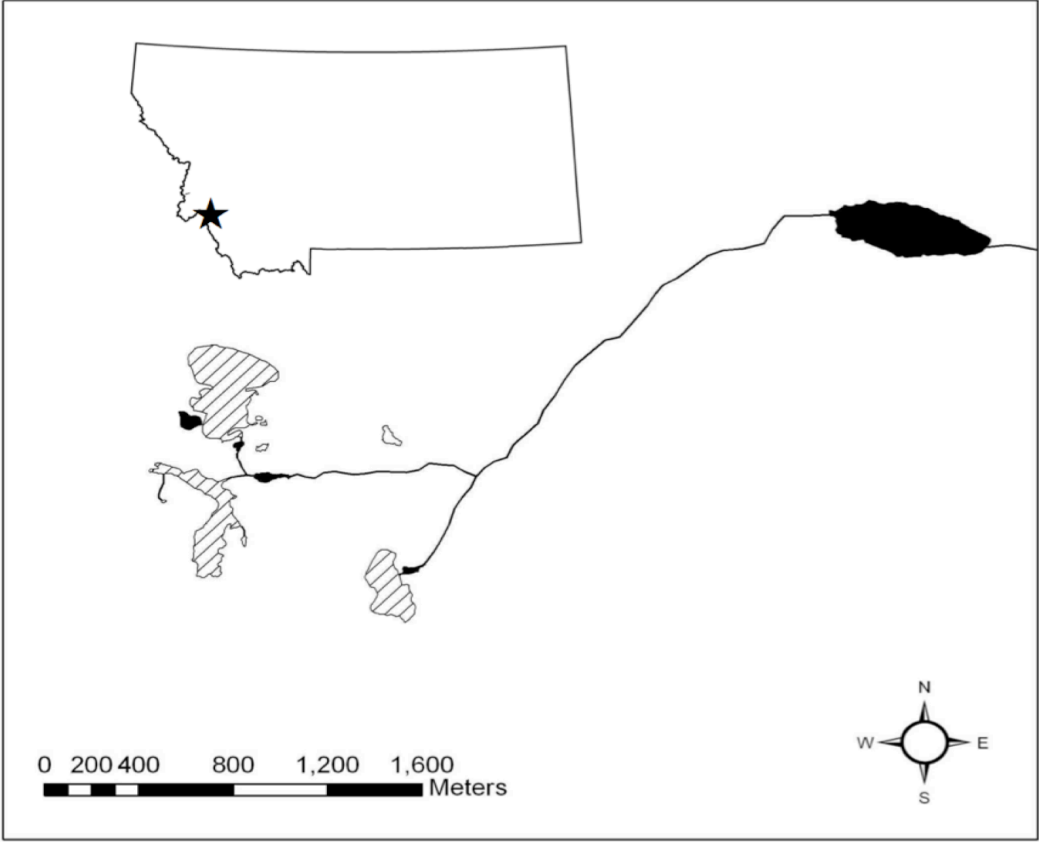
Figure 2.1. The Little Rock Creek drainage, Bitterroot Mountains, Montana, USA. All analyses were based on data collected in the upper basin. Habitat used by *R. luteiventris* includes: (1) permanent water bodies with no emergent vegetation used for summer foraging and overwintering (hatch marks); (2) permanent ponds and lakes with emergent vegetation used for breeding, foraging, and overwintering (solid); and (3) ephemeral ponds with emergent vegetation used for breeding and foraging (open).

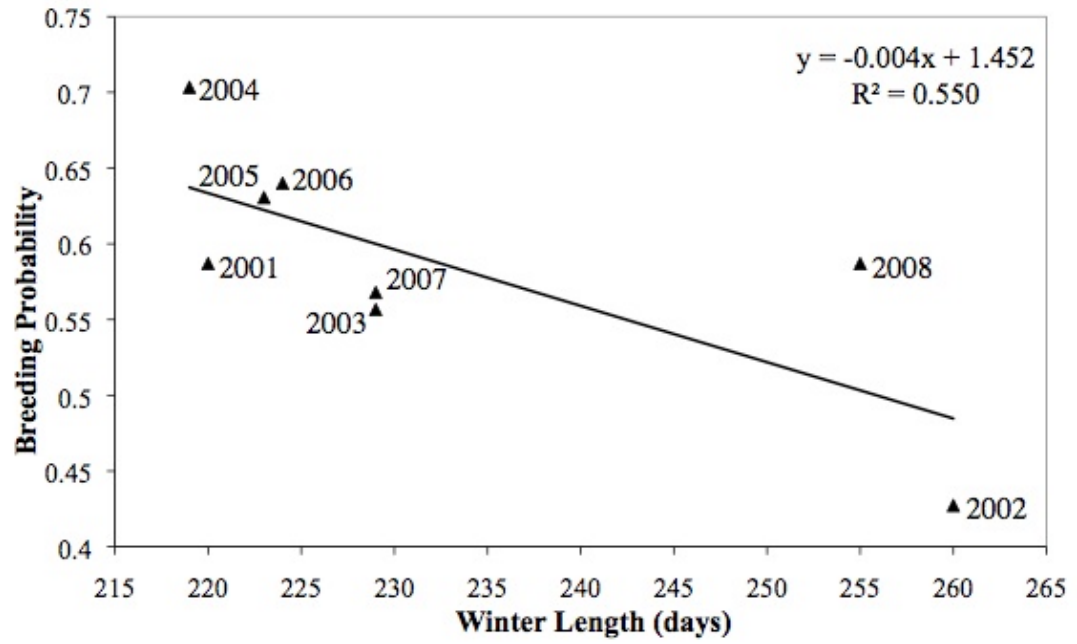
Figure 2.2. Linear regression of female breeding probability with length of previous winter. Longer winters were associated with lower breeding probabilities in the following spring ($p=0.002$).

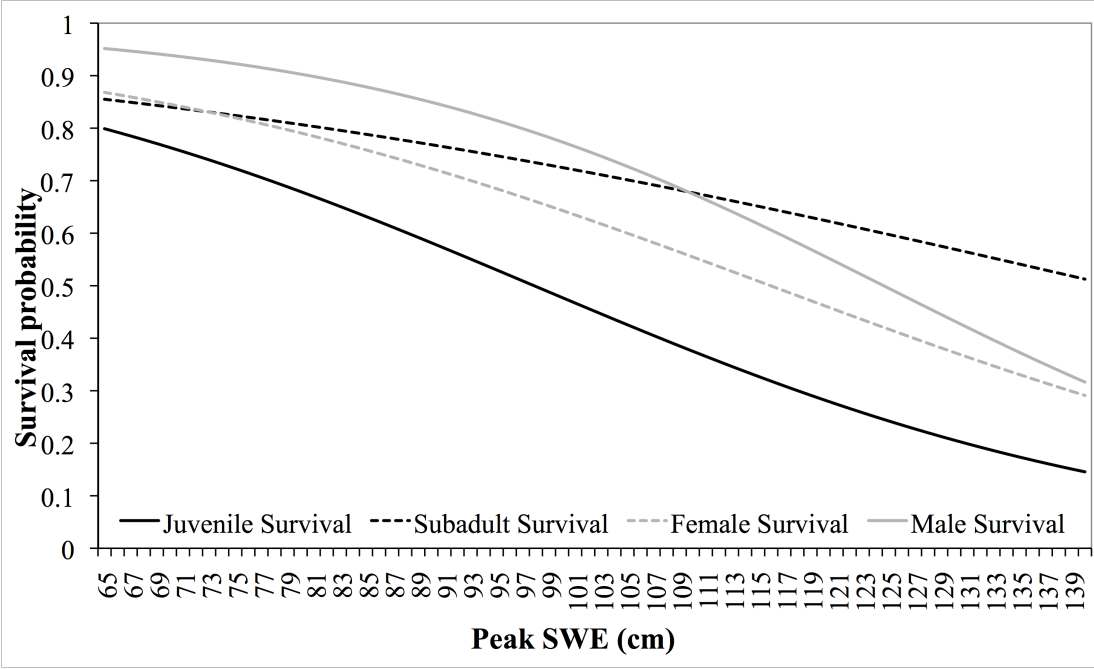
Figure 2.3. Relationship between stage-specific survival rates in *R. luteiventris* and SWE for four age/sex classes: juvenile, subadult female, adult male, and adult female. The lines are the predicted survival curves for different values of SWE from the top model.

Figure 2.4. Female-based, post-birth pulse matrix model for *R. luteiventris*. Each year, average values for survival, growth, and fecundity were used to calculate the asymptotic population growth rate. Average clutch size was 406 female eggs for all years based on measurements of clutch size.

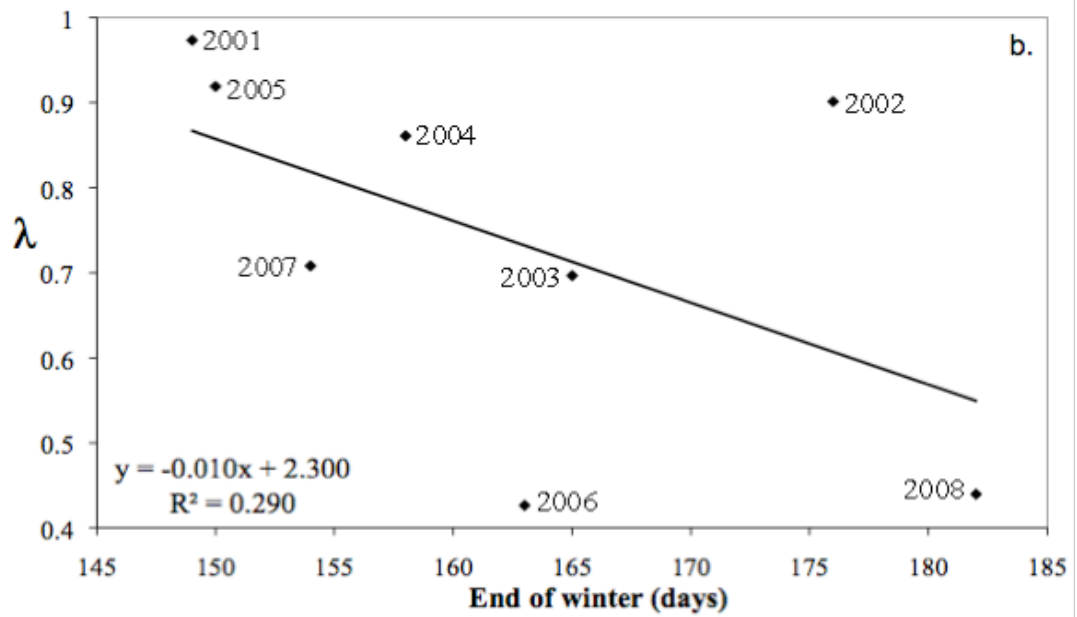
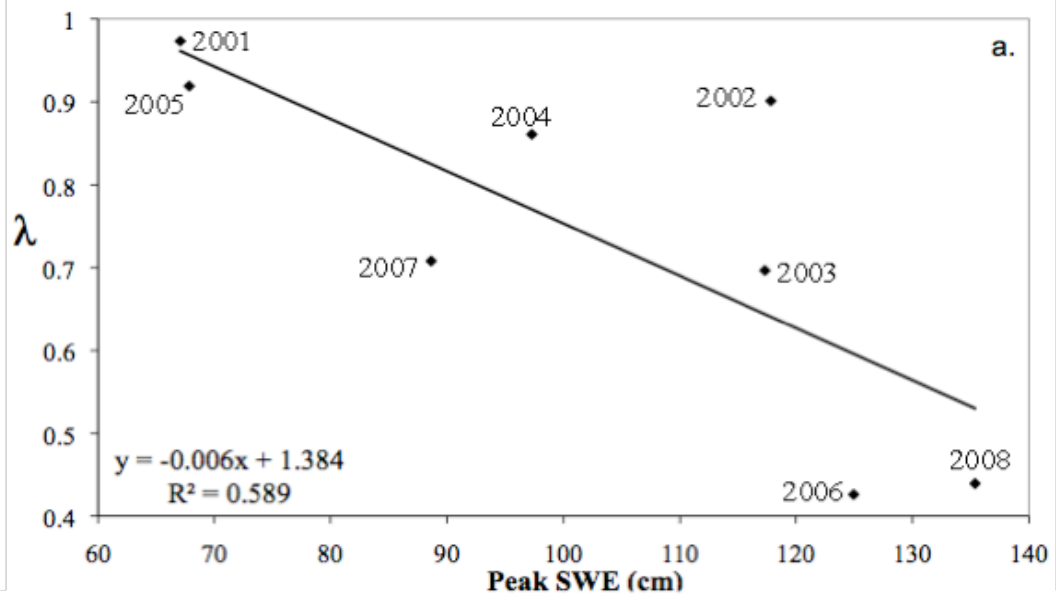
Figure 2.5. Linear regression of annual asymptotic λ values and winter variables, including (a) SWE ($p=0.021$) and (b) end of winter Julian date ($p=0.185$).







$$\begin{bmatrix} 0 & 0 & P_b * S_s * C_s & P_b * S_f * C_s \\ S_0 & P_{jj} * S_j & 0 & 0 \\ 0 & P_{js} * S_j & P_{ss} * S_s & 0 \\ 0 & P_{jf} * S_j & P_{sf} * S_s & S_f \end{bmatrix}$$



CHAPTER 3
FORECASTING EFFECTS OF CLIMATE CHANGE ON THE COLUMBIA
SPOTTED FROG (*RANA LUTEIVENTRIS*) USING BAYESIAN CAPTURE-
RECAPTURE MODELS

Abstract

Worldwide extinctions of amphibians are at the forefront of the biodiversity crisis, with climate change figuring prominently as a potential driver of continued amphibian decline. As in other taxa, changes in both the mean and variability of climate conditions may affect amphibian populations in complex, unpredictable ways. In western North America, climate models predict a reduced duration and extent of snowpack and increased variability in precipitation, which may have consequences for amphibians inhabiting montane ecosystems. We used Bayesian capture-recapture methods to estimate vital rates in a high elevation population of the Columbia spotted frog (*Rana luteiventris*) over 10 years, and then related these rates to interannual variation in peak snowpack. Population models based on snowpack during our study period predicted a strongly declining population. However, snowpack data from the recent past predicted a viable population. This difference was mostly due to changes in snowpack mean, not variance. Similarly, over a range of future scenarios, changes in mean snowpack had a greater effect on viability than changes in the variance of snowpack. Since vital rates in this species are highly variable and only some of the variation is explained by snowpack, mean changes in climate may have a greater effect on long-term dynamics of the population. However, for a given mean snowpack depth, increases in variability could change a population from increasing to decreasing. Therefore, both mean and variance in snowpack conditions can influence predictions of population viability, though future changes in snowpack are generally predicted to increase viability.

Introduction

Climate change has emerged as one of the greatest threats to global biodiversity, and ecologists and conservation biologists will be increasingly called upon to determine how a changing climate will affect individual species. Studies of climate change impacts have involved tracking changes in phenology (Root et al. 2003), distribution (Walther et al. 2002), survival (e.g. Post and Stenseth 1998, Wang et al. 2002), and interspecific interactions (e.g. Kaeriyama et al. 2004) in relation to climatic variables. Documenting changes in phenology and distribution is important, but we ultimately want to know whether changes in climate will affect the viability of plant and animal populations. Predicting changes in population viability is a fundamental challenge, because knowledge of demographic vital rates (i.e. survival, growth, and fecundity) is required, and the demographic research needed to quantify these parameters over appropriate time scales is logistically daunting. Research must also account for other stressors that may interact synergistically with climate change in complex, often non-linear ways.

The majority of attention has been focused on change in mean climate conditions (Payne et al. 2004, Stewart et al. 2004, Mote et al. 2005, Knowles et al. 2006), and some authors have begun to address how changes in mean climate conditions might affect wild populations (Post and Stenseth 1998, Wang et al. 2002, Scherer et al. 2008, Brodie and Post 2010, McCaffery and Maxell 2010). However, climate models also predict an increase in climatic variability (Easterling et al. 2000, MacCracken et al. 2001, Raisanen 2002, Watterson 2005), and fewer researchers have examined how changes in variability of climate across years might affect population viability and species distributions (but see Colchero et al. 2009, Zimmermann et al. 2009). In one of the few studies to look at variance in climate indices, Zimmerman et al. (2009) found that predictions of spatial distributions of tree species in Switzerland were improved by including climatic extremes in their models. In contrast, studies of two long-lived species found that after other factors were taken into account, mean changes in drought and precipitation were more important to population viability than changes in the interannual variation of those variables (Colchero et al. 2009, Jonzen et al. 2010). Determining to what extent changes in climatic variation affect our predictions of population viability relative to changes in

the mean is key to developing meaningful forecasts of climate change on individual species.

In this paper, we assess the importance of changes in the mean and variance of snowpack for *Rana luteiventris*, a frog species that inhabits the Rocky Mountains of western North America. Understanding the impact of climate change on amphibians is an issue of particular urgency: a third of all amphibian species are considered threatened, more than twice as many amphibians are critically endangered compared to mammals or birds (Stuart et al. 2004), and amphibian decline is considered evidence that the sixth mass extinction in the Earth's history is underway (Wake and Vredenburg 2008). Habitat destruction and disease are considered the principal causes of amphibian declines, but there is little doubt that climate change can and will interact with these factors to influence the rate and extent of declines (Corn 2005). However, we know relatively little about how specific changes in climate may affect the demography of individual amphibian populations. Demographic studies of amphibians are essential to determine which life stages are affected by various stressors, and how these impacts combine to affect population growth rates and viability (Biek et al. 2002, Vonesh and De La Cruz 2002, Govindarajulu et al. 2005).

Our study of Columbia spotted frog (*Rana luteiventris*) population viability is based on 10 years of demographic data from a high elevation population (McCaffery and Maxell 2010). From a mark-recapture analysis of the population in relation to a suite of winter summer climate variables, we found that juvenile and adult survival rates were inversely correlated with peak snowpack (McCaffery and Maxell 2010). Recent snowpack in western mountains has been reduced in volume and duration, a trend predicted to continue (Stewart et al. 2004), and one that has direct consequences for the hydrologic and temperature regimes of montane wetlands (McMenamin et al. 2008, Adam et al. 2009). This trend should increase *R. luteiventris* population viability. However, snowpack is also predicted to become more variable, the consequences of which are unknown.

