1-1-2011

Effects of the aquatic to terrestrial habitat ratio on an amphibian predator and its prey

Amber Kramer
Washington University in St. Louis

Recommended Citation

Kramer, Amber, "Effects of the aquatic to terrestrial habitat ratio on an amphibian predator and its prey" (2011). *All Theses and Dissertations (ETDs)*. 602.
https://openscholarship.wustl.edu/etd/602

WASHINGTON UNIVERSITY

Division of Biology and Biomedical Sciences

Evolution, Ecology, and Population Biology

Dissertation Examination Committee:
Tiffany Knight, Chair
Allan Larson
Kenneth Olsen
Barbara Schaal
Kevin G. Smith
Alan Templeton

EFFECTS OF THE AQUATIC TO TERRESTRIAL HABITAT RATIO ON AN AMPHIBIAN PREDATOR AND ITS PREY

By

Amber Burgett Kramer

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

December 2011

Saint Louis, Missouri

ABSTRACT OF THE DISSERTATION

Effects of the aquatic to terrestrial habitat ratio on an amphibian predator and its prey

by

Amber Burgett Kramer

Doctor of Philosophy in Evolution, Ecology and Population Biology

Washington University in St. Louis, 2011

Professor Tiffany Knight, Chairperson

This dissertation explores the effects of varying the composition of aquatic and terrestrial habitats in a landscape (the aquatic to terrestrial ratio) on amphibians that use both the aquatic and terrestrial habitats during their lives. In Chapter 1, I first used meta-analysis and simulations to demonstrate that as the longevity of an amphibian increases, the elasticity of the population growth rate to perturbations in the aquatic (larval) habitat decreases. In Chapter 2, I examined the abundance of larvae of a long-lived amphibian, *Ambystoma maculatum*, across landscapes that varied in their aquatic to terrestrial ratios and found that larvae of this species were more dense in landscapes where aquatic habitat was scarce relative to terrestrial habitat. Because larval *A. maculatum* are top predators, they had more dramatic effects on the community composition of their prey in these isolated habitats, suggesting a result opposite to traditional metacommunity theory. In Chapter 3, I monitored the population level response of two common prey species, tadpoles of grey tree frogs (*Hyla versicolor*) and Blandchard's cricket frogs (*Acris crepitans)* to the presence and absence of predatory laval *A. maculatum* in large-scale experimental ponds. These prey species have very different longevities, and therefore differential use of the aquatic and terrestrial habitats. Population-level results suggest that, as expected, *A. maculatum* had a larger influence on the population dynamics of the shorter-lived *A. crepitans* than on *H. versicolor.* Finally, in Chapter 4, I found that the abundance of aquatic habitat in an area influences the ability of *A. maculatum* females to discern between oviposition sites of varying qualities. Studies of declining populations of amphibians typically focus on aquatic habitat and factors that affect larval survivorship and growth therein. However, this dissertation highlights the importance of both the aquatic and terrestrial habitats, and the ratio between the two, to overall population dynamics of amphibian species. These results will become more important as anthropogenic habitat destruction not only leads to an absolute loss of habitat, but also potentially alters the ratio of aquatic to terrestrial habitats on which amphibians depend.

Acknowledgements:

This research could not have been possible without the assistance and help of many people throughout the last five and a half years. First, I would like to thank my advisor from June of 2006 until July of 2011, Dr. Jon Chase. Without his guidance, patience, and academic counsel, much of this research would not have been possible. He has taught me how to be a better researcher and scientist while inspiring me to develop my research interests and to pursue my own passions. Additionally, I would like to thank Dr. Tiffany Knight for serving as my advisor in the final stages of my dissertation research. Her expertise and assistance in both developing my dissertation ideas, implementing them, seeing them through to fruition, and her patience during the writing phase have been invaluable and I am extremely grateful. I would also like to thank my dissertation committee, Dr. Allan Larson, Dr. Kenneth Olsen, Dr. Barbara Schaal, Dr. Kevin G. Smith, and Dr. Alan Templeton for their support and advice as I developed and executed my dissertation.

I would like to acknowledge my funding sources, which allowed me the means necessary to execute much of my research. First, I would like to thank Washington University and the Tyson Research Center for funding that allowed me to undertake a large-scale experiment, which required building 12 experimental ponds. I would like to thank Washington University's Division of Biology and Biomedical Sciences and the Department of Biology for the years of financial support. Additionally, I would like to acknowledge and thank the National Science Foundation for funding support in the form of the awarded Doctoral Dissertation Improvement Grant. Funds from this grant allowed

me to begin my mark recapture studies and to explore the population level impacts of a predator on amphibians.

Much of this research and data collection could not have been possible without the support of many local agencies. The Missouri Department of Conservation (MDC) allowed me to access conservation sites after hours in order to conduct frog call surveys and issued numerous special use permits, collectors permits, and access to sample ponds, without which I would not have been able to collect much of the data necessary for this dissertation. Additionally, I would like to thank the Missouri Botanical Garden's Shaw Nature Reserve for access to conduct frog call surveys, pond surveys, and construction of ephemeral ponds. In particular, I would like to thank Shaw Nature Reserve's restoration biologist, Dr. James Trager for all of his support, encouragement, and interest in my research over the years.

I would also like to express my gratitude to the EEPB community and Tyson Research Center for their support, advice, and assistance. I would like to thank the members of the Chase lab past and present for all of their encouragement, field work assistance, and advice over the years. In particular, I would like to thank Dr. Brian Allan, and Dr. Wade Ryberg for their assistance in the field countless times. The staff and researchers at Tyson Research Center have also been critical to the success of my dissertation research. I would especially like to thank Meghan Kelly for her patience in answering questions and assistance with logistical support. Pete Jamerson assisted with the construction of experimental ponds 4 years ago and has been providing me with invaluable assistance in constructing and implementing my research ever since. I am extremely grateful to Beth Biro for not only her help with fieldwork and research advice, but her support as a friend and colleague. I would especially like to thank Dr. Kevin G. Smith for all of his advice, guidance, and support both in the field and on my committee. Numerous high school students assisted with data collection and field work through the Tyson Environmental Research Fellowship program, and Chloe Pinkner in particular spent two years assisting me in sampling ponds and catching frogs. I would like to thank Mary Lueder, a Washington University undergraduate, who spent her summer nights catching and marking frogs with me. Her independent project has provided wonderful supplemental data for this dissertation and I look forward to collaborating with her on publishing her project in the future. I would like to acknowledge all of the behind the scenes support provided by the staff of Washington University's biology department. Without their assistance, much of this work could not have been possible.

Finally, I would like to thank my family for their support, love, and encouragement over the years as I pursued a rather different career path than many were accustomed. My parents have been critical in encouraging me to pursue my dreams and instilling in me the value of education from a very early age. They have provided me with unconditional love and support and even the manual labor needed to dig 12 ponds. I am forever grateful for all of the sacrifices they have made in their lives in order to put my brothers and I through college and provide us with the opportunities that they themselves did not have. Lastly, I would like to thank my husband, John, for his tolerance of the crazy hours I worked during field seasons, the numerous ticks that would inevitably make their way into our house, and the complaints and itching that would often consume me during the numerous poison ivy outbreaks. He has given me the strength to see this research through and provided me with emotional support and love. I am excited to start the next phase of our life together with our future son or daughter, whom I would also like to thank for staying put long enough for me to finish this dissertation!

Dedication:

I dedicate this dissertation to my parents who have taught me that with hard work, anything is possible.

Table of Contents

List of Tables

List of Figures

Introduction

Introduction:

Many scientists consider habitat destruction the single greatest threat to global biodiversity (Hoekstra et al. 2005, Brooks et al. 2006). Loss of habitat can change the shape and isolation among remaining habitats, and thus can have dramatic consequences on community dynamics (Gibbs 2000, Fahrig 2003). Less appreciated, however, is that habitat alterations may change the ratio of distinct habitat types available in a landscape. For example, when wetlands are drained, this not only decreases the amount of aquatic habitat in an area, but also decreases the ratio of aquatic to terrestrial habitats. For organisms with ontogenetic habitat shifts, in which two distinct habitats are required during the life cycle (Wilbur 1980, Werner and Gilliam 1984), the ratio of distinct habitat types within a landscape may have dramatic consequences for population dynamics as well as for community interactions in either habitat type.

Most amphibians exhibit a classic complex life cycle in which most larvae grow and develop in aquatic habitats and metamorphose to spend their juvenile and adult life stages in terrestrial habitats (Wilbur 1980). As a result, amphibians may be particularly vulnerable to anthropogenic perturbations such as habitat destruction, due to their reliance on both aquatic and terrestrial habitats (Beebee and Griffiths 2005), and this may contribute to the rapid declines that have been observed over the past several decades (reviewed in: Collins and Storfer 2003, Stuart et al. 2004). Additionally, amphibians occupy a wide range of trophic positions within both aquatic and terrestrial food webs, ranging from primary consumers to top predators (e.g.: Holomuzuki et al. 1994, Wellborn et al. 1996, Altig et al. 2007), and thus habitat perturbations may have large consequences not only for amphibian population dynamics but for aquatic and terrestrial communities as well (Hamer and McDonnell 2008, Vaugh 2010).

The overall goals of this dissertation are explicitly to examine the role of complex life-cycles on amphibian populations, their responses to changes in habitat ratios, and their influences on and within food webs. As a first step, in Chapter One, I sought to identify the population-level responses of amphibian species with varying longevities to aquatic and terrestrial habitats. As has been shown by meta-analysis of numerous other taxa (Silvertown et al. 1996, Heppel 1998, Sæther and Bakke 2000, Heppel et al. 2000, Forbis and Doak 2004), I found that as the longevity of an organism increases, the population growth rate (λ) becomes less sensitive to vital rates of early life stages (e.g., larvae in the aquatic habitat) and more sensitive to survivorship in later life stages (e.g., juveniles and adults in the terrestrial habitat). This pattern may be particularly useful in developing conservation plans for declining or threatened populations because it can focus conservation efforts on the habitat that is most critical for population growth of the species.

Based on the pattern presented in Chapter One, I predicted that changes in the number of aquatic habitats (e.g., breeding ponds) relative to terrestrial habitats would have little influence on the population growth of long-lived amphibian species. Instead, as the ratio of aquatic habitat goes down, the density of long-lived species breeding in those habitats should increase. I tested this prediction in Chapter Two by examining how the availability of aquatic and terrestrial habitats in a landscape influences the abundance of a long-lived amphibian, the spotted salamander (*Ambystoma maculatum*), in breeding ponds, as well as the consequences of varying densities of this aquatic predator on the rest of the food web. In 2007-2008, I surveyed 39 ponds throughout eastern Missouri and found that isolated ponds with low aquatic: terrestrial habitat ratios (ATR) had higher densities of *A. maculatum* larvae than ponds that were more connected (high ATR), a pattern opposite to that expected from most metapopulation/metacommunity expectations (see B**ackground Information: *Principles of metacommunity theory*** section below). Furthermore, high densities of predatory larval *A. maculatum* reduced the species richness of the aquatic community in ponds with low ATR.

Many other aquatic species, including several of *A. maculatum's* preferred prey, have a complex life cycle (e.g., many insects and other amphibians). Larval *A. maculatum* often prey upon tadpoles of the grey treefrog (*Hyla versicolor*) and Blandchard's cricket frog (*Acris crepitans*) in Missouri due to the phenological overlap between tadpole size/vulnerability and larval *A. maculatum* development. However, these two species differ in their life history strategies: *Acris crepitans* lives for approximately one year and could be considered an annual species (McCallum et al. 2011), whereas *H. versicolor* can live for up to 7 years, with multiple opportunities for reproduction over the course of its life (Snider and Bowler 1992, Wright and Wright 1995). In Chapter Three, I empirically examined the effects of larval *A. maculatum* predation on the population dynamics of *H. versicolor* and *A. crepitans.* I projected the population dynamics of both species in 12 experimental ponds at Tyson Research Center in response to the presence or absence of larval *A. maculatum* using capture-mark-recapture techniques and matrix population models. As expected, predation is projected to decrease population growth rate of both species. This suggests that predation in the aquatic habitat is an important driver in population dynamics of both species. In addition, two unexpected results emerged. First, I expected that *A. crepitans* populations would be more affected by predation than *H. versicolor* due to its shorter lifespan and higher elasticity to tadpole survivorship. However, decreases in population growth rate due to predation were similar for the species, likely because *H. versicolor* tadpoles experienced higher predation rates. Second, changes in population size observed across the sampling interval did not match matrix projections. This is likely because vital rate estimates for matrix population models overestimated predation effects or because of the low power to detect differences between treatments in population size.

The longevity of amphibian species may also interact with the ratio of habitat availability across landscapes to influence female use of aquatic habitats for oviposition. Female amphibians often select oviposition sites based on the presence or absence of conspecifics, predators, and resources in addition to abiotic factors such as hydroperiod or soil characteristics (Resetarits and Wilbur 1989, Kats and Sih 1992, Kiesecker and Skelly 2000). However, one main assumption of most oviposition site selection studies is that females have abundant aquatic habitats to choose from and are able to make oviposition decisions based on the variability of the aquatic habitat (Spieler and Linsenmair 1996, Rudolf and Rodel 2005). In Chapter Four, I examined the use of marginal aquatic habitats (aquatic habitats that did not allow the successful metamorphosis before drying completely) by female *A. maculatum* in landscapes with a range of aquatic habitat availabilities. When aquatic habitat was scarce, *A. maculatum* oviposited more frequently in marginal aquatic habitats relative to when aquatic habitat was widely available at a site

Overall, the body of research in this dissertation highlights the important implications of variation in the ratios of habitat types across a landscape. Studies of declining amphibian populations typically focus on factors that affect larval survivorship and growth in the aquatic habitat. Yet, there is increasing evidence of the importance of terrestrial habitat for amphibians (e.g., Biek et al. 2002, Semlitsch 2002, Vonesh and de la Cruz 2004). Understanding how amphibians will respond to different types of habitat destruction (e.g., deforestation, draining of wetlands) requires considering the entire life-cycle of amphibians and the ratio of aquatic and terrestrial habitats in landscapes within which amphibian populations are embedded. Further, variation in landscape context can cascade to influence other members of the community.

Background information

Demographic matrix modeling

A central focus of this dissertation examines how populations respond to habitat ratios differently. I used demographic matrix modeling in chapters 1 and 3 (and application of these models in chapters 2 and 4), to determine the impacts of perturbations to amphibian populations both through simulations and experimental manipulations. Demographic matrix models take the form:

$$\mathbf{N_{t+1}=A(N_t)}$$

Where $\mathbf{N_t}$ is a vector representing the abundance of individuals in each stage class of the population at time t, while $\mathbf{N_{t+1}}$ is a vector indicating the abundance of individuals in each stage class the next year. $\mathbf{A}$ is a matrix containing elements (a_{ij}), which indicate the survival rates of particular stage classes of individuals and their transition rates between stages, in addition to the fecundity of reproductive stage classes (Caswell 2001).

Properties of the demographic matrix **A** are useful for determining how populations might respond to perturbations. For instance, the dominant eigenvalue of **A, λ,** represents the population growth rate, where λ >1 means the population is increasing and λ<1 indicates a declining population. Additionally, elasticity analysis of the demographic matrix is a useful tool in determining how small perturbations in particular life stages can influence the population growth rate, λ. The elasticities of particular vital rates (e_{ij}) can be calculated using the equation (de Kroon et al. 1986):

$$e_{ij} = \frac{a_{ij}}{\lambda} * \frac{\delta\lambda}{\delta a_{ij}} = \frac{\delta(\log\lambda)}{\delta(\log a_{ij})}$$

Demographic matrix modeling is thus a useful tool for exploring the potential population level impacts of particular perturbations on amphibian populations and is therefore a critical tool used throughout my dissertation.

Principles of metacommunity theory

A metacommunity is a network of local communities that are linked through the dispersal of organisms (Wilson 1992, Leibold et al. 2004). Often, metacommunities are thought to represent a series of habitat patches, in which the area between patches is considered matrix habitat and is inhospitable for individuals, therefore organisms only disperse through the matrix habitat, but do not spend any length of time in the matrix. There are four main theoretical frameworks of metacommunity theory that look to explain the mechanistic processes that lead to patterns of species distributions within a metacommunity. They are patch dynamics, species sorting, source-sink, and neutral model frameworks (Leibold et al. 2004). Although these frameworks lead to many explanations for how species are distributed within a metacommunity, there are a several patterns that emerge in regards to predator and prey species richness, which are particularly relevant to this dissertation.

Metacommunity theory predicts that increases in the isolation of habitats within a metacommunity will typically alter patterns of biodiversity and composition (reviewed in Saunders et al. 1991, Cadotte 2006). Isolation of a habitat generally reduces the overall species richness and diversity of that patch, while highly connected patches within the metacommunity often have higher species richness and diversity (Cadotte 2006). However, predators are thought to be more sensitive to habitat isolation than their prey (Terborgh et al. 2001, Holt and Hoopes 2005, Holt 2009, Chase et al. 2010). This is often attributed to several common features of predator species, in particular their lower population sizes, which increases the likelihood of local extinctions. In habitats that are isolated within the metacommunity, it is more difficult for predators to thus re-colonize isolated habitats once extinctions occur, leading to the observed pattern of decreased predator diversity of isolated habitats (Holt and Hoopes 2005). Consequently, it has been shown that a reduction in predator diversity and abundance in isolated habitats can lead to increases in particular prey species abundance and richness (Chase et al. 2010).

However, one of the main tenets of metacommunity theory centers on species that live in distinct habitat patches and disperse amongst patches through an inhospitable matrix (Leibold et al. 2004). This general assumption of metacommunity theory may lead to predictions of predator and prey species distributions which are not necessarily accurate if the predator or prey do not respond to isolation in a similar way. Habitats that may be considered isolated by traditional metacommunity standards could actually be irrelevant if species are using both the patch habitat as well as the matrix habitat. For instance, amphibians use both the terrestrial and aquatic habitat extensively throughout their life. Therefore, both the patch habitat and the matrix habitat are required by these species. When a predator species uses the “matrix” habitat to a greater degree than the actual patch habitat, the ratio of these habitats could influence their density and thus food web interactions in each habitat, leading to inaccurate predictions of predator and prey interactions based on traditional metacommunity theory. In this dissertation, I develop and use a new framework for exploring the distribution of predators and prey within a metacommunity, which relies not on patch isolation but rather on ratios of habitat types within a landscape. Instead of classifying patches or habitats as isolated or connected as is done in traditional metacommunity studies, the ratio of available habitats would reflect not only the isolation of a habitat (with a skewed ratio towards the matrix habitat), but also the abundance of that habitat (additionally capturing the proportion of matrix habitat to patch habitat). Thus the new framework could provide a more accurate measure of “connectivity” for organisms that spend a proportion of their life in multiple habitats.

Literature Cited

Beebee, T.J.C. and R.A. Griffiths. 2005. The amphibian decline crisis: A watershed for conservation biology? Biological Conservation 125:271-285

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313:58–61.

Cadotte, M.W. 2006 Dispersal and species diversity: a meta-analysis. The American Naturalist 167: 913–924.

Caswell, H. 2001. Matrix population models: Construction, analysis and interpretation. 2 Ed. Sinauer Associates, Sunderland, Massachusetts.

Chase, J.M., A.A. Burgett, and E.G. Biro. 2010. Habitat isolation moderates the strength of top down control in experimental pond food webs. Ecology 91: 637–643.

Collins, J.P. and A. Storfer. 2003. Global amphibian declines: Sorting the hypotheses. Diversity and Distributions 9: 89-98.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. Ecology 67:1427-1431

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and systematics 34:487-515.

Forbis, T.A. and D. F. Doak. 2004. Seedling establishment and life history trade-offs in alpine plants. American Journal of Botany 91: 1147-1153.

Freda, J. 1983. Diet of larval *Ambystoma maculatum* in New Jersey. Journal of Herpetology 17: 177-179.

Gibbs, J. P. 2000.Wetland loss and biodiversity conservation. Conservation Biology 14: 314-317.

Hamer, A.J. and M.J. McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: A review. Biological Conservation 141: 2432-2449.

Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998: 367-375.

Heppell, S.S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Holomuzki, J.R., J.P. Collins, and P.E. Brunkow. Trophic control of fishless ponds by tiger salamander larvae. Oikos 71:55-64.

Holt, R.D., and M.F. Hoopes.2005. Food web dynamics in a metacommunity context: modules and beyond. In: Holyoak M, M.A. Leibold, and R.D. Holt. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press: 68–93.

Kats, L.B. and A. Sih. 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). Copeia 1992:468-473.

Kiesecker, J. M. and D. K. Skelly. 2000. Choice of oviposition site by grey treefrogs: The role of potential parasitic infection. Ecology 81:2939–2943.

Leibold, M.A, M. Holyoak, B. Mouquet, P. Amarasekare, J.M. Chase, M.F. Hoopes, R.D. Holt, J.B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601–613.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum.* Journal of Herpetology 31(4): 542-551.

McCallum, M.L., C. Brooks, R. Mason, and S.E. Trauth. 2011. Growth, reproduction, and life span in Blanchard's Cricket Frog (*Acris blanchardi*) with notes on the growth of the Northern Cricket Frog (*Acris crepitans*). Herpetology Notes 4: 025-035.

Nyman, S. 1991. Ecological aspects of syntopic larvae of *Ambystoma maculatum* and the *A. laterale-jeffersonianum* complex in two New Jersey ponds. Journal of Herpetology 25: 505-509.

Polis GA, Myers CA (1985) A Survey of intraspecific predation among reptiles and amphibians. Journal of Herpetology 19:99–107.

Resetarits, W.J. and H.M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis:* role of predators and competitors. Ecology 70: 220-228.

Sæther, B. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* 10: 591-597.

Snider, A.T. and J. K. Bowler. 1992. Longevity of reptiles and amphibians in North American collections. Society for the Study of Amphibians and Reptiles. 2nd ed.

Spieler, M. and K.E. Linsenmair. Choice of optimal oviposition sites by *Hoplobatrachus occipialis* (Anura: Ranidae) in an unpredictable and patchy environment. Oecologia 109: 184-199.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786.

Vaughn, C.C. 2010. Biodiversity losses and ecosystem function in freshwaters: Emerging Conclusions and research directions. BioScience, 60: 25-35.

Welborn, G.A., D.K. Skelly, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337-363.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393-425.

Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology, 73, 1984–2000.

Wright, A.H. and A.A. Wright 1995. Handbook of Frogs and Toads of the United States and Canada 3rd ed. Comstock Publishing Associates, Ithaca NY.

Chapter 1

Amphibian longevity predicts their susceptibility to habitat alterations: A meta-analysis

Co-authors: J.M Chase, J. Vonesh, T.M. Knight

Abstract

Given the rapid decline of amphibian species across the globe, matrix population models provide an important tool in understanding the relationship between environmental factors and population growth and identifying priorities for conservation. Elasticity analysis can identify key life stages for which changes would be expected to produce the largest change in the population growth rate of a species. General patterns between the longevity of a species and it’s elasticity to vital rates occurring in early vs. late life stages has been shown in numerous other taxa, but have not yet been demonstrated in amphibians. Further, since most amphibians spend early life stages in aquatic ecosystems and later life stages in terrestrial ecosystems, determining which vital rates most directly affect the population growth rate would allow habitat conservation priorities to be set. Here, we review 27 matrix population models for amphibians and show that as the longevity of an amphibian increased, population growth rates were less sensitive to changes in vital rates associated with the aquatic relative to the terrestrial habitat. In simulations that considered larger perturbations in vital rates, we found that over a range of increasing larval mortalities (using a realistic range found in studies that manipulate concentrations of the insecticide, carbaryl), the expected change in population growth rate was higher in species that were shorter-lived. Similarly, with increasing levels of adult mortality (terrestrial perturbation), the expected population growth rate was lower in species that were longer-lived. When both aquatic and terrestrial perturbations occur, this pattern is more complicated for long-lived amphibian species, and depends on the intensity of mortality, as well as the ratio of available habitat types. Adding density

dependence in the larval stage did not qualitatively alter our predictions for short-lived amphibians, but it can lead to more unpredictable population-level responses of long-lived species to habitat perturbations. The relationship between the longevity of an organismal amphibian species and the elasticity of its population growth rate to the aquatic or terrestrial habitat will be useful in situations where collecting demographic data is difficult.

Introduction

Matrix population models are an important tool for population viability analyses (PVA) in conservation biology (Beissinger and McCullough 2002, Morris and Doak 2002). These models can be designed to capture key aspects of a population's biology, including stage- or age-structure, environmental stochasticity, and density dependence (Caswell 2001). Matrix projections, such as the long-term rate of population growth (λ) and elasticity analysis are particularly useful in a conservation context. For example, projections of population growth rates are often used to compare the relative health of different populations and different management scenarios, enabling more efficient conservation planning (Silvertown et al. 1996, Caswell 2001). Elasticity analyses quantify how small changes in a vital rate would alter the population growth rate, and can focus conservation efforts on improving survivorship, growth and fecundity at stages in the life cycle that would most benefit the population (Mills et al. 1999, de Kroon et al. 2000).

