

ABSTRACT

FIELDS, WILLIAM ROBERT. Ecology and Conservation of Rare Amphibians. (Under the direction of Nicholas M. Haddad).

Understanding the distribution and status of populations of rare amphibians is a critical task in understanding their ecology and conservation needs. Rare species are impacted by various global environmental changes that change the distribution of suitable habitats, affect demographic processes in local populations, and alter the ability of individuals to disperse from one population to another. To better understand how amphibian species respond to global changes, I studied how regional variation in breeding habitat, climate change, and the use of dispersal habitat affects rare amphibians. I examined the effects of these factors on three rare species of amphibians in the southeastern coastal plain of the U.S.

To assess the effects of regional variation in breeding habitat on rare amphibians, I used locality data from breeding sites of the US federally threatened flatwoods salamander (*Ambystoma cingulatum*) in Georgia to build logistic regression models to predict both presence and absence of this species using data on wetland habitat and landscape structure. I then tested these predictive models with data from additional breeding sites in Florida. Models constructed with data from localities in Georgia failed to discriminate among suitable and unsuitable breeding sites from Florida. Hierarchical clustering revealed that sites in Georgia were more similar to one another than they were to sites in Florida. I concluded that accurate assessment of suitable habitat across a species range must consider regional variation in environmental conditions.

To assess the effects of climate change on the ecology and conservation of rare amphibians, I incorporated downscaled climate projection data into population models for the

tiger salamander (*Ambystoma tigrinum*). I constructed population models with field data on adult survival, and I used climate data with predictive models of wetland hydrology to constrain larval recruitment. Analysis of a deterministic population model suggested that adult survival was more critical to population growth than larval recruitment. However, stochastic population models suggested that high carbon emissions scenarios produced a greater frequency of dry wetland conditions, and this increased the importance of larval recruitment to population growth. My results demonstrate that accounting for interannual variability in future climate scenarios is critical for assessing the response of populations to climate change and prioritizing conservation actions.

To study the effects of habitat loss and fragmentation on the movement of amphibians, I used data from field experiments to predict dispersal routes of ornate chorus frogs (*Pseudacris ornata*) using circuit models. I then used nonlinear regression to determine whether isolation from breeding habitat or dispersal habitat quality was more strongly associated with the likelihood of a location being used by dispersing frogs. I found that dispersal habitat quality predicted the use of areas by dispersing frogs better than wetland isolation, but the spatial context of the landscape was most important in determining dispersal paths.

Finally, I examined the effects of larval conditions on the dispersal behavior of juvenile ornate chorus frogs by conducting field experiments with frogs reared at high and low densities. I found that frogs reared at low densities moved more rapidly through poor quality dispersal habitat. This suggests that understanding larval conditions could be as important as mapping dispersal habitat for assessing landscape connectivity.

In sum, my studies demonstrate that climate change and habitat loss and fragmentation can affect the dynamics of amphibian populations and provide important lessons for how to conserve populations of declining species in the face of global changes in the environment.

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Ecology and Conservation of Rare Amphibians

by
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DEDICATION

To Catherine and Madeline: may your curiosities lead you in interesting directions.

BIOGRAPHY

I was born in 1978 in Indianapolis, IN, to Richard and Cynthia Fields. I graduated from North Central High School in 1997, and enrolled at Ohio University the following fall. After a year at Ohio University, I transferred to Iowa State University, where I completed my B.S. in Animal Ecology in 2001. I then worked with The Nature Conservancy in Texas, the University of California Cooperative Extension, and the Florida Fish and Wildlife Conservation Commission prior to enrolling in graduate school at North Carolina State University in 2005.

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CHAPTER 1: ECOLOGY AND CONSERVATION OF AMPHIBIANS IN THE FACE OF GLOBAL CHANGE

Introduction

The loss of biological diversity is one of the most urgent problems facing ecologists and conservation biologists today (Butchart et al. 2010). Among all the different taxa that have undergone declines in recent years, amphibians are especially notable because the current rate of amphibian extinctions is several orders of magnitude greater than what has been documented from the fossil record (McCallum 2007, Wake and Vredenburg 2008). Not only have amphibian species been lost to typical threats like habitat loss and fragmentation, but there are also amphibian species that are declining for enigmatic reasons in places where the most common factors associated with species extinctions appear to be absent (Pechmann et al. 1991, Beebee and Griffiths 2005, Wake and Vredenburg 2008). The enigmatic nature of many declines in amphibian populations highlights our limited understanding of how global environmental changes affect the population dynamics of species. Although habitat loss and fragmentation is a putative factor that plays a role in many declines,

My dissertation research focuses on three areas that improve our knowledge of how rare species like amphibians respond to global changes in the environment. First, I examine the limits of the application of knowledge about habitat associations of rare amphibians across their range. Second, I examine how climate change may affect the importance of different life stages in limiting amphibian population growth. Third, I examine the potential for restoration to improve connectivity. Finally, I consider how variation in larval conditions of amphibians may affect dispersal behavior. Amphibians

present an effective model system for addressing the effects of global change because of how they use spatially disjunct habitats that are influenced directly by variation in climate. In combination, my dissertation addresses a range of threats, and in doing so provides a number of lessons from studying the ecology and conservation of amphibians that are broadly relevant to understanding the effects of global change on the loss of biodiversity.

Assessing Amphibian Distributions

My dissertation opens with a chapter examining the utility of habitat models for a rare salamander species (Chapter 2). This research was part of a larger project that was aimed at reducing the uncertainty associated with interpreting absence data from surveys for species that are hard to detect (Bevelhimer et al. 2008). This project used habitat models for the flatwoods salamander in conjunction with field studies that quantified the capture efficiency of different sampling methods along with modeling studies that assessed the tradeoffs between the increased costs associated with greater sampling effort and the reduced uncertainty associated with additional survey data. Habitat modeling provided a key component of the project to direct field sampling in areas that would be most suitable for a rare species and to avoid allocating survey effort to areas that did not contain suitable habitat.

Describing species distributions is a fundamental task for ecologists, who seek to describe the niche of a species, and for conservation biologists, who seek to reverse population declines of imperiled species. Some research has focused on predicting amphibian distributions at a biogeographic scale by examining the efficacy of climate

data in predicting amphibian distributions, with a goal of providing insights into how climate change may affect amphibian species (Lawler et al. 2010, Early and Sax 2011). However, such analyses are necessarily coarse in nature due the scale of the analysis, and this provides limited insights to understanding the suitability of fine-scale features in landscapes like breeding ponds that are critical in the life cycle of amphibians. Although recent statistical advances have made it possible to model detection probabilities of species while examining the relationship between the presence of a species in different habitat types, habitat modeling studies typically focus on sites within a particular landscape rather than comparing sites between landscapes (Welsh and Lind 2002, Goldberg and Waits 2009). This is done for obvious logistical reasons, but it leaves a key question unanswered: how general is our understanding of habitat associations for a species across its range? I explore this issue by examining the importance of wetland- and landscape-scale habitat features in predicting the presence of the flatwoods salamander (*Ambystoma cingulatum*) at breeding wetlands in Georgia, and testing these habitat models with data from breeding sites in Florida. Results from this study provide a cautionary tale for those who might seek to extrapolate from one study area to another, whether additional sites are located elsewhere within the range of a species or in fundamentally different types of habitats.

Assessing Population Viability

Although considerable effort is put into field surveys for rare amphibians, information on the distribution of a species is not necessarily a good indicator of its status where it occurs. Species may be present in areas because of source-sink dynamics

(Pulliam 1988), so population modeling is needed in order to provide critical insights into the relative importance of different vital rates to population growth (Biek et al. 2002). For wetland-breeding amphibians, assessing the status of species from field survey data is especially challenging. Although surveys of wetland-breeding amphibians like the tiger salamander (*Ambystoma tigrinum*) often focus on the larval aquatic stage because it is easier to sample than adults, many wetland-breeding amphibians are scarce in wetlands in many years, even when their populations are relatively stable, because wetland hydrology itself is often unsuitable for amphibian reproduction (Pechmann et al. 1991). Moreover, the successful recruitment of one year's cohort of larvae does not guarantee that these individuals will survive to reach maturity and return to breed in a wetland. If clarity about the status of wetland-breeding amphibians is to be gained, it must be done through modeling population dynamics under variable environmental conditions in order to assess the long-term viability of a species and the relative importance of different life stages to population growth.

I used data on wetland hydrology, tiger salamander demography, and future climate scenarios to assess the viability of an isolated tiger salamander population under different climate regimes (Chapter 3). This research provides novel insights into the dynamics of amphibian populations by explicitly examining two key issues related to wetland hydrology. First, I developed a predictive model of wetland hydrology based on field data that was then used to simulate wetland conditions under different climate scenarios, and, second, I accounted for year-to-year variability in wetland hydrology in simulations that modeled several decades. This research suggests that moderate to high rates of adult survival could be necessary but insufficient on its own for viable

populations of pond-breeding amphibians. More importantly, my results highlight the need to account for increasing variability in climate patterns. Recent studies demonstrate that variability is increasing as a result of climate change (Mearns et al. 2003); I show that this variability makes larval recruitment more important for amphibian population growth.

Assessing Dispersal Behavior and Landscape Connectivity

Promoting movement of individuals among different subpopulations of amphibians is ultimately desirable to maintain more robust populations, but it can be difficult to infer how isolated different subpopulations are from field surveys and population modeling alone. One approach for assessing the capacity of amphibians to move among disjunct areas of breeding habitat is to utilize least cost paths to quantify the relative difficulty of dispersing through different habitats. However, such analyses are often conducted without empirical data on movement because successful dispersal events can be infrequent or difficult to observe, and collection of detailed movement data from telemetry studies may present logistical challenges (Moody et al. 2011). It is often the case that assessments of dispersal or landscape connectivity are based on the use of data from surrogate species or expert opinion, but such studies frequently do not test the sensitivity of dispersal models to assumptions about the data that are used (Beier et al. 2008). Even in cases where movement behaviors are quantified, however, scientists frequently make the simplifying assumption that all individuals within a population behave in a similar manner when dispersing. This assumption contrasts with field studies documenting that larval conditions may affect the survival of juvenile frogs as they disperse

(Chelgren et al. 2006), and this could have consequences for their movement behavior as well. In chapter 2, I assessed landscape connectivity for rare amphibians based on rigorous, empirical data on amphibian movement behavior.