To examine how this relationship with snowpack might affect population viability under historical and future climate scenarios, we estimated *R. luteiventris* vital rates using Bayesian capture-recapture methods, established relationships between vital rates and

snowpack, and simulated population growth under a variety of scenarios. Bayesian statistical methods provide a natural framework for examining relationships between climate variables and life history parameters, and for forecasting future effects of climate on amphibian populations (Wade 2000, Ellison 2004, Clark 2005). Parameters are expressed as probability distributions rather than point estimates, which allows a more explicit representation of uncertainty in the estimates and relates more naturally to forecasting. We used these probability distributions to simulate the distribution of population growth rates under future climate scenarios. We compared the sensitivity of population viability metrics to changes in mean snowpack versus variance in snowpack in a frog population with highly stochastic dynamics.

Methods

Study area and climate data

We conducted demographic monitoring of a Columbia spotted frog population in the Bitterroot Mountains of western Montana, USA from 2000-2009. Our study population was located at 2200 m in the Little Rock Creek drainage of the Selway-Bitterroot Wilderness. This basin is delineated by glacial headwalls, and the frog population here is isolated from other nearby populations (Funk et al. 2005). For a complete description of the study site, see McCaffery and Maxell (2010). We obtained precipitation data from the Twin Lakes SNOTEL site, located approximately 18 km northwest of our study site at 1950 elevation (www.wcc.nrcs.usda.gov/snow). We recorded the peak snow-water equivalency (hereafter “SWE”) for each year of our study. SWE is the depth of water that would result if the snowpack were melted instantaneously, and is a commonly used metric of snowpack that takes into account both the depth and the density of the snow. We also examined the mean and variance in peak SWE recorded at this site historically (1970-2000).

Vital rate estimation

In the spring, we searched all standing water bodies for egg masses one to two times a week for the duration of the breeding season. We determined the total number of

egg masses deposited annually across the basin. From 2000 to 2003, we estimated clutch size and variance in a range of egg masses across all breeding ponds using volumetric displacement (Morris and Tanner 1969, Corn and Livo 1989, Werner et al. 1999). To calculate the total number of eggs produced annually in each pond, we multiplied the number of egg masses for each pond by an average of 806 eggs/mass, the mean clutch size estimated from our volumetric displacement calculations. Egg mass counts were used to estimate breeding probability, and total egg abundance was used to estimate survival from egg to one year (see below).

Juvenile and adult frogs were captured in mid-summer using a robust sampling design (Pollock 1982). For this method, we captured animals for multiple consecutive secondary sessions (days) within the primary sampling period (year). Across the secondary sessions, we assumed that the population was closed to immigration, emigration, births, and deaths. This closure allowed population size, corrected for capture probability, to be estimated. Between primary sessions, we estimated survival and transitions among life stages. We monitored three female life stages; juveniles were frogs that were too young to be sexed, subadults were frogs that could be identified as female, but were smaller than the smallest documented breeding female, and adults were frogs large enough to breed. During each primary sampling period, we systematically surveyed all the ponds and lake shores in the basin each year and captured animals by hand or net. We individually marked animals by clipping unique combinations of toes using an alphanumeric coding system (Waichman 1992) and weighed and measured snout-vent length. From these surveys, we had ten-year capture histories for 4362 individuals.

We developed a software package in MATLAB that implements a Bayesian technique for estimating population vital rates from mark-recapture data with multiple life stages. The package is based on the approach described in Clark et al. (2005). Here, raw mark-recapture data are entered directly into the model, where two state vectors summarize the capture history for a given individual (Dupuis 1995). This model is developed for structured populations, where the population can be stratified by life stage at each time step (Dupuis 1995). These include a vector for the observed state of the individual (where a 0 is entered when the individual is not observed), and one vector for the true states at each sample date (which includes both the observed and unobserved

states). The first vector consists of raw data, and state values for the other vector are estimated as Bayesian posterior probabilities using a Markov chain Monte Carlo (MCMC) algorithm.

Our approach extends the methods described in Clark et al. (2005) because we incorporate a robust sampling design, which we implement by only estimating survival and transition probabilities between years. Within a year, survival was set to 1 and probability of transition to any other life stage than the current stage was set to 0. While frogs could have died within our secondary sampling sessions, this constraint on survival fit the assumptions of the robust design sampling method, and allowed us to easily calculate the annual survival estimates needed for the matrix population models. Recapture probabilities were estimated for each year and life stage. For all survival and transition estimates among years, we used uninformative priors. Thus, from our ten-year capture histories, we estimated posterior probability distributions for annual survival and transition parameters, and annual recapture probabilities.

We also used a Bayesian model to calculate annual breeding probabilities and survival from egg to one year. For each year, we estimated a probability distribution for abundance of breeding females in the basin using our raw capture histories, corrected for recapture probabilities. We then divided the number of egg masses by the number of females to determine the proportion of females breeding each year. To estimate survival from egg to one year, we isolated capture histories for one-year-old frogs (identified as frogs 34 mm and smaller) and estimated population sizes for this age class. We then divided the number of one-year-old frogs by the number of eggs laid in the basin the previous spring.

Further details about the mathematical formulation of these estimates can be found in Appendix A. Notably, results are highly concordant with previous, non-Bayesian analyses of these data using program MARK (McCaffery and Maxell 2010; see Results).

Forecasting the effects of climate change

In all steps of the forecasting process, analyses were numerically integrated over posterior probability distribution functions by calculating predictions separately for 4000

MCMC samples. We performed a logistic regression of annual vital rate parameter distributions with peak SWE measured in that year to determine the relationship between SWE and each vital rate across the ten years of the study. We then used these relationships to predict vital rate values for various combinations of mean and variance in peak SWE. We added process variance to the vital rates predicted using SWE using the residual differences between the model predictions and the observations. For consistency, we used the regressions for all vital rates, even if they did not show a strong relationship with SWE. We parameterized a 4-stage, female-based projection matrix model with the vital rates predicted from the mean and variance in SWE (Figure 3.1). We used these models to estimate stochastic population growth rates, and extinction probabilities under various scenarios where we changed mean and variance in SWE.

We took two approaches to evaluate the effect of changing mean and variance in SWE on *R. luteiventris*. First, we examined how periods of historical variation in snowpack recorded at our site affected population viability. Specifically, we compared the mean and variance in SWE from our 10-year study (“current”) to a period from 1983-1995 where both mean and variance in SWE were lower than the current values. We examined four scenarios: (i) current mean and variance, (ii) 1983-1995 mean and variance, (iii) current mean and 1983-1995 variance, and (iv) 1983-1995 mean and current variance. We compared the relative effect of changing mean snowpack versus changing variation in snowpack between these two time periods. For these scenarios, we forecasted population dynamics for 30 years, and this was repeated 1000 times for each of the 4000 MCMC samples. We set ten female frogs as our quasi-extinction threshold. For our starting population size vector, we assumed 100 adult females and the stable stage distribution predicted by the mean matrix.

Second, we examined effects of future changes in mean and variance of SWE on population viability. Climate models for the northwestern United States, which include our study site, predict a 10% to 40% decrease in mean peak SWE by 2100, depending on the model and the area within this region (Payne et al. 2004). Therefore we examined scenarios within this range. Although variance in precipitation is expected to change, there are no model predictions for the magnitude of this change, so we picked a range of hypothetical scenarios to explore the effects of changes in this parameter. The mean SWE

values encompassed everything from a slight increase in SWE to a 40% decrease in SWE, and the standard deviations cover a 50% reduction in variance to a 3-fold increase in variance. To quantify how viability would change across different combinations of future mean and variance in SWE, we estimated mean stochastic lambda, extinction probabilities, and the proportion of samples with a lambda \geq 1.0 for each of 260 different combinations of mean and variance in SWE. Mean SWE ranged from 25 to 44 inches, and standard deviation in SWE ranged from 7 to 19 inches. We compared the effect of changing mean peak SWE versus variance in peak SWE by examining the slope of the relationship between the three viability metrics and the mean and standard deviation of SWE. For each scenario, we ran 4000 model predictions for 30 years, with different possible values for the vital rates given by our Bayesian vital rate estimation. This was repeated 100 times. We used the same extinction threshold and starting population size vector as above.

To illustrate how distribution of stochastic lambda would change under specific scenarios, we simulated distributions for stochastic lambda where we (1) kept variance in SWE constant but changed the mean, and (2) kept mean SWE constant but changed the variance. For these scenarios, we forecasted dynamics for each of the 4000 MCMC predictions for 30 years. This was repeated 1000 times, using the same starting population vector and quasi-extinction threshold.

Results

Vital rate estimates and climate variables

Peak SWE values at this site decreased slightly over the 40 years, though the decrease was not statistically significant (slope = -0.2, p = 0.26; Figure 3.2). Variability among years was high. Both mean (35.3 in) and variance (15.2) in peak SWE were notably lower in the period from 1983-1995 than over the 1969-2009 period (mean = 41.8 in, variance = 116.2) or over the years of our study (mean = 40.7 in, variance = 84.5; Figure 3.2). We examine the importance of this variance in our scenarios.

Breeding probability and first year survival were extremely variable across the ten years of our study, and showed no relationship with peak SWE (Figure 3.3). Breeding

probability ranged from 0.38 to 1.0, and there was considerable uncertainty in many of the estimates. First year survival ranged from 0.001 to 0.009. Notably, first year survival was the highest and most variable in one of the lowest snow years and in the highest snow year.

There was a strong inverse relationship between juvenile and adult survival and peak SWE (Figure 3.4). There was no relationship between subadult survival and SWE. Transition probabilities from juvenile to subadult stage classes had a negative relationship with SWE, but there were no relationships between other transitions and SWE (Figure 3.5). These results confirm our previous analysis of *R. luteiventris* vital rates in relation to snowpack, where we found significant relationships between the same vital rates and peak SWE (McCaffery and Maxell 2010).

Climate scenarios

When we compared scenarios using the period from 1983-1995 to our current conditions (2000-2009), we found that the earlier period had a mean stochastic lambda of 1.01 (0.95-1.05 credibility interval; hereafter “CI”) with 68% probability of lambda being greater than one (probability of growth), while the current conditions had a mean lambda of 0.90 (0.79-0.99 CI) and a 0.95% probability of growth (Figure 3.6). Thus, the early period generally predicted a growing population while the current period predicted a declining population, which was consistent with our observation of a declining population from 2000-2009 (McCaffery and Maxell 2010). Decreasing the variance in our current conditions to what was seen in 1983-1995 resulted in a slight increase in lambda to 0.92 (0.82-0.99 CI), with 1% probability of growth, but the population would still be declining. When we increased variance in SWE in the earlier period to what we saw in 2000-2009, lambda decreased to 0.99 (0.92-1.05 CI), with 34% probability of growth, illustrating how increased variance can influence viability. When we examined the contribution of changing mean versus changing variance to stochastic lambda, we found that changing mean SWE had a greater effect than changing variance in SWE. The mean difference in lambda caused by changing mean SWE from earlier to current conditions was 0.09 (0.05-0.13 CI), while the mean difference in lambda caused by changing variance in SWE was 0.02 (0.0-0.04 CI).

Across all of our scenarios for future changes in the mean and variance of SWE, a decrease in mean SWE had a positive effect on population viability, and an increase in variability had a small negative effect. Overall, all metrics of viability had a higher sensitivity to changes in mean than to changes in variance (Figure 3.7). Decreases in mean SWE resulted in an increase in mean stochastic lambda (slope = -0.014), an increase in the proportion of samples with a lambda \geq 1.0 (slope = -0.069) and a decrease in percent of runs going extinct (slope = 0.48). In contrast, increases in variance of SWE had smaller effects on these viability metrics, and resulted in a decrease in mean stochastic lambda (slope = -0.004), a decrease in the proportion of samples with a lambda \geq 1.0 (slope = -0.015) and an increase in the percent of runs going extinct (slope = 0.17). Populations mostly changed from decreasing to increasing around a mean 33 inches SWE, which represents a 20% decrease relative to current conditions. Increasing variation in SWE had a slightly larger effect on percent of runs going extinct than on other parameters, because the increased spread around mean stochastic lambda meant that a greater number of runs had low lambda values.

When we kept variance in SWE constant but decreased mean SWE, stochastic lambda increased (Figure 3.8). A 20% decrease in SWE shifted populations from mostly declining to mostly growing. No populations were decreasing with a 40% decrease in mean SWE. When we explore the effect of changing variance in SWE while keeping mean SWE constant, we found that stochastic lambda increased with a decrease in variance, and decreased with an increase in variance (Figure 3.9). Increasing variance also widens the distribution of lambda values. A doubling of the variance changes the mean stochastic lambda value from 1.016 to 0.997, with only 45% of samples having a lambda \geq 1.0. When the variance is tripled, there was a 73% probability of decline.

Discussion

Two key results emerged from these analyses. The first was that decreases in mean snowpack, as projected by climate models for the region (Payne et al. 2004), promoted population viability of *R. luteiventris* in this system. This result agrees with our previous, deterministic analysis of climate and vital rates for this population (McCaffery

and Maxell 2010). However, our Bayesian analysis incorporated uncertainty in our vital rate estimates, and demonstrated that this result is robust to increasing levels of variation in snowpack. This result challenges the overarching dogma that climate change will generally be negative for amphibians, or exacerbate declines (Corn 2005, Wake 2007, McMenamin et al. 2008). Rather, this case study offers the more nuanced perspective that in some circumstances, climate warming could benefit some populations and species, provided that suitable habitats remain intact. Frogs in this system persist at the upper elevational limit of their range, and endure long cold winters on many years. Populations of *R. luteiventris* inhabiting these elevations have broad thermal tolerances, and fitness may be enhanced by a warming climate if they are currently spending much of their time below their physiological optimum (Deutsch et al. 2008). Our results indicate that *R. luteiventris* and similar species inhabiting harsh alpine environments may be unlikely beneficiaries of climate change, at least in the short term.

Our second key result is that population viability metrics were more sensitive to changes in mean SWE conditions than to changes in the variance in these conditions. Decreases in SWE systematically increased mean stochastic lambda, increased the probability of population growth, and decreased extinction probabilities; increases in variability had less of an effect. In contrast, other researchers have argued environmental stochasticity is the most important determinant of extinction risk based on times series analysis of past population trends (Fagan et al. 2001). However, other research examining the effects of mean and variability in climatic change on wild populations has corroborated our conclusion. Colchero et al. (2009) found that an increase mean drought severity had a larger effect on the viability of a population of desert bighorn sheep (*Ovis canadensis*) than an increase in the variability in drought. Similarly, Jonzen et al. (2010) found that changes in average rainfall had a greater impact on population growth rates of the red kangaroo (*Macropus rufus*) than increased variability in rainfall. These results agree with the findings of Morris et al. (2008) that in general, long-lived species are more resilient to increases in climatic variability than short-lived species (insects and annual plants). Columbia spotted frogs may live up to ten or more years old in our system, and do not become sexually mature until 3 to 5 years of age at high elevation (Werner et al.

2004). Thus, it may be that for this long-lived frog species, populations can be resilient to substantial environmental variation.

The influence of environmental stochasticity cannot wholly be discounted, however. We found that increases in variability generally decreased stochastic lambda, and could change populations from increasing to decreasing (Figure 3.6 and 3.9). Similarly, in a meta-analysis of 15 plant and 21 animal taxa, Morris et al. (2008) emphasized that increased vital rate variability decreased long-term population growth rates. Although the relative importance of changes in variance may be less than changes in the mean, increases in variability can have consequences for population viability. The patterns of variability in climate may also influence the importance of including variability, as highlighted by our comparison of population viability using SWE values from 1983-1995 and 2000-2009. The SWE values from 1983-1995 predicted a growing population, while the SWE values for the more current time frame predicted a declining population. Mean and variance values from the 40-year record of SWE at this site would also predict a declining population, yet the population is persisting at this site. Thus, short periods of favorable conditions may promote viability even within longer-term predicted declines.

Peak snowpack only explains some of variability in our vital rates, and only relates to some vital rates. Undoubtedly other factors are influencing these rates, and could include both extrinsic and intrinsic factors. For example, timing of spring snowmelt is related to breeding probability in this population (McCaffery and Maxell 2010). Density dependence at either the larval stage or the adult stage could influence vital rates over time (Wilbur 1976, Semlitsch 1987a, Berven 1990, Harper and Semlitsch 2007), although densities of larvae and frogs at this site are lower than what has been measured in other species. Vital rate variability might also be influenced by current predation rates and resource availability. Finally, there could be potential effects of toe-clipping in survival probabilities over time, as has been noted in other species (McCarthy and Parris 2004). Integrating the effects of climate with other potential drivers of variation in this population's dynamics could clarify the relative importance of climate changes to population persistence. However, even with these potentially confounding factors, changes in snowpack do appear to contribute to population dynamics.

Our models predict the effects of future snowpack decline on *R. luteiventris* population viability in isolation from other climate-related ecosystem changes that could be occurring alongside declines in snowpack. These may include habitat loss and changes in the abundance and distribution of food resources. Decreases in the total availability of breeding habitat due to drought could have negative impacts on the population (e.g. McMenamin et al. 2008), and may be accompanied by reductions in the quality of remaining habitat. Reductions in snowpack may be accompanied by changes in the timing, quantity or quality of food resources, which may reduce body conditions and survival rates in juvenile and adult frogs. Thus, models that simultaneously evaluate different ways a given population or species may be impacted by climate could help disentangle the relative influences of different results of changes in climate on population dynamics and viability.

Our results are based on analyses of one population, and we might expect other populations, even at high elevations, to have different relationships with snowpack. In the alpine ibex (*Capra ibex*), spatial covariation in climate variables did not synchronize population dynamics over large spatial scales, suggesting that the effects of climate variables on populations are heterogeneous over a broader spatial landscape (Grotan et al. 2008). In amphibians, configuration of breeding habitat (Karraker and Gibbs 2009), presence of non-native fish (Knapp and Matthews 2000, Pope 2008), and presence of disease (Scherer et al. 2005) may all influence the way climate changes affect population viability. For example, populations dependent on a single, ephemeral breeding pond may be more highly impacted by recruitment failures due to drought than changes in juvenile and adult survival, if the relative magnitude of recruitment failures is greater than increases in survival. Amphibian populations whose breeding is limited to a few fishless ponds may experience greater habitat constrictions with climate change than populations where fish have not been introduced. Finally, if climate change makes conditions more favorable for disease, then increases in survival due to milder winters may be offset by decreases in survival due to disease. Conducting similar analyses and forecasts on other populations and species would help determine the extent to which the patterns we observed are generalizable across a broader landscape.

Despite the above discussion points, it remains that decreases in mean peak SWE increased viability of this frog population, while variance in SWE was less important for viability. Thus, provided that suitable habitat remains intact, projected changes in climate promote viability in this frog population, even in the face of increased variation.