Further, because standard methodology is typically employed to create and to parameterize matrix models, synthetic reviews are available for many taxa, providing a more general understanding of population dynamics of species and how these might be influenced by environmental perturbations (Silvertown et al. 1996, Heppel 1998, Seather and Bakke 2000, Heppel et al. 2000, Forbis and Doak 2004). For example, comprehensive meta-analyses on birds (Seather and Bakke 2000, Stahl and Oli 2006), mammals (Heppel et al. 2000, Oli and Dobson 2003), fish (Mangel et al. 2006) turtles (Heppel 1998), and perennial plants (Forbis and Doak 2004) demonstrate that as the longevity of a species increases, the influence of fecundity and juvenile survivorship decreases relative to adult survivorship. This relationship can be useful for informing conservation decisions when data on specific species may be limited. For example, in the absence of a more detailed demographic study, it might be reasonable to prioritize conservation efforts that increase adult survivorship for species that are extremely long-lived.

Over the last 20-30 years, amphibians have been declining at an unprecedented rate across the planet (Collins and Storfer 2003, Stuart et al. 2004). Several factors have been identified as possible agents of this decline including disease, climate change, UV-B radiation, agricultural run-off and pollution, and habitat destruction (e.g., Biek et al. 2002, Collins and Storfer 2003, Blaustein et al. 2003, Beebee and Griffiths 2005, Cushman 2006). All of these agents have been found to have large effects on demographic vital rates; however, to date, their effects on amphibian population dynamics are largely unknown because studies typically do not measure vital rates across the entire life cycle. It is possible that the same environmental perturbations will have large effects on some species and small effects on others if the population dynamics of the species differ in their sensitivity to changes in the vital rate that is perturbed (Biek et al. 2002, Vonesh and De la Cruz 2004). Given the concern for global amphibian decline, and the limited data available on amphibian population dynamics, a framework for understanding which types of species are most likely to be affected by which types of environmental perturbations is paramount.

The elusive nature of adult amphibians makes demographic data on the adult life stages challenging to collect (Storfer 2003); however, there are demographic data available across the entire life cycle for 27 amphibian species (see Methods), allowing the potential for a synthetic review of this taxon. If there are general patterns in the demography of amphibians with different longevities, as might be expected from studies on other taxa, then it may be possible to make synthetic statements about which environmental perturbations are likely to have the largest influence on the population dynamics of an amphibian species based on its longevity.

Unlike most other organisms that have been the subject of quantitative reviews, amphibians have a complex life cycle, which restricts larval life stages to aquatic habitats and juvenile and adult life stages to the terrestrial habitat. Therefore, it is possible to determine the elasticity of the population growth rate to perturbations in a particular habitat by summing the elasticity values for all life stages that occur in that habitat. This should help set conservation priorities for amphibian species for which limited demographic data is available by focusing efforts on the particular habitat that will have the biggest impact on overall population growth.

The extreme variability seen in vital rate estimates for amphibian species creates an additional complication to establishing actual patterns between the longevity of a species and habitat elasticities. If the elusive nature of juvenile and adult amphibians leads to estimates in survivorship that vary substantially from actual adult survivorships, than the longevity of the species may be either over- or under-estimated when calculated using the matrix model (Forbis and Doak 2004). Therefore, independent estimates of species longevities obtained through skeletal-chronology, captive individuals, or mark recapture studies could allow for a comparison between actual age of amphibians and that obtained through the matrix model. If variations within vital rate estimates artificially inflated longevities that were calculated by the matrix model, we might predict that the patterns observed between the longevity of species and habitat elasticities would not withstand such variation in vital rates.

Although patterns of habitat elasticities and longevity of amphibian species have the potential to inform conservation decisions, elasticity analyses focus on how small perturbations in a particular habitat influence λ. However, factors suspected of contributing to global amphibian population declines are causing large reductions in vital rates. For example, adult habitats can be destroyed through fragmentation and loss of forested terrestrial habitats causing large reductions in juvenile and adult survivorship, while agricultural practices create chemical contamination that threatens larval amphibian survivorship (Blaustein et al. 2003, Hayes et al. 2006, Boone and Bridges-Britton 2006). Thus, it is useful to examine the population-level responses of amphibian species that differ in longevity to large perturbations in vital rates. Furthermore, many anthropogenic factors that cause large reductions in vital rates in a particular habitat are not the only perturbation facing amphibian species, with many factors occurring simultaneously (e.g., terrestrial habitat reduction due to agricultural lands paired with chemical contamination from runoff) (Collins and Storfer 2003, Sih et al. 2004). A modeling approach that examines how larger perturbations and multiple types of perturbations acting synchronously would provide a framework to examine how realistic anthropogenic effects may influence the population dynamics of amphibian species with different longevities.

Many amphibian species have been shown to demonstrate strong density dependent larval survival in the aquatic habitat. Synthetic reviews of other taxa typically include only density-independent matrix models and do not examine whether density-dependence influences the relationship between longevity and elasticities to early life stages (but see Mangel et al. 2006). Through simulation modeling of an aquatic or terrestrial perturbation, we can examine how the relationship between longevity and habitat elasticity is affected by density dependence. For example, density-independent models might predict that for short-lived species, aquatic perturbations would have the greatest effect on population dynamics. However, strong density dependent survivorship of individuals in the aquatic habitat could temper the importance of aquatic perturbations on population dynamics. Depending on the strength of density-dependence and aquatic perturbations, elasticity patterns and longevity may not show the same relationship for density-independent and density-dependent populations.

The aim of this study is to conduct a synthetic review of amphibian matrix population models in order to achieve the following goals: (1) determine the relationship between amphibian longevity and elasticity of the population growth rate to changes in each demographic vital rate, and to all vital rates associated with the aquatic vs. terrestrial habitat; and (2) examine how robust this relationship is to larger vital rate perturbations and adding density-dependent larval survivorship. Finally, we address the utility of these findings for amphibian populations for which few demographic data are available, and the role of future studies on amphibian population dynamics.

Methods

We exhaustively searched the literature for studies containing amphibian matrix population models or studies that contained sufficient demographic data for us to construct a matrix population model. To do so, we used ISI Web of Science in combination with Google scholar, searching the following key words: amphibian matrix model, amphibian population viability analysis, amphibian demography, amphibian modeling. We partitioned search results into papers that presented a full matrix model for an amphibian species, and those that contained sufficient demographic data for us to create a matrix model. Several amphibian species (n=6) had more than one matrix model present in the literature. For three of those six species, *Ambystoma jeffersonianum, Bufo calamita,* and *Rana catesbeiana,* the studies used demographic rates drawn from similar sources [*A. jeffersonianum*: Mullin and Klueh (2009) used estimates of adult and juvenile survivorship from Williams (1973), while Rubbo et al. (2006) calculated most parameters within the context of the study; *B. calamita:* Stevens and Baguette 2008 used Beebee et al. 1996 and others for parameterization of their model,; *R. catesbeiana:* Doubledee et al. (2003) used estimates of survivorships from Raney (1940) and Bury and Whelan (1984), while Govindarajulu et al. (2005) obtained estimates of survivorship “from the literature”], and thus the models behaved qualitatively similarly; in these cases, one model was randomly selected to represent the species within our meta-analysis. Two species (*Bufo boreas* and *Rana aurora*) had two models present in the literature, but the populations had very different population growth rates; here, both were left as separate populations in the meta-analysis. For the sixth species (*Bufo marinus*), both a native and an invasive population were studied, showing large discrepancies between population growth rates and stage-specific elasticities; these matrices were also kept separate for analyses. Density-dependent matrix models were presented for several species (Lampo and De Leo 1999, Trenham and Shaffer 2005, Vonesh and De la Cruz 2004), but since the majority of models in the meta-analysis were linear, we removed density-dependent functions for the first analyses synthesizing the relationship between longevity and elasticities. To do so, we used the mean larval survivorship rate instead of the negative power function presented in Trenham and Shaffer (2005) and Lampo and De Leo (1999), and by setting the larval coefficient of density-dependence equal to zero for the species from Vonesh and De la Cruz (2004). Two additional studies (Pellet et al. 2006 and Sutherland et al. 2000) present results from matrix population models for amphibians, but do not contain data sufficient to recreate the matrix models; therefore we were unable to include these two species (*Hyla arborea* and *Ascaphus truei*) in the meta-analysis.

For each species, we calculated the population growth rate (λ) and elasticity matrix using Matlab (Version R2009B) and standard methods described in Caswell (2001). We summed elasticity values for all life stages that occurred in the aquatic habitat (typically egg and larval survivorship) to determine one elasticity value for each species in the aquatic habitat. Likewise, we summed elasticity values for all life stages that occurred in the terrestrial habitat (usually juvenile and adult survivorship) to produce one elasticity value for the terrestrial habitat. Two species in the meta-analysis (*Geocrina alba* and *G. vitellina*) have a shortened aquatic stage which occurs in small puddles of water located in bromeliad leaves, however it can still be considered as a distinct habitat from that of adult frogs.

We determined the longevity of each species from the density-independent matrices using methods described in Forbis and Doak (2004). For each species, we set the reproductive rates to zero and estimated the number of years it would take one individual in the first juvenile stage class to reach 0.001 individuals. Since these age estimates are dependent on population specific vital rates, there is the potential for circularity between habitat elasticity values, also calculated from population specific vital rates, and age estimates. To address this, we obtained independent age estimates from the literature (when available) for each species, using species name and age, longevity, or skeletal-chronology as key words. We compared the estimates of longevity for each species calculated through the matrix to those where independent estimates were found in the literature, and found a significant correlation (linear regression: $r^2 = 0.7173$, $F=10.855$ $p<0.0001$). As a result, below we only present estimates of age calculated from the matrix model. We used linear regression (using Systat version 12.0) to analyze the relationship between amphibian longevity and the elasticity of the population growth rate to matrix elements in either the aquatic or terrestrial habitats. Furthermore, to determine whether variability in species-specific vital rates contributed to the overall outcome of the relationship between longevity and habitat elasticities, we examined the correlation between independent estimates of longevity and species specific vital rates in the most error-prone life stages; adult and juvenile survivorship using linear regression in Systat (version 12.0).

Simulating larger scale perturbations

From the group of species, we chose six (*Ambystoma jeffersonianum, A. maculatum, A. tigrinum, Bufo boreas, Rana temporaria, and Pseudacris triseriata)* that differ widely in their longevities (between two and eleven years, with three species classified as short-lived, and three species classified as long-lived; see Table 1), but have similar rates of density-independent population growth (between 1.201 and 1.401). Elasticity values are a function of the population growth rate (Silvertown et al. 1996) and therefore other species within our meta-analysis with highly divergent λ's would not necessarily be comparable to each other.

We simulated the effects of two factors that have been shown to cause large decreases in amphibian vital rates: carbaryl contamination in the aquatic habitat, and terrestrial habitat destruction. Carbaryl is the most widely used pesticide in the United States and has been shown to have adverse effects on the survivorship of larval amphibians (Peterson et al. 1994, Relyea 2003). We searched the literature (key words: amphibian, carbaryl, survival) for studies (n=23) that documented larval mortality rates of amphibians due to carbaryl at ecologically relevant concentrations (approximately 3.5 mg/L, Peterson et al. 1994). From this, we varied larval mortality due to carbaryl from 0% to 60% representing the range of responses found within the literature search. For each of the six species, we varied larval mortality in 5% increments and calculated a new λ. Likewise, to explore the effects of terrestrial habitat loss, we simulated a reduction in terrestrial habitat that increased adult mortality from 0% to 75%. The ubiquitous nature of terrestrial habitat loss for amphibians produced a wide range of values within the literature (keywords: amphibian, terrestrial habitat, reductions) ranging between 0 and almost complete loss of terrestrial habitat (summarized in: Cushman 2006). Therefore, we restricted our simulations to values less than 75%, which might be likely if habitat destruction maintains a small buffer zone around aquatic habitats (Semlitsch 2002). For all six species, we only applied a decrease in survivorship to the adult, but not the juvenile, stages for consistency between species, which had varying numbers of juvenile stages.

We plotted the incremental change in λ over the range of increased mortalities for both the addition of carbaryl and increased terrestrial habitat destruction to obtain the slope of the relationship for each species. We used linear regression in Systat (Version

12.0) to regress this slope with the species' longevity to determine how dramatically their population growth rate was affected by an aquatic or terrestrial perturbation.

To examine the interactive effects of both a terrestrial and aquatic environmental perturbation, we simulated the simultaneous reductions in survivorship that could be caused by both carbaryl and habitat destruction on the same six species used previously. We first quantified the expected change in λ for each species between natural and simulated terrestrial habitat loss using the same methods as above. We considered four levels of adult mortality due to terrestrial habitat loss: 10%, 25%, 50% and 75%. We also quantified the expected change in λ for each species between natural and simulated mortality due to carbaryl in the aquatic habitat. Here, we consider one level of carbaryl-induced larval mortality: 50%. If the simultaneous effects of mortality at the aquatic and terrestrial stages are additive, we would expect that the change in λ for each species would be equal to the change in λ due to elevated tadpole mortality (i.e., similar to mortality that could be caused by carbaryl contamination) plus the change in λ due to elevated adult mortality (i.e., similar to mortality levels that could be caused by terrestrial habitat loss). Therefore, we summed the simulated decrease in λ at 50% larval mortality, which is likely at moderate levels of carbaryl contamination, with the decreases in λ expected at 10%, 25%, 50%, and 75% reductions in adult survivorship, which would be likely if terrestrial habitat was destroyed and plotted this as the expected line. We obtained observed estimates of the change in λ at 50% carbaryl contamination over the same range in reductions of terrestrial habitat by re-running matrix models with the incorporated perturbations in Matlab (Version R2009B), obtaining new estimates of λ and calculating the change in λ from the original model. We plotted the expected and observed changes in λ for the three long-lived and three short-lived species to determine the interactive effects of both an aquatic and terrestrial perturbation on amphibians. Similar to the previous simulations, we calculated the difference between the slope of the observed line and the slope of the expected line for each species due to simultaneous aquatic and terrestrial perturbations. We used a student's t-test to examine the difference between the observed and expected slopes between short-lived and long-lived species (Systat, version 12.0).

Density-Dependent Simulations:

To explore the relationship between longevity and the elasticity of the population growth rate to perturbations while incorporating density-dependence, we simulated the effects of reductions in adult and larval survivorship on the equilibrium population sizes of 14 species. We chose these 14 species due to the availability of density-dependent data in the larval stage (presented either in the original study or elsewhere in the literature; see Table 1). Using values of larval survivorship at varying densities, we fit a negative power function, to a minimum of three data points. We chose a negative power function because it is one common function applied to the density dependent relationship of larval amphibian survivorship (Wilbur 1976, Vonesh and De la Cruz 2002, Trenham and Shaffer 2005) and is also a more conservative approach than a negative linear relationship might be given the lack of data often obtained for some species (only 3 survivorship estimates at different densities). Occasionally, a lack of larval survivorship data at low densities produced a Y-intercept greater than 1, indicating survivorship over 100%. In these cases, we set low-density survivorship to the maximum larval survivorship documented in the study. For all species, we started the population with one individual in each stage class, and calculated the average equilibrium density after 100 years. We simulated a decrease in terrestrial habitat availability by decreasing the adult survivorship by 75% and obtaining a new equilibrium density estimate. When species had more than one stage in the terrestrial habitat, we only applied the decrease in survivorship to the adult stage to standardize our simulations across species. We simulated reductions in larval survivorship by 50%; this is a realistic perturbation since studies have documented this drop in survivorship for larval amphibians in the presence of carbaryl contamination. To simulate a decrease in larval survivorship by 50%, we reduced larval survivorship for each of the three larval densities used to create the density-dependent functions by 50% and then created a new density dependent function at the reduced larval survivorship by re-fitting a new negative power function to the data. For species that included density-dependence within the original matrix model, we reduced the overall maximum larval survivorship by 50%.

Due to the wide variability in the strength of density-dependence and in the mean vital rates across species, there is wide variation in equilibrium population sizes across species. To compare the magnitude by which aquatic vs. terrestrial perturbations influence equilibrium population sizes across species, we can calculate a percent change in the equilibrium population size due to either aquatic or terrestrial perturbations. As above, we separated species into either long-lived (7-11 years) or short-lived (1-6 years) categories. Within short-lived species, we conducted a paired t-test to examine the relationship between the percent decreases in equilibrium density due to aquatic or terrestrial perturbations. Likewise, we conducted a second paired t-test within the long-lived species group to see if the aquatic or terrestrial perturbation had a larger effect on equilibrium density. Although the strength of the aquatic and terrestrial perturbations were not equal (50% reduction in larval survivorship vs. a 75% reduction in adult survivorship), these estimates mirror realistic differences in the strengths of perturbations within the aquatic and terrestrial habitats. Thus, we might predict that the 75% reduction in adult survivorship (simulating terrestrial habitat disturbance) should have a larger impact on equilibrium density than the smaller 50% reduction in larval survivorship if species respond to either habitat equally.

Results

We obtained a total of 27 matrix population models that were presented in the literature, or were created from demographic data available in published studies. The longevity of species' ranged from 2 to 30 years with a median age of 6 years. Independent estimates of longevity that were obtained from the literature (from skeletochronology, mark-recapture studies, captive individuals) were highly correlated with adult survivorship, despite the large variation in accuracy within this vital rate (Linear regression, $r^2=0.33547$, $f=11.1061$, $p=0.003$). The elasticity of λ to vital rates associated with the aquatic habitat and to fecundity declined with increasing longevity (Figure 1.1a; $R^2= 0.4443$, $F=19.402$, $p<0.0001$; $R^2=0.486$, $F=23.623$, $p<0.0001$, respectively), while the elasticity of λ to vital rates associated with the terrestrial habitat increased with increasing longevity (Figure 1.1b; $R^2=0.640$, $F=44.500$, $p<0.0001$).

Simulating larger scale perturbations

For the six species for which we conducted density-independent simulations of large perturbations in survivorship, we found that as the longevity of a species increased, the effect of aquatic perturbations decreased (Figure 1.2a and b: $R^2=0.962$, $F=100.923$,

$p<0.0001$) whereas the effect of terrestrial perturbations increased (Figure 1.2c and d: $R^2=0.850$, $F=22.621$, $p=0.009$). However, when survivorship rates in both the aquatic and terrestrial habitat were altered, long-lived species showed non-additive effects of these perturbations on population growth rate. Specifically, as terrestrial habitat was reduced, long-lived species experienced a greater decrease in population growth rate due to the aquatic perturbation than shorter-lived species (Figure 1.3, t-Test, $n=3$, $p=0.0208$).

<u>Density-Dependent Simulations:</u>

Simulation results using density dependent models were congruent with those of density independent models. In the density-dependent models, aquatic perturbations reduced the equilibrium density more than terrestrial perturbations for short-lived species (Figure 1.4: $n=7$, T-test: aquatic mean: 0.616, terrestrial mean: 0.113, $p<0.0001$). Terrestrial and aquatic perturbations did not differentially influence on the equilibrium population density of long-lived species (Figure 1.4; $n=7$, T-test $p=0.454$).

Discussion

Our quantitative synthesis showed that the population growth rate of shorter-lived amphibians is more sensitive to small changes in the vital rates associated with younger life-stages (e.g., fecundity, larval survivorship), whereas longer-lived species are more sensitive to small changes in adult survivorship and growth. Additionally, our simulations of larger perturbations in vital rates demonstrate that amphibian longevity was an important predictor in understanding which types of perturbations would have the largest influence on their population dynamics. Specifically, short-lived species are more strongly influenced by perturbations to vital rates in the aquatic (larval) habitat, whereas long-lived species were most strongly influenced by perturbations to vital rates in the terrestrial (adult) habitat. However, when both aquatic and terrestrial vital rates were altered simultaneously, the susceptibility of longer-lived species to aquatic vital rate perturbations increased when the availability of terrestrial habitat decreased (e.g., as would be expected with habitat destruction). Finally, incorporating density-dependence into these simulations did not change the overall qualitative patterns for short-lived species; however, it complicated predictions for long-lived species.

Meta-analyses on other taxa have revealed that the elasticity of vital rates in younger stage classes declines as the longevity of a species increases (e.g.: Silvertown et al. 1996, Heppel 1998, Seather and Bakke 2000, Heppel et al. 2000, Forbis and Doak 2004, Stahl and Oli 2006); our study confirms this pattern in amphibians. To demographers and population ecologist these results will not necessarily be surprising; despite the unique qualities of amphibians such as their complex life cycles and larval density dependence, the same general patterns between life history and population elasticity apply. However, these results provide insights about agents that have previously been implicated in amphibian population declines. Previously, most researchers studying amphibian declines have focused on a few particular vital rates that are dramatically affected by environmental perturbations and they have concluded that these factors must contribute to amphibian population declines. However, here we show that large reductions in particular vital rates do not necessarily lead to changes in the population dynamics of species. Similarly, small reductions in particular vital rates may lead to large changes in population growth rates if the population dynamics are particularly sensitive to that life stage and have high elasticity values. Therefore, although the apparent relationship between longevity and elasticity to particular life stages is neither surprising nor unique to amphibians, it draws attention to an often-neglected aspect of amphibian conservation in which large changes in specific vital rates do not always produce changes in population dynamics of species.

Although the observed relationship between longevity and habitat sensitivity can inform conservation and restoration decisions, it does not alleviate the need for more, and more accurate, demographic matrix models for amphibian species. Knowledge of the longevity of a species can provide a critical first step towards focusing conservation efforts. For example, in commercially harvested rock fishes, is it known that these species are extremely long-lived, thus, management aimed at reducing harvest-induced mortality of the largest stage classes would appear to be most important to improving population growth. However, with more detailed demographic study of rougheye rockfish, Mangel et al. (2006) found that the elasticity of λ to changes in the juvenile stage was four times higher than that of the adult stage. Conservation recommendations aimed at maximizing juvenile survivorship would provide the greatest increase in population growth rates. Unfortunately, this is a harder stage to place restrictions on because it is not the stage that commercial fishing focuses on. If conservation actions aimed at reducing adult harvests could increase the survivorship of adult stages four times as much as they could juvenile stages, then the same increase in the population growth rate would be obtained with easier management techniques (Mangel et al. 2006). Therefore, although patterns between longevity (or life history strategy) and habitat elasticity can help inform conservation priorities when data or resources are limited, it does not alleviate the need for species-specific demographic models. Furthermore, habitat importance based on longevity and habitat elasticity values alone should not be misconstrued to mean that only one particular habitat is crucial for population persistence. Although λ may not be as sensitive to perturbations in one habitat, elimination of or large disturbances within that habitat are still able to reduce population persistence.

One common cause of terrestrial habitat loss comes from the conversion of upland terrestrial habitats to agriculture. As a result, amphibian populations that experience terrestrial habitat loss also likely experience contamination in their aquatic habitats from common agricultural practices (Collins and Storfer 2003). When we simulated a reduction in survivorships that might be expected if terrestrial habitat availability were reduced and if aquatic habitats were contaminated with carbaryl, we found an interactive effect on long-lived species. Specifically, although long-lived species tended to not be sensitive at the population level to aquatic perturbations alone, they can become so when terrestrial habitat availability is also reduced. This effect arises because reductions in terrestrial habitat cause a decrease in adult survivorship, effectively shortening the life span of those previously long-lived species. As mortality rates in the terrestrial habitat increase (decreasing longevity), λ becomes more sensitive to vital rates occurring in the aquatic habitat. Therefore, instead of an additive effect between carbaryl contamination and terrestrial habitat destruction for long-lived amphibians, the increase in aquatic habitat elasticity leads to a non-additive decrease in λ. Thus, an important lesson here is that the entire landscape of a species' population must be considered in order to fully elucidate the influence of various anthropogenic stressors.

When we incorporated density-dependence into the models, we found similar results to the density-independent models for short-lived but not for long-lived species. For all species, we would expect that reductions in larval survivorship would have little effect on population growth rate, up to a point, since larval survivorship is density dependent. As expected, for most species, small decreases in larval survivorship led to little change (or an increase) in λ as a result of increased survivorship for remaining larvae. However, when reductions in larval survival become substantial (in this case, 50% reduction for most species), then λ decreased for short-lived species. Perturbations in the aquatic habitat always had a stronger influence on the equilibrium population density than perturbations in the terrestrial habitat for short-lived species, which is congruent with our density-independent simulations. However, we note that we incorporated a reduction in larval survivorship (simulating carbaryl's effects) by decreasing the survivorship of each estimate at each density by 50% and recalculating the negative power function that describes the density dependence. In reality, carbaryl might change the shape of the density dependent function. Therefore, more work explicitly examining how aquatic perturbations impact density-dependent survivorship and how that translates to the population dynamics of the species would be useful.