I addressed these issues in collaboration with other researchers through a combination experiments and modeling studies. Together we examined three critical assumptions that are frequently made in landscape connectivity studies: that closely related species have similar movement behavior, that species respond to variation in canopy rather than microhabitat, and that individuals within a population exhibit similar movement behavior (Chapter 4). We tested these assumptions through a series of field experiments with amphibians, and we later used these data to parameterize spatially explicit movement models (Moody et al. 2011). These experiments suggest that assumptions regarding movement behavior need to be carefully considered because they may be violated more frequently than is commonly believed. Careful modeling of dispersal and landscape connectivity needs to evaluate how robust model behavior is to having its assumptions violated. Although I made significant contributions to each of these studies that will appear in a single manuscript, I was solely responsible for experiments testing how variation within populations affected movement rates, and that is the subject of Chapter 4.

I also used data from field experiments to parameterize a circuit model of landscape connectivity for ornate chorus frogs in order to assess how strongly associated landscape connectivity was with breeding habitat, dispersal habitat, and the spatial configuration of the landscape (Chapter 3). Although many studies assess landscape connectivity, few have explicitly considered how landscape connectivity is affected by

breeding and dispersal habitat. There is often a disconnect between the value of particular parcels of land as dispersal habitat and maps depicting landscape connectivity: areas of high landscape connectivity are recognized as such without examining the degree to which connectivity results from the quality of dispersal habitat within an area. This is not a trivial consideration for those concerned with designing habitat restoration with the intent to restore landscape connectivity. Effective conservation planning should prioritize areas within a landscape with good dispersal habitat that contribute the most to landscape connectivity.

A New Perspective for Ecology and Conservation

Understanding the ecology and conservation of rare amphibians depends on having an appreciation for how the spatial and temporal variation in the environment affects these species. Although numerous factors may play a role in amphibian declines, their impact is ultimately determined by how they interact with variation in populations in space and time. My research addresses this environmental variation by considering the spatial variation in suitable habitat for rare amphibians, assessing the effects of variation in breeding conditions over time on demography, and examining assumptions related to dispersal behavior and the consequences of these assumptions for landscape connectivity. These findings have broader lessons not just for the ecology and conservation of amphibians, but for species facing threats from many different global changes in the environment. Although ecologists have long recognized the important role of habitat loss and fragmentation in the loss of biodiversity (Wilcove et al. 1998), variation in habitats over time will become an increasingly important factor in the face of climate change.

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CHAPTER 2: TESTING HABITAT MODELS FOR A RARE SALAMANDER ACROSS ITS RANGE

Abstract

Habitat models are a critical tool for the effective management of rare species, but rarity often makes modeling species distributions problematic. We explored the effects of limited data on habitat modeling with the flatwoods salamander, a federally threatened amphibian, by testing habitat models developed at the northern part of its range in Georgia with locality data from the southern part of its range in Florida. We developed logistic regression models with data on landscape scale variables and wetland vegetation to predict whether wetlands were suitable or unsuitable breeding sites for this species. We also used hierarchical clustering to examine the difference in suitable breeding sites across the range of this species. Logistic regression models that included a combination of landscape scale and wetland vegetation data did the best at predicting presence or absence of flatwoods salamanders from potential breeding sites. When tested with new data from Florida, logistic regression models developed in Georgia did not predict presence of flatwoods salamanders well, even when plant species were grouped into similar classes based upon their tolerance for wetland conditions or their growth habit. This was corroborated by the hierarchical clustering, which showed that potential breeding sites in Florida were, in general, much more similar to one another than potential breeding sites in Georgia. Although habitat models for rare species can be developed, they need to be validated empirically before being applied to new areas of a species range. While accurate predictions of the probability of a species occurring in a

site may be difficult to obtain with limited data, multivariate analyses provide a useful approach for understanding the similarity among potential habitat.

Introduction

Rare or declining species present a challenging paradox to managers: they may have critical management needs because of the status of their populations, but their rarity often leads to a lack of important ecological information to guide management decisions. This scenario becomes even more challenging when detecting a species is difficult or highly variable over time, or when a species undergoes dramatic fluctuations in population size. One such species is the federally threatened flatwoods salamander (*Ambystoma cingulatum*). The current distribution of this species is restricted primarily to areas around temporary wetlands where it breeds on a handful of public lands in Florida, Georgia, and South Carolina. Populations may skip breeding in some years due to fluctuations in hydrological conditions, and populations may be present in relatively low densities when breeding actually occurs. Habitat assessments for this species have been problematic because the species is frequently known from only a few sites in a management area. This limits sample sizes for research, and pooling data from multiple areas across the range of the species may not improve the predictive capacity of models if wetland habitats are highly variable. In response to these issues, we developed habitat models for the flatwoods salamander at the Fort Stewart Military Reservation, Georgia, based upon knowledge of the life history of this species. We then tested these models at other flatwoods salamander breeding sites in Florida and explored the variation in

wetland habitats across the range of the species to better understand the performance of our habitat models.

Predicting the suitability of sites for amphibians involves understanding habitat characteristics within or among different wetlands. Within wetlands many amphibian larvae are susceptible to predators associated with permanent water and show a preference for breeding in temporary wetlands (Wellborn et al. 1997). Moreover, a study with tree frogs found that when adult frogs were presented with a choice of artificial ponds that contained or did not contain fish, they showed a strong preference for ponds without fish (Binckley and Resitarits 2002). Since wetland plants vary in their tolerances for flooded conditions, it is possible that wetland plant species may reflect wetland hydroperiods and be used to improve predictions of where flatwoods salamanders breed. Within wetlands that have a similar hydroperiod, canopy cover may also affect the fitness of larval amphibians. Thurgate and Pechmann (2007) demonstrated that competitive interactions between amphibians may be influenced by canopy cover, and other studies have documented shifts in amphibian communities associated with canopy cover at ponds that result from effects on larval growth (Skelly et al. 2002).

Among wetlands, landscape structure may also improve our ability to predict the suitability of wetland breeding sites for amphibians. Metapopulation theory predicts that occupancy of breeding sites should be associated with proximity to other suitable habitat and the ability of individuals to move through the landscape. Amphibian populations show an increased likelihood of using breeding ponds that were in closer proximity to adjacent occupied ponds (Gulve 1994), and in some cases local habitat conditions appear to be less important in determining amphibian distributions than factors associated with

spatial population processes (Schmidt and Pellet 2005). Moreover, studies of amphibian movement indicate that some landscape features benefit amphibian populations by reducing the risk of desiccation and facilitating movement (Mazerolle 2005, Rothermel and Semlitsch 2002). Landscape structure might also affect the suitability of amphibian sites by determining the distributions of potential predators. Many larval amphibians that develop in temporary wetlands suffer reduced survivorship and growth rates in the presence of predators like fish that are associated with permanent water (Gregoire and Gunzberger 2008). However, studies of fish populations in temporary wetlands in the southeastern coastal plain have found that wetland position is more important than wetland habitat in predicting fish presence (Baber et al. 2002, Sun et al. 2001, Snodgrass et al. 1996), so wetland position within a landscape may be important in predicting the use of sites by amphibians.

In this paper we use knowledge of amphibian ecology to test competing models based on wetland and landscape habitat characteristics for predicting the presence and absence of flatwoods salamanders. We then quantify the similarity among sites from across the range of the species. While predicting the presence of a rare species is a common task, predicting sites where a species is absent may be just as important for management purposes. In addition to understanding where a species is likely to be present or absent, obtaining a broad perspective about the variation of habitat across the range of a species is important if habitat models are to be extrapolated to areas that have not been as extensively sampled. Failure to appreciate the variation in habitat across a species range could lead to inappropriate application of models to areas with different environmental conditions. Moreover, understanding the variation in potential habitats

reveals whether areas sampled for a species are representative of other sites that have yet to be surveyed (Hargrove et al. 2003). We used logistic regression to predict the presence and absence of flatwoods salamanders from breeding sites, and we used hierarchical clustering to explore the variation in habitat across the range of the species.

Methods

Study Area

We compiled locality data for the flatwoods salamander from Fort Stewart and two additional sites in Florida: the Apalachicola National Forest and St Marks National Wildlife Refuge. Fort Stewart is a 113,000-ha military installation located in the coastal plain of Georgia. It contains flatwoods salamander breeding sites in both wet flatwoods and sandhill landscapes. The Apalachicola National Forest covers over 228,000 ha in the Florida panhandle and contains flatwoods salamander breeding sites primarily in wet flatwoods and savannah landscapes. St. Marks National Wildlife Refuge includes over 27,000 ha of coastal wetlands and wet flatwoods with most of its known flatwoods salamander breeding sites occurring in depressional wetlands dominated by sawgrass.

Amphibian Data

We conducted dipnet surveys for larval flatwoods salamanders and other aquatic amphibians between January and May of each year from 2005 – 2007 at 81 wetland sites on Fort Stewart, and we only found flatwoods salamander larvae at one pond during this period (Bevelhimer et al. 2008). This site was the only location within the state of Georgia where flatwoods salamanders have been documented since a drought that lasted from 2001 – 2003. As a result of our limited occurrence data for this species, we decided

to pool data from larval surveys conducted for flatwoods salamanders between 1994 and 2007.

This resulted in the selection of 81 survey sites for our study, with 14 of these being documented flatwoods salamander breeding sites, 16 being considered unsuitable for flatwoods salamander breeding, and 51 considered as having some potential as flatwoods salamander breeding sites. We also selected 50 additional sites in the Apalachicola National Forest and St. Marks National Wildlife Refuge for the purpose of testing our habitat models developed with data from Fort Stewart. Twenty-one of these sites were known to have had flatwoods salamander breeding activity between 2002 and 2007, while the remaining 29 sites were considered to be potential flatwoods salamander breeding sites.

Presence was determined if the flatwoods salamander had been documented in a wetland site between 1994 and 2007, and absence was based upon expert opinion about wetlands being unsuitable for breeding due to the permanence of water or vegetation (personal communication, D. Stevenson). Thus, while presence and absence can be viewed as being opposite extremes in habitat suitability, they are not complements of one another: our set of wetlands included some sites that were not classified as having presence or absence of our focal species. Our research was conducted in accordance with the approval of the Oak Ridge National Laboratory's Animal Care and Use Committee.