Figure Legends

Figure 3.1. Female-based, post birth pulse matrix projection model for *R. luteiventris*. Vital rates are fully described in McCaffery and Maxell (2010).

Figure 3.2. Peak SWE recorded at the Twin Lakes SNOTEL site from 1970-2009. Underlined periods are used to contrast a period with low mean and variance in SWE with the conditions observed over the course of our study ('current period').

Figure 3.3. Annual Bayesian posterior estimates (with 95% credibility intervals) for breeding probability and first year survival in relation to SWE. The line shows predicted values for breeding probability and first year survival for different values of SWE, with 50% (dark gray) and 95% (light gray) confidence envelopes.

Figure 3.4. Annual Bayesian posterior estimates (with 95% credibility intervals) for juvenile, subadult, and adult female survival in relation to SWE. The line shows predicted values for survival for different values of SWE, with 50% (dark gray) and 95% (light gray) confidence envelopes.

Figure 3.5. Annual Bayesian posterior estimates (with 95% credibility intervals) for juvenile-subadult, juvenile-adult, and subadult-adult female transition probabilities in relation to SWE. The line shows predicted values for transition probabilities for different values of SWE, with 50% (dark gray) and 95% (light gray) confidence envelopes.

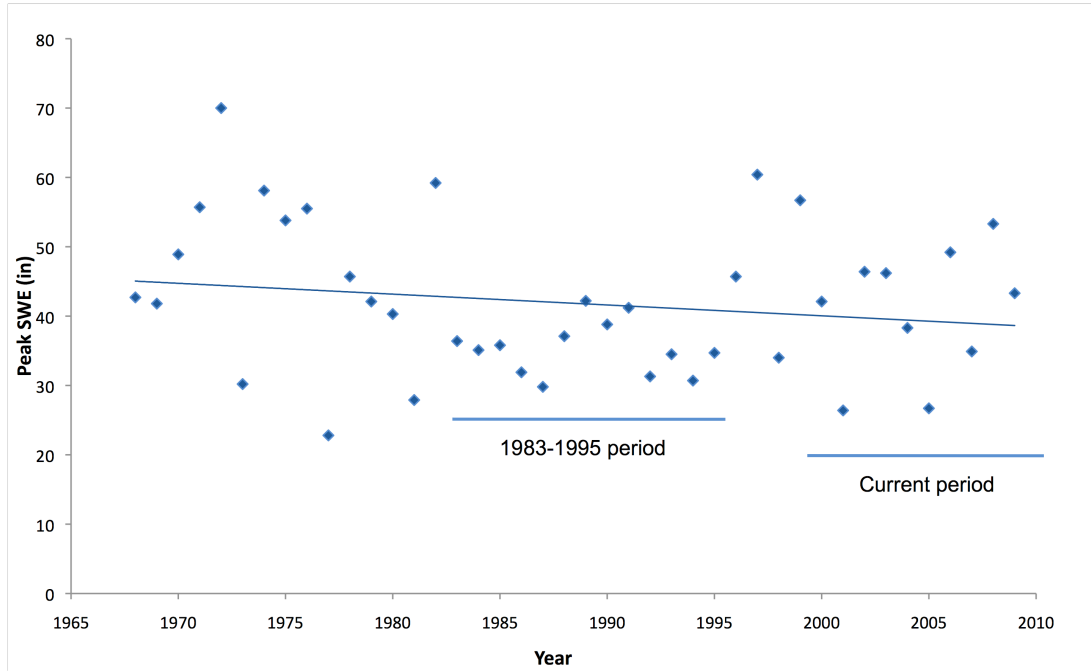
Figure 3.6. Posterior probability density estimate for stochastic lambda under 4 scenarios, comparing effects of changes in both mean and variance of peak SWE in two historical periods: (i) 2000-2009 mean and variance of peak SWE (current mean & var); (ii) current peak SWE and 1983-1995 variance in peak SWE (current mean, 83-95 var); (iii) 1983-1995 mean in peak SWE and current variance (83-95 mean, current var); and (iv) 1983-1995 mean and variance in peak SWE (83-95 mean & var).

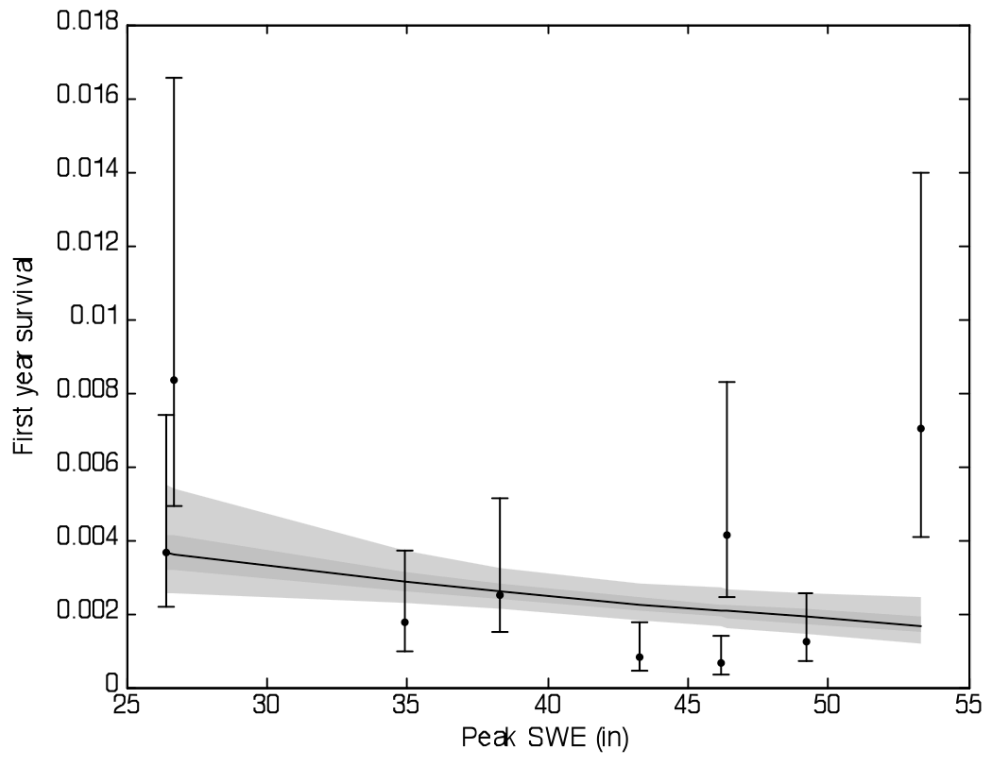
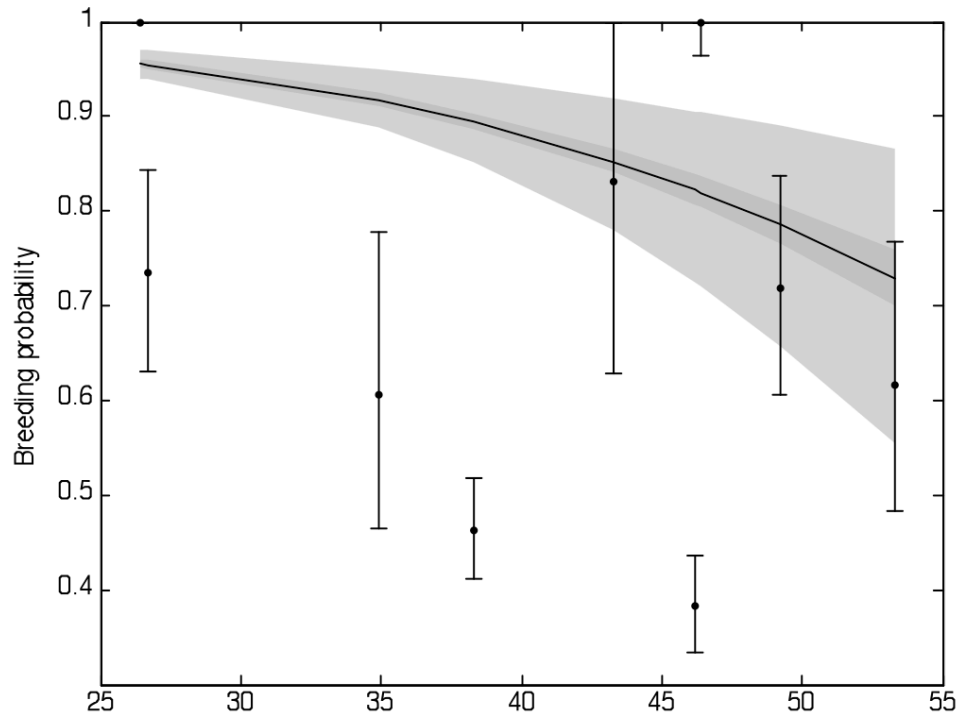
Figure 3.7. Contour plots showing the effect of changes in mean SWE and standard deviation of SWE on (a) mean stochastic lambda, (b) proportion of samples with lambda ≥ 1.0 , and (c) percent of runs going extinct. Stars indicate the mean and standard deviation of SWE for 2000-2009 and 1983-1995.

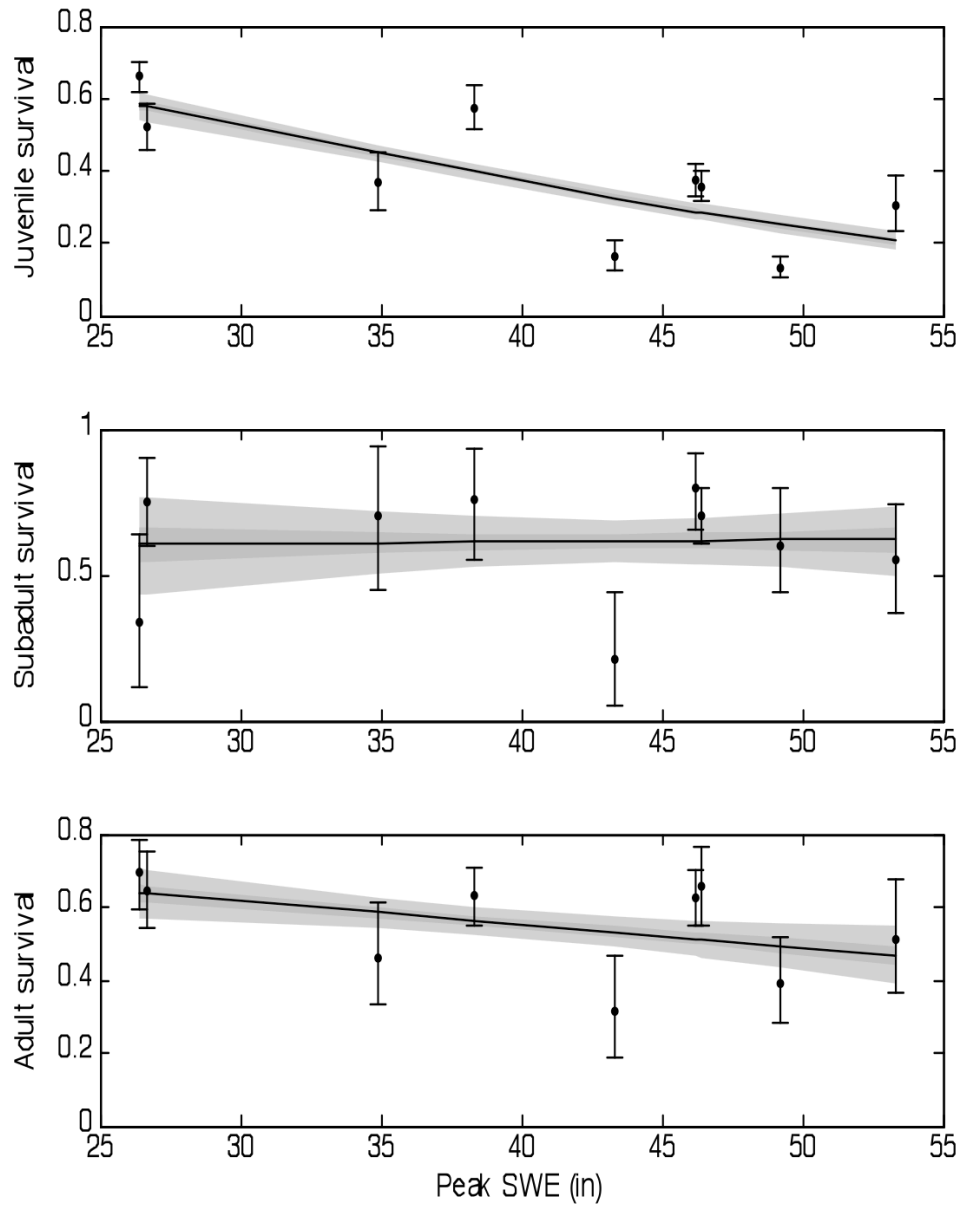
Figure 3.8. Posterior probability density estimates for lambda under 5 scenarios, where mean peak SWE changed but variance in peak SWE was constant (variance from 2000-2009 data): 2000-2009 mean peak SWE (current); 10% decrease from the current mean (-10%); 20% decrease (-20%); 30% decrease (-30%); and 40% decrease (-40%).

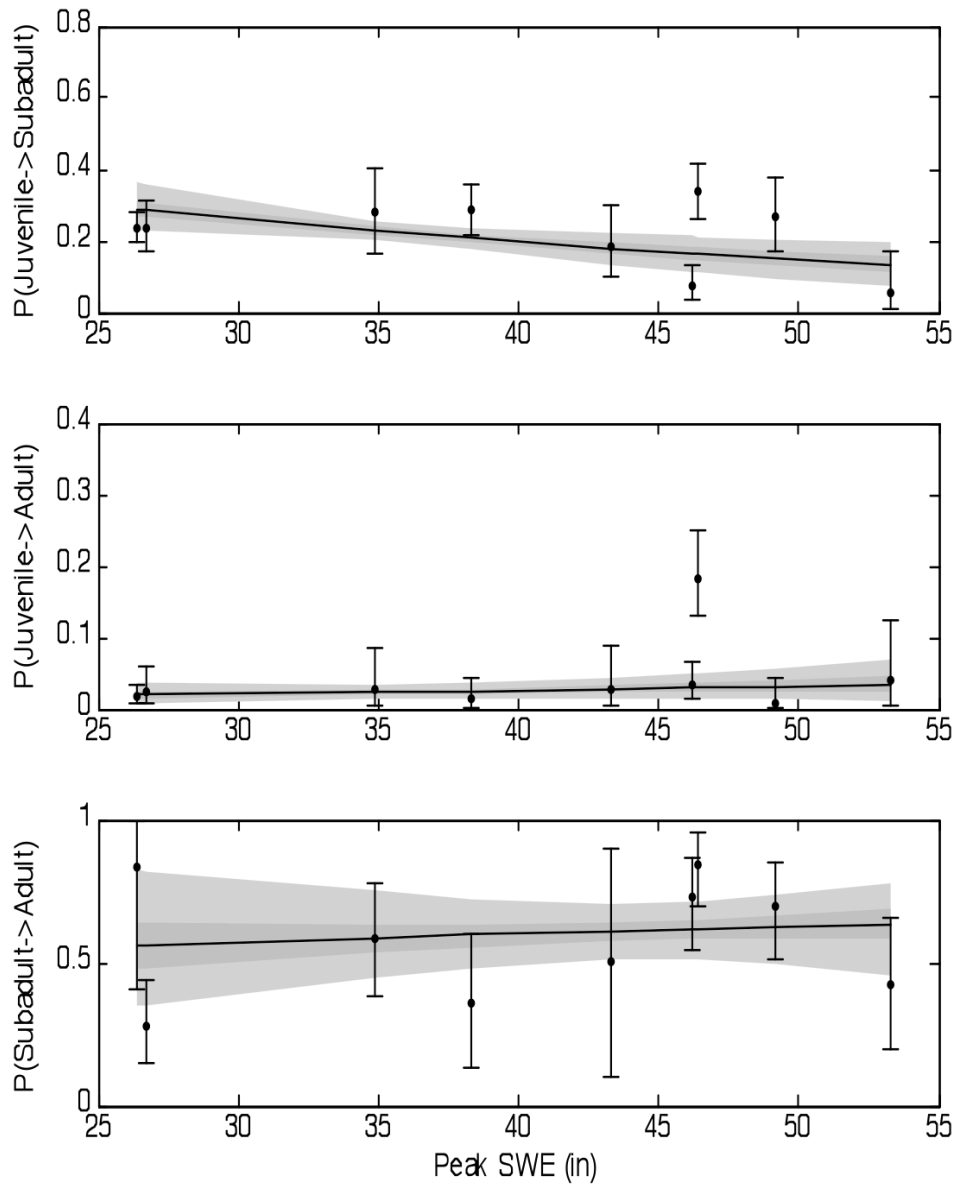
Figure 3.9. Posterior probability density estimate for lambda under 4 scenarios, where mean peak SWE was constant (20% reduction in current mean) but variance in peak SWE changed with reference to the 2000-2009 variance in peak SWE: current variance (1*var); half the current variance in peak SWE (1*var); twice the variance (2*var); and three times the variance (3*var).