For density-dependent long-lived amphibians, decreases in adult survivorship (due to terrestrial perturbations) did not necessarily decrease equilibrium densities more than decreases in larval survivorship (simulating carbaryl contamination). Indeed, decreases in adult survivorship (due to terrestrial perturbations) led to increases in equilibrium population size for several species. This occurred because the smaller number of breeding adults led to fewer eggs and larvae, and higher larval survivorship (Vonesh and de la Cruz 2004). Interestingly, one might predict that declining or threatened amphibian populations may not experience much density dependence in the larval stage as a result of declining numbers of individuals in the population (Holmes

2001). Although density dependence complicates predictions of habitat susceptibility and longevity of amphibians, in instances where rapid action is needed to prevent declines in amphibian populations, density dependence may not be as strong of a contributing factor.

There are substantially fewer demographic matrix models on amphibians relative to other species, and this is largely due to the challenges associated with collecting demographic parameters for the adult and juvenile stages of amphibians. Consequently, our knowledge of the terrestrial life-stage for many amphibians is lacking, hindering our comprehension of how anthropogenic changes influence their populations. The majority (n=20) of matrix models for species included in this study did not explicitly determine adult and juvenile survivorship rates, the vital rates to which λ is most sensitive for long-lived species, but rather acquired estimates of these vital rates from the literature or from related species (exceptions: Hels and Nachman 2002, Conroy and Brook 2003, Funk and Mills 2003, Beebee and Griffiths 2005, Zambrano et al. 2007, and McCaffery and Maxell 2010). Mark-recapture studies are the most common way to determine adult and juvenile survivorship of amphibians, although they tend to underestimate survival rates due to detection probabilities (Jung et al. 2000, Storfer 2003). If the actual rates of survivorship are higher than those included in our analyses, then we expect that the elasticity values for adult survivorship would increase for all species; however the pattern that longer-lived species have higher elasticities for these terrestrial vital rates than shorter-lived species should not change.

Additionally, the quality of the demographic data we obtained for adult and juvenile survivorship was highly variable, with several of the matrix models incorporating vital rates from multiple populations, over variable times, and occasionally from closely related but different species (e.g., Lampo and DeLeo 1998, Rustigian et al. 2003, Vonesh and de La Cruz 2004, Karracker et al. 2008). Independent estimates of longevity that were obtained from the literature (from skeletochronology, mark-recapture studies, captive individuals) were highly correlated with adult survivorship, despite the large variation in accuracy within this vital rate (Linear regression, $r^2=0.33547$, f=11.1061, p=0.003). Had the pattern between longevity and habitat elasticity been purely a product of inaccuracy in vital rate estimation, then independent age estimates would not correlate strongly with adult survivorship. Therefore, the pattern we observed between the longevity of a species and the elasticity of λ to aquatic or terrestrial perturbations is robust to the large variation in species-specific vital rates seen in amphibian matrix models.

An additional limitation of this study arises from the manner in which we calculated habitat elasticities. In order to determine the elasticity for both the aquatic and terrestrial habotat of each species, we assumed that the adult and juvenile stage for all species used the terrestrial habitat only. However, for some species, such as *R. catesbeiana*, juveniles and adults may actually use the aquatic habitat to a greater degree than the terrestrial habitat. In these cases, although they are a relatively long-lived species, aquatic habitat perturbations may have a larger impact on λ than longevity alone would predict. Therefore, it is important to consider the specific habitat requirements of the species of concern when the life history does not conform to a basic structure of aquatic larvae and terrestrial adults.

To date, no amphibian matrix model has included density-dependence in the terrestrial stage, although studies have illustrated the importance of terrestrial density dependence in amphibians (Altwegg 2003, Harper and Semlitsch 2007). We might expect that as terrestrial habitat is destroyed, juvenile and adult amphibians would have to compete for limited space in higher densities, leading to decreases in survivorship. Our simulations provide a simplistic view of how terrestrial habitat destruction might affect amphibian population growth rates and equilibrium population sizes. Further studies are needed to determine the importance of density dependence in the terrestrial habitat, and how the shape of density dependent vital rate functions varies with habitat alterations.

The rapid decline of amphibian populations across the globe necessitates further investigation into not only the causes of these declines, but ways to prevent or reverse the trends. The connection between amphibian longevity and sensitivity towards survivorship in particular habitat-types provides an important first step to understanding potential causes and solutions for declining amphibian populations. For example, matrix population model projections for the threatened long-lived California tiger salamander, *Ambystoma californiens*, revealed that conservation efforts should focus on the critical terrestrial habitat around natal ponds (Trenham and Shaffer 2005). Our quantitative synthesis suggests that similar recommendations are likely for other long-lived amphibians. When demographic data are not available for a rapidly declining species, a good rule of thumb for conservation can be gained by understanding the relationship between longevity and habitat sensitivity. Rapid assessment of the habitats most critical for protection or restoration based on the longevity of the species may help to slow the decline of the species while buying time to collect demographic data and construct more detailed population viability analysis models.

Literature Cited

Altwegg, R. 2003. Multistage density dependence in an amphibian. Oecologia 136: 46-50.

Beebee, T.J.C., J.S. Denton, and J. Buckley. 1996. Factors affecting population densities of adult natterjack toads *Bufo calamita* in Britain. Journal of Applied Ecology 33:263-268.

Beebee, T.J.C. and R.A. Griffiths. 2005. The amphibian decline crisis: A watershed for conservation biology? Biological Conservation 125:271-285 9

Beissinger, S.R., and D.R. McCullough. 2002. Population Viability Analysis. The University of Chicago Press. Chicago, IL.

Belden, L. K., E.L. Wildy, and A.R. Blaustein. 2000. Growth, survival and behaviour of larval long-toed salamanders (*Ambystoma macrodactylum*) exposed to ambient levels of UV-B radiation. Journal of Zoology 251: 473–479.

Biek, R., W.C. Funk, B.A. Maxell, and L.S. Mills. 2002. What is missing in amphibian decline research: Insights from ecological sensitivity analysis. Conservation Biology 16:728-734.

Blaustein, A.R., J.M. Romansic, J.M. Kiesecker, and A.C. Hatch. 2003. Ultraviolet radiation, toxic chemicals and amphibian population declines. Diversity and Distributions 9: 123-140.

Boone, M.D. and C.M. Bridges-Britton. 2006. Examining multiple sublethal contaminants on the gray treefrog (Hyla veriscolor): Effects of an insectivide, herbicide and fertilizer. Environmental Toxicology and Chemistry 25:3261-3265.

Bowler, J.K. 1975. Longevity of reptiles and amphibians in North American collections as of 1 November, 1975. Society for the Study of Amphibians and Reptiles, Miscellaneous Publications, Herpetological Circular 6:1-32.

Briggs, C. J., V. T. Vredenburg, R. A. Knapp, and L. J. Rachowicz. 2005. Investigating the population-level effects of chytridiomycosis: An emerging infectious disease of amphibians. Ecology 86:3149–3159.

Bury, R.B. and A . J. Whelan. 1984. Ecology and management of the bullfrog. U.S. Fish and Wildlife Service Resource Publication 155.

Caswell, H. 2001. Matrix population models: Construction, analysis and interpretation. 2 Ed. Sinauer Associates, Sunderland, Massachusetts.

Collins, J.P. and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9: 89-98.

Conroy, S.D.S, and B.W. Brook. 2003. Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia. Population Ecology 45: 105-114.

Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128: 231-240.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

Doubledee, R.A., E.B. Muller, and R.M. Nisbet. 2003. Bullfrogs, disturbance regimes, and the persistence of California red-legged frogs. *The Journal of Wildlife Management* 67: 424-438.

Dougherty, C.K. and G.R. Smith. 2006. Acute effects of road de-icers on the tadpoles of three anurans. Applied Herpetology 3: 87-93.

Flageole, S. and R. Leclair. 1992. Demography of a salamander (*Ambystoma maculatum)* population by skeletochronology. Canadian Journal of Zoology 70: 740-749.

Forbis, T.A. and D. F. Doak. 2004. Seedling establishment and life history trade-offs in alpine plants. American Journal of Botany 91: 1147-1153.

Francillon-Vieillot, H., J.W. Arntzen, and J. Geraudie. 1990. Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): A skeletochronological comparison. Journal of Herpetology24:13-22.

Funk, W.C. and L. S. Mills. 2003. Potential causes of population declines in forest fragments in an Amazonian frog. Biological Conservation 111: 205-214.

Goin, C.J., O.B. Goin, and G.R. Zug. 1978. Introduction to Herpetology, 3rd ed. San Francisco: W. H. Freeman and Company.

Govindarajulu, P., R. Altwegg, and B. R. Anholt. 2005. Matrix model investigation of invasive species control: Bullfrogs on Vancouver Island. Ecological Applications 15:2161–2170.

Grafe, T.U., S.K. Kaminsky, J.H. Bitz, H. Lussow, and K.E. Linsenmair. 2004. Demographic dynamics of the afro-tropical pig-nosed frog, *Hemisus marmoratus*: effects of climate and predation on survival and recruitment. Oecologia 141:40-46.

Griffiths, R.A. 2004. Great Crested Newts (*Triturus cristatus*) in Europe: Effects of metapopulation structure and juvenile dispersal on population persistence. In

Species Conservation and Management: Case Studies. Edited by H. R. Akcakaya, M.A. Burgman, O. Kindvall, C.C. Wood, P.Sjogren-Gulve, J.S. Hatfield, and M.A. McCarthy. Oxford University Press, Oxford NY.

Guarion, F.M, I. Di Gia, and R. Sindaco. 2008. Age structure in a declining population of *Rana temporaria* from Northern Italy. Acta Zoologica Academiae Scientiarum Hungaricae: 54 99–112.

Harper, E.B. and R.D. Semlitsch. 2007. Density dependence in the terrestrial life history stage of two anurans. Oecologia 153: 879-889.

Hatch, A.C. and A.R. Blaustein. 2003. Combined effects of UV-B radiation and nitrate fertilizer on larval amphibians. Ecological Applications 13:1083–1093.

Hatfield, J.S., A. H. Price, D.D. Diamond, and C.D. True. 2004. Houston toad (*Bufo houstonensis)* in Castrop County, Texas: Need for protecting multiple subpopulations. In Species Conservation and Management: Case Studies. Edited by H. R. Akcakaya, M.A. Burgman, O. Kindvall, C.C. Wood, P.Sjogren-Gulve, J.S. Hatfield, and M.A. McCarthy. Oxford University Press, Oxford NY.

Hayes, T.B., P. Case, S. Chui, D. Chung, C. Haeffele, K. Haston, M. Lee, V.P. Mai, Y. Marjuoa, J. Parker and M. Tsui. 2006. Pesticide mixtures, endocrine disruption, and amphibian declines: Are we underestimating the impact? Environmental Health Perspectives 114:40-50.

Hels, T. and G. Nachman. 2002. Simulating viability of a spadefoot toad *Pelobates fuscus* metapopulation in a landscape fragmented by a road. Ecography 25: 730-744.

Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998: 367-375.

Heppell, S.S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Holmes, E.E. 2001. Estimating risks in declining populations with poor data. *PNAS* 98: 5072-5077.

Jennings, M. R. and M. P. Hayes. 1990. Final report on the status of the California red-legged frog (*Rana aurora draytonii*) in the Pescadero Marsh Natural Preserve. Prepared for the California Department of Parks and Recreation under contract No. 4-823- 9018 with the California Academy of Sciences.

Jung, R.E., S. Droege, J.R. Sauer, and R.B. Landy. 2000. Evaluation of terrestrial and streamside salamander monitoring techniques at Shenandoah National Park. Enivronmental Monitoring and Assessment 63: 65-79.

Karraker, N.E., J.P. Gibbs, and J.R. Vonesh. 2008. Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecological Applications 18: 724-734.

Korky, J. K. and R. G. Webb. 1999. Resurvey, biogeography and conservation of the Natterjack Toad *Bufo calamita* Laurenti (Anura: Bufonidae) in the Republic of Ireland. Bulletin of the Irish Biogeographical Society 23: 2-52.

Lampo, M. and G. A. De Leo. 1998. The invasion ecology of the toad *Bufo marinus:* From South Ameica to Australia. Ecological Applications 8:388–396

Mangel, M., P. Levin, and A. Patil. 2006. Using life history and persistence criteria to prioritize habitats for management and conservation. Ecological Applications 16: 797-806.

Matthews, K.R. and C. Miaud. 2007. A skeletochronological study of the age structure, growth, and longevityof the mountain yellow-legged frog, *Rana muscosa*, in the Sierra Nevada, California. Copeia 4: 986-993.

McCaffery, R.M. and B.A. Maxell. 2010. Decreased winter severity increases viability of a montane frog population. Proceedings of the National Academy of Sciences 107: 8644-8649.

Mills, L.M., D.F. Doak, and M.J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13: 815-829.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: The theory and practice of population viability analysis. Sinauer, Sunderland, MA.

Mullin, S.J. and S. Klueh. 2009. Demographics of a geographically isolated population of a threatened salamander (Caudata: Ambystomatidae) in central Illinois. Herpetological Conservation and Biology 4: 261-269.

Oli, M.K. and F.S. Dobson. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole’s prediction revisited. The American Naturalist 161: 422-440 .

Pellet, J., G. Maze, and N. Perrin. 2006. The contribution of patch topology and demographic parameters to population viability analysis predictions: the case of the European tree frog. Population Ecology 48: 353-361.

Raney,E. C. 1940. Summer movements of the bullfrog, *Rana catesbeiana Shaw*, as determined by the jaw-tag method. American Midland Naturalist 32:733-745

Reaser, J. K. 2000. Demographic analysis of the Columbia spotted frog (*Rana luteiventris*): Case study in spatiotemporal variation. Canadian Journal of Zoology 78: 1158–1167.

Rubbo, M.J., K. Shea, and J.M. Kiesecker. 2006. The influence of multi-stage predation on population growth and the distribution of the pond-breeding salamander, *Ambystoma jeffersonianum.* Canadian Journal of Zoology 84: 449-458.

Russell, A.P., G.L. Powell, and D.R. Hall. 1996). Growth and age of Alberta long-toed salamanders (*Ambystoma macrodactylum krausei*): a comparison of two methods of estimation. Canadian Journal of Zoology 74: 397–412.

Rustigian, H.L., M.V. Santelmann, and N.H. Schumaker. 2003. Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landscape Ecology 18:65-81.

Sæther, B., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Sagor, E.S., M. Ouellet, E. Barten and D.M. Green. 1998. Skeletochronology and geographic variation in age structure in the wood frog, *Rana sylvatica*. Journal of Herpetology 32:469–474.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology, 12: 1113–1119.

Sih, A., A.M. Bell, and J.L. Kerby. 2004. Two stressors are far deadlier than one. Trends in Ecology and Evolution 19: 274-276.

Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* 10: 591-597.

Smith, H.M. and R.B. Smith. 1971. Synopsis of the Herpetofauna of Mexico. University Press of Colorado.

Snider, A. and J. Bowler. 1992. Longevity of Reptiles and Amphibians in North American Collections, 2nd Ed. Herpetological Circular No. 21, Society for the Study of Amphibians and Reptiles.

Stahl, J.T. and M.K. Oli. 2006. Relative importance of avian life-history variables to population growth rate. Ecological Modelling 198: 23-39.

Stevens, V.M. and M. Baguette. 2008. Importance of habitat quality and landscape connectivity for the persistence of endangered natterjack toads. Conservation Biology 22: 1194-1204.

Storfer, A. 2003. Amphibian declines: future directions. Diversity and Distributions 9: 151-163.

Storrs, S.I and J.M. Kiesecker. 2004. Survivorship patterns of larval amphibians exposed to low concentrations of atrazine. Environmental Health Perspectives 112:1054-1057.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786.

Sutherland, G.D., J.S. Richardson, and F.L. Bunnell. 2000. Uncertainties linking tailed frog habitat and population dynamics with riparian management. Proceedings of a

Conference on the Biology and Management of Species and Habitats at Risk 2: 477-484.

Taylor, B.E. and D.E. Scott. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum.* Herpetologica 53:132-145.

Tocher, M.D., D. Fletcher, and P.J. Bishop. 2006. A modeling approach to determine a translocation scenario for the endangered New Zealand frog *Leiopelma hamiltoni.* Herpetological Journal 16: 97-106.

Trenham, P.C. and H.B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15: 1158-1168.

Tyler, M.J. 1998. Australian Frogs: a natural history. Cornell University Press, Ithaca, New York.

Vonesh, J.R. and O. de la Cruz. 2004. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325-333

Whiting, A. 2004. Population ecology of the Western Chorus Frog, *Pseudacris triseriata*. M.Sc. Thesis, McGill University, Montréal, Québec, Canada.

Wilbur, H.M. 1976. Density-dependent aspects of metamorphosis in *Ambystoma* and *Rana sylvatica*. Ecology 57: 1289-1296.

Williams, P.K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. Dissertation, Indiana University. Bloomington, Indiana, USA. 47 p.

Zambrano, L., E. Vega, L.G. Herrera M., E. Prado, and V.H. Reynoso. 2007. A population matrix model and population viability analysis to predict the fate of endangered species in highly managed water systems. Animal Conservation 10: 297-303.

Zug, G.R. 1993. Herpetology: An Introductory Biology of Amphibians and Reptiles. San Diego: Academic Press.

Table 1.1: Species included in our study, their source, longevity, and whether density dependence was included, or where the data to create density dependent functions was obtained. * indicate studies not used in meta-analysis (see Methods). For those species with “Common” listed under the density dependence column, it is known that density dependence is common in larval life stages, however species specific estimates of density dependent larval survival were insufficient in the literature to create density-dependent larval survivorship functions. “Not Found” in the density dependence column means that we were unable to locate any studies in the literature that addressed the presence or absence of density dependence for that species.

Species	**Study**	**Matrix longevity**	**Independent longevity**	**Independent longevity source**	**Density dependence**
Ambystoma californiense	Trenham and Shaffer 2005	10	Max: 11, Average:6	Trenham et al. 2000	Included in model
Ambystoma jeffersonianum	Rubbo et al. 2006	11			Brodman 1996
Ambystoma jeffersonianum	Mullin and Klueh 2009*	11			N/A
Ambystoma macrodactylum	Vonesh and De la Cruz 2002	10	Max:10, Average: 6	Russell et al. 1996	Included in model
Ambystoma maculatum	Karracker et al. 2008	9	Max: 32, Average: 11	Flageole and Leclair 1992	Brodman 1996
Ambystoma opacum	Taylor and Scott 1997	8	Average: 11.3	Snider and Bowler 1992	Included in model
Ambystoma tigrinum	Rustigian 2003	10	Max: 25, Average: 16	Snider and Bowler 1992	Petranka 1989*
Bufo americanus	Rustigian 2003	5	Average: 5	Bowler 1975, Zug 1993	Brockelman 1969*
Bufo boreas	Biek et al. 2002	5	Average: 6	Bowler 1975	Common
Bufo boreas	Vonesh and de la Cruz 2002	4	Average: 6	Bowler 1975	Included in model (for *B. americanus)*
Bufo marinus native	Lampo and De Leo 1998	4	Max: 15 average: 5	Tyler 1999	Calculated from data given
Bufo marinus invasive	Lampo and De Leo 1998	3	Max: 15 average: 5	Tyler 1999	Calculated from data given
Bufo calamita	Beebee et al. 1996	6	Average: 7	Korky and Webb 1999	Tejado and Reques 1992*
Bufo calamita	Stevens and Bagguette 2008*	6	Average: 7	Korky and Webb 1999	N/A
Bufo houstonensis	Hatfield et al. 2004	2	Max: 4	Snider and Bowler 1992	Not found
Colostethus stepheni	Funk and Mills 2003	28			Not found
Geocrinia alba	Conroy and Brook 2003	5			Not found
Geocrinia vitellina	Conroy and Brook 2003	5			Not found
Hemisus marmoratus	Grafe et al. 2004	4			Calculated from data given*
Hyla versicolor	Rustigian 2003	4	Max: 7	Snider and Bowler 1992	Resetarits et al. 2004
Leiopelma hamiltoni	Tocher et al. 2006	30	Max: 30	Tocher et al. 2006	No estimates available
Pelobates fuscus	Hels and Nachman 2002	6	Max: 11	Goin et al. 1978	Common
Pseudacris triseriata	Rustigian 2003	2	Max: 4 average: 3	Whiting 2004	Smith 1990
Rana catesbeiana	Doubledee et al. 2003	9	Average: 10	Zug 1993	Common
Rana catesbeiana	Govidarajulu et al. 2005*	9	Average: 10	Zug 1993	N/A
Rana luteiventris	McCaffery and Maxell	12	Max: 7 Average: 6	Reaser 2000	Not found

	2010				
Rana muscosa	Briggs et al. 2005	17	Average: 14	Matthews and Miaud 2007	Common
Rana sylvatica	Karracker et al. 2008	6	Average: 4	Sagor et al. 1998	Berven 1990 and Wilbur 1976
Rana temporaria	Biek et al. 2002	4	Average: 5	Guarino et al. 2008	Riis 1991 (appendix)
Rana aurora draytonii	Doubledee et al. 2003	8	Average: 9	Jennings and Hayes 1990	Calef 1973
Rana aurora draytonii	Biek et al. 2002	8	Average: 9	Jennings and Hayes 1990	Calef 1973*
Triturus cristatus	Griffiths 2004	9	Max: 14 Average: 5	Francillon-Vieillot et al. 1990	Not found

Figure 1.1: a) Results of elasticity analyses of density independent matrix population models. The elasticity of population growth rate to vital rates associated with the aquatic habitat decreases with the longevity of the species. The relationship remains significant even when the longest-lived species is removed. b) Relationship between the longevity of amphibian species and the elasticity of the population growth rate to changes in vital rates associated with the terrestrial habitat.

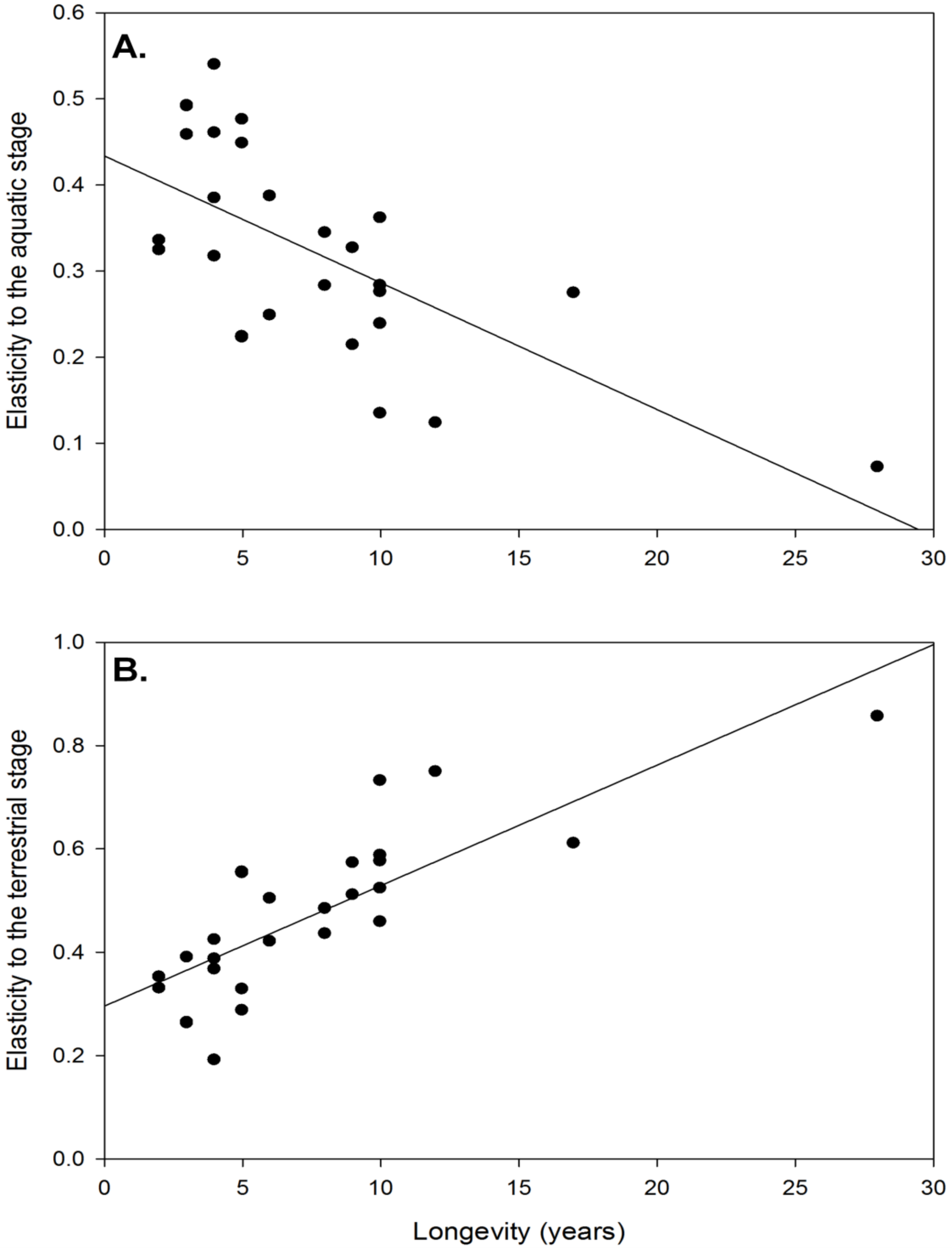

A.
Elasticity to the aquatic stage
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
5
10
15
20
25
30
B.
Elasticity to the terrestrial stage
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
25
30
Longevity (years)

Figure 1.2: a) Change in λ over a range of % decreases in larval mortality that might be expected from carbaryl contamination in the aquatic habitat b) Relationship between the rate at which the population growth rate of each species decreases over a range of larval mortality (slope from each species in a) and the longevity of the species. c) Change in λ over a range in % decreases in adult mortality that might be expected from terrestrial habitat loss d) Relationship between the rate at which the population growth rate of each species decreases over a range of adult mortality (slope from each species in c) and the longevity of the species. Numbers in parentheses after each species indicates the longevity in years.