Wetland Vegetation Surveys

Within each wetland we sampled wetland vegetation at points 8 m apart along two perpendicular transects. At each point, we estimated the percent cover of ground,

water, and herbaceous and emergent wetland plants within a 1-m radius of the point. We estimated the percent cover of shrubs and trees within a 5-m radius of each point. Plant species were identified to the lowest possible taxonomic unit, and we grouped plants according to both structural characteristics and their wetland indicator status. Plants were placed into one of the following structural groups: graminaceous vegetation emergent vegetation, submerged aquatic vegetation, ferns, shrubs, and trees. Plants were also placed into one of the following wetland indicator status categories designated by the U.S. Fish and Wildlife Service (1988): obligate, facultative wetland, facultative, and upland. Wetland indicator status reflects the likelihood that a plant occurs in a wetland and does not reflect the degree of wetness at a site.

GIS Data

We compiled spatial data on wetlands, streams, roads and land cover within 2 km of wetland survey sites into a geographic information system for the analysis. We selected a buffer of 2 km based upon maximum movement distances of congeneric salamanders and other amphibians (USFWS 1999, Smith and Green 2005). We obtained National Wetlands Inventory (NWI) Data at a scale of 1:24,000 from the USFWS. Wetlands were identified as being temporary or permanent based upon their NWI category. We calculated the distance to the nearest permanent and temporary wetland as well as the total area of permanent and temporary wetlands within the buffer for each site. Road data and stream data were also compiled at a 1:24,000 scale, and we calculated both the Euclidean distance to the nearest road or stream and the total length of roads and streams within the 2 km buffer. Road data were obtained from the Department of Public

Works at Fort Stewart and the Florida Geographic Data Library for sites in Florida, and stream data were obtained from the U.S. Geological Survey's National Hydrography Dataset. Finally, we collected National Land Cover Data from the U.S. Environmental Protection Agency for each 2 km buffer around a survey site. These data were available in a raster format with a pixel size of 30 x 30 m.

Data Analysis

We analyzed our data both to predict whether sites should be occupied by flatwoods salamanders and to quantify the variation in habitat across the range of the species. We conducted two analyses to predict presence and absence of the flatwoods salamander in wetland sites. Prior to conducting analyses, we checked variables for normality and applied appropriate transformations when necessary. We also screened the data for variables with high correlations (>0.7). To avoid problems associated with collinearity, we retained the variable with the greatest among-group variance when variables were strongly correlated (McGarigal et al. 2000).

Logistic regression was performed separately for both presence and absence of the flatwoods salamander. We used forward and backward stepwise variable selection to identify models that fit the data well, and we compared these models with *a priori* models for salamander presence. We ran stepwise selection procedures on wetland vegetation and landscape data separately. Model selection criteria were evaluated, and the parameters from the best models in each category were then combined into a new set of variables that had forward and backward stepwise regression procedures performed on it.

We then compared these models with models for presence and absence of flatwoods salamanders based upon wetland vegetation and landscape structure.

We expected that some variation in plant species across the range of the flatwoods salamander might make models from Fort Stewart perform poorly with data from Florida, so we analyzed wetland vegetation in three ways. First, we used cover estimates of different plant species in logistic regression analyses. Then we grouped cover estimates of plant species by type of vegetative structure (i.e., tree, shrub, herbaceous vegetation, emergent aquatic vegetation, submerged aquatic vegetation). Finally, we grouped cover estimates of plant species by wetland indicator status. We anticipated that grouping similar types of plant species might improve model performance when testing models with new data from other regions of the species range, for example, if different plant species in Georgia and Florida provided a similar structural component in salamander habitat. We evaluated logistic regression models in two ways after comparing model selection criteria. First, we compared the predicted probabilities of presence or absence in ponds at Fort Stewart or in both the Apalachicola NF and St Marks NWR that were known to contain or lack flatwoods salamanders. Second, we compared the predicted probability of presence or absence in ponds at Fort Stewart with an expert assessment of pond suitability.

We also used hierarchical clustering to analyze the similarity of vegetation and landscape characteristics associated with wetland sites in Florida and Georgia. For wetland vegetation, we compared dendrograms generated with complete, single, and average linkages. We standardized data prior to conducting all analyses.

Results

Logistic Regression

Two models based upon wetland vegetation predicted presence of flatwoods salamanders better than the other candidate models (Table 2.1). The model based upon wetland indicator status of plants performed slightly better than the model based upon plant species alone. Landscape data did not predict presence of flatwoods salamanders well on its own, but the addition of landscape data significantly improved the fit of models for presence in ponds. Our *a priori* model of presence being related to hatpin, beakrush, and wiregrass did not perform as well as the alternative models produced by stepwise selection procedures.

The average predicted probability of presence for known salamander breeding sites was only 0.34, but known breeding sites from Florida were predicted to have a much lower probability of occupancy by both of these models (Figure 2.1). Predicted probabilities of presence were highest in known and suitable ponds, while predicted probabilities of absence were highest in unsuitable ponds (Figure 2.2).

Hierarchical Clustering

Our cluster analysis reveals 2 general patterns in wetland vegetation. First, wetland vegetation within different management areas has a high degree of similarity, and, second, known breeding sites tend to be most similar to other suitable breeding sites rather than unsuitable breeding sites (Figure 2.3). These patterns were consistent with all of 4 of the different linkages used.

Discussion

Our results from modeling flatwoods salamander habitat at Fort Stewart corroborate prior studies that identified both landscape and wetland vegetation features associated with pond-breeding amphibians. First, we found that the presence of flatwoods salamanders was positively associated with a native iris species and the presence of facultative and obligate wetland plants. This is consistent with a previously published study that found a positive relationship between fire frequency and herbaceous vegetation, which in turn was associated with wetland use by flatwoods salamanders (Bishop and Haas 2005). We also found that increased canopy cover was strongly associated with unsuitable wetlands, and this is consistent with other studies that have found a negative association between increased canopy cover and suitability of ponds for larval amphibians (Skelly et al. 2002).

Although cover estimates of plant species are an obvious starting point for assessing habitat relationships of flatwoods salamanders, we found evidence that the tolerance of plants to flooding conditions as defined by the NWI may also be useful in describing habitat. A preliminary analysis of grouping plants by both tolerance to flooding and structural attributes was not very informative because many of the categories only contained a few species, so this analysis was not substantially different from considering species alone. Grouping of wetland plants based upon traits like structural characteristics or tolerance of flooding may be more informative than simply including plant species.

We found that landscape structure was an important predictor of habitat use in both logistic regression and discriminant function analyses. Including distance from

streams improved prediction of habitat in regression analyses. Previous research has also shown that landscape structure predicts presence of amphibians well (Van Buskirk 2005). Examining landscape pattern may be a useful starting point when habitat models are used to direct surveys and other management actions. Because the course and hydroperiods of many of the streams on the base have been largely modified due to base activities, the streams often interact with the wetlands in ways that are potentially harmful such as introducing predatory fish or reducing water quality through siltation. Although our model predictions were improved by the inclusion of landscape features, we were not able to detect specific impacts related to base activities and these features. Because most of the flatwoods salamander habitat is found in close proximity to red-cockaded woodpecker colonies, the flatwoods salamanders benefit from conservation measures intended to preserve and protect woodpecker habitat, such as controlled burning and limitations on military training.

The poor performance of habitat models in predicting occupancy of known breeding sites located in other different regions within the range of flatwoods salamanders is striking (Figure 2), and this reflects the differences in wetland vegetation and landscape structure among the sites in Florida and Georgia. These results are of general interest because many rare species persist on larger tracts of publicly managed lands scattered across their ranges. Although rare species may be well studied in one area, changes in habitat structure may cause models that are statistically robust where they are developed to perform poorly in new areas. A second consideration in applying habitat models is the status of the species in question. A species may decline for reasons that are not directly related to habitat structure (such as persistent drought), and if populations

become restricted in their distribution or shift habitat associations as a result of other ecological factors such as disease, predation, and competition, then this may cause habitat models to perform poorly. In short, the amount of suitable habitat may not always be a limiting factor for rare species. If this is the case, then development of robust habitat models becomes more difficult.

Finally, the taxonomic status and biogeography of a species in question may also be important to consider. Pauly et al. (2007) recently proposed splitting *Ambystoma cingulatum* into two species with the Apalachicola River as a boundary between them. Although all of the sites included in this study were east of the Apalachicola River, this study also identified significant genetic differentiation between populations in Georgia and Florida. Unique habitat requirements for sister taxa or variation in habitats across ecoregional boundaries may make multiple habitat models for different taxa or regions more desirable.

Habitat modeling is a fundamental task related to the management of rare species. Models may be used to predict both the presence and the absence of a species, but validation is essential before using models to guide management activities, especially in areas that were not sampled for the development of the model. In addition to understanding what factors are related to the presence or absence of a rare species, it is important to understand the variation in habitat across a species range. While small numbers of potential sites may limit efforts to predict the presence or absence of a rare species, multivariate analyses need not be limited to sites where the presence of species has been documented. Thus, even in cases where locality data for a species are very sparse, it is still possible to determine if previously surveyed sites reflect the variation in

habitat types in a landscape and the degree of similarity between known localities of a rare species. When confronted with the case of very rare species managers should remember that rarity affects the types of management questions that can be addressed by researchers, but rarity itself need not be viewed as an obstacle to further research that would better inform management actions.

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Table 2.1. Logistic regression models for predicting presence and absence of the flatwoods salamander at potential breeding sites on Ft. Stewart, GA.