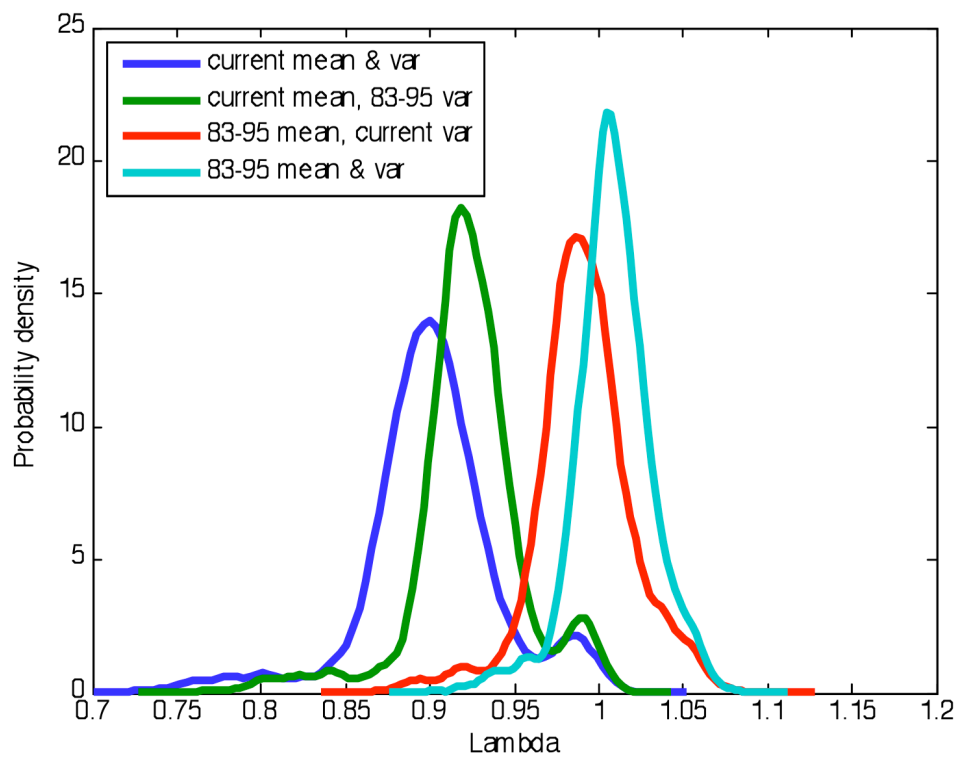
$$\begin{bmatrix}
 0 & 0 & P_b * S_s * C_s & P_b * S_f * C_s \\
 S_0 & P_{jj} * S_j & 0 & 0 \\
 0 & P_{js} * S_j & P_{ss} * S_s & 0 \\
 0 & P_{jf} * S_j & P_{sf} * S_s & S_f
 \end{bmatrix}$$

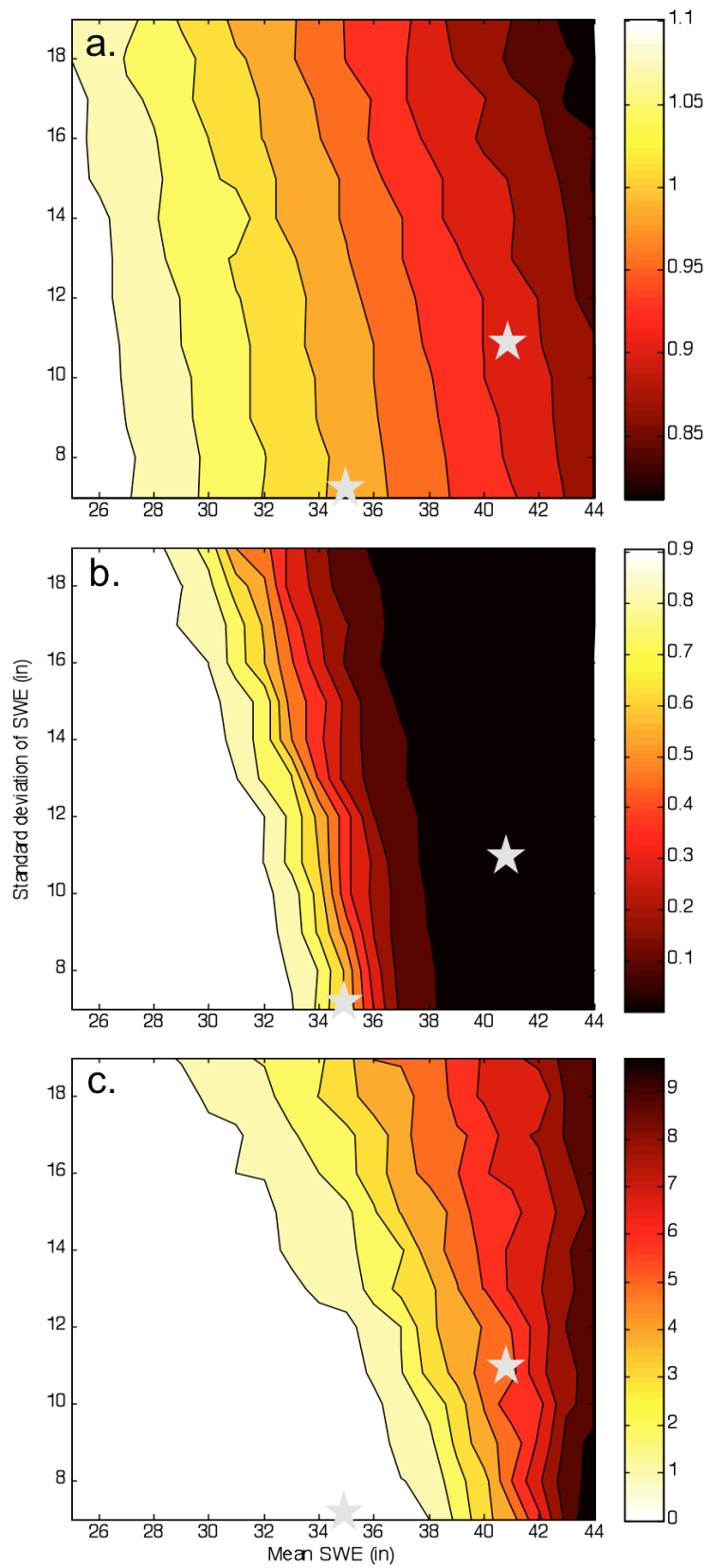


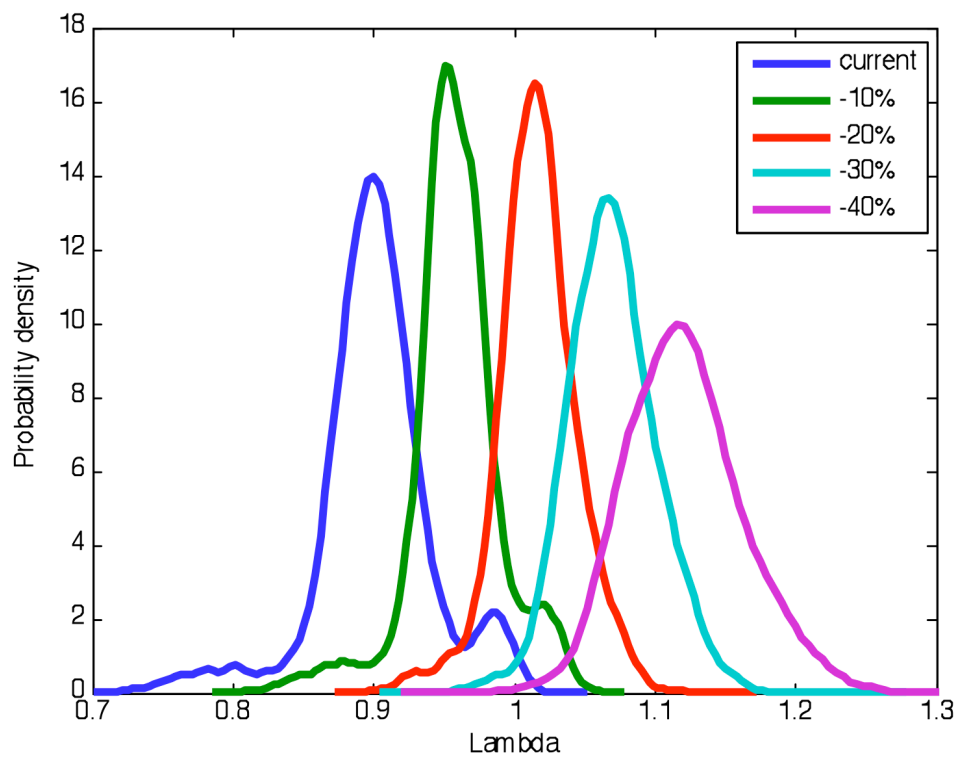


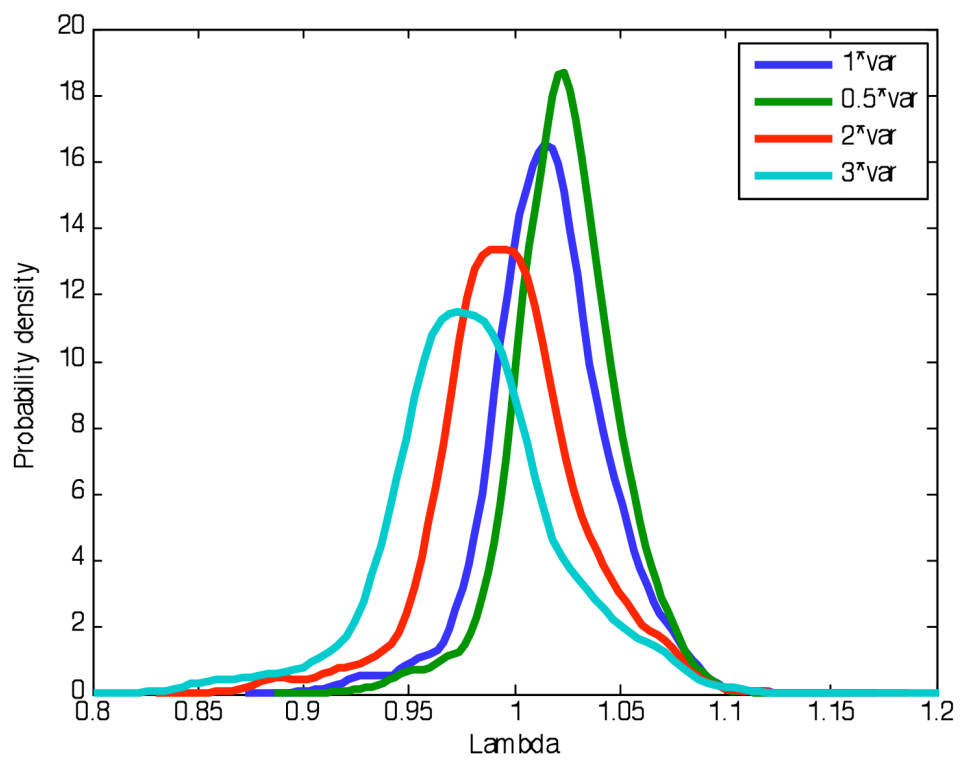












CHAPTER 4
THE EFFECTS OF BREEDING SITE HETEROGENEITY ON COLUMBIA SPOTTED
FROG (*RANA LUTEIVENTRIS*) RECRUITMENT AND POPULATION DYNAMICS

Abstract

Environmental stochasticity can have profound effects on the dynamics of wild populations, and is arguably often the most important determinant of population viability. Habitat heterogeneity provides one mechanism by which populations may be buffered against climatic fluctuations. For example, heterogeneity in pond hydroperiod may allow amphibian populations to persist despite variable interannual precipitation. We examined recruitment dynamics over ten years in a high-elevation Columbia spotted frog (*Rana luteiventris*) population that uses both ephemeral and permanent ponds for breeding. We combined these data with models to quantify the consequences of heterogeneity in pond hydroperiod on net recruitment (i.e. number of metamorphs produced) and long-term population growth rates. We compared our heterogeneous system to hypothetical homogeneous environments with (1) only long hydroperiod ephemeral ponds, (2) only short hydroperiod ephemeral ponds, and (3) only permanent ponds. We found that most eggs were laid in permanent ponds each year, but egg to metamorph survival was higher in longer hydroperiod ephemeral ponds than either short ephemeral ponds or permanent ponds. There were weak negative correlations in egg to metamorph survival among all pond types, suggesting that the different pond types have better recruitment success on different years. Net recruitment and stochastic population growth rate were highest in the scenario with longer hydroperiod ephemeral ponds, but variability in recruitment was lowest in the scenario with all ponds. These results suggest that the presence of a diversity of hydroperiods on the landscape may reduce variability in amphibian recruitment. However, longer hydroperiod ephemeral ponds have the highest long-term growth rates, because of consistent recruitment success across years and occasional bonanzas. These results do not consider habitat loss though, and if climate change causes drought frequency to increase, permanent ponds may become more critical to population dynamics.

Introduction

Fluctuations in the environment can have profound effects on the population dynamics of species by increasing the variability of survival, fecundity, and other vital rates over time. Variability in vital rates increases interannual changes in population size, and can ultimately lead to decreased long-term population growth rates and increased risk of extinction. Indeed, changes in the variability of population growth rate may have a stronger influence on extinction risk than changes in mean population growth rate or population size (Fagan et al. 2001, Inchausti and Halley 2001). Recent climate change models predict increasing variability in climate in addition to changes in mean values (Boer et al. 2000, Raisanen 2002, Rowell 2005, Watterson 2005). This could lead to a magnification in the contrast between wet and dry years as well as an increase in the frequency of extreme weather events such as drought. This augmentation in stochasticity due to climate change could have dire consequences for species already sensitive to stochastic changes in environmental conditions. The consequences of changing climatic variability on plant and animal populations, and our ability to conserve populations in light of this variance, are largely unexamined (but see Boyce et al. 2006, Morris et al. 2008). However, they are urgent questions in population ecology and conservation biology.

Habitat heterogeneity has the potential to reduce the effects of environmental stochasticity on populations. Two observational studies of insects have posited that heterogeneity in habitat features promotes population persistence. Kindvall (1996) demonstrated a decrease in population variability of the bush cricket (*Metrioptera bicolor*) with increased heterogeneity in patch vegetation types, concluding that patch heterogeneity may be more important for species persistence than patch size. McLoughlin et al. (2002) showed that a population of Bay Checkerspot butterflies (*Euphydryas editha bayensis*) inhabiting a more topographically diverse habitat had a lower extinction risk than a population occupying a more homogeneous habitat. Additionally, researchers conducting a meta-analysis of 35 butterfly species in Britain found that both topographic and habitat heterogeneity are associated with more stable population dynamics (Oliver et al. 2010). These studies provide some empirical evidence that a diversity of habitats can

help populations persist despite high interannual variation in weather conditions. However, the relationship between habitat heterogeneity and stability of population dynamics has rarely been examined in other taxa.

In amphibians, variability in the length of breeding pond hydroperiod (the number of days ephemeral ponds have water) can have strong effects on recruitment dynamics (Pechmann et al. 1991, Semlitsch et al. 1996, Daszak et al. 2005). Simply put, if ponds dry too quickly, tadpoles do not have time to complete metamorphosis and recruitment fails. However, permanent ponds can be poor breeding sites if temperatures are too cold for development or predators reduce recruitment (e.g. Meyer et al. 1998, e.g. Knapp and Matthews 2000). As such, several researchers have alluded to the potential benefits of maintaining diverse pond types or hydroperiods on the landscape to promote amphibian population persistence (Semlitsch and Bodie 1998, Semlitsch 2000, Snodgrass et al. 2000, Babbitt et al. 2003). However, few studies have examined recruitment dynamics in heterogeneous landscapes over multiple years. In a 16-year study of Arizona tiger salamanders (*Ambystoma mavortium nebulosum*), Whiteman and Wissinger (2005) documented that successful recruitment in semi-permanent ponds occurred less frequently than in permanent ponds. However, individuals metamorphosing from semi-permanent habitats tended to be larger and in better condition than individuals from permanent ponds. Recruitment from semi-permanent ponds may be important for overall population dynamics in some systems since larger individuals are known to have higher survival rates (Smith 1987, Morey and Reznick 2001, Chelgren et al. 2006), higher fecundity (Semlitsch 1987a, Berven 1988), and shorter time to reproductive maturity (Smith 1987, Semlitsch et al. 1988). In a three-year study of the breeding dynamics of the yellow-bellied toad (*Bombina variegata*), Hartel et al. (2007) found that toads exploit breeding habitat differently in wet and dry years. Though toads primarily used permanent or semi-permanent ponds, they readily bred in a number of ephemeral ponds in wet years, increasing the percent of ponds with successful recruitment from 40 to 90%. In dry years, breeding in these ephemeral ponds resulted in complete failure of metamorphosis. While these studies show some differences in recruitment in different pond types over years, they do not quantify the relative contribution of multiple pond types to recruitment over time, or relate the effects of pond heterogeneity to population dynamics.

As climate change alters global precipitation patterns, hydroperiod dynamics in wetland systems are changing (Winter 2000), which may have consequences for amphibian recruitment and population dynamics. The presence of heterogeneous pond types on the landscape could help buffer populations against stochasticity in precipitation by providing suitable breeding habitat over a wide range of environmental conditions. We examined the recruitment dynamics of a high elevation population of Columbia spotted frogs (*Rana luteiventris*) in a heterogeneous landscape over ten years. *Rana luteiventris* are thought to have high breeding site fidelity, but different pond types appeared to be more successful in different years. We asked how important this diversity in pond type was for net recruitment (i.e. number of metamorphs produced) and population dynamics in the system. First, we compared recruitment dynamics in ephemeral and permanent breeding ponds over a ten-year period. Second, we examined how number of recruits would change if all recruitment came from ephemeral ponds, or from permanent ponds. Finally, we used stochastic simulations to examine how the source of recruitment affected long-term population growth rates in the system. We hypothesized that net recruitment and stochastic growth rate from a mixture of permanent and ephemeral ponds would be higher and less variable than recruitment and stochastic growth rate from either permanent or ephemeral ponds alone.

Methods

Site description and field methods

All data were collected in the Little Rock Creek basin, which is located in the Selway-Bitterroot Wilderness in western Montana. Our analyses were focused on the upper basin (2200 m), which contains 11 breeding sites, of which four are permanent and seven are ephemeral (Figure 4.1). Permanent ponds are defined as ponds that never dry; these ponds are all fed by streams and lakes. Ephemeral ponds are those that dry by mid- to late summer in most years. The basin also contains three large lakes, which are not used for breeding, but are used for summer foraging and overwintering. These were monitored for juvenile and adult frogs each summer. Neither the ponds nor the lakes support fish populations. *Rana luteiventris* are the primary amphibian species in all

ponds, though long-toed salamanders (*Ambystoma macrodactylum*) breed in small numbers in some of the ponds. The chief predators in the ponds are garter snakes (*Thamnophis sirtalis* and *T. elegans*), but odonate and dystiscid beetle larvae are also present at these sites. Although this basin contains many water bodies, genetic analyses indicate that the upper basin groups as one population (Funk et al. 2005). We obtained weather data from the Twin Lakes SNOTEL site located approximately 18 km northwest of our field site at 1950 m elevation (www.wcc.nrcs.usda.gov/snow). The range and magnitude of variability in precipitation and snowpack recorded during our study encompasses the 40-year historical range of variation in this site.

Nine of the eleven breeding ponds were monitored annually from 2000 to 2009. Of these ponds, three small, adjacent ephemeral ponds were analyzed as one unit (ILP3-5) because we were unable to separate recruitment among them. Therefore, our analyses are based on three permanent ponds and four ephemeral ponds (Figure 4.1). Permanent and ephemeral ponds differed in surface area and depth (Table 4.1). Permanent ponds were deeper (>1 m) and never dried over the course of the study. Of the four ephemeral ponds, two had longer hydroperiods (hereafter “long ephemeral”) and two had shorter hydroperiods (hereafter “short ephemeral”). Long ephemeral ponds were only fed by snowpack. These ponds dried between late August and late September in warmer summers, but retained some water throughout the year in cooler summers. They were unsuitable for overwintering. Short ephemeral ponds were all <1-m deep at high water, fed only by snowpack, and dried every year. During hotter summers, these ponds dried by early August, but during cooler summers, they held water until late September.