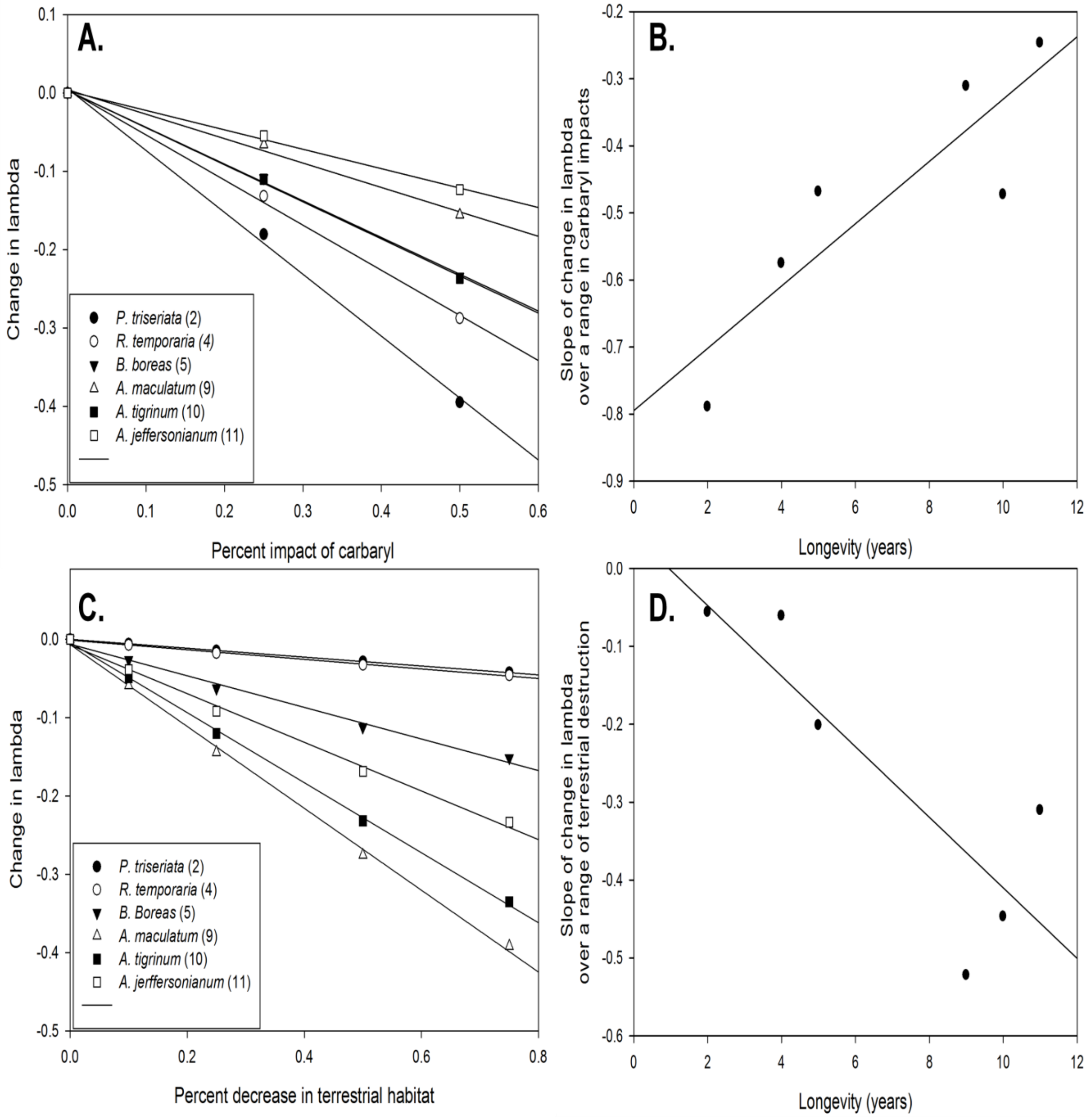

A.
Change in lambda
Percent impact of carbaryl
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
0.0
0.1
0.2
0.3
0.4
0.5
0.6
● P. triseriata (2)
○ R. temporaria (4)
▼ B. boreas (5)
△ A. maculatum (9)
■ A. tigrinum (10)
□ A. jeffersonianum (11)
B.
Slope of change in lambda over a range in carbaryl impacts
Longevity (years)
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
0
2
4
6
8
10
12
C.
Change in lambda
Percent decrease in terrestrial habitat
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
0.0
0.2
0.4
0.6
0.8
● P. triseriata (2)
○ R. temporaria (4)
▼ B. Boreas (5)
△ A. maculatum (9)
■ A. tigrinum (10)
□ A. jerffersonianum (11)
D.
Slope of change in lambda over a range of terrestrial destruction
Longevity (years)
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
0
2
4
6
8
10
12

Figure 1.3: Results of simulations on simultaneous exposure to mortality in both the aquatic and terrestrial habitats. Dashed lines and open symbols represent an expected change in λ if simultaneous effects of increasing larval and adult mortalities are additive. Closed symbols and solid lines represent the observed change in λ when matrix models were re-analyzed including both perturbations. *P. triseriata* (longevity=2 years) and *R. temporaria* (longevity=4 years) are representative of short-lived amphibians, while *A. tigrinum* (longevity=10 years) and *A. maculatum* (longevity=9 years) are representative of long-lived species.

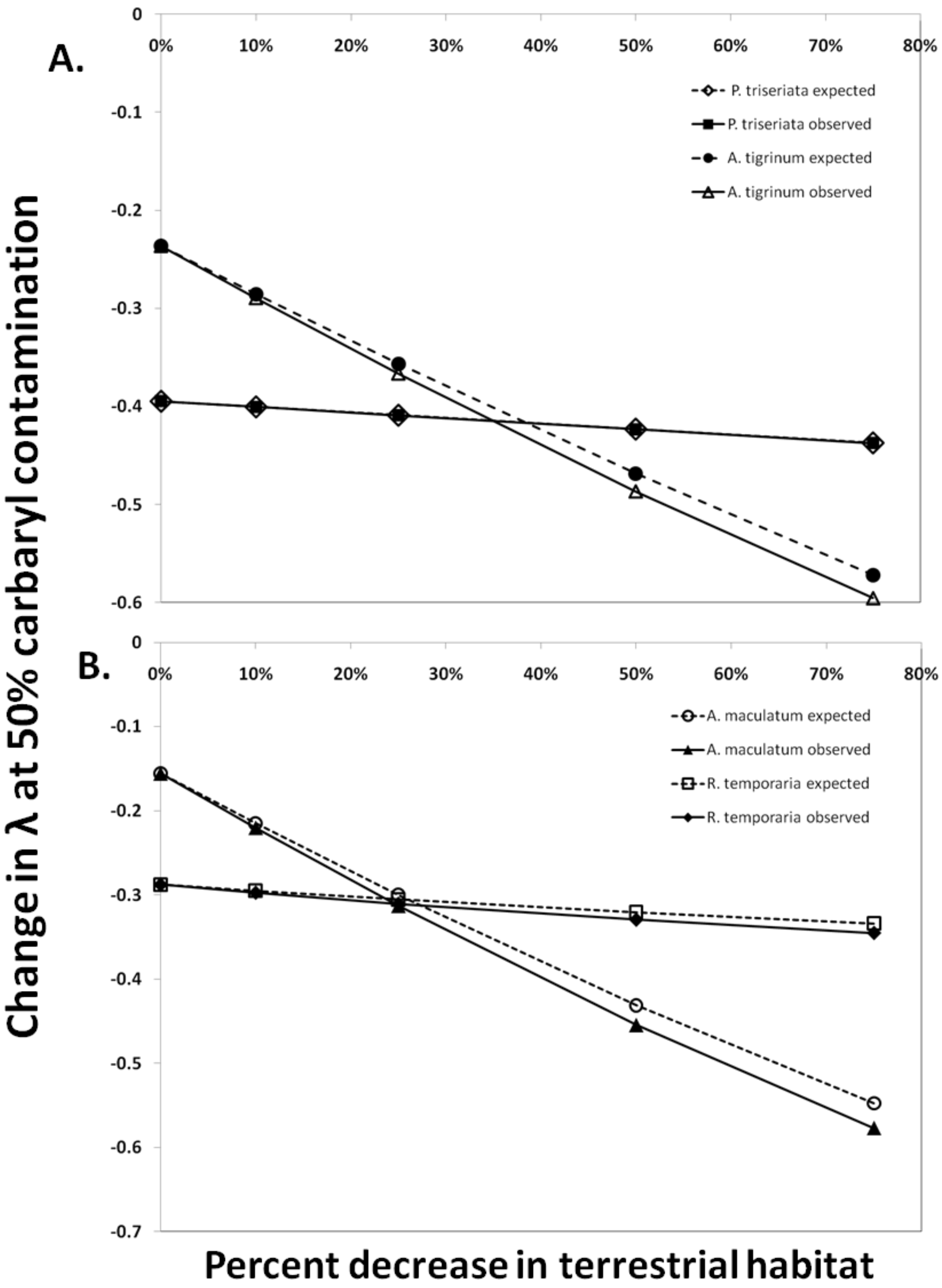
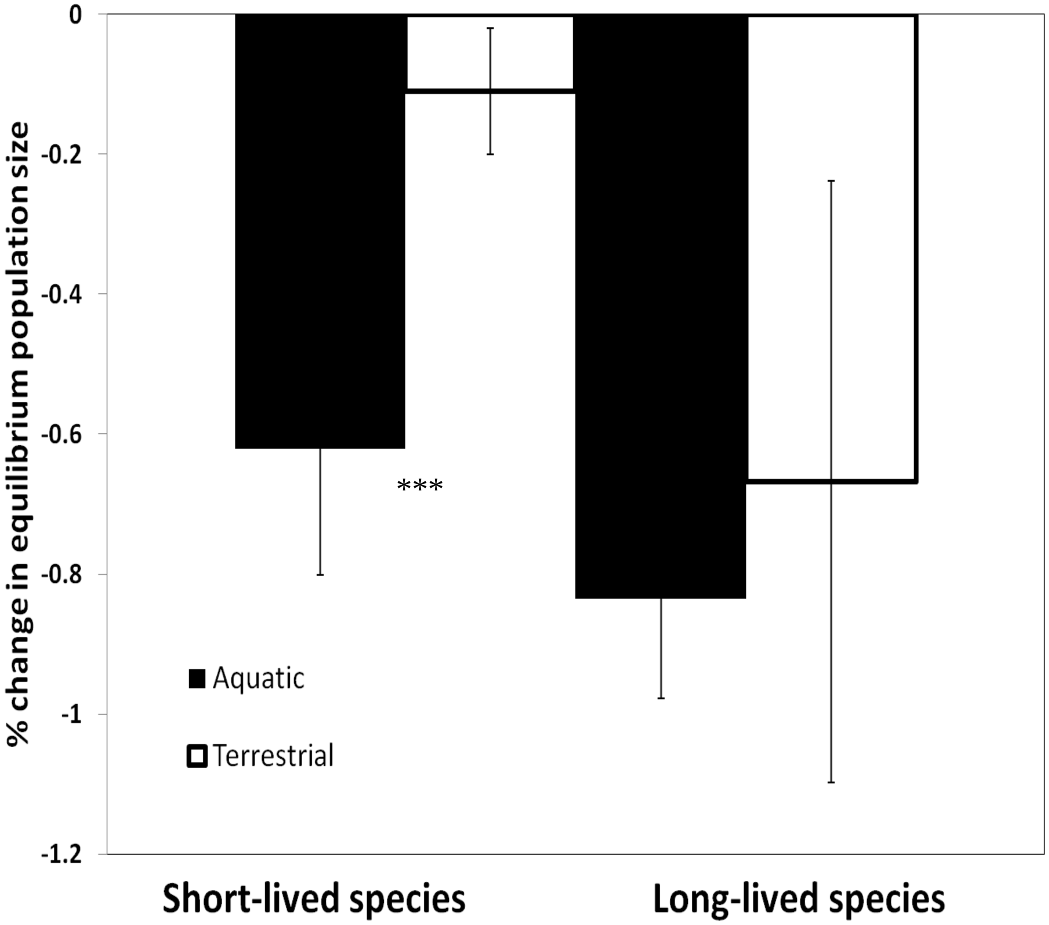

A.
B.
Change in λ at 50% carbaryl contamination
Percent decrease in terrestrial habitat
0%
10%
20%
30%
40%
50%
60%
70%
80%
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
P. triseriata expected
P. triseriata observed
A. tigrinum expected
A. tigrinum observed
A. maculatum expected
A. maculatum observed
R. temporaria expected
R. temporaria observed

Figure 1.4: The percent change in equilibrium density for density-dependent short-lived (n=7) and long-lived species (n=7) experiencing a 50% decrease in adult (terrestrial) or larval (aquatic) survivorship (these decreases would be expected to result from to terrestrial habitat loss and carbaryl contamination respectively). ***denotes significant difference in mean values between aquatic and terrestrial perturbations. Error bars represent standard deviation.



0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
% change in equilibrium population size
***
■ Aquatic
□ Terrestrial
Short-lived species
Long-lived species

Chapter 2

The ratio of aquatic to terrestrial habitat alters the role of a top-predatory salamander in pond food webs

Chapter 2 currently submitted for publication and is under review.

Abstract

A wide variety of species use distinct habitat types throughout their life-cycle, switching among them through a process known as an Ontogenetic Niche Shift (ONS). Standard metacommunity theory is inadequate for capturing the complexities of community interactions for ONS species by only considering spatial connections among one habitat. We suggest using the ratios of habitat types as a predictor variable for species with ONS to examine the influence of landscape structure on those species' abundances and interspecific interactions. We surveyed *Ambystoma maculatum*, a salamander with predaceous aquatic larvae and terrestrial adults, as well as the species richness of their prey, in ponds embedded within landscapes of different Aquatic to Terrestrial Ratios (ATRs). Structural equation modeling revealed that landscapes with higher ATRs had fewer larval *A. maculatum*, and that aquatic species richness was not directly influenced by ATR; richness was instead indirectly influenced through the ATR's direct effect on *A. maculatum*. In contrast to standard metacommunity expectations, this predator had a stronger influence on prey richness in ponds in more isolated (low ATR) landscapes. This study also highlights an important consequence of landscape changes by altering the ratios of habitat types, which can disrupt the interactions of species with ONS.

Introduction

Landscapes are inherently heterogeneous, comprising resources distributed unevenly among several habitat types (Risser et al. 1984, Turner 1989, Danielson 1991). Most efforts to examine the influence of spatial processes on species interactions implicitly or explicitly assume that species in communities interact within relatively homogeneous discrete patches that are interconnected by dispersal (i.e., a metacommunity) (Leibold et al. 2004). However, interactions among species within a given landscape are often not confined to just one habitat type (Polis et al. 1997). When species require the use of multiple distinct habitat types, both regional processes(dispersal) and local processes(trophic interactions, environmental variables) are influenced by the juxtaposition of habitats within the landscape. As a result, when species that utilize multiple habitat types are common, the assumptions of standard metacommunity theory may inadequately capture the complexities of community interactions at the landscape level (Knight et al. 2005, McCoy et al. 2009).

Species with ontogenetic niche shifts (ONS) often require two (or more) distinct habitat types during their life-history (Wilbur 1980). For example, many species of insects (e.g., Lepidoptera, Coleoptera, Diptera, Odonata), amphibians, and fishes, among others, utilize one habitat type for larval growth and then transition (e.g., via metamorphosis) into a separate habitat for continued growth, dispersal, and reproduction. Species with ONS may occupy different trophic roles in each habitat/life-stage they occupy (e.g., herbivore in larval habitat, predator in adult habitat), however, growth and survival in each habitat differentially contribute to the overall population dynamics of the species (Wilbur 1980). Consequently, the abundance of individuals in one habitat depends upon the availability of both essential habitat types (Chase and Leibold 2003). Examining the influence of spatial processes on species with an ONS thus requires consideration of both habitats they require. Furthermore, the proportional availability of either habitat type may shift patterns of abundance of the ONS species, altering their interactions with other species in the food web.

We propose an approach that explicitly estimates the ratio of essential habitat types required by the species within a landscape to capture the effects of spatial processes on the dynamics of species with ONS. Because species with an ONS require different habitats for larval and adult growth, the population growth of the species is influenced by both the availability of larval habitat (H_l) and adult habitat (H_a) in the landscape, and the survival of individuals within those habitats (Wilbur 1980). Thus, if one habitat is particularly limiting, this will restrict the abundance of individuals of a species with ONS in the other habitat the species occupies, limiting the overall population size. Importantly, the limiting habitat type for a population is not necessarily the habitat with the lowest abundance in the landscape. The population growth rate (λ) of the species depends upon survivorship and growth of individuals in both H_l and H_a, and the elasticity (i.e., relative importance) of a given life stage to overall λ (Caswell 2001). Therefore, the limiting habitat for the population depends on H_l:H_a ratio as well as the importance of each habitat to overall population growth rate.

To estimate the relative contribution of survivorship in each habitat type—the 'habitat elasticity'—to λ we can sum all the elasticities of stages that occur in H_l (e.g., egg survivorship+ larval survivorship = E_l) and all the elasticities of stages that occur in H_a (e.g., juvenile survivorship + adult survivorship = E_a). Consequently, the ratio of the two habitats, H_l and H_a, can have differential influences on species with ONS depending upon the values of E_l and E_a. When species have an ONS, classifying patches according to their degree of isolation from one another as is typically done in metacommunity theory (Leibold et al. 2004), may not provide the complete story. If a species has a considerably higher E_a than E_l, its abundance in H_l will be more a function of the availability of H_a than any feature of H_l. As a result, the interactions of that species with other species in H_l (e.g., competition, predation) will be strongly influenced by the $H_{a:}H_l$ ratio, rather than more traditionally considered metacommunity features such as patch isolation.

Here, we examine the effects of a top predator with an ONS on the structure of food webs in small freshwater ponds that vary in the ratio of habitat availability. The top predators in small ponds without fish include larvae of long-lived salamanders (Holomuzki et al. 1994, Davic and Welsh 2004) and odonates (McPeek 1990, Batzer and Wissinger 1996), which often spend a significant part of their lives as adults in the terrestrial habitat. If survivorship in the terrestrial habitat represents a significant contribution to the populations of these top predators (high E_a), species interactions within the ponds may be more strongly influenced by adjacent terrestrial habitats than the distribution of the ponds themselves. Although previous studies have shown that the species richness of invertebrates and amphibians in ponds depends to some extent on the degree of isolation within a metacommunity (McCauley 2006, Howeth and Leibold 2008) and the interaction between dispersal and predator dynamics (Chase et al. 2009, Chase et al. 2010), here, we suggest that top predator species with ONS are expected to respond differently to processes of habitat isolation, such that patterns might not conform to the expectations from traditional metacommunity theory.

In east-central Missouri (USA), we examined the influence of larval and adult habitat availability (aquatic to terrestrial habitat ratios; ATR) on a wide-spread, long-lived salamander, *Ambystoma maculatum* (Caudata: Ambystomatidae), which spends its short larval stage in small temporary ponds, and its long-lived adult stage in the surrounding terrestrial matrix. Larval *A. maculatum* remain in fishless ponds for 4-6 months, where they are typically top predators, exerting strong pressure on the abundance and diversity of other amphibians and invertebrates in the food web (Freda 1983, Nyman 1991). However, because *A. maculatum* are long-lived as adults (average life-span 7-15 years; Flageole and Leclair 1992), they likely have large E_a to the terrestrial habitat (e.g., Biek et al. 2002, Vonesh and De LaCruz 2002, Burgett et al. unpublished manuscript). Therefore, we hypothesized that the abundance of *A. maculatum* at focal ponds would increase in landscapes with abundant terrestrial relative to aquatic habitat (low ATR). We quantified the ATR surrounding 42 focal ponds, and examined the relationships between the ATR, the abundance of *A. maculatum*, and the richness of other amphibians and invertebrate prey at focal ponds. We used structural equation modeling to disentangle the direct and indirect effects of the landscape on aquatic species richness.

Methods

Pond selection and ATR

We identified 42 focal ponds in eastern Missouri that were fishless, of moderate size (between $50m^2$ and $275m^2$), with at least 15% tree canopy cover over the pond, and which maintained permanent standing water during most years. For each focal pond, there was at least 40% forested habitat [preferred habitat for adult *A. maculatum* (Petranka 1998)] within a 500m radius around each focal pond (determined using ARC GIS software and land cover data from Missouri Spatial Data Information Service [MSDIS]). In our choice of focal ponds, we minimized abiotic differences such as canopy cover, size, and water chemistry.

For each focal pond, we calculated the aquatic to terrestrial ratio (ATR) to examine the relationship between landscape structure, *A. maculatum* abundance in focal ponds, and the richness of the aquatic invertebrate community. We classified the terrestrial habitat within 500m of the focal pond by using a combination of ground-truthing, and Arc GIS land cover data from MSDIS. The land cover data identified 15 categories of ground cover ranging from impervious urban streets to deciduous forest. For this study, we considered the available terrestrial habitat as deciduous forest, deciduous woody herbaceous, and evergreen forest (Vasconsuelos and Calhoun 2004). Aquatic habitat within the 500m radius of the focal pond was largely determined by ground truthing, as most small ponds did not appear in the land cover data.

The average dispersal distance of *A. maculatum* has been shown in several studies to be less than approximately 400 m (Phillips 1989, Smith and Green 2005) with a maximum dispersal of 756m away from a focal pond (Madison 1997). Therefore we calculated the ATR within a 500m radius around each focal pond as a reasonable estimate of the ATR a population of salamanders would experience. For analyses presented in this paper, we restricted our definition of terrestrial and aquatic habitat to only those habitats that *A. maculatum* would typically utilize, excluding agricultural, urban, and open grassland for the terrestrial habitat, and ponds, lakes, and rivers with fish for the aquatic habitat. However, the results from this study are robust to changes in the definition of ATR; the results are qualitatively the same when we relaxed the definition of ATR to include all aquatic habitats (Burgett and Chase unpublished data). Given the relatively small amount of aquatic habitat compared to the amount of terrestrial habitat surrounding focal ponds, terrestrial habitat availability drives the ATR values in this study. However, we advocate for the use of the habitat ratios approach regardless of H_a or H_l availability within a landscape, since ONS species may respond differently depending upon its E_a or E_l.

Pond Surveys

in late February to early March in Missouri, *A. maculatum* lay conspicuous egg masses, which remain intact for approximately 3 to 4 weeks prior to hatching (depending upon water temperatures) (Sexton et al. 1990). We conducted egg mass surveys following standard methods (Crouch and Patton 2000) in 30 ponds in early March 2007 and an additional 12 ponds in early March of 2008. We assured that all adult *A. maculatum* had left the pond for at least a week prior to our surveys to ensure accurate egg mass counts.

The aquatic community was sampled twice (mid-May and late-June) to capture phenological differences among species. To sample macro-invertebrates and amphibian larvae, we used standard box sampling methods (Turner and Trexler 1997) by deploying a 500 cm diameter cylinder thrust into the soil. The contents of the cylinder were exhaustively sampled with a net (0.33mm mesh size) until 10 sweeps turned up no organisms. This process was repeated three times, stratified across each pond. In each cylinder, amphibian larvae were collected, identified, sorted into size categories, counted and released. Macroinvertebrates were stored in 70% ethanol and later identified in the lab, using a dissecting microscope and appropriate keys when necessary. Zooplankton (including cladocerans, copepods, and rotifers) were sampled by collecting 1L of water at 5 random locations and depths from each pond, filtered through a 80 μm mesh zooplankton net, and preserved in acid Lugol's solution for later identification and enumeration under a dissecting microscope.