<i>Models for Presence</i>	<i># Parameters</i>	<i>AIC</i>
Landscape + Plant Species	4	62.83
Wetland Indicator Status	2	64.61
Plant Species	4	66.37
Landscape	2	69.74
Landscape + Wetland Indicator Status	4	70.87
Hatpin + Beakrush + Wiregrass	3	72.62
<i>Models for Absence</i>	<i># Parameters</i>	<i>AIC</i>
Wetland Indicator Status	3	63.04
Plant Structure	2	64.79
Plant Species	3	74.04
Landscape + Plant Species	6	85.60
Landscape + Wetland Indicator Status	4	90.03
Landscape	2	98.29

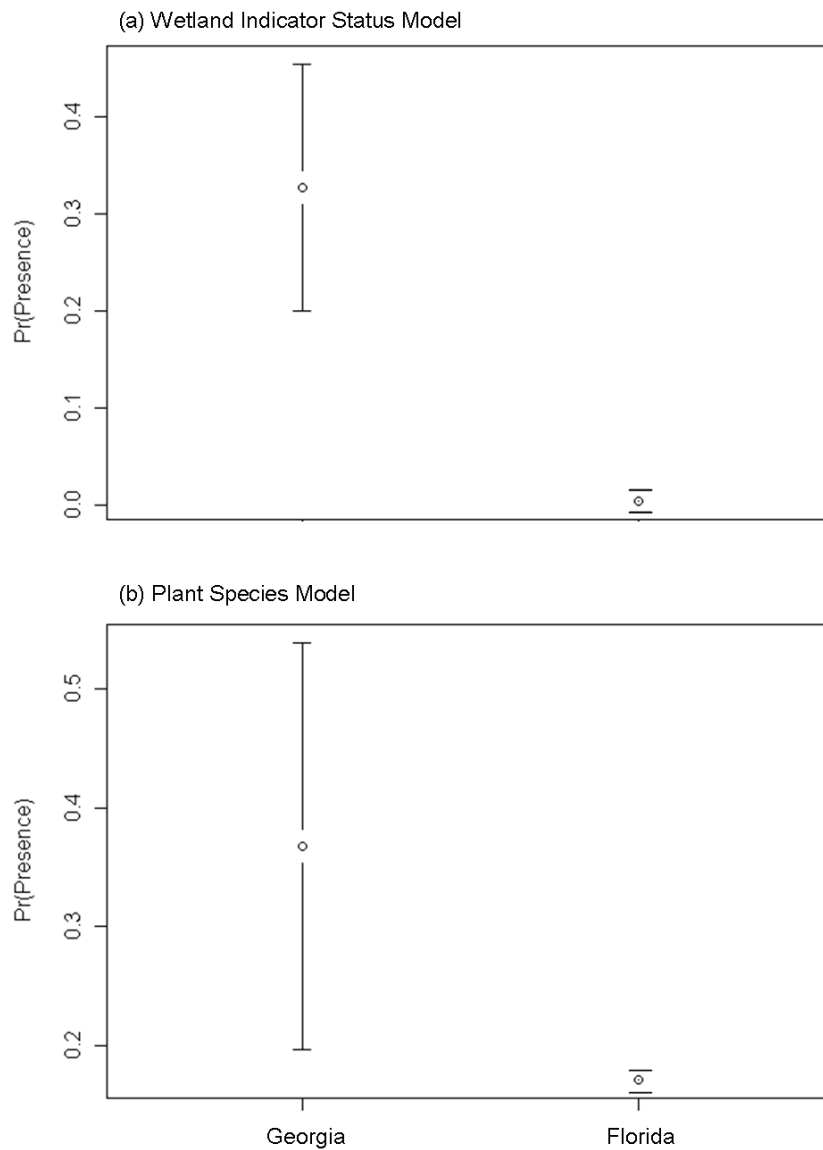


Figure 2.1. Predicted probabilities of presence of flatwoods salamanders at known breeding sites at Fort Stewart (GA) and the Apalachicola National Forest (FL) and St.Marks National Wildlife Refuge (FL) derived from logistic regression models based upon (a) wetland indicator status and (b) plant species.

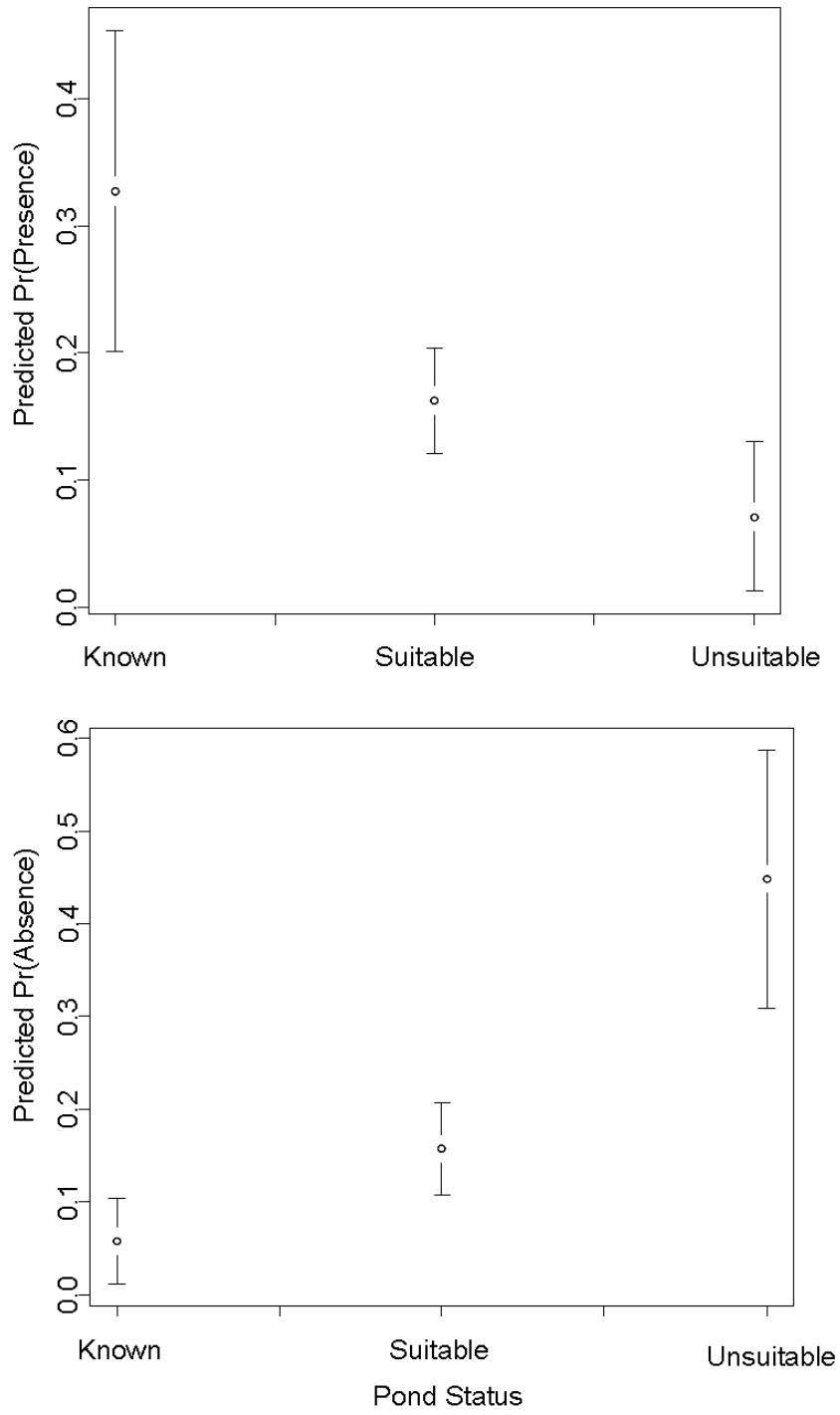


Figure 2.2. Predicted probabilities of presence and absence of flatwoods salamanders from wetlands at Fort Stewart, GA.

CHAPTER 3: ASSESSING THE VALUE OF BREEDING AND DISPERSAL HABITAT FOR LANDSCAPE CONNECTIVITY

Abstract

Habitat restoration is frequently used to mitigate the effects of habitat loss and fragmentation. Although the protection and restoration of breeding and dispersal habitat is implicitly assumed to enhance landscape connectivity, the relative influence of protecting these habitats on landscape connectivity is unknown. I test three hypotheses about factors that best predict landscape connectivity: the proximity hypothesis states that areas closest to breeding habitat should have higher values of landscape connectivity; the dispersal hypothesis predicts that areas of high landscape connectivity should contain good dispersal habitat; and the location hypothesis states that landscape connectivity is driven by the spatial configuration of the landscape rather than the locations of breeding or dispersal habitats. I tested these hypotheses by assessing landscape connectivity for a rare amphibian, the ornate chorus frog, in the sandhills region of North Carolina. I first developed predictive models to identify suitable breeding sites. I then collected data on frog movements in different habitat types and at habitat boundaries in order to calculate the resistance of different habitat types to frog movement. Landscape connectivity was predicted with a circuit model that used a map of breeding habitat and the resistance of dispersal habitat to frog movement, and this map of predicted landscape connectivity was then subjected to a reserve selection algorithm to create a map that prioritized locations within the landscape according to how much they contributed to landscape connectivity. I then selected 4,000 sites within the study area to test my hypotheses using generalized additive models. I found that the best model for predicting landscape connectivity and

prioritization scores included terms for spatial location, proximity to breeding sites, and quality of dispersal habitat. However, the ranking of these predictors changed between the models for landscape connectivity and prioritization scores, reflecting some support for all three hypotheses. These differences between landscape connectivity and prioritization scores reflect the spatial process of prioritizing areas with higher values of landscape connectivity. My results show that the effectiveness of conservation plans seeking to enhance landscape connectivity can be improved by directly testing the relative contributions of breeding and dispersal habitat to landscape connectivity.

Introduction

Conservation actions often focus on habitat restoration as a means to mitigate the effects of habitat loss and fragmentation on rare species, but its potential effects on enhancing landscape connectivity are not fully understood. Habitat loss and fragmentation may reduce populations in two ways. First, as habitat patches are reduced in size, they support smaller populations, which are more likely to go extinct. Second, habitat loss and fragmentation also make remaining habitat patches more isolated, reducing species ability to recolonize suitable habitat when local populations become extinct (Brown and Kodric-Brown 1977). Habitat restoration can address these two problems by increasing the amount of available breeding or dispersal habitat, thus increasing landscape connectivity. Yet, few studies have examined the effects of the amount of breeding and dispersal habitat on landscape connectivity. Here I examine how landscape connectivity is affected by isolation from breeding habitat and the quality of dispersal habitat.

Three problems are especially challenging in assessing landscape connectivity with the purpose of conserving rare species. First, rare species may be absent from or undetected in suitable patches of breeding habitat, so the current knowledge of occupied breeding sites may present an incomplete picture of the true distribution of breeding habitat across a landscape (MacKenzie et al. 2006). Second, even when breeding habitat can be identified, it is often difficult to directly observe dispersal behavior (Kuefler et al. 2010). This means that assessments of landscape connectivity frequently rely upon expert opinion rather than empirical data, and ascertaining the veracity of the assumptions made in these models can be difficult (Beier et al. 2008). Finally, even when landscape connectivity is mapped for a rare species, it must still be placed into the context of conservation actions in order for it to be truly useful in setting conservation priorities to protect rare species.