In the spring, we searched all standing water bodies for egg masses one to two times a week for the duration of the breeding season. We determined number of egg masses deposited at each pond in each year. From 2000 to 2003, we estimated clutch size and variance in a range of egg masses across all breeding ponds using volumetric displacement (Morris and Tanner 1969, Corn and Livo 1989, Werner et al. 1999). In the late summer and fall, we captured new metamorphs emerging from all breeding ponds and marked them with a pond-specific batch mark. We estimated the number of new metamorphs as they emerged from the ponds using Chapman’s unbiased version of the Lincoln-Peterson estimator (Seber 1982). The batch marks allowed us to track production

of metamorphs from the different pond types every year. Due to forest fires and other logistical constraints, we were unable to estimate metamorph population size in 2000 and 2005.

Juvenile and adult frogs were captured in mid-summer using a robust sampling design (Pollock 1982) that is fully described by McCaffery and Maxell (2010). Mark-recapture data from juvenile and adult frogs were used to parameterize matrix models (see below).

Ephemeral and permanent pond recruitment

To calculate the total number of eggs produced annually in each pond, we multiplied the number of egg masses for each pond by 806, the mean clutch size estimated from our volumetric displacement calculations in 2000-2003. We then calculated the proportion of all eggs laid in each pond in each year.

We calculated pond-specific egg to metamorph survival rates for each year by dividing the number of metamorphs produced in each pond by the number of eggs laid in that pond in that year. To calculate survival from metamorphosis to one year, we divided the number of one year-old frogs for each year by the total number of metamorphs produced the fall before. One year-olds were defined as animals 34 mm snout-vent length (SVL) or smaller that were captured in our mid-summer surveys and individually marked. This maximum length represented a natural break in frog size, with the next largest frogs typically >40 mm SVL. We estimated their population size using Huggins closed capture models (Huggins 1989) in Program MARK (White and Burnham 1999). These models allow estimation of population size from initial capture probabilities and recapture probabilities of individually marked animals (Huggins 1989). One year-olds could not be assigned to their natal pond because of high metamorph dispersal in the basin.

We calculated proportion of egg masses laid, egg to metamorph survival, and number of metamorphs produced for each of seven breeding ponds annually. Then, we compared these variables among the three pond types (permanent, long ephemeral, and short ephemeral). Proportional and survival rate data were arcsine square root transformed, and metamorph counts were square root transformed for normalization prior

to statistical analysis. We compared the mean of these recruitment parameters using analysis of variance (ANOVA) and multiple comparison procedures. We compared the variance in these parameters using Levene's test for equality of variances.

Effects of pond heterogeneity on net recruitment

Using the proportions of egg masses laid in each pond and pond-specific egg to metamorph survival rates, we determined net recruitment under hypothetical scenarios where the number of eggs laid remained constant, but was shifted to either (1) only permanent, (2) only long ephemeral, or (3) only short ephemeral ponds. For each scenario, we calculated the proportion of eggs laid in each pond once the other pond types had been removed for each scenario and estimated the new number of eggs that would be produced annually in each pond. For example, in the first year of the permanent pond scenario, total annual eggs laid across the whole population was proportionally shifted to the three permanent ponds (which originally comprised 72% of total eggs laid), so that P1 had 57%, P2 had 10%, and P3 had 33% of the eggs. We multiplied the new number of eggs by the egg to metamorph survival rate for that pond and year to determine the number of metamorphs produced in the new scenario. We calculated the net recruitment in each year for each scenario. We compared net recruitment from these homogeneous scenarios to the net recruitment when all ponds contribute to recruitment. We compared the mean net recruitment using ANOVA and multiple comparison procedures, and compared variance in net recruitment using Levene's test for equality of variances. In all analyses, years were the unit of replication (N=8, 2001-2004, 2006-2009).

Effects of pond heterogeneity on population growth rate

We parameterized a female-based, post birth pulse Leftkovich matrix (Leftkovich 1965) using vital rate means and variances for the ten years of our study. Survival and transition parameters for juvenile, subadult, and adult survival rates were estimated using capture-mark-recapture (CMR) analysis (see McCaffery and Maxell 2010 for model details and description of life stages). These models also estimated annual population size for each life stage. Breeding probability was estimated by dividing the

number of egg masses deposited by the closed population estimate for adult females each year. For all juvenile and adult vital rates, we used White's (2000) method to correct variance estimates for sampling error, using code from Morris and Doak (2002; Box 8.1) in MATLAB. We estimated recruitment separately for each individual breeding pond, resulting in seven fecundity terms and seven egg to metamorph survival terms.

We examined population growth rates for the same four scenarios described above: all ponds, permanent, long ephemeral, and short ephemeral. For each scenario, we calculated new breeding proportions to reflect the shift in breeding proportions to each pond type, as described above. We examined two metrics of population growth rate. First, we calculated asymptotic growth rates, which show the expected growth rate if all vital rates were to remain constant over time. Then, we used stochastic projection matrix model simulations to estimate stochastic population growth. Here, each annual vital rate value is drawn from a distribution using the mean and variance (across years) of that vital rate from our field estimates. For all simulations, we used code in MATLAB modified from Morris and Doak (2002; Box 8.10). We did not include within year correlations among vital rates because the number of significant correlations among vital rates was close to what we would expect by chance. We started our simulations with 100 adult females and a stable stage distribution.

Results

Ephemeral and permanent pond recruitment

More eggs were laid in permanent ponds than ephemeral ponds across all years, but the number of egg masses laid in both permanent ponds and ephemeral ponds declined over the course of the study (Figure 4.2). The proportion of egg masses laid differed among the three pond types (ANOVA, $F=270$, $p<0.001$; Figure 4.3). The proportion of eggs laid in permanent ponds was over four times higher than in either of the ephemeral pond types (Tukey's HSD, $p<0.001$), and there was no difference in the proportion of eggs laid in short ephemeral and long ephemeral ponds (Tukey's HSD, $p=0.298$).

Egg to metamorph survival fluctuated among years for all breeding ponds (Figure 4.4). There were weak negative correlations in egg to metamorph survival among all three pond types, suggesting that different pond types had more successful recruitment in different years. None of these correlations were statistically significant (Table 4.2), but most correlations were negative. Survival to metamorphosis also differed among pond types (ANOVA, $F=4.25$, $p=0.028$; Figure 4.5). Egg to metamorph survival averaged three times higher in long ephemeral ponds than short ephemeral (Tukey's HSD, $p=0.032$) and permanent ponds ($p=0.087$). This was driven by one year of extremely high survival in a long ephemeral pond. There was no difference in survival between short ephemeral and permanent ponds ($p=0.877$). There was no difference in the variability of egg to metamorph survival among the three pond types.

Metamorph production differed among the pond types (ANOVA, $F=3.73$, $p=0.041$). Successful recruitment in ponds was most consistent in long ephemeral ponds (Table 4.3), where ponds produced metamorphs in all but one year of the study. In permanent ponds, metamorphs were produced all years except for the last two years of the study. Successful recruitment was much more sporadic in the short ephemeral ponds. Every pond varied in the number of metamorphs produced across years (Figure 4.6). Two of the permanent ponds produced most of the metamorphs in the early years of the study, but ephemeral ponds produced all of the metamorphs in the last two years. Despite the higher survival rates in long ephemeral ponds, there was no difference in the number of metamorphs produced from permanent ponds and long ephemeral ponds across years (Tukey's HSD, $p=0.796$; Figure 4.7). However, on average there were over four times more metamorphs produced in permanent ponds than short ephemeral ponds ($p=0.041$), and over two times more metamorphs produced in long ephemeral than short ephemeral ponds ($p=0.143$). Permanent ponds had eight times higher variance in metamorph production than short ephemeral ponds (Levene's test for equality of variance, $F=6.569$, $p=0.023$) and four times higher variance than long ephemeral ponds ($F=4.113$, $p=0.062$). This was driven by the last two years of the study, where permanent ponds had no successful recruitment due to cooler summer and early onset of winter, in contrast to years where several hundred metamorphs emerged from these ponds (Figure 4.6).

Effects of pond heterogeneity on net recruitment

Total metamorphs produced differed among scenarios where we varied the source pond type but kept total eggs laid constant (ANOVA, $F=3.468$, $p=0.029$; Figure 4.8). Specifically, the scenario with all reproduction in long ephemeral ponds resulted in more metamorphs than the scenarios with only short ephemeral (Tukey's HSD, $p=0.029$) or only permanent ($p=0.075$) ponds. However, this scenario did not differ from the scenario where all ponds contribute in their current proportions ($p=0.368$). Production of metamorphs did not differ between any other pairs of scenarios. The scenario with all ponds contributing was less variable than the scenarios with only short ephemeral (Levene's test for equality of variances, $F=8.149$, $p=0.013$) or only long ephemeral ($F=0.060$, $p=0.060$) ponds, but was not different from the scenario with only permanent ponds ($F=0.875$, $p=0.365$). Therefore, breeding site heterogeneity can decrease interannual variability in metamorph production.

Effects of pond heterogeneity on population growth rate

The deterministic growth rate for the population was highest in the scenario with reproduction only in long ephemeral ponds ($\lambda=0.87$), lowest with reproduction in only permanent ponds ($\lambda=0.72$), and intermediate with reproduction in all ponds ($\lambda=0.75$) or only short ephemeral ponds ($\lambda=0.75$). These values reflect the higher mean egg to metamorph survival rates found in long ephemeral ponds compared to other pond types. However, this metric does not incorporate variance in the recruitment parameters.

When we conducted stochastic simulations, the scenario with only long ephemeral ponds still had the highest growth rate ($\lambda=0.80\pm 0.0006$ SE), followed by the scenario with all ponds ($\lambda=0.72\pm 0.0005$). Scenarios with only permanent ponds ($\lambda=0.67\pm 0.0005$) and only short ephemeral ponds ($\lambda=0.68\pm 0.0006$) had the lowest growth rates (Figure 4.9). The standard errors represent the precision of our stochastic lambda estimates across 1000, 20-year simulations. Variance in egg to metamorph survival for both long and short ephemeral ponds was higher than that for permanent ponds, and likely contributed to stochastic λ being proportionally lower than deterministic λ in scenarios that only included these ponds (8.1 and 7.9% lower, respectively, versus 5.8% for only permanent ponds). The scenario with all ponds

contributing to recruitment declined proportionally less than the other scenarios in the stochastic simulations (4.9%).

Discussion

Ephemeral and permanent pond recruitment dynamics

Our study demonstrates complex recruitment dynamics for *R. luteiventris* in a heterogeneous breeding landscape. Part of this is because long ephemeral, short ephemeral, and permanent ponds show contrasting dynamics in different years. In particular, recruitment from ephemeral ponds dominated in two cool wet years (2008-2009), and recruitment from permanent ponds dominated in years that were hotter or had less snow the preceding winter (2003-2007; Figures 4.3 and 4.4). As a result, over this dynamic ten-year time period, we never witnessed complete recruitment failure, even though all but one pond experienced recruitment failure at least once over that time period (Table 4.2). From these descriptive analyses, there is evidence that heterogeneity in hydroperiod stabilized recruitment dynamics, because variability in dynamics across the whole population was lower than what we measured in individual ponds. These results are similar to what has been observed for the wood frog (Karakker and Gibbs 2009), the yellow-bellied toad (Hartel et al. 2007), and the tiger salamander (Whiteman and Wissinger 2005). Our results corroborate other researchers' recommendations to conserve of a diversity of pond hydroperiods on the landscape to promote pond-breeding amphibian population persistence (Snodgrass et al. 2000, Babbitt et al. 2003).

Recruitment dynamics in pond-breeding amphibians have been monitored in various ways for different species, and each adds to our understanding of factors affecting amphibian recruitment. At larger landscape levels, researchers have monitored the presence or absence of breeding in large networks of ponds, often over long time periods (Skelly et al. 1999, Trenham et al. 2003). These studies examine the dynamics of breeding pond use, but generally do not measure recruitment at any particular pond or pond network. Therefore, it is difficult or impossible to quantify differential recruitment success at different ponds across years. In other studies, researchers have monitored egg mass counts in networks of ponds in one or more years (Meyer et al. 1998, Baldwin et al.

2006). This has allowed us to determine breeding effort in relation to hydroperiod (e.g. Baldwin et al. 2006), but not to quantify successful recruitment (i.e. number of metamorphs produced). Intensive studies at individual ponds over a number of years have quantified recruitment success under a variety of environmental conditions (e.g. Semlitsch et al. 1996). These studies, however, do not examine how the presence of multiple ponds on the landscape may affect population-level recruitment success over time, unless the population only uses one breeding site. A few recent studies have quantified recruitment in networks of nearby ponds (Whiteman and Wissinger 2005, Karraker and Gibbs 2009), thus beginning to address how different ponds contribute to recruitment in different years. Our study combines the strengths of these approaches by quantifying recruitment success in diverse breeding ponds across the landscape over a relatively long time period.

Studies that have examined amphibian recruitment dynamics in a diversity of pond types or over long time periods typically find that longer ephemeral hydroperiods (Semlitsch 1987b, Semlitsch et al. 1996, Baldwin et al. 2006) or permanent ponds (Whiteman and Wissinger 2005, Karraker and Gibbs 2009) have the highest net recruitment. Ponds with very short hydroperiods dry before successful metamorphosis, but ponds with permanent hydroperiods are often colonized with aquatic predators like fish, which can have strong negative impacts on recruitment (Knapp and Matthews 2000, Pilliod and Peterson 2001). These generalities are similar to what we found, except that fish are absent from the permanent ponds in our system, making them more generally suitable for recruitment. Rather, in our system cooler wet summers limited recruitment from permanent ponds. For *R. luteiventris* inhabiting mountain systems, the ability of tadpoles to develop to metamorphosis within a short growing season is key to recruitment success. However, other montane amphibians have multiple year larval stages, making permanent, fishless breeding ponds more critical to recruitment success (Whiteman and Wissinger 2005, Lacan et al. 2008). For species like the mountain yellow-legged frog (*R. muscosa*), cool summers would slow the development of first year larvae, but hot summers with non-permanent ponds would ensure recruitment failure.

Effects of pond heterogeneity on net recruitment and population growth rate

Our modeling results for metamorph production show that a heterogeneous system had less variability in net recruitment than a hypothetical system composed of only ephemeral ponds, and similar variability to one with only permanent ponds. This finding agrees with other observations that net recruitment can be extremely variable in ephemeral ponds (Semlitsch et al. 1996). The scenario with all ponds produced an equivalent number of metamorphs to the permanent pond scenario or the long ephemeral scenario. These results suggest that although individual pond types have the potential to produce equivalent numbers of metamorphs over time, their dynamics will generally be more variable than a system with heterogeneous pond types. In contrast, Karraker and Gibbs (2009) predicted that beaver ponds (i.e., semi-permanent to permanent hydroperiod) would produce 1.2 to 23 times more metamorphs than vernal (ephemeral) pools in the northeastern United States. Thus, permanent wetlands contribute disproportionately to regional wood frog production, similar to what Whiteman and Wissinger (2005) found for salamanders. However, for a western montane system, we found that a mixture of pond types provided the most stable recruitment. It is possible that these western montane systems experience more dramatic fluctuations in precipitation among years, but our study also captured a greater range of weather conditions by being conducted over a ten-year time period. The importance of hydroperiod variation for net recruitment will likely be different for various habitats, latitudes, and elevations.

The effect of pond type on egg to metamorph survival and number of metamorphs produced was still evident when we examined the repercussions of pond heterogeneity on population growth rate. The scenario with long ephemeral ponds had the highest population growth rate, followed by the scenario with all ponds. This result was largely due to extremely high egg to metamorph survival in one long ephemeral pond in 2008. It is possible that occasional bonanzas in these pond types have a true influence on recruitment dynamics, where some conditions promote exceptionally high survival. Our results do not qualitatively change if we remove this data point from our study, because long ephemeral ponds had the highest egg to metamorph survival in most years. This suggests that a landscape of long ephemeral ponds would have the highest long-term

growth rate, provided that environmental conditions did not systematically change over time.

Overall, population growth rates were low, and this is likely driven by changes in juvenile and adult survival rates over the course of the study. Both juvenile and adult survival rates declined from 2000 to 2009, while egg to metamorph survival rates remained relatively constant across ponds. Given these juvenile and adult survival rates, differences we measured in egg to metamorph survival among pond type scenarios altered our estimates of population growth rates. Thus, changes in breeding pond types in a population could alter population growth rates considerably. In amphibian population ecology, few studies have used matrix population models to examine the contribution of different vital rates to overall population growth (Biek et al. 2002). As such, variation in recruitment has rarely been put into a population context (but see Vonesh and De La Cruz 2002, Govindarajulu et al. 2005). Our study shows that differences in recruitment vital rates due to hydroperiod differences can impact long term growth rates. As long as juvenile and adult survival rates do not change systematically over time, changes in hydroperiod type or heterogeneity could alter long-term growth rates and population viability.

Whereas other studies examining the effect of habitat heterogeneity on population dynamics examine fluctuations in estimates of total population size (Kindvall 1996, McLoughlin et al. 2002, Oliver et al. 2010), our study only examines the effect of heterogeneity on egg to metamorph life stages. Other habitat features, such as foraging and overwintering habitat, may be more important to juvenile and adult frogs, and be less tied to hydroperiod. If landscape heterogeneity were able to promote persistence of adult frog populations, as suggested by Piha et al. (2007) for the common frog (*Rana temporaria*), population growth rates might be more impacted by homogenization of terrestrial habitats. Although habitat heterogeneity has the potential to decrease variability in production of metamorphs, it may not be critical to population viability if other factors are causing declines in post-metamorphic life stages.

Conservation and management implications

Climate change models around the world predict an increase in the climate variability (Easterling et al. 2000). Analyses of climate data for Montana indicate an increase in the number of extremely hot days (≥ 32.2 C) per year and an increase in the frequency of years with an extreme number of hot days (Pederson et al. 2010). These trends might be positive for recruitment from permanent ponds, which is highly correlated with growing degree days (an index of the growing season; $R=0.79$, $p=0.035$), but could have deleterious consequences for recruitment from ephemeral wetlands. An increase in extremely hot years could increase the frequency of recruitment failure in ephemeral wetlands. Additionally, decreases in snowpack could ultimately lead to the loss of short ephemeral ponds, and the conversion of long ephemeral ponds to short ephemeral ponds. Therefore, permanent ponds may become increasingly important to stabilizing montane amphibian recruitment dynamics as global warming progresses. This study examined the impacts of habitat shifts but did not quantify this type of habitat loss. Undoubtedly, permanently losing breeding ponds in this landscape would lead to a loss in recruitment. Although the population may be able to sustain some loss of recruitment, permanent loss of breeding ponds would almost certainly lead to a decrease in population viability. Future climate changes will likely reduce both the number and diversity of ponds on the landscape.