Statistical analysis

To examine the direct effect of ATR on *A. maculatum* egg mass abundance (an indicator of both their breeding adult and larval abundance), we square root transformed ATR and egg mass data to comply with assumptions of normality and used linear regression analysis in SYSTAT version 12.0. We also examined the relationship between *A. maculatum* egg mass abundance and ATR on macro-invertebrate species richness using linear regressions in SYSTAT version 12.0. To partition the direct and indirect effects of ATR and *A. maculatum* egg mass abundance on macro-invertebrate species richness, we used structural equation modeling (SEM) in AMOS 5.0.1 (Amos Development Corp. 2003). The accuracy of the model was examined using χ^2 values as well as AIC and BIC indices (Akaike's information criterion, Bayesian information criterion). Path coefficients were evaluated using z tests. Given our particular interest in spatial processes influencing *A. maculatum* abundance and their potential effects on prey species richness, we focused on a simple model including *A. maculatum* egg mass density, the ATR, and prey species richness. We present other models that include the effects of abiotic factors on prey species richness and *A. maculatum* egg mass density in the Appendix.

Results

The number of *Ambystoma maculatum* egg masses in focal ponds significantly increased as the ATR of the focal pond decreased (Fig. 2.1a, linear regression, R^2=0.23, P=0.002, F=8.03). Macro-invertebrate species richness significantly decreased as *A. maculatum* egg mass abundance increased (Fig. 2.1b, linear regression, R^2=0.15; P=0.02). Macro-invertebrate species richness was not influenced by ATR (R^2=0.02; P=0.37). Our base-line SEM (structural equation modeling) excluded the path between ATR and macro-invertebrate species richness, due to the non-significant relationship between the two endogenous variables. The model yielded a $\chi^2 = 0.77$ (Fig. 2, df=1, P=0.38) and AIC and BIC values suggesting adequate model fit (default model AIC=10.78 and BIC=19.09). The indirect effect of the aquatic to terrestrial ratio (ATR) on species richness yielded $R^2 = 0.12$. The χ^2 did not improve with the addition of a path between ATR and macro-invertebrate species richness (saturated model: AIC=12.00, BIC=21.98), thus confirming that the original model was the most parsimonious. Abiotic factors such as pond size, canopy cover, and pH influenced species richness in the aquatic habitat and yielded adequate models, but inclusion of these variables into the model did not reduce the χ^2 further (Online Resource 1). The R^2 value of overall aquatic species richness in the system improved to 0.37 with the addition of pH and canopy cover into the model, however, none of the adequate models containing abiotic factors included a direct effect of ATR on aquatic species richness.

Discussion

Overall, our results show that the abundance of *Ambystoma maculatum* present at a focal pond was lower as the aquatic to terrestrial ratio (ATR) of a site decreased.

Furthermore, the increased abundance of larval *A. maculatum* at ponds with a low ATR was negatively related to the richness of species in the aquatic food web, suggesting their strong control over the food web. In all, the species richness of other amphibians, macro-invertebrates, and zooplankton appeared to be indirectly influenced by the effect of ATR on *A. maculatum*, but not directly by ATR itself.

The increased abundance of larval *A. maculatum* in isolated ponds is most likely explained by their complex life cycle and strong dependence on the terrestrial habitat as long-lived adults. Population growth rates of long-lived species are typically less sensitive to juvenile life-stages (Heppell et al. 2000, Seather and Bakke 2000, Forbis and Doak 2004). For long-lived amphibians which only utilize aquatic habitats for a brief larval stage, their populations should be relatively less sensitive to larval than adult survivorship (Biek et al. 2002,Vonesh and De la Cruz 2002), and as a result most limited by the availability of terrestrial relative to aquatic habitats. Indeed, we used the demographic matrix model presented in Karracker et al. (2008) to calculate E_l (0.275) and E_a (0.587) values for *A. maculatum*, and we found that processes in the terrestrial habitat (E_a) have a larger proportional effect on λ than processes in the aquatic habitat (E_l). As a consequence, we suggest that landscapes with higher ATR, and thus higher availability of larval (pond) habitat, will have a negligible influence on overall population size of *A. maculatum*. Instead, in lower ATR landscapes, with higher inter-pond isolation, a similar density of adult *A. maculatum* oviposit in fewer ponds, concentrating larval *A. maculatum* relative to higher ATR landscapes.

The increase in larval *A. maculatum* in ponds with a low ATR likely led to a significant decrease in macro-invertebrate species richness in those ponds. Larval *A.*

maculatum are typically top predators in these ponds, consuming a wide range of prey species throughout their larval development (Freda 1983). Thus, higher densities of larval *A. maculatum* reduce the overall species richness of ponds in low ATR landscapes. While traditional metacommunity theory would predict similar results of lower species richness in habitats that are more isolated (reviewed in Cadotte 2006), when predation is strong, species richness of prey can be higher in more isolated habitats (Sheffer et al. 2006, Chase et al. 2010). Here, we find that isolated habitats have higher predation and resulting lower prey species richness, most likely a result of the ONS of the top predator and its extensive reliance on the terrestrial habitat.

Although our study demonstrates one specific example of when the availability of different habitats can influence the abundance of a species and the strength of its' interactions in a metacommunity, there are many examples where the ratios of habitat availability may play a critical role in trophic interactions of other species with ONS. For example, many lepidopterans (butterflies and moths) use host-plants in one habitat type for larval development, and other resources in a separate habitat for adult persistence. The well-studied metacommunity interactions among the Glanville fritillary butterfly, *Melitaea cinxia*, might provide an exemplary system to explore this question, as it requires larval host-plants (*Plantago lanceolata* and *Veronica spicata*) which occur in restricted meadows (van Nouhuys and Hanski 2002, van Nouhuys et al. 2003), while adult resources are concentrated in adjacent woodland flowering plants (van Nouhuys and Hanski 2002). If adult survivorship is important to the overall population dynamics of this species, we might expect that *M. cinxia* larvae will be more concentrated, and exert greater damage, on the host plants in landscapes where the availability of larval host plants are less abundant. Another example of where this effect might influence the strength of food web interactions is in the well-studied case of bluegill sunfish (*Lepomis macrochirus*), which require both lentic and lotic habitat in lakes (Osenberg et al. 1988, Werner and Hall 1988); the influence of bluegill on prey in each habitat type could depend critically on the bathymetry of the lake and the resulting proportional availability of lentic:lotic habitat.

By explicitly considering the ratios of habitat availability for species with ONS, we can make more specific predictions about the influence of landscape structure on species abundances and the strengths of their interspecific interactions. In this paper, we focus on a top-predator with an ONS, and its influence on its prey community. Importantly, however, there are often many species with ONS that co-occur, and thus will be variably influenced by the ratios of available habitat. In the pond communities we studied here, many of the species of prey also have ONS and utilize terrestrial habitats in their adult stage (e.g., several insects and anurans). Therefore, the influence of predation in the aquatic habitat on the populations of these prey species with ONS will depend on the relative importance of their survivorship in aquatic and terrestrial habitats. For example, we might expect that the influence of predation by larval *A. maculatum* would have a larger influence on ONS species whose population dynamics are more limited by aquatic habitats (e.g., short-lived species) than on species with an ONS whose population dynamics are more limited by terrestrial habitats (e.g., longer-lived species).

The alterations of habitats by humans, most notably habitat loss and the resulting fragmentation, have become one of the greatest threats to global biodiversity (Fahrig 2003, Foley et al. 2005, Fisher and Lindenmayer 2007). Our study emphasizes an important, but underappreciated, consequence of habitat destruction; potentially altering the ratios of qualitatively distinct habitat types. For example, the draining of wetlands and conversion of forests to agricultural or urban land can dramatically alter the ratios of aquatic to terrestrial habitats in a landscape, which in turn can alter the relative abundance of species and the strengths of their interactions with other species in the food web. Progress in understanding the ultimate consequences of habitat alterations will necessitate ecologists to embrace, rather than avoid, the heterogeneities observed in ecological systems, and to break down the barriers of studying different types of ecosystems, such as aquatic versus terrestrial ecosystems, without considering their interconnections (Knight et al. 2005, McCoy et al. 2009)

Acknowledgements

We thank W. Ryberg, B. Allan, P. Hanly, J. Mihaljevic, and especially E. Biro for assistance with surveys and pond sampling. We would like to thank the Chase lab, K.G. Smith, and T. Knight for helpful comments, and Tyson Research Center for logistical support. Funding was provided by the National Science Foundation (DEB 0241080, 0816113 to J. M. C. and DEB 10-11433 to A. A. B. and J. M. C.), and Washington University.

Literature Cited

Batzer DP and Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Ann Rev of Entomol 41:75-100 doi: 10.1146/annurev.en.41.010196.000451

Biek R, Funk WC, Maxell BA, and Mills LS (2002) What is missing in amphibian decline research: Insights from ecological sensitivity analysis. Conserv Biol 16:728-734 doi: 10.1046/j.1523-1739.2002.00433.x

Cadotte MW (2006) Dispersal and species diversity: A meta-analysis. Am Nat 167: 913–924 doi: 10.1086/504850

Caswell H (2001) Matrix population models: Construction, analysis and interpretation. 2 Ed. Sinauer Associates, Sunderland, Massachusetts.

Chase JM and Leibold MA (2003) Ecological niches: Linking classical and contemporary approaches. Univ. of Chicago Press, Chicago, IL.

Chase JM, Biro EG, Ryberg WA and Smith KG (2009) Predators temper the relative importance of stochastic processes in the assembly of prey communities. Ecol Lett 12: 1210-1218 doi: 10.1111/j.1461-0248.2009.01362.x

Chase JM, Burgett AA, and Biro EG (2010) Habitat isolation moderates the strength of top down control in experimental pond food webs. Ecology 91: 637–643 doi: 10.1890/09-0262.1

Crouch WB and Patton PWC (2000) Using egg-mass counts to monitor wood frog populations. Wildl Soc Bul 28:895–901.

Danielson BJ (1991) Communities in a landscape: The influence of habitat heterogeneity on the interactions between species. Am Nat 138: 1105-1120.

Davic RD and Welsh HH (2004) On the ecological roles of salamanders. Ann Rev of Ecol and Syst 35: 405-434 doi: 10.1146/annurev.ecolsys.35.112202.130116

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Ann Rev of Ecol and Syst 34:487-515 doi: 10.1146/annurev.ecolsys.34.011802.132419

Flageole S and Leclair R (1992) Demography of a salamander (*Ambystoma maculatum)* population by skeletochronology. Can J of Zoology 70: 740-749.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, and Snyder PK (2005) Global consequences of land use. Science 309: 570-574 doi: 10.1126/science.1111772

Forbis TA and Doak DF (2004) Seedling establishment and life history trade-offs in alpine plants. Am J of Bot 91: 1147-1153 doi: 10.3732/ajb.91.7.1147

Franklin JF and Lindenmayer DB (2009) Importance of matrix habitats in maintaining biological diversity. Proc of the Nat Acad of Science 106: 349-350 doi: 10.1073/pnas.0812016105

Freda J (1983) Diet of larval *Ambystoma maculatum* in New Jersey. J of Herpetol 17: 177-179.

Heppell SS (1998) Application of life-history theory and population model analysis to turtle conservation. Copeia 1998: 367-375.

Holt R D, and Hoopes MF (2005) Food web dynamics in a metacommunity context: modules and beyond. In: Holyoak M, Leibold MA, and Holt RD.

Metacommunities: spatial dynamics and ecological communities. Univ of Chicago Press: 68–93.

Holomuzki JR, Collins JP, and Brunkow PE (1994) Trophic control of fishless ponds by tiger salamander larvae. Oikos 71: 55-64.

Howeth JG and Leibold MA (2008) Planktonic dispersal dampens temporal trophic cascades in pond metacommunities. Ecol Lett 11: 245–257.

Karraker NE, Gibbs JP, and Vonesh JR (2008) Impacts of road de-icing salt on the demography of vernal pool-breeding amphibians. Ecol App 18:724-734.

Knight TM, McCoy MW, Chase JM, McCoy KA, and Holt RD (2005) Trophic cascades across ecosystems. Nature 437: 880-883.

Leibold MA, Holyoak M, Mouquet B, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, and Gonzalez A (2004) The metacommunity concept: A framework for multi-scale community ecology. Ecol Lett 7: 601–613.

Madison DM and Farrand L (1997) Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. Copeia 1997: 402–410.

McCoy MW, Barfield M, and Holt R (2009) Predator shadows: Complex life histories as generators of spatially patterned indirect interactions across ecosystems. Oikos 118: 87 100.

McPeek MA (1990) Determination of species composition in the enallagma damselfly assemblages of permanent lakes. Ecology 71: 83-98.

Nyman S (1991) Ecological aspects of syntopic larvae of *Ambystoma maculatum* and the *A. laterale-jeffersonianum* complex in two New Jersey ponds. J of Herpetol 25: 505-509.

Osenberg CW, Werner EE, Mittelbach GG, and Hall DJ (1988) Growth patterns in bluegill (*Lepomis macrochirus)* and pumpkinseed (*L. gibbosus)* sunfish: Environmental variation and the importance of ontogenetic niche shifts. Can J of Fish and Aqua Sciences 45: 17-26.

Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution Press, Washington and London.

Phillips, C. A. 1989. Population structure, breeding pond fidelity and phylogeography in the spotted salamander, *Ambystoma maculatum*. PhD. Washington University, St. Louis.

Polis GA, Anderson WB and Holt RD (1997) Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Ann Rev of Ecol and Syst 28: 289-316.

Risser PG, Karr JR, and Forman RT (1984) Landscape Ecology: Directions and Approaches. Special Publ. 2. IL Nat History Survey, Urbana, IL.

Seather, BE and Bakke O (2000) Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653.

Scheffer M, Van Geest G J, Zimmer K, Jeppesen E, Søndergaard M, Butler M G, Hanson M A, Declerck S, and De Meester L (2006) Small habitat size and isolation can promote species richness: Second-order effects on biodiversity in shallow lakes and ponds. Oikos 112: 227–231.

Sexton OJ, Phillips C, and Bramble JE (1990) The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum*). Copeia 1990: 781-787.

Smith AM and Green MD (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28: 110–128

Turner AM and Trexler JC (1997) Sampling aquatic invertebrates from marshes: Evaluating the options. J of the North Am Benthol Soc 16: 694-709.

Turner MG (1989) Landscape ecology: The effect of pattern on process. Ann Rev of Ecol and Syst 20: 171-197.

Van Nouhuys S and Hanski I (2002) Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. Journal of Animal Ecology 71: 639–650

Van Nouhuys S, Singer MC, and Nieminen M (2003) Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. Ecol Entomol 28: 193–202

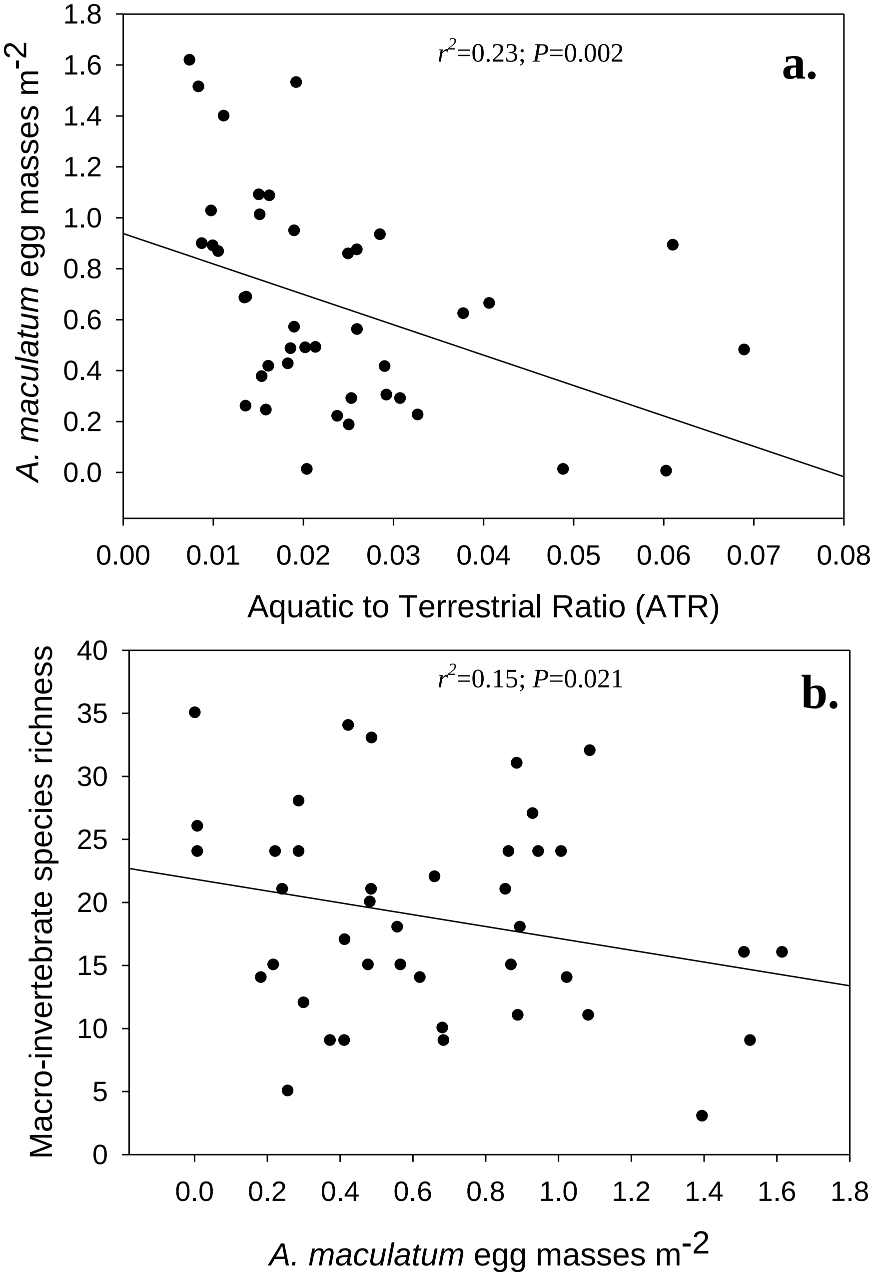
Vasconcelos D and Calhoun AJK (2004) Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. J of Herpetol 38: 551-561.

Vonesh JR and de la Cruz O (2004) Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325-333.

Werner EE and Hall DJ (1988) Ontogenetic Habitat Shifts in Bluegill: The Foraging Rate-Predation Risk Trade-off. Ecology 69: 1352-1366.

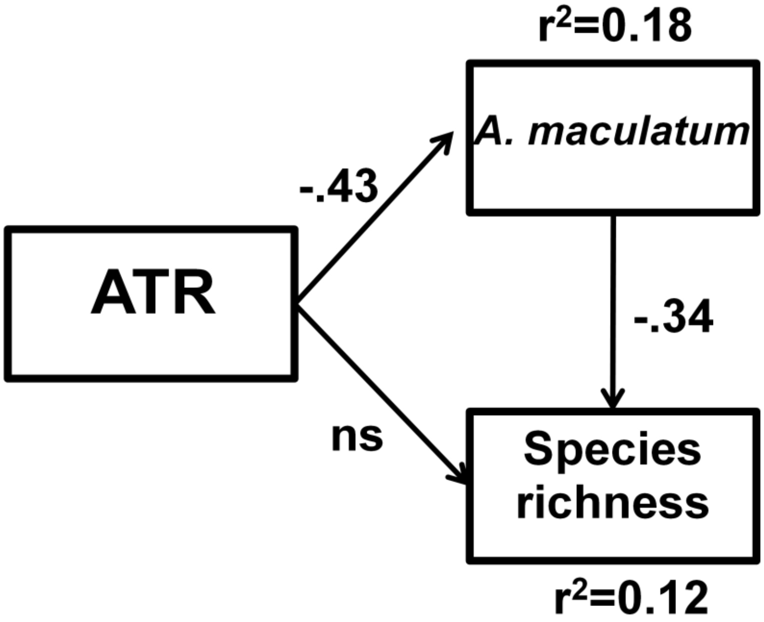
Wilbur HM (1980) Complex life cycles. Ann Rev of Ecol and Syst 11: 67-93.

Figure 2.1: a) The relationship between the ratio of aquatic to terrestrial habitats of focal ponds and the abundance of *Ambystoma maculatum* egg masses m^{-2}. (both variables are square root transformed to improve normality, n=42). b) The relationship between *A. maculautm* density and the species richness of other amphibians, macro-invertebrates, and zooplankton in focal ponds (n=42).



a.
r²=0.23; P=0.002
A. maculatum egg masses m⁻²
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
Aquatic to Terrestrial Ratio (ATR)
b.
r²=0.15; P=0.021
Macro-invertebrate species richness
40
35
30
25
20
15
10
5
0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
A. maculatum egg masses m⁻²

Fig. 2.2: SEM model showing the indirect effect of aquatic to terrestrial ratio on species richness. Path coefficients are standardized values. r^2 values represent the proportion of variance explained by upstream factors.


r²=0.18
A. maculatum
-.43
ATR
-.34
ns
Species richness
r²=0.12

Apendix:

Table 2.1: Table 1: Models that included abiotic variables. The simple model is nested within these models. An X indicates that the model includes an arrow from the factor going to either species richness or *A. maculatum.* An * indicates an adequate model fit to the data.

Variable	**Affecting Spp richness**	**Affecting A. mac**	χ^2	**DF**	**Probability level**	**AIC**	**BIC**	**CAIC**
pH*	X		1	3	0.801	15	26.645	33.645
pH*	X	X	0.905	2	0.636	16.905	30.213	38.213
Canopy cover*	X		5.322	3	0.15	19.322	30.967	37.967
canopy cover*	X	X	3.1	2	0.215	19.076	32.385	40.385
pond size	X		14.4	6	0.025	32.44	47.416	56.416
pond size	X	X	6.196	2	.045	22.196	35.505	43.505
Chlorophyll A*	X		1.8	3	0.618	15.788	27.433	34.433
canopy cover + pH*	X	X	9.1	5	0.104	29.125	45.761	55.761
pH + chlor	pHX CH X		15.171	6	.019	33.171	48.143	57.143
Canopy cover+ chlor *	CC X CHX	CCX	4.544	5	.474	24.544	41.179	51.179
All variable model	X	X	39.6	13	0	69.595	94.549	109.549

Appendix Discussion: Canopy cover, pH, and Chlorophyll A had a significant effect on overall aquatic species richness (R^2=.359, p>.0001; R^2=.107, p=.042; R^2=.001, p=.864 respectively). Although adding these abiotic explanatory variables into the model yielded significant models that adequately fit the data, they did not lower the χ^2 value of the original simplified model significantly. Most importantly, none of the models that included a direct effect of ATR on species richness were supported, further demonstrating the importance of salamander predation in this system. Abiotic factors do help to explain an additional 25% of the variation in aquatic species richness yielding an overall R^2=0.37 for this observational study.

Chapter 3

Population-level response of two anurans (*Hyla versicolor* and *Acris crepitans*) to an aquatic predator

Abstract

Interspecific interactions (ie: predation) shape the structure of communities and can influence the population dynamics of the species involved. For stage-structured organisms, the influence of one species on the population dynamics of another depends on which stage class the interaction influences, the magnitude of the effect on the survivorship, growth or fecundity of that stage class, and the relative sensitivity of the population growth rate to changes in those vital rates. For amphibians, most studies have focused only on the interactions between species in the aquatic habitat and their subsequent effects on larval survivorship. To understand the population-level influence of an aquatic predator on amphibian larvae, their effect on survivorship in the larval (aquatic) habitat must be combined with demographic information across the rest of the life cycle. In this study, we followed the population-level effects of an aquatic predator (*Ambystoma maculatum*) on two species of Hylidae frogs with different longevities (*Hyla versicolor* and *Acris crepitans*). My quantitative synthesis in Chapter One suggests that the population growth rate of longer-lived species tends to be less sensitive to fecundity and juvenile life stages, leading to the hypothesis that an aquatic predator would likely have larger population level impacts on the shorter-lived species (*A. crepitans*). We found that the population growth rate of *A. crepitans* had a higher elasticity to the aquatic stage than the longer-lived species, *H. versicolor*. The presence of predatory *A. maculatum* larvae decreased the projected population growth rate of both species. However, over the three study-years, we found no significant effect of predator presence on overall population size of either species. The discrepancy between model projections and actual changes in population size likely resulted from overestimation of larval *A. maculatum*

impacts on larval survivorship, and climatic variation between years that was not reflected in the demographic matrix models. Although interspecific interactions between larval *A. maculatum* and its prey *H. versicolor* and *A. crepitans* led to large decreases in larval survivorship, this did not translate into differences in population size at experimental ponds. Therefore, to fully understand the impacts of interspecific interactions on the population dynamics of amphibians, one must consider the entire life cycle of the species.

Introduction

The relationship between a predator and its prey is a fundamental ecological interaction that shapes the structure of communities (May 1973, Paine 1980). Often, the relationship between predators and their prey can drive the population regulation of either or both species causing cyclical dynamics in abundances (e.g.: lynx and hare, MacLulich 1937, voles and lemmings, Elton 1942), increases in predator abundances (Gause 1934), and/or decreases and even extinction of prey species (Huffaker and Kennett 1956, Estes and Palmisano 1974). Countless studies on community interactions document the effects of a predator on prey species, and are especially common in aquatic and amphibian community studies (e.g: Morin 1985, Morin 1986, Wilbur and Fauth 1990, Welborn et al. 1996).