I address these problems associated with applying reliable knowledge about landscape connectivity to conservation planning in four stages. First, I use statistical models to predict locations of breeding habitat. Second, I incorporate detailed movement data from animals in field experiments to determine the resistance of different habitats to animal movement. Third, I combine information on movement data and the locations of suitable breeding sites to predict landscape connectivity. I define landscape connectivity as a measure of the relative likelihood of individuals dispersing to places within the landscape because I am interested in how different habitat types affect the likelihood of dispersing individuals passing through particular places in the landscape. Finally, I prioritize areas for landscape connectivity by selecting larger contiguous areas with relatively high values of landscape connectivity.

Amphibians provide an excellent model system for studying the effects of restoration on landscape connectivity because wetland-breeding amphibians use distinct habitats for breeding and dispersal. I use the ornate chorus frog (*Pseudacris ornata*) as a case study. This species is rare and declining throughout much of its historic range in the southeastern coastal plain of the U.S., where it uses both natural and artificial wetlands as breeding sites (NatureServe 2011). Like many amphibians, ornate chorus frogs leave breeding wetlands and disperse through upland forest habitat, and both wetland and upland habitats need to be considered in restoration.

Distinct breeding and dispersal habitat in amphibians allows me to compare three hypotheses about landscape connectivity. First, the proximity hypothesis suggests that landscape connectivity is determined primarily by the proximity of a location in a landscape to suitable breeding habitat (Tischendorf and Fahrig 2000). This hypothesis is implicit in many conservation actions that seek to benefit species by protecting additional patches of habitat in a landscape. Second, the dispersal hypothesis states that landscape connectivity is determined by the ability of dispersal habitat to facilitate movements of individuals from one breeding habitat patch to another. This hypothesis guides many large-scale conservation efforts to reestablish regional corridors to promote movement of species like large carnivores. Third, the location hypothesis considers landscape connectivity as an emergent property of the spatial configuration of habitats in the landscape more generally. Although these hypotheses for landscape connectivity have not been explicitly tested before, they encompass the perspectives of different ecological disciplines that are relevant to planning conservation actions that are intended to improve landscape connectivity. The proximity hypothesis reflects insights gained from

considering patch isolation metrics that have their basis in metapopulation biology (Hanski 1994), which tends to focus on the location of patches rather than areas between habitat patches. In contrast to this, landscape ecology may focus on the different types of dispersal habitats separating patches of breeding habitat or the spatial arrangement of habitats explicitly (Wiens et al. 1993). Together these hypotheses provide a useful framework for conservation planning that seeks to protect or restore landscape connectivity for rare species by isolating factors that increase landscape connectivity, and, most importantly, permitting well-justified prioritization of areas to target with restoration actions. Although support for these three hypotheses may vary across rare species, this analytical framework provides an approach for assessing what conservation actions benefit landscape connectivity.

Methods

Study Area

I focused my analyses on an area encompassing a 10-km buffer around the Fort Bragg Military Reservation, located in the Sandhills of the inner coastal plain of North Carolina, USA. Fort Bragg is a 62,400-ha active military installation that contains areas of pine forest. I used field surveys and data from prior surveys of potential habitat for ornate chorus frogs in our study area to identify 4 categories of sites: natural wetlands that are suitable breeding sites for ornate chorus frogs, artificial wetlands that are suitable breeding sites for ornate chorus frogs, wet areas that are too ephemeral to be ornate chorus frog breeding sites, and depressions in the landscape that do not retain water. I reclassified National Land Cover Data (Gesch et al. 2002) into three categories of

potential dispersal habitat for our study area: riparian forest, upland forest, and open habitat.

Predicting Breeding Habitat

To determine the location of potential breeding ponds for ornate chorus frogs, I obtained a 20-ft digital elevation model (DEM) created by the GIS Unit of the Department of Transportation of North Carolina and from LiDAR data collected by the Federal Emergency Management Agency's North Carolina Floodplain Mapping Program. My models of natural and artificial wetlands focused on environmental features derived from a DEM, rather than soils data, because amphibian breeding sites like those used by ornate chorus frogs are ephemeral in nature and very small in size, and other data have a very coarse spatial resolution relative to the size of ephemeral ponds. Although soils data can be used to map wetland sites, soils data are not available at a higher resolution for many areas. The Floodplain Mapping Program has created DEMs at a high resolution for much of North Carolina, and I relied heavily on these data in order to develop an approach that could be easily transferred to other landscapes.

In order to predict the locations of breeding wetlands, I derived several different environmental variables from the DEM. Natural and artificial wetlands that are suitable breeding sites for ornate chorus frogs are typically isolated from more permanent water sources like streams and rivers (Petranka 1998), and I expected human activity that is associated with the creation of artificial wetlands to be more frequent in areas closer to dirt roads. Thus, to predict breeding wetlands, I calculated the Euclidian distance from streams and dirt roads for each site. I calculated slope and elevation from the original

DEM before processing the DEM to calculate a topographic wetness index (Beven and Kirkby 1979) and classify landform types (Pennock et al. 1987). The topographic wetness index is a ratio of the catchment area of a place within a landscape and the slope at that point, and should be associated with low places in landscapes where ponding of water occurs. The classification of landform types provides a way to determine whether the flow of water to a point is converging or diverging and whether a point within the landscape is located on a ridge, the side of a slope, or the base of the slope. These properties are associated with the development of different soil types, and I anticipated that they could also be related to the distribution of wetlands within a landscape. I followed standard procedures for smoothing DEMs prior to conducting our analyses.

To predict natural and artificial wetlands, I followed conventional methods for variable selection with generalized additive models (Wood 2006). I evaluated model accuracy separately for two sets of models for suitable ornate chorus frog breeding sites: one for predicting the locations of natural wetlands, and one for predicting the locations of artificial wetlands. Artificial wetlands result from human activity and were expected to have a weaker association with environmental variables derived from the DEM. Although model selection procedures are well developed for logistic regression models, generalized additive models fit smoothing functions to data using a cross validation procedure that iteratively removes a small proportion of a data set, and this precludes a model selection approach. Backward elimination of variables from generalized additive models has been advocated as an alternative method for assessing the importance of different predictor variables (Wood 2006). I initially fit a model with smoothing functions for all predictor variables: elevation, slope, wetness index, distance to nearest

stream, distance to nearest dirt road, and landform type. The significance of nonparametric smoothing functions can be evaluated by computing a χ^2 statistic that is analogous to a z-statistic for a predictor variable in a logistic regression model. This χ^2 statistic only reveals the significance of a smoothing function, so plots that show the change in the linear predictor of a smoothing function in relation to the range of values for the predictor variable can be examined to determine the nature of the relationship between environmental variables and the presence of wetland sites. The backward elimination procedure with generalized additive models proceeds by identifying the smoothing function with the weakest relationship to the data, dropping this smoothing function to create a new model with a reduced number of smoothing functions, and then using a goodness-of-fit test to compare the original model with the reduced model. If the reduced model provides a better fit to the data, then this process is repeated until the elimination of a smoothing function stops improving model fit. Significance of smoothing functions in reduced models was evaluated with $\alpha=0.10$.

In addition to assessing the fit of models to data, I also assessed model accuracy. Just like logistic regression models, generalized additive models predict a binary response like the presence or absence of a wetland. I used these predicted probabilities to assess how well the models that best fit the data actually predicted the presence or absence of wetland sites. Receiver operating characteristic plots provide one way to assess model accuracy by looking at the proportion of sites that are correctly classified as having or lacking wetlands over the range of probabilities predicted by a model. This is shown graphically by plotting, as the predicted probability of the model changes, the true positive rate as a function of the false positive rate. Since the range of probability is

bounded by 0 and 1, the maximum area under this curve is 1. Models with an area under the curve (AUC) above 0.9 are generally considered to have a high degree of accuracy (Guisan et al. 2002), and I report AUC values here as a measure of model performance in correctly classifying the presence or absence of wetland sites. I verified our predictive models with extensive field surveys to confirm the location of predicted wetland sites.

Movement Experiments

In order to obtain empirical data on habitat resistance values, I conducted release experiments with ornate chorus frogs (*Pseudacris ornata*). Twenty-nine ornate chorus frogs were released at boundaries between upland forest and open habitats, 78 were released within upland forest, 32 were released within open habitat, and 27 were released within riparian forest. Because of a lack of boundaries between riparian and open habitats within our study area, it was not possible to conduct releases at boundaries between riparian and open habitat. I assumed behavior at this boundary was similar to behavior at the boundary of riparian forest and open habitats. The proportion of time frogs moved into one habitat at a boundary was used as a measure of the probability of a frog entering that habitat type. Frogs were captured and released at night after being marked with fluorescent dye powder (Moody et al. 2011). An individual was allowed to move for 15 – 20 minutes before the movement trail was tracked with an ultraviolet light. Frogs deposited dye powder on the ground as they hopped away from their release point. I marked clusters of dye powder where a frog had landed along the movement path. I used a compass to measure the angle between subsequent points of dye powder along a path, and in cases where there were two new points of dye powder, I assumed that the

frog moved to the closest point of powder first. New points that did not deviate from the previous segment by more than 5 degrees were considered to be part of the same straight segment. The length of each segment of the movement path was recorded to the nearest centimeter, and the turning angle between subsequent segments was recorded to the nearest 5 degrees. I marked segments of the movement trail and measured the distance travelled and turning angle from one segment to the next. I conducted releases at 8 sites in upland forest, 2 sites in open habitat, and 2 sites in riparian habitat between January and March 2010 (Moody et al. 2011).

After collecting movement data on frogs, I used mean-squared displacement rates and probabilities of entry for each habitat type to calculate habitat-specific resistance values (Kuefler et al. 2010, Karieva and Shigesada 1983). The mean-squared displacement, or the average square of the distance travelled, can be calculated as a function of the number of moves in a movement path:

$$R_n^2 = nm_2 + 2 m_1^2 (c/(1-c)) (n - (1-c^n)/(1-c))$$

Where m_1 is the mean length of a segment on a movement path, m_2 is the mean squared movement length, and c is the mean cosine of the turning angle, and n is the number of moves. I divided the estimates of resistance values by the largest resistance value to generate relative resistance values for habitat types that were incorporated into the connectivity analysis.

Assessing Landscape Connectivity

I used data on the location of suitable breeding sites and the resistance of different habitats to amphibian movement to predict landscape connectivity for ornate chorus frogs

using circuit models (McRae et al. 2008). Landscape connectivity was defined as the likelihood that a dispersing individual passes through any point on the landscape as determined by a circuit model (McRae et al. 2008). Other approaches for assessing connectivity include quantifying landscape pattern, individual-based movement models, and analytical methods using graph theory or least-cost path models (McRae et al. 2008). However, these methods all have limitations that circuit theory overcomes. Pattern indices, while useful for quantifying spatial structure of habitats, may fail to capture variation in habitats relevant to dispersing organisms (Tischendorf and Fahrig 2000). Movement simulations can be computationally intensive, and often require additional movement data to parameterize models (Hudgens et al., in press). Finally, analytical approaches for assessing connectivity with graph theory or least-cost path models often focus on identifying a single route between patches of habitat, but dispersing individuals may not always select an optimal dispersal route. Circuit theory circumvents these issues through the relationship of electrical networks and random walk models on graphs.