Climatic trends may be out of our control, but the potential to manage for heterogeneous habitat may help sustain populations into the future. For example, eradication of non-native fishes from permanent lakes and ponds can have positive consequences for amphibian populations (Knapp et al. 2007). The eradication of fishes from mountain lakes may be critical to sustaining amphibian populations in the face of climate change if recruitment from semi-permanent lakes and wetlands becomes less frequent due to summer drought and snowpack declines (Lacan et al. 2008). In montane systems, the presence of permanent, fishless lakes and wetlands on the landscape may be critical to the long-term persistence of amphibian populations.

No studies have explicitly examined the potential for habitat heterogeneity to stabilize recruitment dynamics in amphibian populations in stochastic environments. We monitored recruitment dynamics in seven breeding ponds over a ten year period with

extremely high interannual environmental variability, and demonstrated the dynamic contribution of ephemeral and permanent pond types to annual production of metamorphs. Our study provides some support to the idea that heterogeneity in pond hydroperiods can lead to less variability in recruitment over time, and demonstrates that changes in egg to metamorph survival rates in relation to pond type can have a large effect on population growth rate. The importance of breeding pond heterogeneity may increase as climate change progresses, especially in montane systems where drought and interannual variability in weather conditions are expected to increase.

Table 4.1. Characteristics of breeding ponds in the Little Rock Creek drainage. Surface area, maximum depth, and emergent vegetation area are approximate values at high water. Emergent vegetation area indicates the approximate area in each pond potentially available for breeding in the spring. Hydroperiod is either characterized as permanent (P), long ephemeral (L), or short ephemeral (S).

Pond Name	Pond ID	Surface area (m²)	Maximum Depth (m)	Emergent Vegetation Area (m²)	Hydroperiod
FP	P1	5354	2	18	P
ILOP1	P2	1484	1.2	32	P
ILOP2	NA	3945	1.1	275	P
BLOP	P3	2097	1.5	350	P
SP	L1	3693	1	12	L
ILP1	L2	1109	1.2	16	L
BLP	NA	205	0.4	150	L
ILP3	S1	394	0.7	8	S
ILP4	S1	166	0.4	2	S
ILP5	S1	434	0.6	400	S
BLAW	S2	681	0.3	24	S

Table 4.2. Pairwise correlations of egg to metamorph survival among permanent (P), long ephemeral (L) and short ephemeral (S) ponds. Pearson correlation coefficients are displayed.

	P1	P2	P3	L1	L2	S1	S2
P1	1						
P2	0.63	1					
P3	-0.166	-0.184	1				
L1	-0.402	-0.472	-0.356	1			
L2	-0.104	-0.167	-0.352	0.855	1		
S1	-0.272	-0.329	-0.219	-0.304	-0.39	1	
S2	-0.215	0.333	-0.176	-0.375	-0.475	0.473	1

Table 4.3. Recruitment at different pond types in different years. 1=years where each pond had successful metamorphosis, (1)=years where each pond had some successful metamorphosis, but less than ten total metamorphs were captured, and 0=years where no individuals successfully metamorphosed.

Year	Pond						
	P1	P2	P3	L1	L2	S1	S2
2001	1	1	1	1	1	1	1
2002	1	0	(1)	1	1	1	1
2003	1	1	1	1	1	0	(1)
2004	1	1	1	1	1	1	(1)
2006	1	0	1	1	1	0	0
2007	1	1	1	1	1	0	0
2008	0	0	0	1	1	(1)	0
2009	0	0	0	1	0	1	0
Total years with successful recruitment	6	4	5 (1)	8	7	4 (1)	2 (2)

Figure 4.1. Distribution of lakes and wetlands in the upper basin at Little Rock Creek. This basin contains three lakes (lined), four permanent breeding ponds (black) and seven ephemeral breeding ponds (white). BLP and ILOP2 were not included in the analysis, and ILPs 3-5 were analyzed as one pond. Therefore, we used three permanent ponds (FP, ILOP2, and BLOP), two long hydroperiod ephemeral ponds (ILP1 and SP), and two short hydroperiod ephemeral ponds (BLAW and ILP3-5) in our analyses.

Figure 4.2. Number of eggs masses oviposited annually in a) permanent (P) and b) ephemeral breeding ponds in the Little Rock Creek basin. Ephemeral ponds include both long hydroperiod (L) and short hydroperiod (S) breeding ponds.

Figure 4.3. Proportion of egg masses laid in permanent, long ephemeral, and short ephemeral ponds across the study period (± 1 SE).

Figure 4.4. Annual egg to metamorph survival estimates in a) permanent and b) ephemeral breeding ponds in the Little Rock Creek basin. Ephemeral ponds include both long hydroperiod (L) and short hydroperiod (S) breeding ponds. Survival rates were calculated by dividing the number of metamorphs produced by the number of eggs laid.

Figure 4.5. Box plots of egg to metamorph survival across years for permanent, long ephemeral, and short ephemeral breeding ponds in the Little Rock Creek basin. Bars indicate median values, boxes show 50th percentiles, and error bars show 95th percentiles. The dot represents egg to metamorph survival in L1 in 2008.

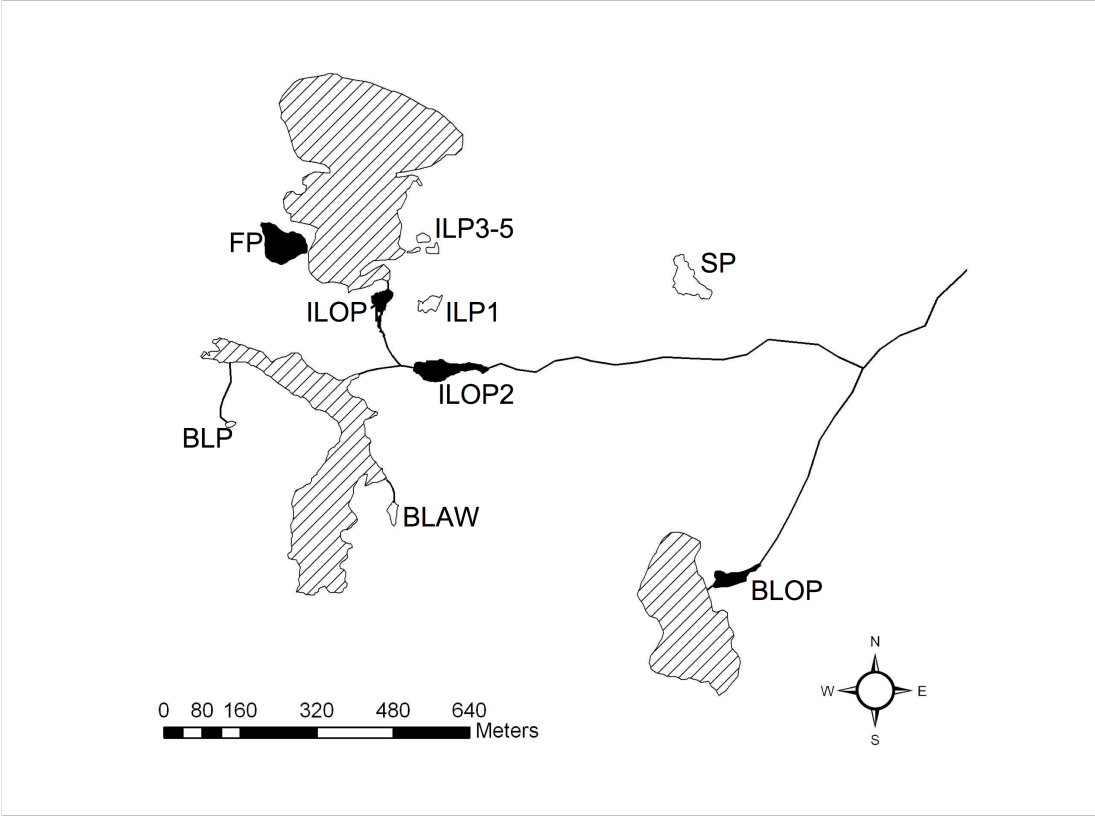
Figure 4.6. Annual metamorph production (± 1 SE) in a) permanent and b) ephemeral breeding ponds in the Little Rock Creek basin. Ephemeral ponds include both long hydroperiod (L) and short hydroperiod (S) breeding ponds. Estimates of metamorph abundance were calculated using mark-recapture methods.

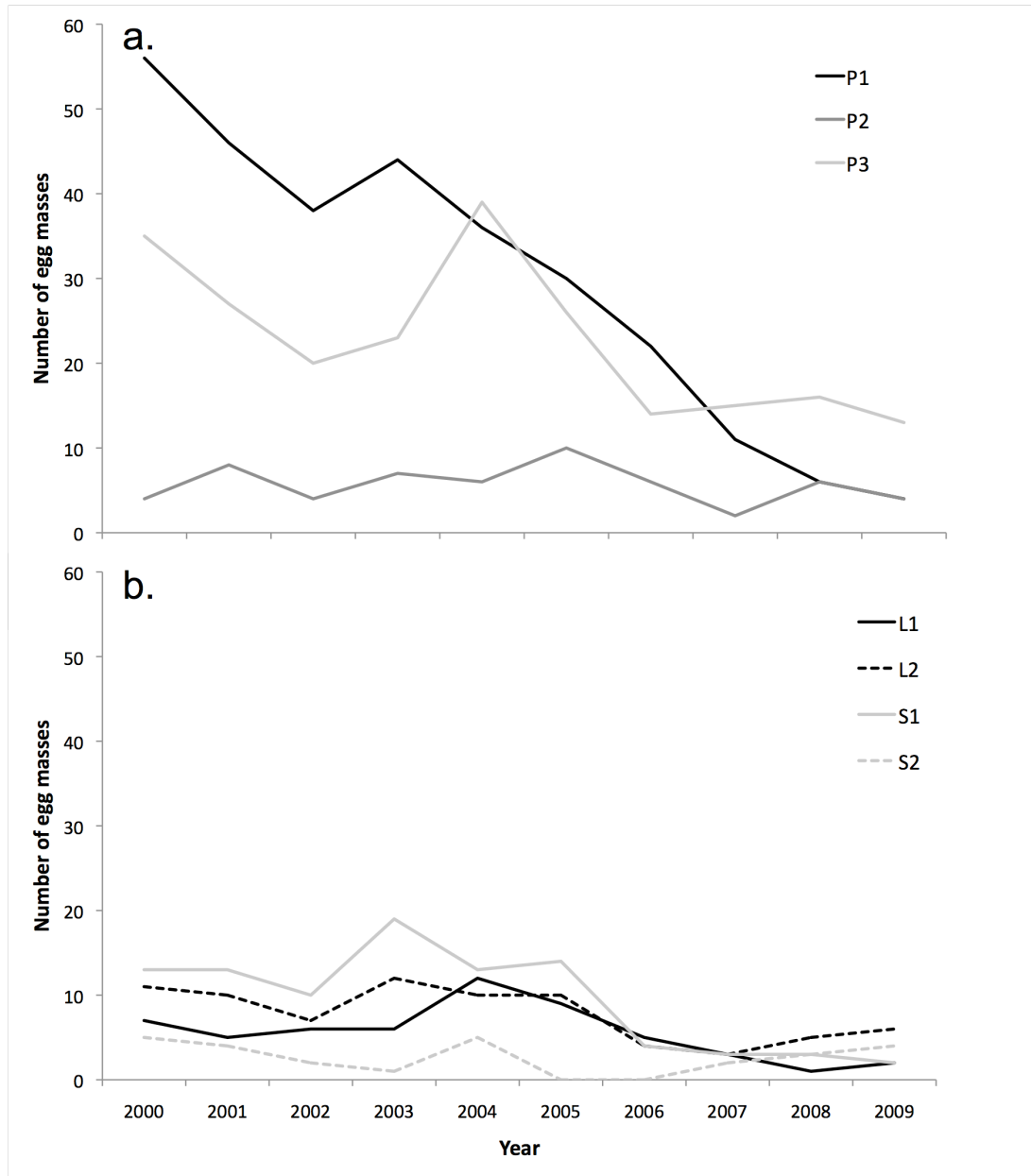
Figure 4.7. Box plots of number of metamorphs produced across years in permanent, long ephemeral, and short ephemeral ponds. Bars indicate median values, boxes show 50th

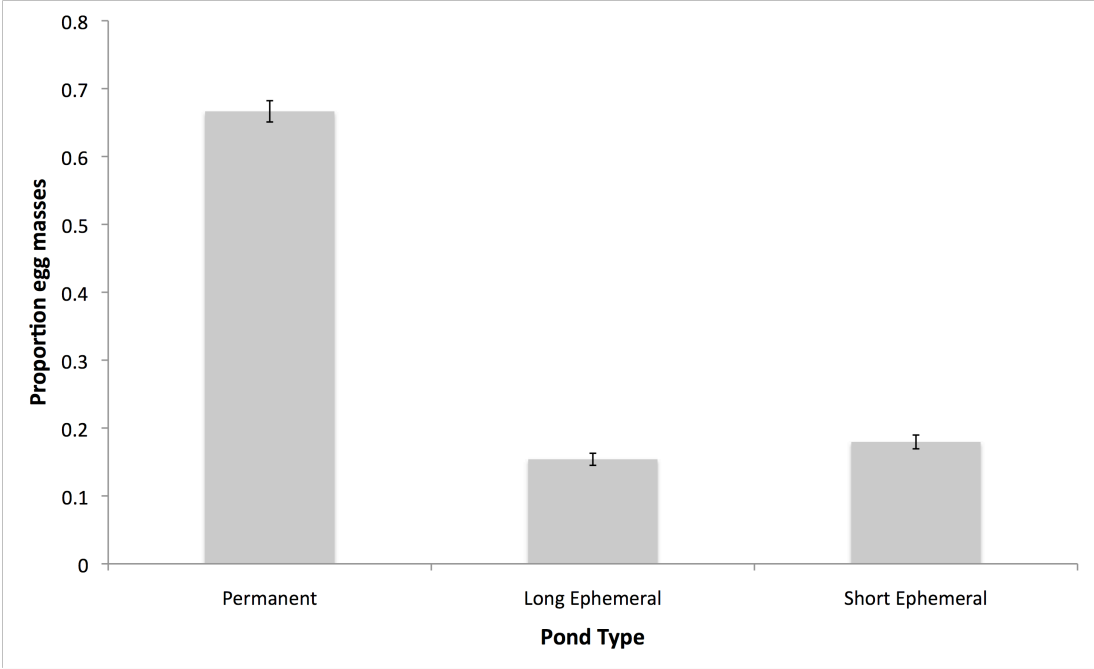
percentiles, and error bars show 95th percentiles. The dot represents net recruitment in L1 in 2008.

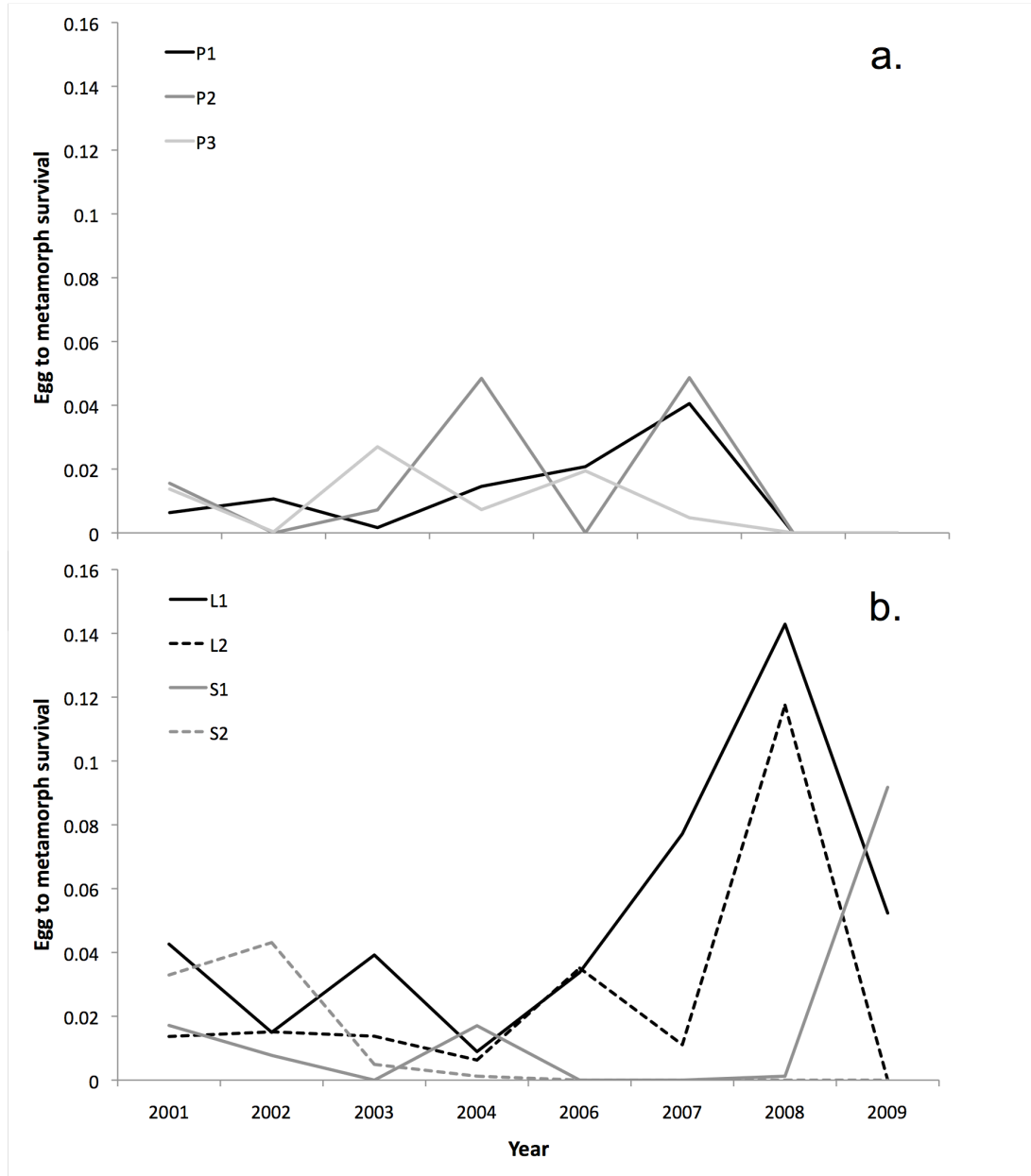
Figure 4.8. Box plots of estimated net recruitment across years for four scenarios: (1) current metamorph recruitment in Little Rock Creek basin (All), (2) all recruitment comes from permanent ponds (Permanent), (3) all recruitment comes from long hydroperiod ephemeral ponds (Long ephemeral), and (4) all recruitment comes from short hydroperiod ephemeral ponds (Short ephemeral). Total number of eggs laid in each scenario is the same, but is shifted to the ponds producing recruits in each scenario.