Understanding how predation shapes population dynamics is complicated for amphibians, since they occupy many different trophic positions in aquatic systems from primary consumer to top predator (Welborn et al. 1996, Altig et al. 2007). Additionally, most amphibians have a complex life cycle in which they use the aquatic habitat for larval growth and development and then metamorphose to spend their juvenile and adult stages in the terrestrial habitat (Wilbur 1980). Therefore, strong interspecific interactions in the aquatic habitat may not necessarily translate into dramatic consequences for the population dynamics of either predator or prey species (Wilbur 1980, Burgett chapter 1). Although the effects of aquatic predators on larval amphibians has been well documented (e.g.: Brodie and Formanowicz 1983, Morin 1983), to my knowledge, no studies to date have examined the influence of an interspecific interaction on the population-level responses of amphibians with complex life cycles.

Matrix population models integrate the effects of environmental factors (e.g., presence/absence of a predator) on vital rates across the life cycle of an organism, and can be used to project population growth (Caswell 2001). Amphibian populations are typically stage-structured, making matrix population models ideal for studying the potential population level effects of interspecific interactions on particular species. In addition to stage-structure and environmental factors, matrix population models can include a variety of other biological features, such as temporal variation and density dependence. It is typically thought that density-independent models that explicitly incorporate environmental factors provide a meaningful way to integrate vital rates and assess the relative importance of environmental factors on populations. However, this assumption is rarely tested (Crone et al. 2011). In this study, we examine the validity of our models by comparing matrix projections (deterministic population growth rate) to observed changes in population size during the same time interval in which the model parameters were estimated. If these do not match, then it suggests that the model is too simplistic or the parameters were poorly estimated.

Elasticity analysis can be used to examine how small changes in vital rates (ie: larval survivorship) influence the overall population growth rate (λ) of the species (deKroon et al. 1986, Caswell 2001). A wide variety of species, including amphibians, demonstrate a similar pattern: as the longevity of a species increases, the population growth rate becomes less sensitive to perturbations in early life stages (Burgett, Chapter 1, Seather and Bakke 2000, Heppell et al. 2000, Forbis and Doak 2004). Thus, amphibians that are short-lived may be particularly vulnerable to threats that occur on the larval stage in the aquatic habitat, while longer-lived amphibians may experience more pronounced population declines in response to perturbations in the terrestrial habitat (Burgett, Chapter 1). Therefore, we expect that predation on larvae will have more dramatic effects on populations of shorter-lived amphibians.

In this study, our primary objective is to examine the effects of an aquatic predator, *Ambystoma maculatum*, on the population dynamics of two anurans with disparate life histories. Throughout much of eastern and Midwestern North America, larval spotted salamanders (*Ambystoma maculatum*) and other related species are often top predators in fishless aquatic habitats such as ponds or wetlands (Freda 1983, Nyman 1991). Larval *A. maculatum* can reach relatively high densities (Burgett, Chapter 2), and prey upon the larvae of two species of anurans in the family Hylidae: Grey treefrogs (*Hyla versicolor)* and Blanchard's cricket frog (*Acris crepitans blanchardi)* (Burgett, unpublished data). Large-scale surveys of fishless ponds throughout eastern Missouri revealed a decrease in *H. versicolor* and *A. crepitans* larval abundance in isolated ponds with dense *A. maculatum* larvae, although night call surveys indicated the presence of substantial numbers of breeding adult *H. versicolor* at those ponds (Burgett, unpublished data).

Hyla versicolor has a larval period of three to four months, can live between seven and nine years as adults, and utilizes the terrestrial habitat extensively (Snider and Bowler 1992, Wright and Wright 1995). *A. crepitans* also has a larval period of approximately four months, but a much shorter adult stage (~eight months) (Burkett 1984, McCallum et al. 2011). Given the disparate life history strategies of *H. versicolor* and *A. crepitans*, we hypothesize that the increase in predation by larval *A. maculatum* will have a larger effect on the population dynamics of *A. crepitans* relative to *H.*

versicolor. Alternatively, if predation rates are relatively low, or if predation is less important than other environmental factors, then the presence of a predator might have little effect on population growth rates of these species.

To examine the population level response of *H. versicolor* and *A. crepitans* to larval *A. maculatum* predation, we constructed 12 experimental ponds at Washington University's Tyson Research Center (TRC) and introduced high densities of larval *A. maculatum* to half of the ponds. Using mark recapture techniques, we monitored stage-specific vital rates for both species as well as overall population size to determine the effects of this aquatic predator on the overall population dynamics of *H. versicolor* and *A. crepitans*. We test our model by independently measuring observed population size over the study interval.

Methods

Experimental set-up

We created 12 experimental ponds (6m diameter, 1m deep) at Tyson Research Center during the winter of 2008. Experimental ponds were located within an oak-hickory forest and were separated by at least 500m from each other and from any existing water bodies at Tyson Research Center, creating isolated ponds with reduced likelihood of migration between populations (Semlitsch 2002). Given the constraints of spacing within TRC, ten of the 12 ponds were located on ridgetops, while two of the 12 ponds were located along a valley bottom. One of the ponds located within the valley became too close to other water bodies and experienced a large influx of migration by *Acris crepitans* following the flooding events of the nearby Meramec river in 2009 and 2010. We removed this pond (a predator-present pond) from analyses since the influx of individuals could potentially inflate population sizes of both *A. crepitans* and *H. versicolor*.

After ponds were excavated, we smoothed and contoured the banks of the ponds, lined them with two inches of gravel, geotextile fabric, and a polyethylene liner to ensure their permanence (PPL-30, BTL Liners Inc.). On the berm above each pond, we dug a two-foot wide trench and secured the edges of the liner into the trench to prevent the liner from slipping during filling. We then spread two inches of topsoil over the liner to allow for submergent plant growth. We filled all ponds by 21 March 2008, with well water from Tyson Research Center using a water hauling truck. We inoculated the experimental ponds with concentrated densities of phytoplankton and zooplankton collected from five ponds at TRC. Both submerged (n=6 species) and emergent macrophytes (n=10 species) were added to all ponds over the course of two years. We allowed macroinvertebrates to naturally colonize ponds. Throughout the spring and summer of 2008, we introduced large numbers of egg masses, larvae, and breeding adults of eight common species of anurans (*Hyla versicolor, Acris crepitans, Pseudacris crucifer, P. triseriata, Rana sphenocephala*, *R. clamitans, R. sylvatica,* and *Bufo americanus*) from existing ponds located at TRC to establish anuran populations.

We randomly assigned one of two treatments to each pond (predator presence or absence) and added *Ambystoma maculatum* egg masses to predator-present ponds on 8 April 2008. In order to achieve the high density of *A. maculatum* egg masses/m^2 observed in isolated ponds in Missouri, we added 75 egg masses to each of the six predator-present ponds. Given the longevity and age to sexual maturity of *A. maculatum* (Flageole and Leclair 1992), we did not expect these populations to breed during the time-span of the project, and thus maintained this treatment by adding 75 egg masses each spring. Although the ponds were designed to be isolated from natural ponds, eight of the 12 ponds received some natural recruitment by *A. maculatum* by 2011. To maintain the treatments, we searched all predator-absent ponds from late February to early April each year and removed any *A. maculatum* egg masses located. We also searched predator-present treatments prior to the addition of egg masses but after female oviposition was complete for the season, and subtracted the number of naturally recruited egg masses into the pond from the 75 added to maintain the treatment density.

Demographic data collection

We collected demographic data for both *H. versicolor* and *A. creptians* in the presence and absence of larval *A. maculatum* to parameterize matrix population models. Although larval amphibians commonly show density-dependent survivorship (e.g. Van Buskirk and Smith 1991, Altwegg 2003, Trenham and Shaeffer 2005), the overall density of tadpoles of both species was substantially lower in the experimental ponds (average density of *H. versicolor* 0.488/m^2 in 2010 in predator-absent ponds, *A. crepitans* were extremely rare in dip net sweeps and chimney sampling of ponds, with only one individual ever detected during pond sampling throughout 2009-2011) than that found in established ponds both at Tyson Research Center and elsewhere in Missouri (average density of *H. versicolor* 1.36/m^2, of *A. crepitans* 0.7878/m^2). The low abundance of both species in experimental ponds indicates that density-dependence is likely not a factor affecting the larval survivorship rates of either species during the time span of our data collection (Burgett and Lueder, unpublished data). Because populations of both *H. versicolor* and *A. crepitans* were recently established at the experimental ponds, populations were likely still in the exponential growth phase. Therefore, we present only density-independent population models for each species with and without predators.

Clutch size

Clutch size was determined by collecting amplectant pairs of both species from experimental ponds, placing them overnight in terrariums (which contained a small container of water for oviposition) located within the lab at Tyson Research Center, and counting the total number of eggs laid the following morning. Egg masses and adult frogs were returned to their respective ponds the following day. In 2010, we obtained a total of 12 *H. versicolor* amplectant pairs from predator free ponds and 13 amplectant pairs from *A. maculatum* present ponds. Amplectant pairs of *A. crepitans* were more difficult to collect due to their rarity within experimental ponds (average number of males was 3.8 at experimental ponds) and we were only able to obtain four amplectant pairs at predator-absent ponds, with only two of these pairs laying eggs in captivity. However, estimates of clutch size for the two pairs was concordant with estimates of clutch size for the species found in the literature (Livezey 1950). Finally, the average clutch size for each species was determined by taking the mean number of eggs/egg mass for ponds with or without *A. maculatum* (for *A. crepitans,* we averaged the number of eggs/egg mass for the two clutches laid in capitivity and used this estimate for both predator-present and absent ponds). We incorporated an even sex ratio of 50% for egg masses within our female-based matrix models.

Egg survivorship

We determined overall egg survivorship of *H. versicolor* in the laboratory using egg masses collected from non-experimental ponds at TRC. We counted the number of eggs within each mass, placed them in 10 gallon aquariums filled with well-water and either the presence or absence of larval *A. maculatum* (n=15 per treatment), and counted surviving tadpoles just after hatching (2 days later, approximately Gosner stage 20). Contamination of egg masses by bacteria or fungi within natural and experimental ponds can cause reductions in egg survivorship as well as water quality characteristics (Bugg and Trenham 2003). Additionally, *A. maculatum* larvae target tadpoles just as they are about to hatch, once embryos begin to elongate and move (Gosner stage 15), which can cause decreases in egg survivorship prior to actual hatching of eggs (Burgett and Lueder, unpublished data). Therefore, we determined a separate egg survivorship rate for both predator present and predator absent ponds by averaging survivorship rates for all 15 replicates. Unfortunately, we were unable to collect enough amplectant pairs of *A. crepitans* to conduct 15 replicates of egg survivorship experiments under the presence and absence of *A. maculatum*, however we were able to obtain estimates for egg survivorship from two replicates each of predator present and predator absent treatments.

Larval survivorship

We used three *in situ* cages (1m^2 x 1m deep with 1 mm mesh screening; e.g., Skelly 1995) in each experimental pond to determine larval survivorship of both *H. versicolor* and *A. crepitans;* cages in the predator-present ponds were stocked with ambient densities of larval *A. maculatum*. Zooplankton were able to pass through the mesh of the cages and cages were open at the top to allow for colonization of macroinvertebrates at the start of the experiment. We stocked ten *H. versicolor* tadpoles and 5 *A. crepitans* tadpoles into each cage approximately one week after hatching (approximately Gosner stage 22), when they could be handled without causing additional stress or mortality in tadpoles. The density of tadpoles was chosen because it approximates the naturally occurring densities of both species in the experimental ponds (for *A. crepitans* this was the density seen in predator free ponds). We removed tadpoles from the cages when their back legs emerged. A mesh lid was placed over the cages after two weeks to prevent any metamorphosed tadpoles from escaping the cages before being counted.

Adult survivorship and growth

To determine adult survivorship, we collected adult frogs of both species and used a mark recapture technique. We visited experimental ponds at night during peak activity times for *H. versicolor* and *A. crepitans* (humid or rainy nights, above ~10°C, with little wind) and collected all individuals present at the ponds. Most individuals collected were males, given the ease in locating these individuals, however females were often captured in or around the ponds edge through visual scanning. Additionally, in the spring of 2009, 10 PVC pipe refugia (Boughton et al. 2000) were placed around the ponds to aid in locating adults during the day. The PVC pipe samplers were readily colonized by *H. versicolor* .

When a frog was captured, it was placed individually into a sandwich size Ziploc bag and received a cohort and pond specific Visible Implant Elastomer (VIE) mark (Northwest Marine Technologies Inc.) beginning in the spring of 2009. In 2010 and 2011 we scanned all captured individuals for existing VIE tags using the purple wavelength detection light. If an individual was marked in a previous year, we recorded the VIE tag pattern and the individual received an additional specific mark to denote that it had been recaptured that year. Using the total number of individuals that were marked in year t, we determined a survivorship rate for adults based on the number of individuals that were recaptured in year t+1. Therefore, we calculated an estimate of survivorship for each species when predators were present or absent between 2009 and 2010, and 2010 and 2011.

We used the mean adult *H. versicolor* survivorship rate from all predator-present treatments and both years to parameterize the *H. versicolor* predator-present model, and used the mean rate from predator-absent ponds to parameterize the *H. versicolor* control matrix. Given the large-scale nature of monitoring and marking individual frogs of two species at 12 experimental ponds, we were unable to individually mark each frog and instead used cohort and pond specific tags. This limited our ability to incorporate detection probabilities into our survivorship rates using traditional methods. One way to account for detection probabilities, would be to penalize adult survivorship (A) by the proportion of individuals that went undetected in a given year (ie: proportion of individuals that were marked in 2009, not recaptured in 2010, but were recaptured in 2011). In our study, no individuals went undetected. That is, all adults recaptured in 2011 that were originally marked in 2009 were also marked in 2010. However, since we had a low sample size available to quantify detection probability, we increased overall adult *H. versicolor* survivorship by 5%, simulating a more conservative approach than our perfect detection probability from recapture data.

Hyla versicolor adults that were two years of age or older showed different patterns of survivorship than first year adults, so an additional second year adult (A2) stage was added for this species. Because we had low sample size, we calculated the survivorship rate for the A2 stage across both predator present and absent ponds (proportion of adults captured in 2010 that were recaptured again in 2011).

From 2009 to 2011, we captured and marked 653 adult *H. versicolor*, and 84 adult *A. crepitans.* We recaptured no adult *A. crepitans* individuals. We recaptured a total of 54 previously marked adult *H. versicolor* in 2010 and 2011. All of the recaptures occurred at the ponds where the individuals were originally marked, indicating limited dispersal between ponds.

Juvenile survivorship

The small size of VIE tags allowed us to mark recently metamorphosed juveniles of each species during the summer and fall of each season in order to estimate juvenile survivorship rates in a similar fashion to that of adult survivorship rates. Recently metamorphosed juveniles were collected from experimental ponds using visual surveys of pond edges in addition to dip net sweeps through the experimental ponds to obtain any individuals that had all four legs, but had not yet reabsorbed their tails. We limited the placement of VIE tags in juveniles to the back legs in order to reduce the potential damage to smaller front limbs. We marked 719 *H. versicolor* metamorphs and 88 *A. crepitans* metamorphs between 2009 and 2010 For *A. crepitans*, juvenile survivorship is based on recaptures in 2010 plus 5% to account for detection probabilities. The recapture rate of juvenile *H. versicolor* was extremely low (1 out of 719 marked juveniles < 0.001 survivorship), and thus we used estimates of juvenile survivorship from other studies of *H. versicolor* and similar species to set a more realistic, yet still very low, juvenile survivorship of 0.01 (Rustigian et al. 2003).

Demographic matrix models

Using the estimated parameters of tadpole, adult, and juvenile survivorship, clutch size and egg survivorship, we parameterized a basic two-stage demographic matrix model for *A. crepitans* with and without predators and a three-stage model for *H. versicolor* with and without predators (Figure 2.1). Matrix models were based on females, however adult survivorship rates were biased towards males given the propensity to collect more males than females. This provides a more conservative estimate of adult survivorship since male anurans tend to have higher mortality rates than females (Berven 1990). The fecundity term in all four matrix models is the product of clutch size, sex ratio, egg survivorship, and tadpole survivorship. Both *H. versicolor* and *A. crepitans* complete the larval life stage and metamorphose into juveniles within the first year, and thus we limited our matrix models to include just the juvenile and adult stage with the spring breeding season as time t and the following spring breeding season one year later as time t+1.

We calculated the population growth rate (λ) and elasticity matrix for each model following the methods outlined in Caswell (2001). We then compared the population growth rate of each species with and without predators for each species. Additionally, we calculated a habitat-specific elasticity value for both the aquatic and terrestrial habitat by summing the elasticities of vital rates that occurred in the aquatic habitat (egg and larval survivorship) and the terrestrial habitat (Juvenile and adult survivorships, clutch size) respectively. Egg and larval survivorship both occur in the aquatic habitat, however it is embedded within the fecundity term in our matrix model. Clutch size is often a product of resources available in the terrestrial habitat, therefore part of the fecundity term occurs in the terrestrial habitat, while part occurs in the aquatic habitat. Consequently, to obtain a habitat specific elasticity value for the aquatic habitat, we separated elasticity values for each individual vital rate instead of each stage. The total elasticity value for the vital rates was then greater than 1 (whereas the total elasticity value for all stages is = 1). In order to determine the proportionate effect of that habitat on population growth, we divided the habitat specific total elasticity value by the total elasticity value of all vital rates combined.

Overall population size

Using the total number of individuals marked in a given year at predator present or absent ponds, we were able to obtain total population size estimates for both species in 2009, 2010, and 2011. We tested whether species, year, predator treatment or their interactions affected the population sizes of *H. versicolor* and *A. crepitans* from 2009 to 2011 using repeated measures ANOVA in Systat (version 11). Overall population sizes (count data) for each species were square root transformed to meet assumptions of normality.

Results

Population growth rates differed between species and treatments. *Hyla versicolor* populations are projected to grow faster than *A. crepitans.* Both species have higher projected rates of population growth in ponds with predators absent compared to those with *A. maculatum* (Figure 3.3). The population growth rate of *Acris crepitans* was more sensitive to changes in occurring in the aquatic stage than *H. versicolor* (Figure 3.4).

Overall population sizes were much smaller for *A. crepitans* than for *H. versicolor* (repeated measures ANOVA: Table 3.1). There was no overall affect of treatment on total population size (Table 3.1), although *A. crepitans* did show a non-significant trend of lower population size at predator present compared to predator absent ponds (Figure 3.2). Overall population sizes varied significantly from 2009 to 2011 (Table 3.1), increasing between 2009 and 2010, and remaining stable or slightly decreasing between 2010 and 2011.

Discussion

Our matrix population models project that the presence of larval *A. maculatum* at high densities decreases the overall population growth rate (λ) of both species. Interestingly, *H. versicolor* populations are still projected to persist in the presence of predators with $\lambda > 1$ despite high levels of larval mortality that result from *A. maculatum* presence. In contrast, *A. crepitans* populations are projected to decline at predator-present ponds ($\lambda < 1$). Elasticity analysis of the demographic matrix models differed between species as expected, with the population growth rate of shorter-lived *A. crepitans* having a higher elasticity to perturbations that occurred in the aquatic habitat than did longer-lived *H. versicolor* (Figure 3.4). Thus, we would have expected predators in the aquatic habitat to have a more dramatic effect on *A. crepitans* population growth than on *H. versicolor*. However, *A. maculatum* decreased the population growth rate of both species similarly (Figure 3.3, *A. crepitans* no predator: λ=1.3663, predator λ=0.7009; *H. versicolor* no predator λ=1.8017, predator λ=1.0259). This discrepancy between the elasticity values and the actual effect on population growth rates likely arises from differences between species in the magnitude of predation that occurred within the experimental ponds. *Hyla versicolor* showed increased activity levels when *A. maculatum* were present relative to *A. crepitans* (Lueder and Burgett, unpublished data). This may have allowed *A. maculatum* to preferentially prey upon *H. versicolor*, leading to much larger effects on larval mortality (*H. versicolor* larval survivorship without predators= 0.52, *H. versicolor* survivorship with predators=0.21; *A. crepitans* larval survivorship without predators=0.31, *A. crepitans* larval survivorship with predators=0.25; Lueder and Burgett, unpublished data).

To test our matrix population models, we compare model projections to real changes in population size over the sampling period. Model projections and population size estimates concur that *H. versicolor* populations grow faster than *A. crepitans* populations. However, our model projects that *Ambystoma maculatum* presence will influence growth rate of populations of both species, and we find no overall effect of the predator treatment on either species (although there was a trend for predators to decrease the population sizes of *A. crepitans* (Figure 3.2)). The faster growth rate and higher population sizes observed in *H. versicolor* as compared to *A. crepitans* likely comes from differences in life history strategies between the two species. *A. crepitans* has a smaller body size in comparison to *H. versicolor*, which likely contributes to differences in mean clutch size between the two species (197 eggs/clutch in *A. crepitans* compared to 1720 eggs/clutch in *H. versicolor*). Additionally, *H. versicolor* has a slightly higher larval survivorship rate. The reduced clutch size of *A. crepitans* and lower larval survival in the absence of predators prevents populations from achieving higher population growth rates and thus higher population sizes in experimental ponds.

Demographic matrix modeling reveals a decrease in population growth rate for both species at predator-present ponds, however, the presence of predators did not influence the overall population size of either species over the course of this experiment. Several factors likely affected this inconsistency. First, our demographic models may have overestimated of larval mortality due to predators. We used standard methodology to quantify the effects of predation on larval mortality (Skelly1995). Specifically, we used *in situ* enclosures that provided alternative prey resources for larval *A. maculatum* and refugia for tadpoles. Despite this, mortality was likely increased in comparison to what tadpoles would experience within the larger experimental pond. Submerged vegetation was quite abundant in experimental ponds, providing increased heterogeneity than experienced within the experimental cages (Lewis and Eby 2002, Kopp et al. 2006). Second, our population size estimates for each pond were relatively low for both species, and there was high variation across ponds in population size. Thus, we had low statistical power to detect effects of predation on population sizes of either species. Finally, our population size estimates might have been more affected by poor abiotic environmental conditions that were present in 2011 than our vital rate estimates.

In 2011, there was a particularly cold winter and spring and a very hot summer, which decreased overall capture probabilities and the number of calling males at experimental ponds compared to 2010. Indeed, the abundances of *H. versicolor* at ponds decreased between 2010 and 2011; this could reflect an actual decrease in population size, or could be indicative of adults skipping the breeding season due to reduced resources or variable weather patterns that prevented them from returning to ponds to breed that year (Penchman et al. 1991). Vital rate estimates for the matrix population models were averaged across years, and were therefore less influenced by 2011 weather than population size estimates. Therefore, predator effects on population size might have been overshadowed by poor abiotic conditions in 2011. It is possible that additional years of data collection will reveal significant effects of predation on population size, and a greater congruence between model projections and population size estimates.

An important assumption of demographic matrix modeling is that populations are at equilibrium (Caswell 2001). In this study, we are likely capturing the exponential growth phase of both species as they begin, or try to begin to establish populations under the presence and absence of larval *A. maculatum.* Overall population size estimates increased dramatically between 2009 and 2010 and then remained somewhat stable (or decreasing) between 2010 and 2011 due to climatic variation in 2011. This suggests that these populations are likely still experiencing population growth. Although both species are likely experiencing rapid population growth, the limited size of the experimental ponds indicates that the population will eventually reach a point where density-dependence in the larval stage will become important. Therefore, it will be interesting to follow these populations as they begin to reach an equilibrium population size and to parameterize density-dependent matrix models to capture how predation then influences population dynamics of both species.

This study highlights the importance of examining how interspecific interactions in the larval life stage can alter the overall population dynamics of an amphibian species. Although many studies suggest that interspecific interactions in the larval stage of amphibians can cause dramatic decreases in survivorship (e.g.: Brockelman 1969, Skelly 1992, Werner and McPeek 1994), this does not necessarily lead to population declines within the species if the population growth rate is not particularly sensitive to that life stage (Burgett, Chapter 1). The structure of aquatic communities is thus not only dependent upon the interactions of species within it, but the dynamics that are occurring in the terrestrial habitat as well. This study highlights the importance of examining interspecific interactions at a population scale when one or more of the species has a complex life cycle and is the first study to examine how interspecific interactions in the aquatic habitat scales up to influence the population dynamics of the species.

Literature Cited

Altig, R., M.R. Whiles, and C.L. Taylor. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. Freshwater Biology 52: 386-395.

Altwegg, R. 2003. Multistage density dependence in an amphibian. Oecologia 136: 46-50.

Berven, Keith A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana Sylvatica*). Ecology 71:1599–1608.

Bessinger, S.R., and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. The Journal of Wildlife Management 62: 821-841.

Biek, R., W.C. Funk, B.A. Maxell, and L.S. Mills. 2002. What is missing in amphibian decline research: Insights from ecological sensitivity analysis. Conservation Biology 16:728-734.