There are several ecological analogs that can be made using circuit theory (McRae et al. 2008). A circuit is a network of nodes connected by resistors that conduct current. Current is the flow of an electrical charge through a circuit, voltage is the difference in electrical charge between two nodes in a circuit, and resistance is the degree to which a resistor impedes the flow of current. In ecological terms, a circuit is a network of nodes that represent habitat patches or populations. Previous research demonstrated that circuit theory identifies the use of random walkers dispersing across a network (Doyle and Snell 1984, Chandra et al. 1996), and this makes it possible to use circuit theory to assess connectivity for a species. In ecological terms the resistance of a path or

edge on a circuit is the inverse of the permeability of the habitat represented in that edge. A map of current is representative of the net movement probabilities for random walkers moving through a graph, while voltages predict the probability of successful dispersal to a point by random walkers moving on a graph. When a circuit is used to consider a network or graph of habitat patches, the nodes represent patches of habitat, and edges connecting nodes are determined by calculating a resistance distance based on the set of multiple pathways connecting nodes. For a single path, resistance is calculated according to resistance values associated with the habitat types along a pathway. The resistance distance accounts for both the least-cost path and additional paths connecting two nodes. As the number of pathways connecting two nodes increases, the resistance distance decreases, which reflects an increase in movement between sites when there are multiple dispersal pathways for individuals.

I constructed a circuit model for amphibian dispersal by using the map of suitable breeding sites as a set of nodes from which individuals (i.e., current) would disperse. I then used data on the resistance of different habitat types to amphibian movement to set the resistance for all of the places in between suitable breeding sites through which amphibians might disperse. I reclassified National Land Cover Data for the study area into upland forest, riparian forest, and open habitats. Riparian habitat included major waterways and their associated bottomland areas, while forest habitat included evergreen, deciduous, and mixed forests. Open habitats were shrubland, grassland, or developed areas. I resampled our habitat resistance map from a resolution of 30-m to 120-m in order to reduce processing time for this analysis. Coarser raster cell sizes generally do not result in failure to detect patterns of connectivity from higher resolution rasters,

provided that important barriers are retained in the habitat resistance raster (McRae et al. 2008). These analyses were conducted using Circuitscape (available at www.circuitscape.org), an open-source program designed to assess circuit models for ecological systems.

After creating maps showing landscape connectivity for amphibians with circuit models, I prioritized areas according to how important they were for landscape connectivity. To prioritize areas within a map for landscape connectivity, I sought to iteratively remove cells from the edge of the map that contributed the least to landscape connectivity. I started with the entire map, searched the edge of the map for the cell that made the smallest contribution to landscape connectivity, and then removed this cell. This process was repeated until all cells in the map had been sequentially removed. Recording the order in which cells were deleted from the map gave us a measure of a cell's value to landscape connectivity: the least valuable cells were removed quickly, while the most valuable cells were retained until the end of the process. To implement this prioritization method, I used program Zonation (Moilanen 2006). The resulting map of prioritization scores was then used in additional analyses described below.

Predicting Landscape Connectivity

After prioritizing sites for conservation, I sought to test three hypotheses about how isolation from breeding habitat, quality of dispersal habitat, and spatial location contributed to both the landscape connectivity of a site and a site's prioritization score. I did this by predicting landscape connectivity and prioritization scores with generalized additive models. I initially fit models with smoothing functions for isolation from

breeding habitat, quality of dispersal habitat, and spatial location on their own before comparing these models to all possible combinations of these variables. Using generalized additive models, I examined the effect of location independently, which is highly desirable for models of landscape connectivity and prioritization because these maps are the result of spatial processes. This analysis can be done by fitting smoothing functions using the spatial coordinates for the location of a site, which has the effect of adding a random effect to the statistical model that is based on the location of each observation (Wood 2006). I then defined isolation from breeding habitat in a similar manner to Hanski's isolation metric (Hanski 1994):

$$S_i = \sum(e^{-\alpha \cdot d_{ij}})$$

where S_i is the i th location in the landscape, α is the mean maximum dispersal distance for a species, and d_{ij} is the distance between the i th location in the landscape and the j th breeding site. This metric does not incorporate information on the size of breeding sites because breeding wetlands used by ornate chorus frogs are small features in the landscape and ornate chorus frog populations may vary by an order of magnitude between breeding sites of similar sizes. Because I lacked estimates for the mean maximum dispersal distance of ornate chorus frogs, I used an estimate of 500 m for the mean maximum marbled salamander (*Ambystoma opacum*) dispersal distances (Scott et al. in press) as a surrogate for the mean maximum dispersal distance. I quantified the quality of dispersal habitat around a particular location within the landscape by calculating the harmonic mean of the habitat resistance values for all cells within the mean maximum dispersal distance of that location. I fit models with 4,000 randomly

selected data points from our landscape and evaluated models for connectivity and prioritization scores by comparing AIC values among the competing models.

Error in Connectivity Models

Because models of landscape connectivity have been criticized for not being based upon empirical data (Beier et al. 2008), I highlight a few issues related to sources of error in the process of modeling landscape connectivity and prioritizing areas for conservation actions. Predictions about landscape connectivity depend upon both information about the distribution of habitats within a landscape and the movement behavior of individuals in response to different habitats. The resistance of a habitat type to an animal could be decomposed into a movement process and a mortality process. A movement process would describe the information about step lengths and turning angles of movement paths, while a mortality process would incorporate the likelihood of a dispersing individual dying while in a particular habitat. Here I have included the information from the movement process in my calculation of habitat resistance values, but I lack data on a mortality process for dispersing frogs. By not including information on mortality in my calculations of habitat resistance, I am implicitly assuming that the mortality process is similar across habitat types.

In the process of modeling landscape connectivity from habitat resistances calculated with movement data, the relative resistance values are likely more important than precision in estimates of habitat resistance values, as these numbers are used to parameterize circuit models. I examined the effect of systematically changing the relative resistance values of different habitat types. First, I assumed that the relative

resistance values of riparian and upland forest were the same and I assigned the habitat resistance value of the upland forest to all areas of riparian forest on the habitat map. Second, I assumed that the difference in relative resistance values was reduced such that the resistances of open habitat and riparian forest were still 1.000 and 0.513, respectively, but the relative resistance of upland forest was doubled from 0.128 to 0.256. I then produced circuit models for both of these scenarios and ran prioritization algorithms on circuit models. These maps are presented for visual comparison with the maps used in the analysis of factors related to landscape connectivity and prioritization score.

Results

Breeding habitat models

The best models for both natural and artificial wetlands included smoothing functions for elevation and distance to stream, and the model for artificial wetlands also included a smoothing function for the distance to dirt roads (Table 3.1). The natural wetland model had an adjusted r^2 of 0.137 and explained 21.7% of the deviance, and the artificial wetland model had an adjusted r^2 of 0.224 explained 29% of the deviance. None of the models had trouble achieving convergence.

Examination of the smoothing functions for elevation reveals no clear relationship with the presence of artificial wetlands, but there is some evidence that natural wetlands are less likely to occur at lower elevations within the study area (Figure 3.1). Natural wetlands and artificial wetlands were both more likely to occur at greater distances from streams, and artificial wetlands were less likely to be found at greater distances from dirt

roads (Table 3.1). Predictive models for natural and artificial wetlands performed well (AUC for model natural wetlands = 0.93, AUC for model of temporary wetlands = 0.94).

Movement experiments

Ornate chorus frogs showed different movement behavior in the three different habitat types. Movement paths of ornate chorus frogs varied according to the different habitats ($F_{134,2} = 3.24$, $p = 0.04$). Frogs had longer step lengths in upland forest ($N = 78$, mean = 1.1m, standard deviation = 0.93m), than in open habitat ($N = 32$, mean = 0.91m, standard deviation = 0.52m) or riparian forest ($N = 27$, mean = 0.67 m, standard deviation = 0.50m). Turning angles of movement paths also differed among the three habitat types ($F_{113,2} = 1.21$, $p < 0.05$), with frogs having smaller turn angles in open habitat ($N = 26$, mean = 30.7 degrees, standard deviation = 18.0 degrees) than in riparian forest ($N = 23$, mean = 41.5 degrees, standard deviation = 37.7 degrees) or upland forest ($N = 67$, mean = 37.3 degrees, standard deviation = 21.4 degrees). In order to assess the likelihood of frogs entering these habitat types, I also conducted 32 additional releases at boundaries between upland forest and open habitat; frogs moved into upland forest after 28 of these releases. The relative resistance values from these movement data indicate that open habitats were the most resistant to ornate chorus frog movement (Table 3.2). Resistance values of upland and riparian forest were approximately one eighth and one half, respectively, of the resistance value of open habitat (Table 3.2).

Connectivity and Prioritization Models

Maps of landscape connectivity and prioritization values show most high priority areas and regions of higher landscape connectivity toward the center of our study region (Figures 3.2 and 3.3). An increase in the resistance value of upland forest produced a similar map to that which resulted from reducing the resistance of riparian forest to equal that of the upland forest. These alternative scenarios of habitat resistances produced prioritization maps that were qualitatively similar to the original prioritization map in that all three maps tend to highlight relatively large interior regions as high priority areas (Figures 3.2 and 3.3).

Two variables consistently showed a strong association with landscape connectivity and prioritization scores: the location of sites and the quality of dispersal habitat (Tables 3.3 and 3.4). Although the best models for landscape connectivity and prioritization scores included smoothing functions for location, dispersal habitat, and breeding habitat, the data also provided support for models with only location and dispersal habitat. The full model for predicting connectivity scores had an adjusted r^2 of 0.61 and explained 60.9% of the deviance, and the full model for predicting connectivity scores had an adjusted r^2 of 0.60 and explained 60.3% of the deviance. All candidate models converged. However, the behavior of smoothing functions for dispersal habitat varied in models for connectivity and prioritization (Figure 3.4). Higher quality dispersal habitat was associated with higher measures of landscape connectivity, but prioritization scores did not show a strong association with the quality of dispersal habitat (Figure 3.4).