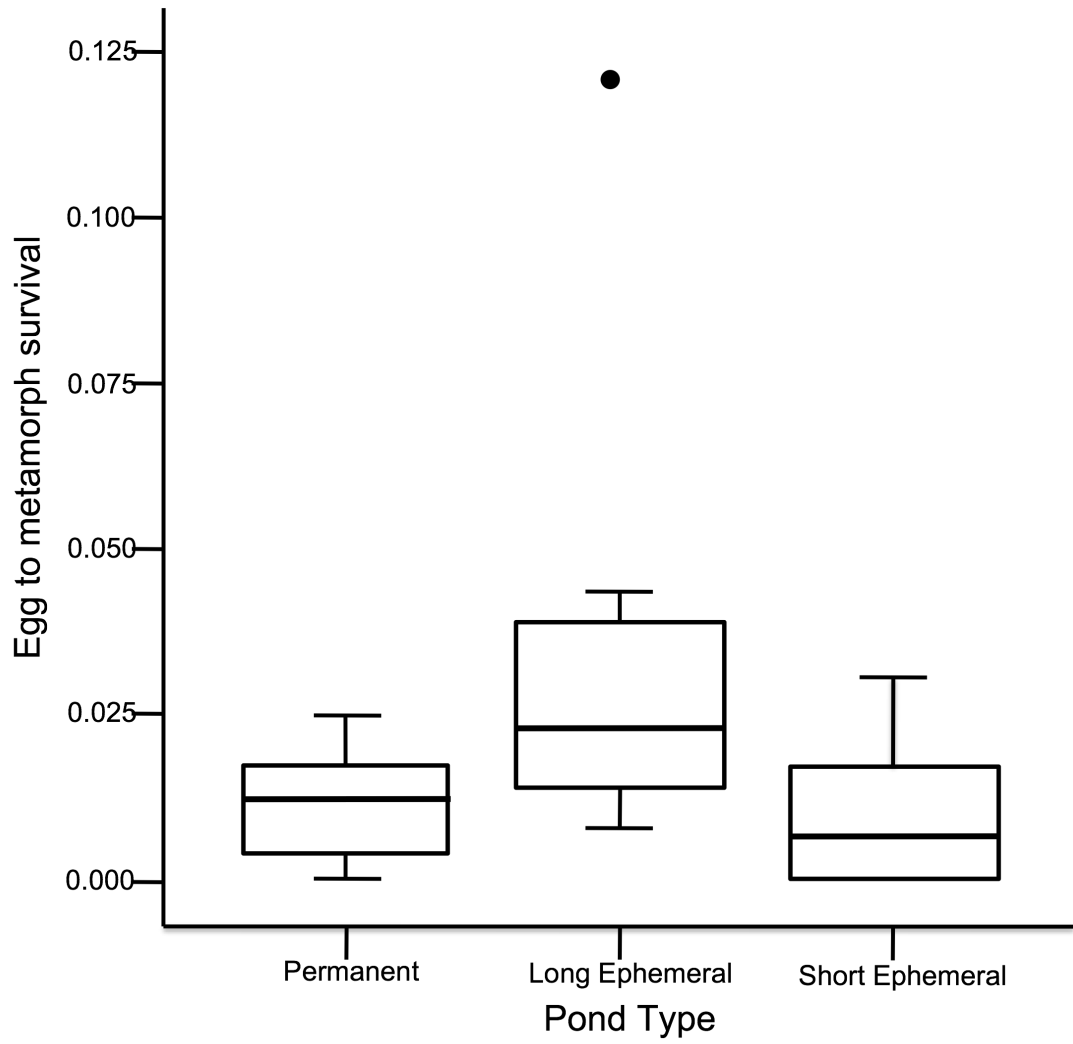
Figure 4.9. Population growth rates for four scenarios: (1) all ponds contribute to metamorph recruitment in current proportions (All), (2) only permanent ponds contribute to recruitment (Permanent), (3) only long hydroperiod ephemeral ponds contribute to recruitment (Long Ephemeral), and (4) only short hydroperiod ephemeral ponds contribute to recruitment (Short Ephemeral). Total recruitment does not change, but is shifted to the ponds producing recruits in each scenario.

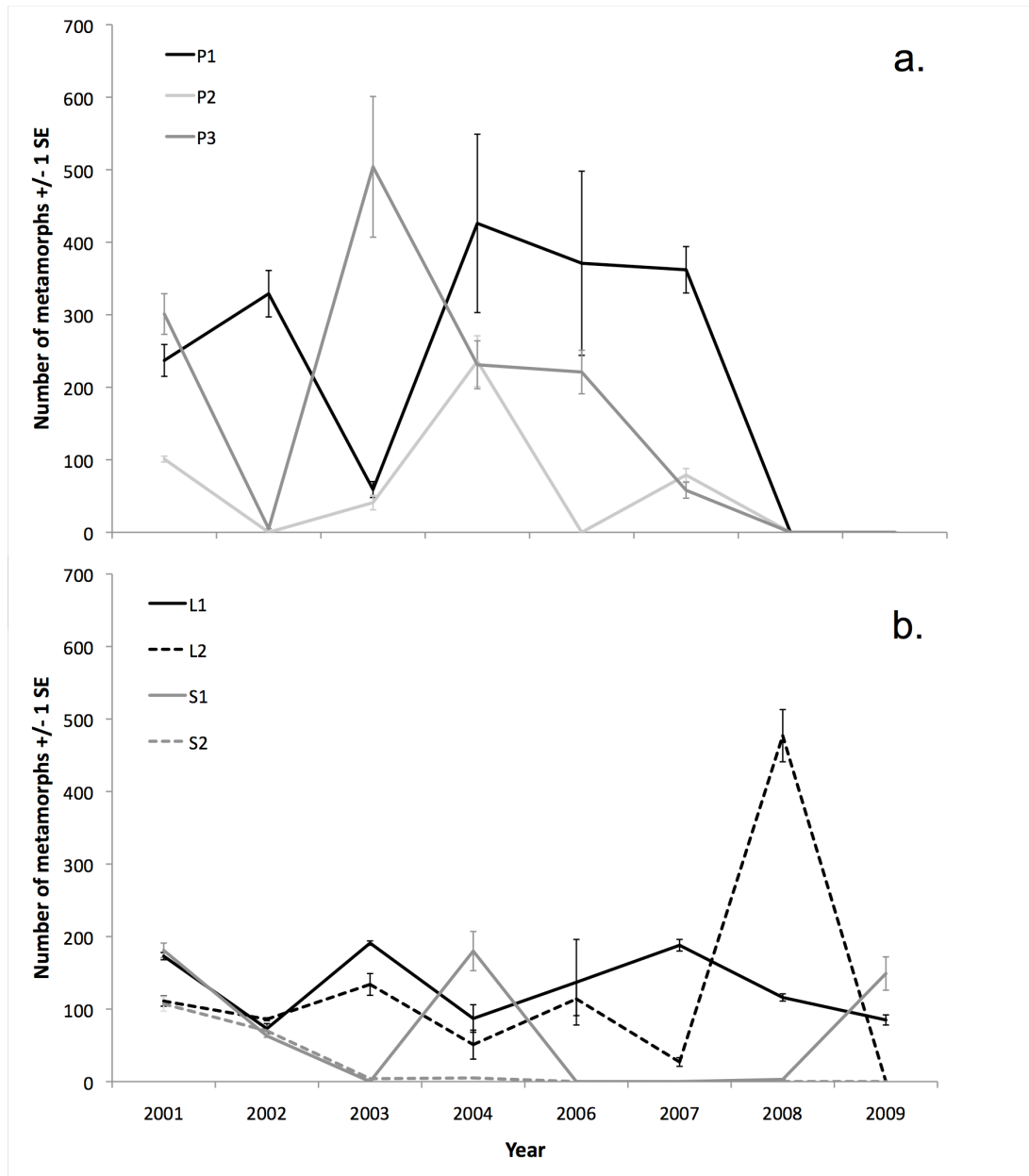


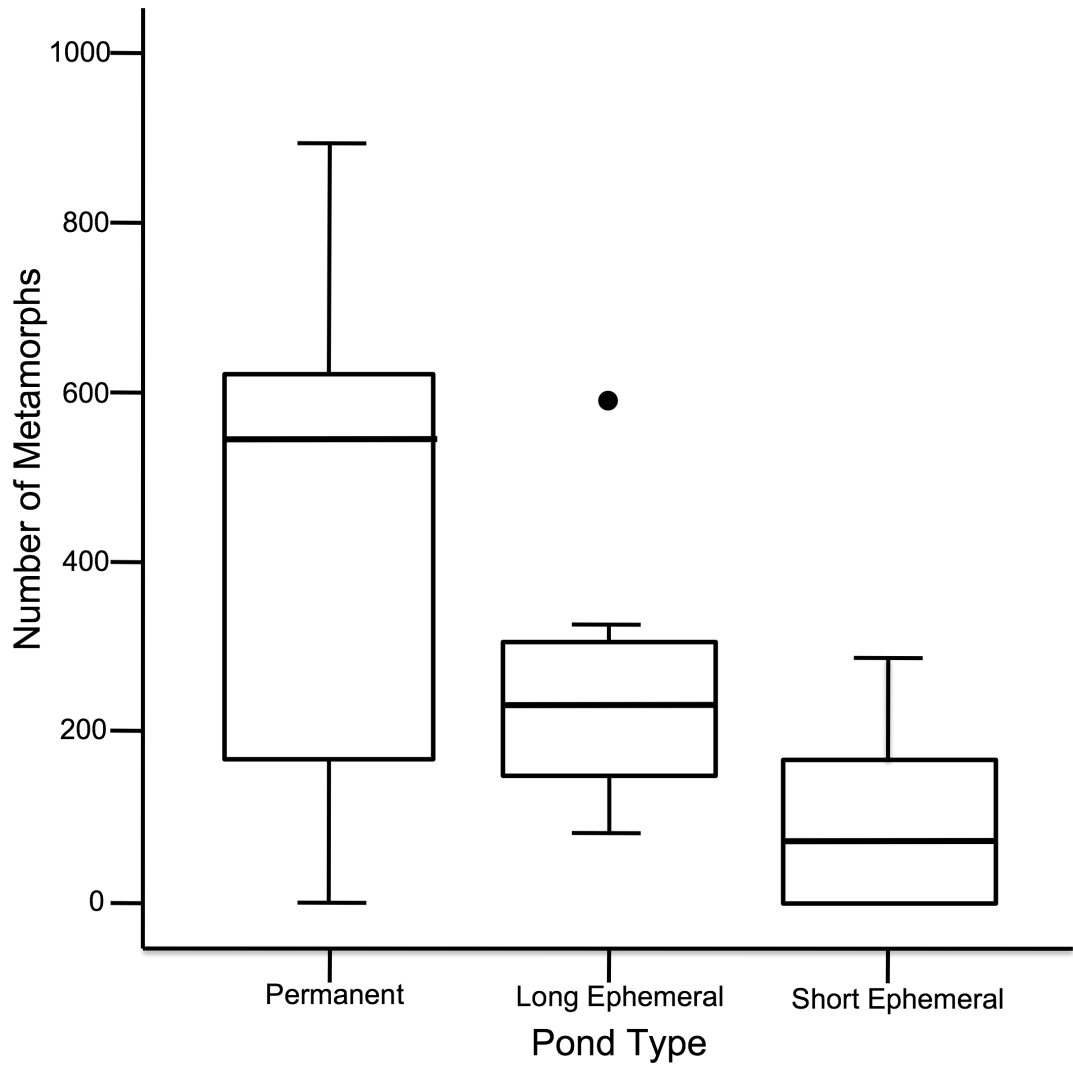


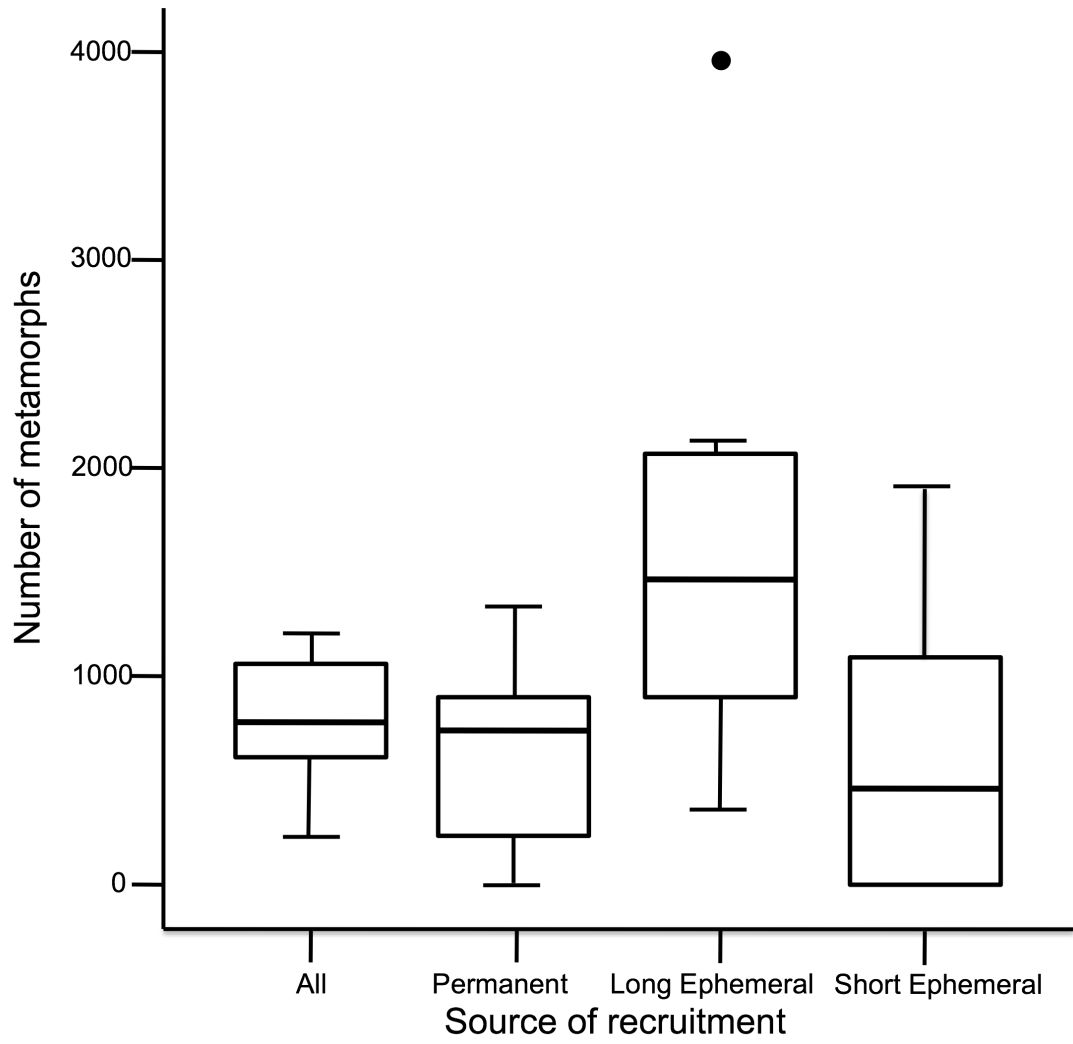


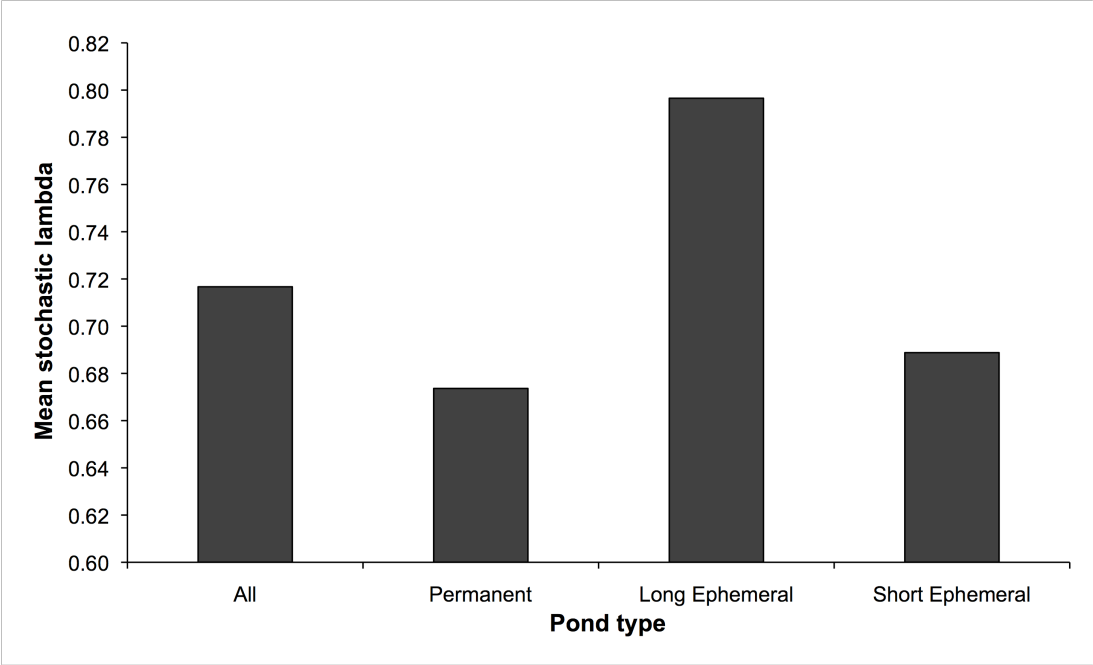












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APPENDIX A

BAYESIAN PARAMETER ESTIMATION FOR MULTI-STATE MARK-RECAPTURE DATA

The Bayesian framework for mark-recapture data allows the probabilistic estimation of vital rate parameters (survival, transition and recapture probabilities). Instead of point estimates, the Bayesian approach gives the solution as a distribution of different possible vital rates that explain the observed data. These distributions are often analytically intractable, but there are numerical methods to approximate the distributions by producing random samples from them. In this paper, we have used a Gibbs sampling algorithm for estimating population vital rates. The algorithm is described in detail here.