Blaustein, A.R., J.M. Romansic, J.M. Kiesecker, and A.C. Hatch. 2003. Ultraviolet radiation, toxic chemicals and amphibian population declines. Diversity and Distributions 9: 123-140.

Boughton, R.G., J. Staiger, and R. Franz. 2000. Ues of PVC pipe refugia as a sampling technique for Hylid treefrogs. The American Midland Naturalist 144: 168-177.

Briggs, C. J., V. T. Vredenburg, R. A. Knapp, and L. J. Rachowicz. 2005. Investigating the population-level effects of chytridiomycosis: An emerging infectious disease of amphibians. Ecology 86:3149–3159.

Brockelman, W.Y. 1969. An analysis of density effects and predation in *Bufo americanus* Tadpoles. Ecology 50: 632-644.

Brodie, E.D. and D.R. Formanowicz. 1983. Prey size preference of predators: Differential vulnerability of larval anurans. Herpetologica 39: 67-75.

Bugg, R.L. and P.C. Trenham. 2003 Agriculture affects amphibians (Part I). Climate change, landscape dynamics, hydrology, mineral enrichment of water. Sustainable Agriculture **15:** 8–11.

Burkett, R. 1984. An ecological study of the cricket frog, *Acris crepitans*, in northeastern Kansas. Vertebrate Ecology and Systematics (Special edition) 10: 89-103.Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. American Naturalist 167:913-924.

Byers, J.E., S. Reichard, J.M. Randall, I.M. Parker, C.S. Smith, W.M. Lonsdale, I.A. Atkinson, T.R. Seastedt, M. Williamson, E. Chornesky, and D. Hayers. 2002. Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16: 630-640.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: Their roles in conservation biology. Ecology 81:619–627.

Caswell, H. 2001. Matrix population models: Construction, analysis and interpretation. 2 Ed. Sinauer Associates, Sunderland, Massachusetts.

Collins, J.P. and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9: 89-98.

Corn, P.S. 1998. Effects of ultraviolet radiation on boreal toads in Colorado. Ecological Applications 8: 18-26.

Crone, E. E., E.S. Menges, M.M. Ellis, T. Bell, P. Bierzychudek, J. Ehrlén, T.N. Kaye, T. M. Knight, P. Lesica, W.F. Morris, G. Oostermeijer, P.F. Quintana-Ascencio, A. Stanley, T. Ticktin, T. Valverde, and J.L. Williams. 2011. How do plant ecologists use matrix population models? Ecology Letters 14: 1–8.

Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128: 231-240.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

Elton, C. 1942. Voles, mice and lemmings: Problems in population dynamics. Clarendon Press, Oxford.

Flageole, S. and R. Leclair. 1992. Demography of a salamander (*Ambystoma maculatum)* population by skeletochronology. Canadian Journal of Zoology 70: 740-749.

Forbis, T.A. and D. F. Doak. 2004. Seedling establishment and life history trade-offs in alpine plants. American Journal of Botany 91: 1147-1153.

Freda, J. 1983. Diet of larval *Ambystoma maculatum* in New Jersey. Journal of Herpetology 17: 177-179.

Gause, F. 1934. Experimental analysis of Vito Volterra’s mathematical theory of the struggle for existence. Science 79: 16-17.

Gillespie, G. 2010. Population age structure of the spotted tree frog (*Litoria spenceri)*: insights into population declines. Wildlife Research 37: 19-26.

Govindarajulu, P., R. Altwegg, and B. R. Anholt. 2005. Matrix model investigation of invasive species control: Bullfrogs on Vancouver Island. Ecological Applications 15:2161–2170.

Hels, T. and G. Nachman. 2002. Simulating viability of a spadefoot toad *Pelobates fuscus* metapopulation in a landscape fragmented by a road. Ecography 25: 730-744.

Heppell, S.S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Irwin, J.T., J.P. Costanzo, and R.E. Lee. 1999. Terrestrial hibernation in the northern cricket frog, *Acris crepitans*. Canadian Journal of Zoology77: 1240-1246.

Karraker, N.E., J.P. Gibbs, and J. R. Vonesh. 2008. Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecological Applications 18: 724-734.

Kopp, K., M. Wachlevski, and P.C. Eterovick. 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84: 136-140.

Lehtinen, R.M. and A. A. Skinner. 2006. The Enigmatic decline of Blanchard's cricket frog (*Acris crepitans blanchardi*): A test of the habitat acidification hypothesis. Copeia: 2006: 159-167.

Livezey, R.L. 1950. The eggs of *Acris gryllus crepitans* Baird. Herpetologica 6:139–140.

Lewis, D. B. and L.A. Eby. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. Oikos, 96: 119–129.

MacLulich, D.A. 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). University of Toronto Studies Biological Series 43:1-136.

McCaffery, R.M. and B.A. Maxell. 2010. Decreased winter severity increases viability of a montane frog population. Proceedings of the National Academy of Science 107: 8644-8649.

Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119–138.

Morin, P.J. 1985. Predation intensity, prey survival and injury frequency in an amphibian predator-prey interaction. Copeia 1985: 638-644.

Morin, P.J. 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. Ecology 67: 713-720.

Mullin, S.J. and S. Klueh. 2009. Demographics of a geographically isolated population of a threatened salamander (Caudata: Ambystomatidae) in central Illinois. Herpetological Conservation and Biology 4: 261-269.

Neil, W. T. 1948. Hibernation of amphibians and reptiles in Richmond County, Gorgial. Herpetologica 4: 107-114.

Nyman, S. 1991. Ecological aspects of syntopic larvae of *Ambystoma maculatum* and the *A. laterale-jeffersonianum* complex in two New Jersey ponds. Journal of Herpetology 25: 505-509.

Penchman, J.H., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, and J.W. Gibbs. 1991. Declining amphibian populations: The problem separating human impacts from natural fluctuations. Science 253: 892-895.

Pough, F. H., and R. E. Wilson. 1970. Natural daily temperature stress, dehydration, and acclimation in juvenile *Ambystoma maculatum* (Shaw) (Amphibia: Caudata). Physiological Zoology 43:194–205

Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A Consuegra, M.P.L. Fogden, P.N. Foster, E. La Marca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, S.R. Ron, G. A. Sanchez-Azofeifa, C.J. Still, and B.E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161-167.

Rustigian, H.L., M.V. Santelmann, and N.H. Schumaker. 2003. Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landscape Ecology 18:65-81.

Sæther, B., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Semlitsch, R.D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 619-629.

Skelly, D.K. 1992. Field evidence for a cost of behavioral antipredator response in a larval amphibian. Ecology 73: 704-708.

Skelly, D.K. 1995. A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. Ecology 76: 150-164.

Snider, A.T. and J. K. Bowler. 1992. Longevity of reptiles and amphibians in North Amercain collections. Society for the Study of Amphibians and Reptiles. 2nd ed.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786.

Trenham, P.C. and H.B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15: 1158-1168.

Van Buskirk, J. and D.C. Smith. 1991. Density-dependent population regulation in a salamander. Ecology 72: 1747-1756.

Vonesh, J.R. and O. de la Cruz. 2004. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325-333.

Wilbur, H.M. and J.E. Fauth. 1990. Experimental aquatic food webs: Interactions between two predators and two prey. The American Naturalist 135: 176-204.

Wilbur H. M. 1980. Complex life cycles. Annnual Review of Ecology and Systematics 11: 67-93.

Welborn, G.A., D.K. Skelly, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337-363.

Werner, E.E. and M.A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:1368-1382.

Wright, A.H. and A.A. Wright 1995. Handbook of Frogs and Toads of the United States and Canada 3rd ed. Comstock Publishing Associates, Ithaca NY.

Zambrano, L. E.Vega, L.G. Herrera, M.E. Prado, and V.H. Reynoso. 2007. A population matrix model and population viability analysis to predict the fate of endangered species in highly managed water systems. Animal Conservation 10: 297-303.

Table 3.1: Repeated measures ANOVA comparing overall population size between *H. versicolor* and *A. crepitans* under the presence or absence of an aquatic predator between 2009 and 2011.

Between subjects							
Source	**SS**	**Df**	**MS**	**F**	**P**		
Species	145.207	1	145.207	56.977	0.0001		
Treatment	6.198	1	6.198	2.432	0.135		
Treatment*Species	67.056	1	67.056	0.939	0.345		
Error	50.971	20	2.549				
Within Subjects							
Source	**SS**	**Df**	**MS**	**F**	**P**	**G-G**	**H-F**
Year	30.235	2	15.118	13.420	0.0001	0.0001	0.0001
Year*Species	13.913	2	6.957	6.176	0.005	0.005	0.005
Year*Treatment	1.796	2	0.898	0.797	0.458	0.452	0.458
Year*Tmt*Spps	29.731	2	14.866	0.222	0.802	0.802	0.802
Error	45.059	40	1.126				

Figure 3.1: General matrix model for *Acris crepitans,* (solid lines) and *H. versicolor,* solid lines and dashed lines, where J= juvenile stage, , A=adult stage and A2 = second year adult stage. Vital rates are represented by lower case letters where j=juvenile survivorship a=adult survivorship (a=0 for *A. crepitans* since does not live more than 1 year) a2= second year adult survivorship, and f= fecundity (clutch size*sex ratio*larval survivorship).

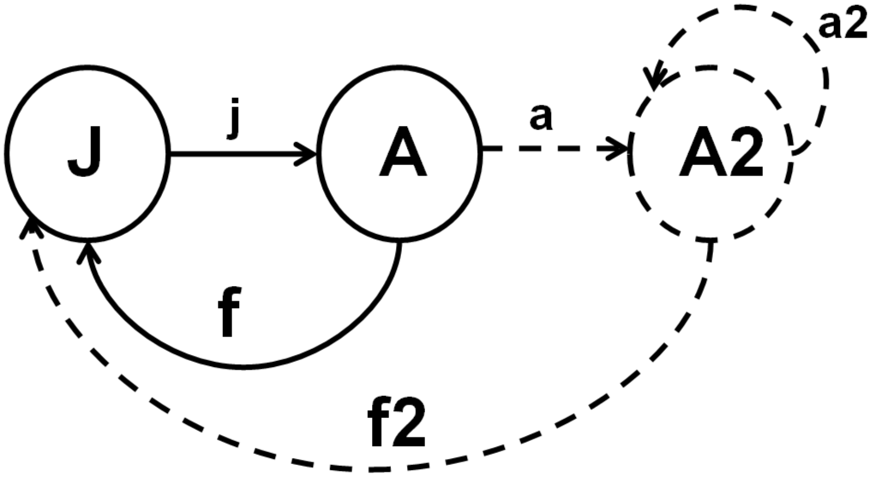

J
j
A
a
A2
a2
f
f2

Figure 3.2: Mean population size and standard deviation of *H. versicolor* and *A. crepitans* at predator present and absent ponds from 2009 to 2011.

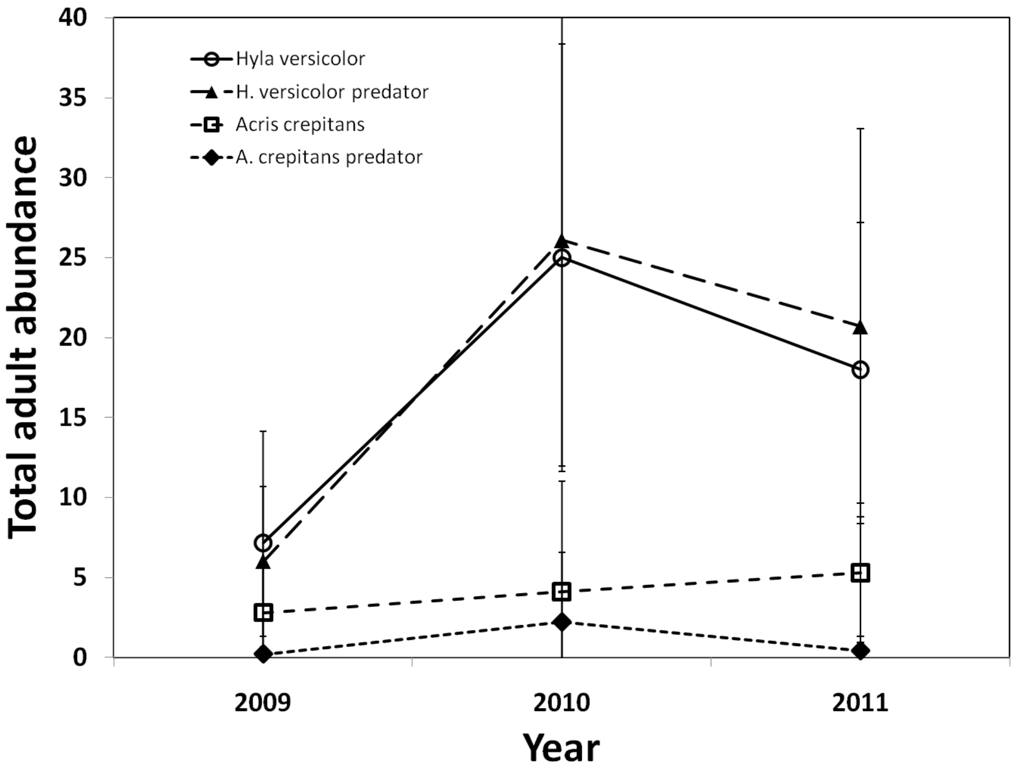

Total adult abundance
0
5
10
15
20
25
30
35
40
Hyla versicolor
H. versicolor predator
Acris crepitans
A. crepitans predator
2009
2010
2011
Year

Figure 3.3: The projected population growth rate of *H. versicolor* and *A. crepitans* in predator present and absent ponds from matrix population models.

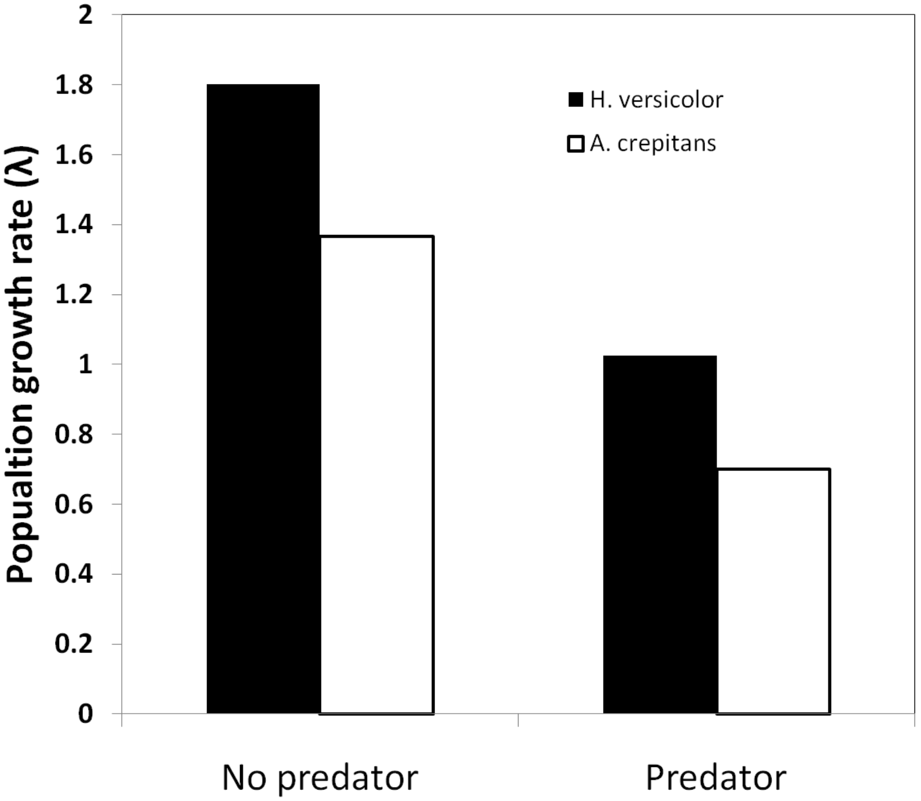
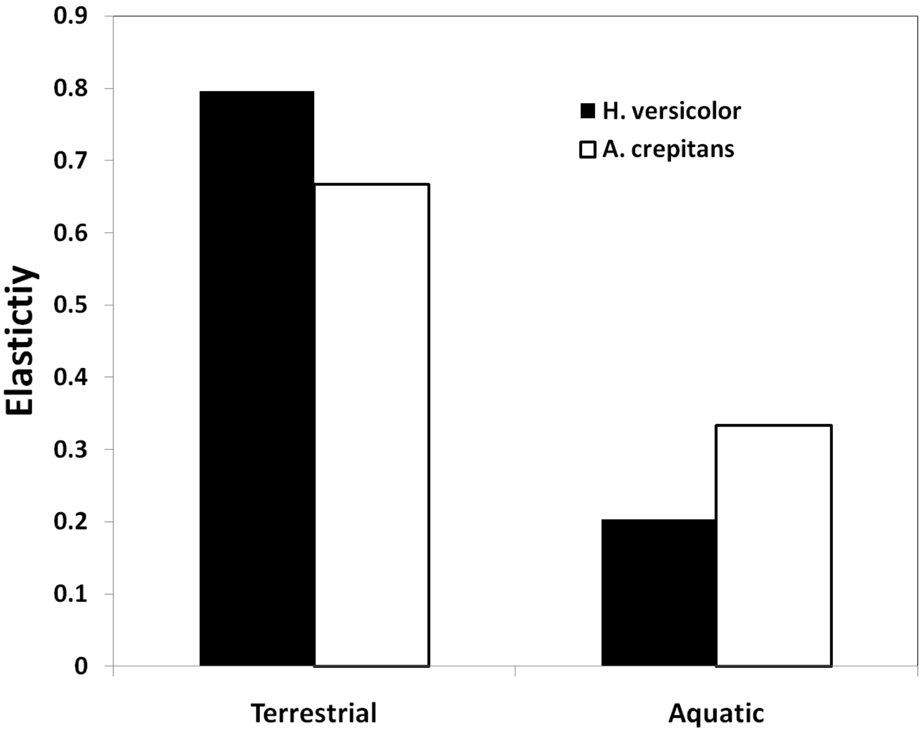

Popualtion growth rate (λ)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
■ H. versicolor
□ A. crepitans
No predator
Predator

Figure 3.4: Elasticity of the population growth rate to perturbations in vital rates associated with the aquatic (egg and larval survivorship which is incorporated into the f term) or terrestrial habitat (j and a from Figure 1 and clutch size which is incorporated in the f term).


0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Elastictiy
■ H. versicolor
☐ A. crepitans
Terrestrial
Aquatic

Chapter 4

Aquatic habitat availability influences oviposition in marginal habitats by the spotted salamander (*Ambystoma maculatum)*

Abstract

Many amphibians choose habitats in which to lay their eggs based on the characteristics of the aquatic habitat. For example, the presence of predators or suboptimal abiotic characteristics has been shown in numerous species to influence where a female will deposit her eggs. Although less studied, the characteristics of the landscape surrounding breeding ponds can also influence the oviposition site selection of breeding females. In this study, I examined the oviposition site-selection of a long-lived salamander, *Ambystoma maculatum,* into marginal breeding habitats: those that are highly ephemeral and thus likely to dry out before larvae are able to metamorphose. I specifically tested the null hypothesis that the oviposition of *A. maculatum* in marginal habitats would be proportional across landscape contexts relative to two alternatives: (1) females may increase their use of marginal habitats in landscapes where aquatic habitat is scarce and intraspecific competition in the few breeding ponds is intense, or (2) females may become more philopatric when aquatic habitat is limited and decrease their use of marginal habitats. I surveyed 19 marginal habitats in landscapes of varying contexts, and found evidence for the hypothesis that *A. maculatum* oviposited more in marginal aquatic habitats when their preferred breeding habitat was scarce. This study highlights the importance of knowing both the landscape context and life-history strategy of the species in question when understanding the context of oviposition habitat selection.

Introduction

Many species have a complex life cycle in which they use one distinct habitat for larval growth and development and a second habitat for adult dispersal and reproduction (Wilbur 1980). For these species, oviposition site selection by females is critical for the success of offspring (Resetarits and Wilbur 1989). For example, most of these species are unable to disperse long distances in the larval stage, if at all, such that oviposition site selection shapes the spatial structure of populations and can be critical to overall population dynamics of the species (Pearman and Wilbur 1990). Additionally, oviposition site selection by females can influence a species' interactions (e.g., competition, predation) in the community in which they reside (Morris 2003). Consequently, selection for the ability of females to discriminate between high and low quality habitats for oviposition is strong (Clausnitzer 1992, Bjorkman et al. 1997, Edgerley et al. 1998, Resetarits 1996).

Among amphibians, several studies have shown that females can discriminate between oviposition sites of high and low quality reflecting both biotic and abiotic factors (Figel and Semlitsch 1995, Reich and Downes 2003, Blaustein et al. 2004). For example, presence of predators, conspecific individuals, and parasites can deter female oviposition (Resetarits and Wilbur 1989, Kats and Sih 1992, Laurila and Aho 1997, Kiesecker and Skelly 2000), and amphibians tend to oviposit more frequently in ponds with shorter hydroperiods, warmer water temperatures, and specific soil compositions (Seal 1982, Reich and Downs 2003). While there have been numerous studies on amphibian oviposition site selection, they have focused either on the factors of the aquatic habitats (e.g., Resetarits and Wilbur 1989, Hopey and Petranka 1994, Kiesecker and Skelly 2000, Rudolf and Rodel 2005), or on the immediate surrounding terrestrial habitat (Hocking and Semlitsch 2007), and have neglected the broader landscape context in which amphibian populations occur (but see Segev et al. 2011).

Long-lived species with complex life-cycles, including many amphibian species, may rely critically on the ratios of available habitats (aquatic to terrestrial) in making their oviposition habitat selection decisions. For example, I have shown that densities of the long-lived salamander, *Ambystoma maculatum*, at breeding ponds depends critically on the landscape context in which they live; their densities are higher in areas with fewer ponds (Burgett, Chapter 2) and this likely occurs because their populations are less sensitive to aquatic parameters relative to terrestrial parameters (Burgett Chapter 1).

In this study, I examined whether oviposition site selection of female *A. maculatum* in marginal aquatic habitats (non-ideal breeding habitats that are likely to dry before development completion) was influenced by landscape context (e.g., the ratios of aquatic to terrestrial habitat). If female *A. maculatum* use marginal aquatic habitats in similar proportions regardless of the habitat context (e.g.: if they are unable to distinguish between high and low quality habitats or are not making oviposition site choices) I would predict the null hypothesis that oviposition in marginal habitats is proportional to that in preferred habitats as the abundance of preferred aquatic habitats across the landscape changes (dashed line in Figure 4.1). If, however, *A. maculatum* oviposition behavior varies in response to habitat context, one of two alternative hypotheses are possible. First, the high densities of conspecifics found in preferred aquatic habitats within landscapes where aquatic habitat is scarce (Burgett Chapter 2) may deter female *A. maculatum* from ovipositing in those habitats (Rosenzweig 1991, Egan and Paton 2004). This could drive females to oviposit more in marginal habitats when the landscape has lower abundance of aquatic habitat (HA_1 in Figure 4.1; dotted line). Alternatively, amphibian breeding and migrations to breeding habitats can change depending on various environmental factors, specifically climate variables during a given season (reviewed in Semlitsch 2008). Therefore, *A. maculatum* females could respond to the decrease in aquatic habitat abundance by either not breeding in a given season or by minimizing risk associated with finding alternative breeding sites, and ovipositing primarily in the limited preferred breeding habitat available (Gamble et al. 2007) (HA_2 in Figure 4.1; dot-dash line). In this study, I tested these hypotheses using surveys of marginal aquatic habitats and the abundance of *A. maculatum* egg masses in reference to the overall landscape structure of habitats throughout eastern Missouri.

Methods

Study system

The availability of aquatic habitats for breeding amphibians can be extremely variable across landscapes (Semlitsch 2002) and ranges from ephemeral wetlands, fishless ponds, streams, lakes and rivers all of which vary in their spatial distribution within landscapes. In particular, Missouri is rather limited in natural ponds and wetlands, and most current amphibian aquatic habitat was man-made to serve as either “wildlife watering holes” (Missouri Department of Conservation “Woodland Resource Guide”), agricultural ponds, or stocked fishing ponds (Perry, MDC: “Missouri Pond Handbook”). The juxtaposition of these aquatic habitats across the landscape is also extremely variable with some areas containing high densities of aquatic habitat, and other areas containing few ponds that are widely spaced. This variability in aquatic habitat distribution provided us with an opportunity to examine how landscape variation in aquatic habitat availability may influence the oviposition site selection of *A. maculatum*.