Discussion

The dispersal and location hypotheses for landscape connectivity were more strongly supported than the proximity hypothesis. The location of sites within the landscape is the strongest predictor of landscape connectivity (Table 3.3), supporting the location hypothesis. This reflects two phenomena: first, the map of landscape connectivity is created by a spatial process, and, second, there is significant spatial structure in dispersal habitat because contiguous areas of forest cover tend to be larger within protected areas. I anticipated that the low number of breeding sites within the landscape would make isolation from breeding sites an important predictor of landscape connectivity, but I found the opposite to be the case. This may result from the fact that distances between breeding sites are large relative to the expected dispersal distance of amphibians, so the variation in the isolation metric I used in our analyses is low.

In contrast to our findings for models predicting landscape connectivity, models predicting prioritization scores were more strongly affected by the location of sites within the landscape (Table 3.4). This can be explained by the prioritization algorithm, which identifies contiguous blocks of habitat with relatively high values for landscape connectivity (Figure 3.3). More interestingly, the effect of habitat predictor variables changes when models for site prioritization and landscape connectivity are compared (Figures 3.4). This initially seems contradictory, but it is actually consistent with the behavior of the site prioritization algorithm. Priority areas identified by this algorithm often contain sites with relatively high landscape connectivity values surrounding areas with lower values for landscape connectivity, so the blending of sites that are higher and lower values breaks down the relationship between landscape connectivity and habitat

types. For example, a small clearing that was the size of one pixel in a map would be expected to have a lower value for landscape connectivity than the surrounding forest, but if the forest around the clearing was a contiguous patch hundreds of hectares in size, then both the clearing and the forest might have relatively high prioritization scores. These findings are potentially confusing, so I make 2 recommendations for conservation plans that seek to enhance landscape connectivity. First, conservation actions across the landscape should focus on managing habitat to improve landscape connectivity by increasing the amount of good dispersal habitat. Second, the prioritization of areas for conservation may depend more on finding areas with an aggregation of sites that have relatively high values of landscape connectivity than it does on merely identifying the points within a landscape that contain the highest values for landscape connectivity.

Accurate maps of suitable breeding and dispersal habitat are vital for assessing landscape connectivity, and our success in developing statistical models to discriminate both natural and artificial wetlands used by rare amphibians strengthens our analysis (Figure 2). I successfully identified breeding habitats even though these habitats are predicted by different environmental factors and are small features in the landscape that are not well mapped by existing spatial data. Our results indicate that while the location of natural wetlands is strongly influenced by elevation, the location of artificial wetlands created by military training activities is not strongly tied to the environmental data I used. Our use of generalized additive models allows us to explicitly test how well different factors predict the location of suitable habitat types in a similar manner to linear regression models, and it also provides a simple approach for dealing with spatial autocorrelation in environmental data.

Although changing the habitat resistance values resulted in slight changes to the connectivity maps (Figure 3.2), this did not translate into large differences in the maps of high priority areas for protecting habitat to enhance landscape connectivity (Figure 3.3). This suggests that for maps with few habitat types, errors in calculating habitat resistance values may have a limited effect on which areas are mapped as high priority areas for conservation. Since the landscape map included only 3 distinct habitat types, the spatial arrangement of habitat types could be as important as the resistances of different habitats. Further research on the effects of the number of habitat classes and the resistance values of habitat classes should be done to corroborate this finding and to test the effect of letting habitat resistances vary within a habitat type across a landscape rather than remaining a fixed value.

The approach presented here provides a way to empirically test hypotheses related to factors associated with a common conservation objective: increasing landscape connectivity. Our approach uses rigorous methods to model landscape connectivity that allow assessment of uncertainty associated with our data at different stages in the modeling process while providing an analytical framework that can be easily updated with additional data. As conservation practitioners become more interested in the implementation of conservation programs operating at larger spatial scales, the success of these conservation programs will need to be assessed. Moreover, limited resources should be allocated to protect the critical areas in order to improve landscape connectivity. Our independent assessment of prioritization values demonstrates that conservation efforts should strategically target larger important blocks of habitat rather

than focusing on trying to protect smaller, more isolated fragments that may have relatively high connectivity in comparison to the surrounding landscape.

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Table 3.1. Smoothing functions for generalized additive models predicting natural and artificial wetlands at Fort Bragg, NC.

	Smoothing function	χ^2 value	p-value
<i>Natural wetland model</i>			
	Elevation	19.47	0.022
	Distance to Stream	10.35	0.066
<i>Artificial wetland model</i>			
	Slope	0.081	0.776
	Elevation	27.373	0.001
	Wetness Index	0.178	0.673
	Distance to Dirt Road	4.084	0.043
	Distance to Stream	4.750	0.029

Table 3.2. Estimates of habitat resistances to amphibian movements from ornate chorus frog release experiments at Fort Bragg, NC.

Habitat Type	Mean Step Distance	Mean Step Distance Squared	Cos (turn angle)	Mean Squared Displacement	P(entry)	Relative Resistance
Open	0.91	1.09	0.82	8.71	0.12	1.00
Riparian Forest	0.67	0.70	0.64	2.32	0.88	0.51
Upland Forest	1.11	2.08	0.64	9.26	0.88	0.12

Table 3.3. Comparison of generalized additive models predicting landscape connectivity values with a combination of smoothing functions for 3 variables: location (spatial coordinates), dispersal habitat (resistance of habitat to movement around a point), and breeding habitat (isolation of a point from all breeding sites within the landscape).

Model	AIC
Location + Dispersal Habitat + Breeding Habitat	32252
Location + Dispersal Habitat	32253
Location + Breeding Habitat	33521
Location	33523
Breeding Habitat + Dispersal Habitat	34795
Dispersal Habitat	34809
Breeding Habitat	35867

Table 3.4. Comparison of generalized additive models predicting prioritization scores with a combination of smoothing functions for 3 variables: location (spatial coordinates), dispersal habitat (resistance of habitat to movement around a point), and breeding habitat (isolation of a point from all breeding sites within the landscape).

Model	AIC
Location + Dispersal Habitat + Breeding Habitat	7733
Location + Dispersal Habitat	7734
Location + Breeding Habitat	7741
Location	7743
Breeding Habitat + Dispersal Habitat	11412
Breeding Habitat	11415
Dispersal Habitat	11420

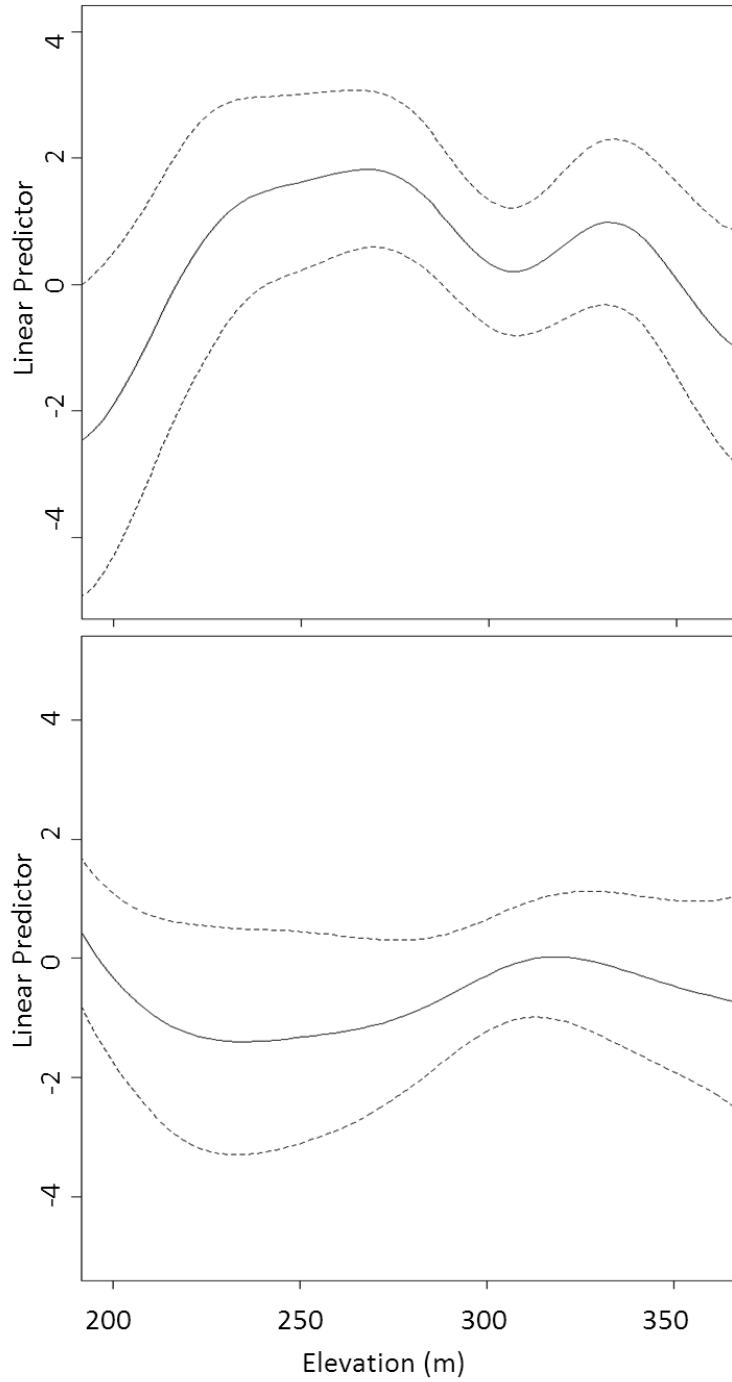


Figure 3.1. Smoothing functions for elevation predicting natural wetlands (top) and artificial wetlands (bottom). Dashed lines indicate 95% limits about the smoothing functions. Lower values for the linear predictor indicate conditions under which wetlands are less likely to occur.