We estimate separate survival, transition and recapture probabilities for each year and each life stage. We have four life stages (juvenile, subadult, adult male, adult female) and 10 years of data. Let us begin by defining the following notation:

- x_{it} observed life stage for individual i at year t
- z_{it} true life stage for individual i at year t
- S_{it} survival probability from year t to year $t+1$ for life stage i
- R_{it} recapture probability in year t for life stage i
- P_{ijt} transition probability from life stage j at year t to life stage i at year $t+1$

Each entry in matrix \mathbf{x} is the observed life stage of an individual. If the individual was not observed, we set $x_{it} = 0$. Following Clark et al. (2005) we define the matrix \mathbf{z} , which contains the estimate of the true life stage of an individual. For the unobserved cases, this is estimated from data and varied in the Gibbs sampling algorithm.

The recapture probabilities can be directly estimated from the observations. We use the secondary sampling sessions within one summer to estimate the recapture probability for that year. Thus, the likelihood for observing \mathbf{x} for a given year t , with recapture probabilities R is

$$P(x_{\cdot,t} | R_{\cdot,t}) \propto \prod_{i=1}^4 R_{it}^{o_{it}} (1 - R_{it})^{u_{it}} \quad (1)$$

where the indicator variables o_{it} and u_{it} indicate the number of observed and unobserved individuals at year t and life stage i , respectively (counted from all secondary capture sessions). For estimating the survival and transition probabilities, we need an estimate of the true life stage \mathbf{z} . Survival and transition probabilities are estimated between primary capture sessions. The likelihood for life stages \mathbf{z} for a given year t , with survival and transition probabilities S and P is

$$P(z_{\cdot,t} | S_{\cdot,t}) \propto \prod_{i=1}^4 S_{it}^{s_{it}} (1 - S_{it})^{d_{it}} \quad (2)$$

$$P(z_{\cdot,t} | P_{\cdot,t}) \propto \prod_{\substack{i=1..4 \\ j=1..4}} P_{ijt}^{\#(i \rightarrow j)_t} \quad (3)$$

where indicator variables s_{it} , d_{it} and $\#(i \rightarrow j)_t$ indicate the number of survivals, deaths and transitions at year t , respectively (counted between primary sessions).

For estimating the true life stages, we follow (Clark 2005) and condition the life stage at time t on life stages at the previous and next time point (surviving previous time, stage transition, not capturing, surviving next time and stage transition):

$$P(z_{it} = j | z_{i,t-1} = k, z_{i,t+1} = l, R, S, P) \propto S_{k,t-1} P_{jk,t-1} (1 - R_{jt}) S_{jt} P_{ljt}. \quad (4)$$

Above, we have defined the likelihood components for observations \mathbf{x} and true life stages \mathbf{z} and a probabilistic model for true life stages \mathbf{z} . The only thing that is missing from the Bayesian estimation framework is the prior. Our prior assumptions follow the robust design framework: since secondary capture sessions are very close to each other (1 day), we can assume that survival probability is one between the secondary sessions and no transitions are possible between them. These priors are explicit in our computations, since we estimate survival and transition only between primary capture sessions.

The total likelihood for observing data \mathbf{x} and having true life stages \mathbf{z} , given the vital rate parameters, is obtained by taking a product of equations (1-3) over years. It is clear that the posterior distributions for the vital rates are binomial for recapture and survival and multinomial for transition. Thus, given our observed data \mathbf{x} and an estimate for life stages \mathbf{z} , we can sample new values for R, S and P from these known distributions.

In contrast, for some given values of the vital rates, we can calculate the probabilities for different z_{it} using equation (4) and sample new values from the resulting multinomial distribution. Alternating these conditional samplings, we arrive at the Gibbs sampler that is given as an algorithm below.

-
1. *Initialize: set initial guesses for R , S , P and z and iteration counter $i=1$*
 2. *Sample R , S and P from their conditional posteriors given x and z using equations (1-3)*
 3. *Loop over individuals and time points where $x_{it} = 0$, sample a new life stage z_{it} using equation (4)*
 4. *Set $i=i+1$ and go to step 2, until a desired number of iterations is obtained*
-

For our stochastic matrix model, we need estimates for breeding probability and survival probability from egg to one year, in addition to the actual vital rates of the four life stages. For the breeding probability, we need an estimate of the number of females for each year. These are calculated by dividing the number of observed females (counted from data) by the recapture probability estimate. To get the estimate for breeding probability as a distribution, this calculation is performed by numerical integration over the distribution of recapture rates given by the Bayesian mark-recapture analysis. Similarly, for survival probabilities from egg to one year, we need estimates of the number of one-year-old frogs. These are calculated from a separate data set which contains capture histories for one-year-old individuals. The above Bayesian algorithm was used for estimating the recapture probability for this age class (in this estimation, we only have one life stage) and the number of observed individuals was then divided by different recapture probability estimates to get a distribution of the number of one-year-old frogs.

Since the Bayesian sampling approach produces vital rate estimates as a set of samples, it is easy to use the samples to estimate the uncertainty of any function of the vital rates and extend the Bayesian analysis to all calculations made with the estimates. In

this paper, we utilize this property in all of our computations of regressions with vital rates and snowpack and matrix model predictions.

In Clark (2005), in addition to the simple Bayesian model, a hierarchical structure is defined for vital rates. In hierarchical estimation, one specifies a common prior for some group of vital rates and estimates the parameters of the prior (called hyperparameters) from data. With hierarchy, one can model stochastic effects; e.g. vital rates that are approximately constant over years and/or life stages but that are allowed to change a bit over the years. We use a non-hierarchical version here, since we estimate vital rates separately for each year and then associate these annual estimates with climate variables. Development of a hierarchical extension to our model will be an interesting area for future research, but is beyond the scope of this analysis.

APPENDIX B
BIRD ECOLOGY ACROSS BOUNDARIES: INTERNATIONAL PEN PALS IN THE
BIOLOGY CLASSROOM

Introduction

The diversity of life on earth is a fundamental concept in biology, but is something that can be difficult to explore in an elementary school classroom. A great place to start is by getting students outside to observe the diversity in their own backyards. I served as a scientist in residence for one year at an elementary school in Missoula, Montana, working on ecological inquiries inside and out of the classroom. To extend the students' understanding of their local biodiversity, I set up an ecological pen pal exchange with students at two schools in northern Scotland. Pen pal relationships have been used to enhance literacy skills (Rankin 1992), create cross-cultural connections (Shandomo 2009), and develop mathematical communication skills (Crespo 2003), among other topics. We focused on writing about bird diversity between the two countries because students can easily observe and listen to birds in their own backyards and schoolyards (Frissell and Cayton 2009, Smith 2009). Additionally, we were able to link into each country's existing citizen science bird monitoring programs, which allowed students to contribute their findings to a real database and see how the data were used in a larger biodiversity context. The goals for this project were (1) to make ecological connections among students in two different countries, (2) to learn about local bird ecology and biodiversity, and (3) to contribute to national bird monitoring programs. These goals fit into the National Science Standards for Teaching and Content (Box A.1). I describe how we developed this project and some of the tangible results of the exchange, with suggestions along the way for how to implement this kind of project in your classroom.

Making ecological connections between countries

Before the school year started, I contacted two teachers I knew in Scotland about getting involved in this project, and they were enthusiastic about participating. Their schools were Udney Green primary school in northeastern Scotland, and Poolewe primary school in northwestern Scotland. Our first letters gave students the opportunity to introduce themselves. They wrote about their favorite things, and described their families and where they live. Once the introductions had been made, we were ready to write about biology! All of the letters exchanged by students and teachers included some information on what the students were learning in their science classes. Although our focal project was on birds, students were able to share stories and information on other outdoor and classroom-based science projects throughout the school year. Students in Scotland and Montana completed their investigations on birds in their own countries and then sent letters, artwork, pictures, graphs, and other reports to each other.

I was fortunate to know teachers in another country, but there are other ways you could set up such an exchange. These could include contacting local universities, which generally have connections with schools overseas, connecting with fellow teachers at conferences or on-line teacher networking sites, or identifying interested teachers and schools through bird education and citizen science websites (Box A.2). This type of eco-pal exchange could also be accomplished with students in a different region of the United States. The ecological and cultural diversity of the United States could make a more local exchange fun, successful, and informative.

Learning about local bird ecology and diversity

Each classroom developed its own set of activities to study bird biodiversity, which also intersected with their art and math curricula. Poolewe students studied and drew pictures of local bird species and made clay birds (Figure A.1); Udney Green students worked on bird feeders and made detailed observations of bird behavior in the schoolyard; and Missoula students learned to identify local species and birdcalls every week (Figure A.2). The different projects were developed by the individual teachers to

compliment what was going on in their classrooms, and winter bird counts were the common link between the three schools. In Missoula, we showed pictures of common local species and practiced recognizing the birdcalls and the pictures of the bird. We had a field guide for western North American birds and a CD of Rocky Mountain bird songs in the classroom. However, birdcalls, pictures, and other information for many North American species can be found on the Internet (Box A.2). The students spent about 15 minutes each week learning about these birds, and the students were soon able to recognize about 10 common winter bird species. Every student had a favorite bird species, and they were soon pointing out the common birds seen out of the classroom window, such as magpies, black-capped chickadees and northern flickers. We kept a log of birds seen at school and at home in the students' backyards (Figure A.3). Parents were encouraged to help their children fill out the log at home. We also built bird feeders, which we placed around the schoolyard and at students' houses (Figure A.4).

The bird project in Missoula culminated in a bird-watching field trip to a local natural area. We practiced using binoculars safely and met two bird experts, who accompanied us on the field trip. Several parent chaperones joined us too to ensure adequate supervision of the class. The class was divided into two groups, and we counted birds in two different areas of the park. We wrote down the number of birds of each species we saw, and recorded the total time we spent looking. Students in Scotland conducted similar counts at their schools, recording numbers of birds seen and total time spent looking. This gave students an introduction to some of the scientific methods that biologists use to collect data.

Back in the classroom, we made bar graphs to visualize how many birds we saw, and Scottish students did the same (Figure A.5). Making bar graphs linked directly with what the students were learning in their math class, and allowed for easy comparison between Scotland and Montana. We practiced making bar graphs by hand, and also made them on the computer. Students from all three schools sent artwork, graphs, and summary information about the bird ecology projects to each other, in addition to their letters. Once we had received the projects from Scotland, we were able to discuss why there are different or similar species in the two different countries and compare our bird counts.

Connecting to national bird-monitoring programs

Citizen science programs monitor long-term trends in bird populations using data collected by the public at certain times of the year. These programs occur in different countries, and have consistent, easy-to-follow protocols. Both Scotland and the United States have established winter bird counts, and all three schools participated in these bird-monitoring programs in their countries. The Scottish schools participated in the Big Schools' Birdwatch (<http://www.rspb.org.uk/schoolswatch>), which is a citizen science program for schoolchildren. Missoula students participated in the Great Backyard Bird Count (GBBC; <http://www.birdsource.org/gbbc>), which is a national program in the United States co-sponsored by the Audubon Society and the Cornell Laboratory of Ornithology. The bird counts conducted during their bird ecology projects used the protocols and forms from these programs, which can be found on their websites. For example, the GBBC is completed over the course of four days, and has an easy-to-use form for recording species seen. We set up our field trip to coincide with the dates of the GBBC. In all cases, the classes followed standardized protocols to record bird observations, and then submitted their data to an online database. Although there were some differences in the protocols for the Big Schools' Birdwatch and the GBBC, the data collected were similar and easy to compare.

Students in Missoula were able to look at their results, as well as the United Kingdom results, on the Internet, and vice versa. Students in both countries were able to see how their results fit into the larger picture of bird diversity, both in Scotland and in the United States. Examining maps of bird diversity throughout the two countries led to discussions of why diversity is higher in some places than in others, when and why birds migrate, and which species were the most common. Maps of local and country-wide bird diversity are available from the bird count websites after the bird counts are over. Students can also compare bird counts from their year to previous years, and examine the abundance of individual species.

Projects like the bird count have amazing potential to be used in national or international pen pal exchanges such as this one. This is largely due to the fact that they are already connected to large, national networks. By getting involved in these national

citizen science monitoring projects, we were able to collect useful data using standardized protocols, and enrich this experience by sharing those results internationally.

Evaluation of the project

Each school participated in a qualitative evaluation of the eco-pen pal project in late spring. Students were asked a series of ten questions designed to determine what they learned in their own investigations and from their pen pals' investigations. Each teacher also completed a questionnaire addressing the greatest successes and challenges of the exchange, and how the exchange enhanced student understanding of ecological concepts.

Student perspective

Generally, students from Missoula enjoyed participating in the exchange and indicated that they learned something new or interesting about Scotland's wildlife, such as identifying which species we had in common and which were different. Most students demonstrated some understanding of the ecological concepts we covered in the short answer questions. For example, in response to the question "why are the birds here different from those in Scotland?" students mention the differing weather and/or climate of the two countries. In response to the question "why do seasonal changes occur at different times here than in Scotland?" one student responded, "[Scotland is] farther from the equator." These answers demonstrated that students were connecting differences in geography and climate to differences in ecology between the two countries. Students from Scotland had similar responses.

Teacher perspective

The teachers benefited from the exchange as well. The Montana teacher felt that the exchange "definitely helped [the students] understand species better because [they] got to exchange data." She felt that receiving the letters and projects from Scotland "allowed for discussions about Scotland and led [them] to extending what [they] were learning [in Montana]." In addition to enriching the students' ecological knowledge, the teacher thought it was interesting to see how schools and cultures differed between the

two countries. Overall, she considered the exchange to be “an incredibly enriching activity.” The teachers from Scotland felt that the letters and projects received generated a lot of discussion, and helped students “appreciate the bigger picture of the diversity of life on Earth.” By participating in the exchange, the teachers in Scotland also reached out to local experts to learn more about their local ecology. The main challenge with the project was the time delay in the exchange of letters. This could be improved by sending some correspondence by email.

From my perspective, the exchange was both fun and informative for the students. In their regular science class, students were just learning the characteristics of birds in a textbook, and this experience allowed them to see those characteristics out in nature, contribute to a national bird monitoring project, and compare birds from two countries. We did not formally test the students on their knowledge gained, but knew that students were excited to be a part of this exchange and to recognize the birds around them.

Conclusion

There are many different ways to organize an ecological exchange like this one. Although this project was conducted with third grade students, eco-pen pal exchanges such as this could be done with all grade levels. Initiating this type of exchange with older students could result in more in-depth ecological inquiries, with analyses that formally compare the results from different countries. Exchanges could also incorporate various classroom technologies. For example, students could exchange videos or pictures through email, or classrooms could set up a blog to chronicle the progress of the project. Nothing can change the experience of receiving hand-written letters, artwork, and colorful reports, but computers and the Internet could certainly enhance and add to the exchange. We used traditional mail to facilitate sending art projects and to work on handwritten letters, but we would incorporate some email writing and more Internet use if we did this again.

In our exchange, we focused on broad differences in biodiversity between two countries. This approach introduced younger students to the concept of biodiversity: they learned about why different species inhabit different places, and compared the species found in Scotland and Montana. They also explored how the environment affects living

organisms by making observations of birds in their schoolyards over multiple seasons (Box A.1).

Connections between students from different regions or countries in the areas of science and ecology have the potential to enhance ecological knowledge and enlarge the worldviews of participants. The students from Montana that were involved in this exchange will probably not go to Scotland anytime soon, but this exchange provided a first glimpse into the ecology of a country thousands of miles from their own home through the eyes of their peers. Similarly, students in Scotland were able to directly communicate with American students. Through this type of exchange, these different worlds were brought a little closer together, while allowing each group of students to get outside, observe their local bird diversity, and develop a stronger ecological understanding of their local environment.

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Box 1. This project connects to the following National Science Education Standards (NRC 1996):

1. Teaching Standards

Standard B: Guide and facilitate learning

- Orchestrate discourse among students about scientific ideas

Standard D: Design and manage learning environments

- Flexible and supportive setting for scientific inquiry
- Identify and use resources outside the school

2. Content Standards (Grades K-4)

Standard A: Science as inquiry

- Abilities necessary to do scientific inquiry
- Understanding about scientific inquiry

Standard C: Life science

- Characteristics of organisms
- Organisms and environments

Box A.2. On-line resources for bird ecology

Citizen science bird counts in various countries (these websites include great resources for educators, and may facilitate connections with teachers in other countries):

- Great Backyard Bird Count: <http://www.birdsource.org/gbbc/>
- Big School's Birdwatch UK: <http://www.rspb.org.uk/schoolswatch/index.aspx>
- Australia School Yard bird survey:
<http://www.birdsinbackyards.net/surveys/schoolground-birds.cfm>
- New Zealand Garden Bird survey:
<http://www.landcareresearch.co.nz/research/biocons/gardenbird/activities.asp>

Resources on North American bird ecology:

- National Audubon Society: www.audubon.org
- Cornell Bird Laboratory: <http://www.birds.cornell.edu>
- Bird calls: <http://www.enature.com/birding/audio.asp>

Figure legends

Figure A.1. Artwork by a Scottish student set to Montana during the winter bird ecology projects.

Figure A.2. Artwork sent to Scotland by a Montana student while we examined signs of spring.

Figure A.3. Winter bird log completed by Montana students inside and out of the classroom.

Figure A.4. Guidelines for making pop-bottle bird feeders in the classroom.

Figure A.5. Sample data collected during winter bird counts in a) Scotland, and b) Montana.



A blue tit likes to eat at a bird feeder
in the winter. It is blue, green
and yellow. It whistles and nests
in holes in trees.

by Annie



Two-liter pop bottle birdfeeders

1. Remove all the labels and stickers from the soda bottle.
2. Wash and dry the bottle.
3. The bottom of the bottle will be top of the feeder.
4. Drill two small holes in the bottom of the bottle. Thread wire through one hole and out the other. Twist the ends of the wire together to make a loop for hanging the feeder. Use a small piece of duct tape or caulk to seal the holes so rain cannot get into the feeder.
5. Using a drill, make 5/16" holes that are on opposite sides of the bottle. Insert 8" - 9" by 5/16" dowels into the pairs of holes.
6. Repeat the above step to make several more perches.
7. If you want a thistle (niger) seed feeder, make 1/4" by 1/8" slots 1 1/2" above the perches.
8. If you want a sunflower seed feeder, make 5/15" holes 1 1/2" - 2" above the perches.