Ambystoma maculatum spend approximately four months as larvae in fishless aquatic habitats before they metamorphose into the terrestrial habitat as juveniles (Flageole and Leclair 1992). Like many other *Ambystoma,* this species is considered philopatric, returning to natal ponds each spring to breed (Phillips 1989, Patrick et al. 2008). They preferentially oviposit in permanent, semi-permanent, and ephemeral aquatic habitats (Welborn et al. 1996, Johnson 2005), and avoid ovipositing in ponds with abundant predators or high densities of conspecifics (Kats and Sih 1992). In this study, I classified preferred breeding habitat for *A. maculatum* as fishless ponds, with varying hydroperiods, but which held water long enough for larvae to complete their development (e.g., at least until mid-June in most years). Despite their philopatry and oviposition site selection abilities, *A. maculatum* egg masses are sometimes observed in marginal aquatic habitats such as tire ruts, roadside ditches, and fishponds (Burgett and Chase, pers. obvs). These marginal habitats are typically smaller than $15m^2$, very shallow, and hold water for less than 30 d at a time; thus it is unlikely that they would not support the completion of the larval stage of *A. maculatum* in most years.

Site selection and data collection

I used a database of existing ponds located within private and public lands in Missouri to look for natural areas that had a range in aquatic habitat availability and established *A. maculatum* populations, allowing me to narrow the search to seven areas. Each natural area had established breeding populations of *A. maculatum* in preferred aquatic habitats (fishless semi-permanent to permanent ponds), had marginal aquatic habitats (aquatic habitats with a hydroperiod of less than 30 days) present in early spring, and had variable numbers of permanent and/or semi-permanent ponds, so that the regions varied in their overall landscape context.

In the first week of March 2009 and 2010, I visited each area and extensively searched for any marginal ephemeral habitats such as puddles, roadside ditches, tire ruts, and holes underneath treefalls. However, given the area of most of these natural areas (mean size: 996 hectares), I was unable to exhaustively search each landscape for all marginal habitats present. Instead, I focused searches along hiking trails and roads, as well as the area surrounding breeding ponds to identify any potential marginal habitats that may have been used for amphibian oviposition.

For each marginal habitat, I quantified the number of *A. maculatum* egg masses visually (Crouch and Paton 2000) and the area of the marginal habitat. I used Google Earth and extensive ground truthing to find and measure the area of all preferred aquatic habitats within a 500m radius of each marginal habitat. For each marginal habitat, I calculated the average density of *A. maculatum* egg masses (number of egg masses/m^2) and the area of preferred habitat within a 500m radius. I averaged these values to have one estimate of each for each natural area. For each preferred aquatic habitat, I calculated the area of all other preferred aquatic habitats within a 500m radius. Burgett (Chapter 2) contains data on the density of *A. maculatum* egg masses in each preferred aquatic habitat. For each natural area, I averaged across these preferred habitats to obtain one estimate of the area of preferred aquatic habitat within a 500m radius and one estimate of egg mass density. The use of a 500m radius to calculate area of surrounding preferred habitat around each focal habitat is better than using a single estimate for each natural area at a broader spatial scale because this approach more accurately detects the abundance of aquatic habitat within a site that *A. maculatum* females are likely able to perceive given their dispersal abilities.

To test the null hypothesis that *A. maculatum* egg mass density in marginal aquatic habitats is proportional to *A. maculatum* egg mass density in preferred aquatic habitats, I used an ANCOVA to detect a difference in the slopes between marginal and preferred aquatic habitat egg mass density (square root transformed to meet assumptions of normality) over the range in aquatic habitat abundances (Systat, Version 11).

Results

I identified 19 marginal aquatic habitats between 2009 and 2010 that were filled with water during the time of female *A. maculatum* oviposition. Overall, I observed 95 *A. maculatum* egg masses that were laid in marginal aquatic habitats. All of the marginal aquatic habitats dried prior to the successful completion of the larval stage of *A. maculatum* (by mid-June) in both years.

Marginal aquatic habitats were embedded within a wide range of landscape contexts, including several that had no other nearby aquatic habitats and others with as many as 11 ponds with breeding populations of *A. maculatum* within a 500m radius. I found that as the amount of aquatic habitat in an area decreased, the density of *A. maculatum* egg masses in marginal aquatic habitats increased (Figure 4.2, Linear regression: R^2= 0.668, P=0.025, F= 10.045), but did so differently from the relationship expected from *A. maculatum* density in preferred aquatic habitats (Figure 4.2: ANCOVA: df=1, P=0.046, F=4.880).

Discussion:

Several studies have shown that female amphibians can discriminate between oviposition sites of high and low quality due to biotic factors such as predators, conspecifics, and parasites (Resetarits and Wilbur 1989, Kats and Sih 1992, Laurila and Aho 1997, Kiesecker and Skelly 2000) and abiotic factors such as hydoperiod, water chemistry, and temperature (Seal 1982, Reich and Downs 2003, Segev 2011). However, thus far, studies have only focused on factors of the aquatic habitat that influence female oviposition choice, neglecting the broader landscape context in which amphibian populations occur. In this study, I examined how the landscape context might affect female oviposition into marginal aquatic habitats, finding that the landscape surrounding marginal aquatic habitats influenced the rate at which *A. maculatum* chose low quality marginal habitats. This supported my first alternative hypothesis (Fig. 1 HA_1) that *A. maculatum* use of marginal breeding habitats increased as the density of preferred habitats decreased.

One possible reason for the observed increase in marginal habitat use when aquatic habitat is scarce would be if female *A. maculatum* detected the increased density of conspecifics in isolated breeding ponds, and chose to oviposit in marginal aquatic habitats to increase the chance of their offspring's survival (Rowe and Dunson 1995, Rudolf and Rodel 2005). Landscapes with numerous aquatic breeding habitats, on the other hand, had lower conspecific densities in breeding ponds, which potentially minimized the relative benefits an individual might gain by using marginal habitats where the chances of survival are risky, but possible in particularly wet years.

Ambystoma maculatum has an average life span of approximately 25 years (Flageole and Leclair 1992), and the population dynamics of such long-lived species are considerably less sensitive to perturbations in the aquatic relative to the terrestrial habitat (Burgett, Chapter 1). Therefore, the complete loss of fecundity within a given breeding season might not affect the overall population size of *A. maculatum* (Burgett Chapter 1) in an area.

Interestingly, some marginal aquatic habitats were located more than 500m from any existing preferred breeding habitats for *A. maculatum*, indicating that females either travel extreme distances to oviposit in marginal habitats, or are philopatric to these marginal habitats. This indicates the possibility that the *A. maculatum* may form persistent populations that use only marginal habitats for breeding. The occasional wet year, in which water could remain in marginal habitats long enough for *A. maculatum* larvae to successfully metamorphose, could be enough to maintain populations where preferred aquatic habitats is non-existent.

Other amphibian species may respond differently to the landscape context depending on their life history strategy and in particular, their longevity. Several other amphibian species, including spring peepers (*Psuedacris crucifer),* chorus frogs (*P. triseriata),* leopard frogs (*Rana sphenocephala),* American toads (*Bufo americanus)* and grey tree frogs *(Hyla versicolor)* oviposited in the marginal aquatic habitats within this study. Short-lived amphibian species have limited opportunities for reproduction and depend more critically on larval survivorship in aquatic habitats (Burgett Chapter 1). As such, their oviposition into marginal habitats would likely have greater repercussions for their population dynamics than for longer-lived species (Burgett Chapter 1).

Although oviposition into marginal aquatic habitats might not have significant effects on the population dynamics of *A. maculatum*, larval *A. maculatum* can significantly alter the dynamics of prey communities in those habitats (Freda 1983, Nyman 1991). Ephemeral pools serve as essential habitats for many invertebrates (Wellborn et al. 1996), and are often used as refugia for prey species to escape predation in more permanent ponds (Jefferies and Lawton 1985). These habitats also house a unique suite of habitat specialists and are of particular conservation concern in many areas (Colburn 2004). Thus, in landscapes where preferred aquatic habitats for *A. maculatum* are limited, ephemeral pond specialists may be particularly vulnerable to predation due to the increased use of these ephemeral habitats by *A. maculatum*.

In conclusion, I have shown that the landscape in which an amphibian population resides can influence the oviposition site-selection by females. Specifically, a long-lived amphibian increases its use of marginal habitats when aquatic breeding habitats are scarce. This study is one of the first to demonstrate how landscape context (the amount of aquatic habitat in a landscape) influences the oviposition site selection of a species (see also Segev 2011). As anthropogenic processes change the availability of aquatic habitats across a landscape (such as wetland draining), female oviposition decisions based on the amount of breeding habitat in an area may lead to not only population level effects for amphibian species, but consequences for both the aquatic and terrestrial communities in which they reside.

Literature Cited

Bjorkman, C., S. Larsson, and R. Bommarco. 1997. Oviposition preferences in pine sawflies: a trade-off between larval growth and defense against natural enemies. Oikos 79:45–52.

Blaustein, L., M. Kiflawi, A. Eitam, M. Mangel, and J.E. Cohen, 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. Oecologia 138:300–305.

Clausnitzer, V. 2002. Reproductive behaviour and ecology in the dendrolimnetic Hadrothemis scabrifrons (Odonata: Libellulidae). International Journal of Odonatology 5:15–28.

Colburn, E.A. 2004. Vernal pools: Natural history and conservation. McDonald and Woodward Publishing Company. Blacksburg, Virginia.

Crouch, W.B. and P.W.C. Paton. 2000. Using egg-mass counts to monitor wood frog populations. Wildlife Society Bulletin 28:895–901.

Edgerly, J.S., M. McFarland , P. Morgan, and T. Livdahl. 1998. A seasonal shift in egg-laying behaviour in response to cues of future competition in a treehole mosquito. Journal of Animal Ecology 67:805–818.

Egan, R.S. and P.W.C. Paton. 2004. Within-pond parameters affecting oviposition by wood frogs and spotted salamanders. Wetlands 24:1-13.

Figel, C.R. and R.D. Semlitsch. 1995. Experimental determination of oviposition site selection in the marbled salamander, *Ambystoma opacum*. Journal of Herpetology 29:452–454.

Flageole, S. and R. Leclair. 1992. Demography of a salamander (*Ambystoma maculatum)* population by skeletochronology. Canadian Journal of Zoology 70: 740-749.

Freda, J. 1983. Diet of larval *Ambystoma maculatum* in New Jersey. Journal of Herpetology 17: 177-179.

Gamble, L.R., K. McGarigal, and B.W. Compton. 2007. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. Biological Conservation: 139: 247-257.

Hocking, D.J. and R.D. Semlitsch. 2007. Effects of timber harvest on breeding-site selection by gray treefrogs (*Hyla versicolor*). Biological Convservation 138: 506-513.

Hopey, M.E. and J.W. Petranka. 1994. Restriction of wood frogs to fish-free habitats: how important is adult choice. Copeia 1994:1023-1025.

Jefferies, M.J. and J.H. Lawton. 1985. Predator-prey ratios in communities of freshwater invertebrates: the role of enemy free space. Freshwater Biology 15:105-112.

Johnson, T.R. 2005. The amphibians and reptiles of Missouri. Missouri Department of Conservation, Jefferson City, MO.

Kats, L.B. and A. Sih. 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). Copeia 1992:468-473.

Kiesecker, J. M. and D. K. Skelly. 2000. Choice of oviposition site by grey treefrogs: The role of potential parasitic infection. Ecology 81:2939–2943.

Laurila, A. and T. Aho. 1997. Do female common frogs choose their breeding habitat to avoid predation on tadpoles. Oikos 78:585-591.

Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.

Nyman, S. 1991. Ecological aspects of syntopic larvae of *Ambystoma maculatum* and the *A. laterale-jeffersonianum* complex in two New Jersey ponds. Journal of Herpetology 25: 505-509.

Patrick, D.A., A.J.K Calhoun, and M.L. Hunter. 2008. The importance of understanding spatial population structure when evaluating the effects of silviculture on spotted salamanders (*Ambystoma maculatum*). Biological Conservation 141: 807-814.

Pearman, P.B. and H.M. Wilbur 1990. Changes in population dynamics resulting from oviposition in a subdivided habitat. The American Naturalist 135:706–723.

Phillips, C. A. 1989. Population structure, breeding pond fidelity and phylogeography in the spotted salamander, *Ambystoma maculatum*. PhD. Washington University, St. Louis.

Reich, P. and B.J. Downes. 2003. Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. Oecologia 136:465–475.

Resetarits, W.J. 1996. Oviposition site choice and life history evolution. American Zoologist 36: 205-215.

Resetarits, W.J. and H.M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis:* role of predators and competitors. Ecology 70: 220-228.

Rosenzweig, M.L. 1991. Habitat selection and population interactions: the search for mechanism. The American Naturalist 137:5-28.

Rowe, C.L. and W.A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of Central Pennsylvania, USA. Oecologia 102:397-403.

Rudolf, V.H. and M.O. Rodel. 2005. Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues. Oecologia 142: 316-325.

Seal, D.B. 1982. Physical factors influencing oviposition by the wood frog, *Rana sylvatica*, in Pennsylvania. Copeia 1982:627-635.

Segev, O., M. Mangel, N. Wolf, A. Sadeh, A. Kershenbacbaum, and L. Blaustein. 2011. Spatiotemporal reproductive strategies in the fire salamander: a model and empirical test. Behavioral Ecology 22: 670-678.

Semlitsch, R. D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology, 16: 619–629.

Semlitsch, R.D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. The Journal of Wildlife Management 72: 260–267.

Welborn, G.A., D.K. Skelly, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337-363.

Wilbur, H.M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11: 67-93.

Figure 4.1: Conceptual figure outlining the relationship between the abundance of aquatic habitat in a landscape (m^2) and the density of *A. maculatum* egg masses. The actual relationship between density of *A. maculatum* egg masses in preferred aquatic habitats decreases as the abundance of aquatic habitat within a landscape increases (Burgett, Chapter 2, solid line). The three other lines are possible relationships between the density of *A. maculatum* egg masses in marginal habitats and the abundance of aquatic habitat within a landscape: (1) The null hypothesis predicts that the abundance of preferred breeding habitat in a landscape will not change the use of marginal aquatic habitats by *A. maculatum* for oviposition (the relationship will be proportionate to their use of preferred aquatic habitat). (2) HA_1 shows the alternative hypothesis that *A. maculatum* may use marginal habitats more than would be expected when preferred aquatic habitat is scarce. (3) HA_2 outlines the expected result if *A. maculatum* use marginal habitats less than expected when preferred aquatic habitat is scarce.

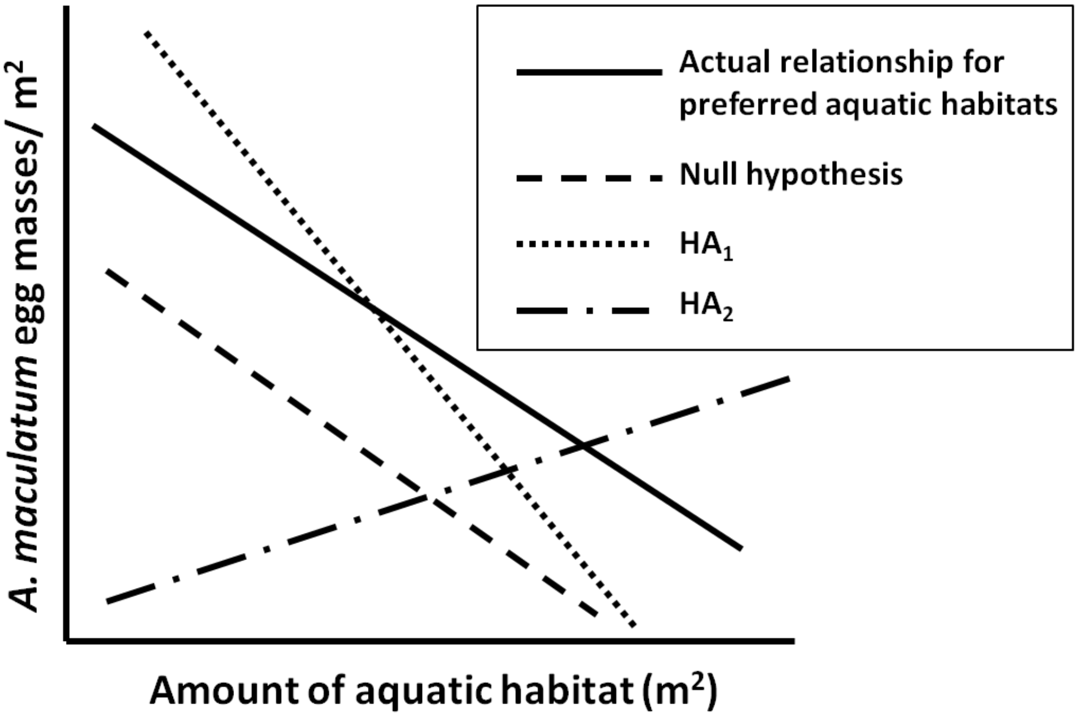
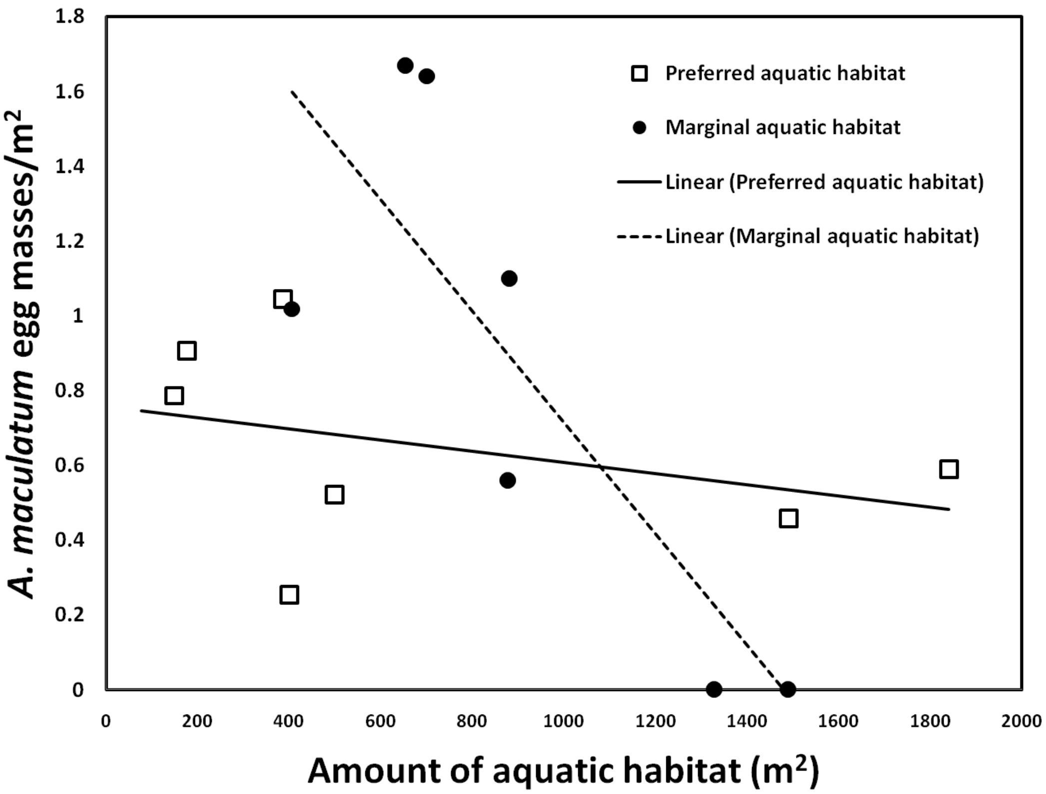

A. maculatum egg masses/ m^2
Actual relationship for preferred aquatic habitats
Null hypothesis
HA_1
HA_2
Amount of aquatic habitat (m^2)

Figure 4.2: Effects of landscape context (amount of aquatic habitat within a 500m radius of focal marginal or preferred habitat) on the abundance of *Ambystoma maculatum* egg masses/m^2 (square root transformed) in marginal and preferred habitats.


A. maculatum egg masses/m²
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Amount of aquatic habitat (m²)
□ Preferred aquatic habitat
● Marginal aquatic habitat
Linear (Preferred aquatic habitat)
Linear (Marginal aquatic habitat)

Dissertation Conclusions

Conclusions:

The overall goal of this research was to determine how landscape characteristics interact with the longevity of amphibian species to influence their population and community dynamics. I combined a meta-analytical and simulation modeling approach with both observational and manipulative empirical experiments on a long-lived amphibian, *Ambystoma maculatum* and its prey to demonstrate that the ratio of aquatic to terrestrial habitats in a landscape alters the abundance and oviposition site selection of *A. maculatum*, decreases prey species richness, and can change the population dynamics of two anuran prey species.

Through meta-analysis and simulation of 27 amphibian species, I first established that as the longevity of a species increases, the population growth rate becomes less sensitive to perturbations in the aquatic habitat and more sensitive to perturbations in the terrestrial habitat. This pattern, although previously demonstrated in other taxa, had yet to be established in species with complex life cycles and where density-dependence in the larval stage is common. Understanding the relationship between amphibian longevity and habitat elasticity provides a useful tool for conservation planning of declining or threatened amphibian species where data is often limited and timely conservation actions are critical. Given the widespread decline of amphibian species across the planet, rapid conservation actions are often required and the pattern between longevity and habitat elasticity provides a useful first step for establishing the habitat in which to focus conservation efforts.

The results of the meta-analysis in chapter one allowed me to establish hypotheses about the abundance of a long-lived salamander, *Ambystoma maculatum* in aquatic habitats that were embedded in landscapes with different proportions of aquatic and terrestrial habitats. In chapter two, I present the results from a large-scale survey of *A. maculatum* and the aquatic community at 39 ponds throughout Eastern Missouri. I found that as the aquatic to terrestrial ratio (ATR) of a habitat increased (more aquatic habitats available across the landscape), the density of *A. maculatum* in individual ponds decreased.. This was likely because decreases in aquatic habitat within a landscape have a relatively small effect on *A. maculatum* population dynamics, and thus the young individuals in the population were condensed into the limited aquatic habitats available, increasing their localized density. Furthermore, because larval *A. maculatum* are strong predators, prey species richness was decreased in isolated ponds (those with low ATR). Metacommunity theory predicts that reductions in species richness in isolated habitats results both due to decreased dispersal abilities as well as reductions in predator densities. However, this chapter highlights that in aquatic habitats where many species have complex life cycles, the ratio between aquatic and terrestrial habitats can strongly influence the community dynamics.

Two of the prey species that showed reductions in abundance due to *A. maculatum* predation in isolated ponds in chapter two also have complex life cycles. *Hyla versicolor* is a moderately long-lived anuran while *Acris crepitans* lives on average for only one year. I predicted that reduced larval survival in the aquatic habitat due to *A. maculatum* predation would have a larger effect on the population dynamics of the shorter-lived *A. crepitans* than on *H. versicolor.* In chapter 3, I found that although *A. maculatum* larvae preferentially consumed *H. versicolor, A. crepitans* was unable to establish populations at ponds with predatory *A. maculatum*, whereas despite large reductions in larval survival, *H. versicolor* was able to maintain increasing populations both in the presence and absence of larval *A. maculatum.*

In chapter two and three, I showed the effects of the aquatic: terrestrial ratio (ATR) on the community interactions between *A. maculatum* and its prey within aquatic habitats. However, the ATR of a landscape also influences the ability of female *A. maculatum* to discern between oviposition site choices, which can have implications for prey species that specialize on ephemeral habitats to avoid predation. Several studies on amphibians have shown that females use both biotic and abiotic cues to select the habitat for their offspring's survival. In chapter four, I demonstrate that the ATR of a landscape also influenced female *A. maculatum* oviposition site selection. When preferred aquatic habitats were scarce, *A. maculatum* oviposited more frequently in marginal aquatic habitats.

In all, this dissertation draws attention to previously ignored aspects of both metacommunity dynamics and amphibian population declines; that of landscape context and the ATR. The population dynamics of organisms with ontogenetic habitat shifts, such as amphibians, depend on the availability and ratio of both habitat types within a landscape. While a majority of studies of amphibians have focused primarily on their interactions in their aquatic (larval) habitats, owing primarily to their ease of study, my work highlights that the insights gained from this work can be limited, particularly for long-lived species that utilize terrestrial habitats for a majority of their lives. The rapid decline of amphibians worldwide highlights the need for consideration of demography information across the entire life cycle of the organism and consideration of the overall landscape context in which populations are embedded in order to curb or prevent future declines.

In addition to the implications for studying amphibian populations, this research has implications for other taxa and for metacommunity theory. Organisms with stage-structured life cycles and those that move long distances or use different ecosystem types during their life cycle will require studies similar to this one in order to fully understand how changes to the environment will affect population dynamics. This is important since ecological research typically is not conducted across the entire life cycle and at landscape scales for these organisms. Metacommunity theory predicts that isolated habitats should contain fewer predators and weaker tropic interactions, since predators tend to have higher extinction rates than prey species owing to their larger body sizes, higher metabolic needs and smaller population sizes. This thesis shows the opposite result. Predator densities were highest in isolated aquatic habitats because population dynamics of these long-lived predators are driven by demography in the terrestrial habitat, and isolated aquatic habitats have stronger tropic interactions. The disconnect between this thesis and the existing theory results from the simple population dynamics assumed in the theory. A broader understanding of how habitat isolation will influence trophic interactions requires expanding metacommunity theory to include stage-structured population dynamics of both predators and prey.