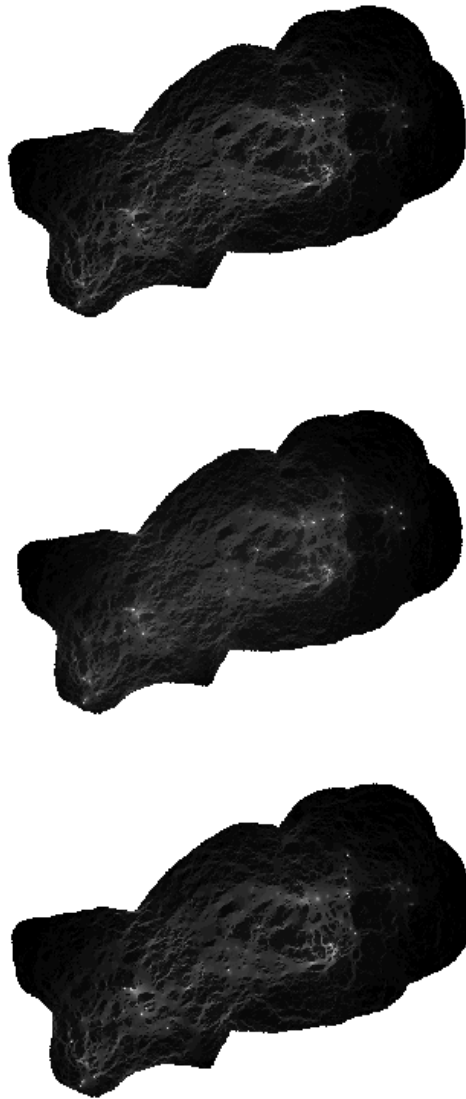


Figure 3.2. Map of landscape connectivity for ornate chorus frogs (white = higher connectivity, black = lower connectivity) based on habitat resistance values estimated from movement data (top), resistance of upland forest set to approximately one half of the resistance of riparian forest, and equal habitat resistances for upland and riparian forest (bottom).

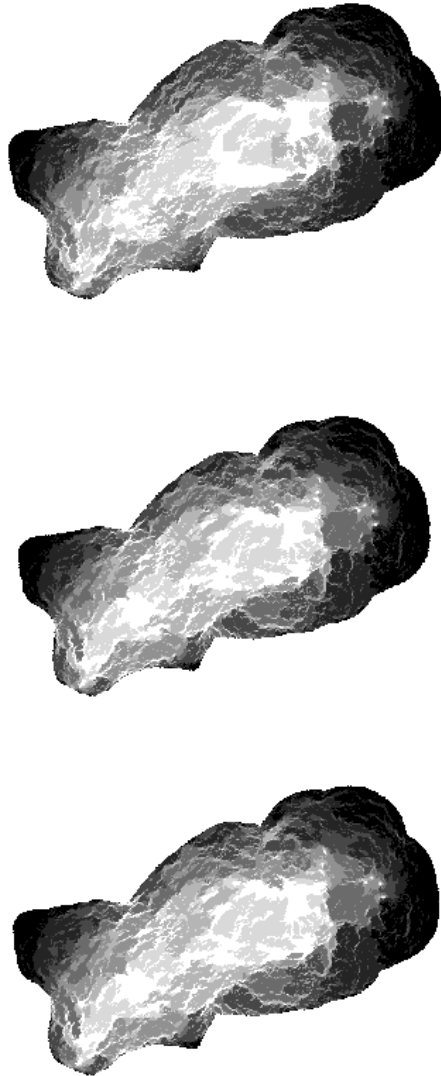


Figure 3.3. Map of prioritization scores for landscape connectivity map of ornate chorus frogs based on connectivity maps created with estimates of habitat resistance from movement data (top), resistance of upland forest set to approximately one half of the resistance of riparian forest, and equal habitat resistances for upland and riparian forest (bottom). Highest priority areas are shown in white, while low priority areas are shown in black.

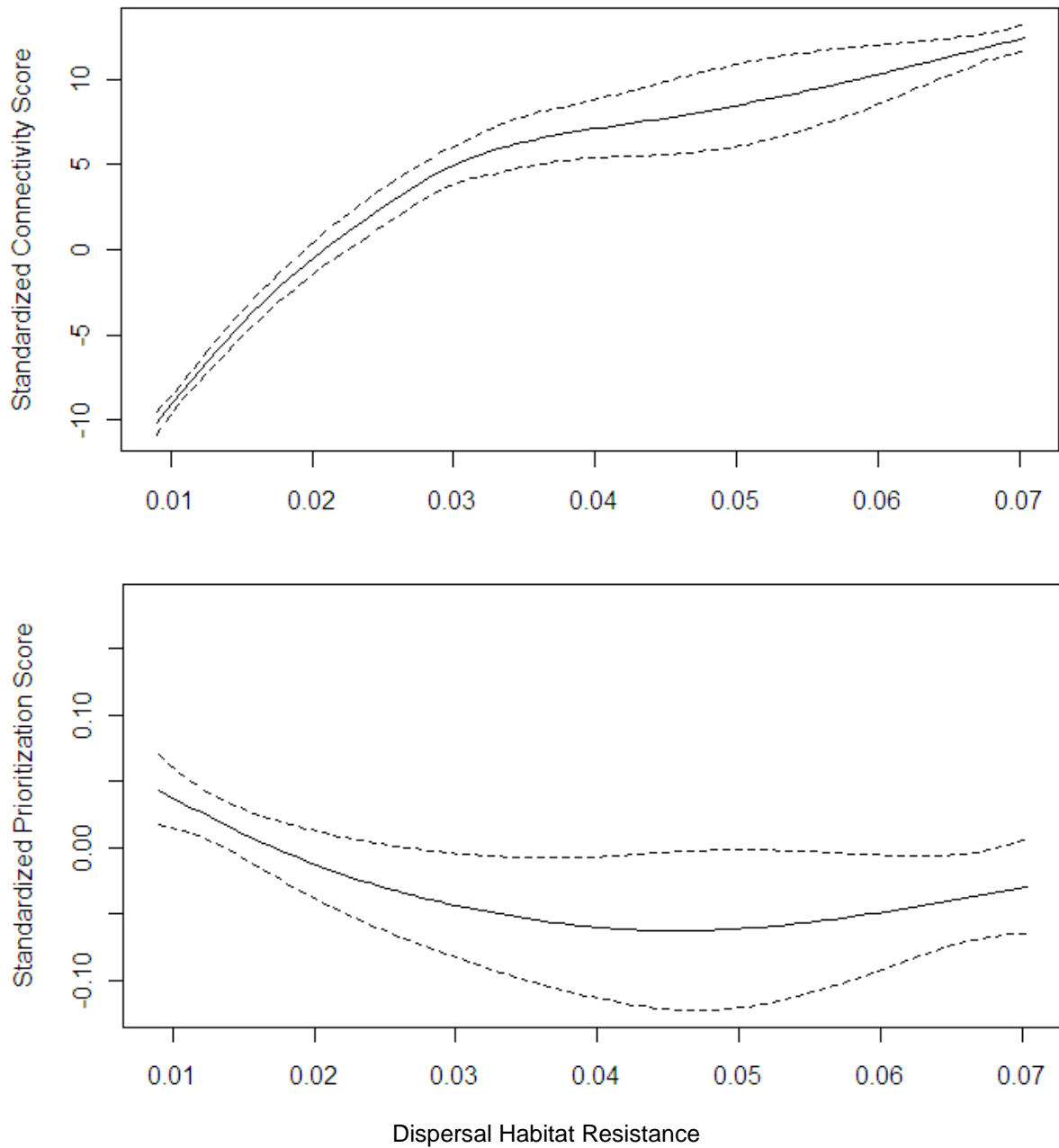


Figure 3.4. Relationship between the harmonic mean of dispersal habitat resistance (low values indicate increased resistance to movement) and predicted values of (a) prioritization scores and (b) landscape connectivity at sites within the study area.

CHAPTER 4: CHANGES IN CLIMATE VARIABILITY REDUCE AMPHIBIAN POPULATION GROWTH

Abstract

Although there is deep concern about the impacts of climate change on biodiversity, research on the mechanisms by which climate change affects populations is rare. I incorporated climate change into demographic models for a wetland-breeding amphibian, the tiger salamander. I developed a predictive model of wetland hydrology based on two years of field data. I then incorporated these models of wetland hydrology into demographic models for the tiger salamander that were parameterized with five years of field data on adult survival, fecundity, and larval growth rates. I used this model to assess how different future climate regimes affected the correlation between different vital rates and population growth. Climate change is not expected to affect mean precipitation in our study region, but it is expected to increase variability in precipitation and wetland hydrology. This change in variability is related to the life stage that most strongly affects population growth and population viability. Although adult survival had higher sensitivity and elasticity values than juvenile recruitment in our deterministic model, this result was affected by future climate change scenarios. At medium and high levels of future carbon emissions, wetlands become more likely to dry too quickly for larval recruitment to occur, and as a result, population growth under these climate change scenarios was more strongly correlated with larval recruitment than it was with adult survival. These results highlight the importance of protecting wetland breeding sites for amphibians, and they also show that the effectiveness of conservation actions may depend upon not just upon mean, but also on variability in climate changes.

Introduction

Climate change is affecting species around the world, and has been implicated in shifting phenology of species, movement of species ranges toward poles, and declines in suitable habitat (Parmesan and Yohe 2002). Research examining abundance or occupancy in association with climate change has documented fluctuations or extinctions of species (McMenamin et al. 2008, Werner et al. 2009, Anchukaitus and Evans 2010). These studies demonstrate a clear and unequivocal pattern of climate change affecting the distribution of species. However, the mechanisms by which climate change drives population dynamics are difficult to discern from patterns of species distributions alone (Doak and Morris 2010). To advance understanding of the effects of climate change on species, two questions about links between demographic processes and climate change need to be addressed. First, does climate change affect the relative importance of different demographic rates in limiting population growth? Second, are populations limited more by long-term trends in variables such as temperature and precipitation or by changes in year-to-year variation in climate? We address these questions by examining how different climate scenarios affect amphibian populations in the southeastern U.S. by changing the hydrology of wetland breeding sites.

Recent developments in climate science have changed the nature of available data and have raised new questions about population responses to climate change. Specifically the most recent projections of future climate have been downscaled, or interpolated to provide projections for finer spatial and temporal scales (Williams et al. 2006). In practice, this means that data are now available for monthly time periods over spatial extents that are much smaller than those traditionally used in global circulation

models of climate. For the southeastern U.S., future climate scenarios indicate that in addition to warming temperatures, precipitation may also increase during summers and decrease during winters (Mearns et al. 2003). More significantly, however, is the finding that in addition to shifts in temperature and precipitation, future climates may become more variable (Mearns et al. 2003). This has important implications for those who seek to incorporate climate change into population models in order to evaluate the potential impacts on species. First, research should identify how changes in both temperature and precipitation affect the physical environments that species inhabit. Second, population models should account for year-to-year variation in environmental conditions that result from climate change, as some studies have indicated that changes in the variability of precipitation may be associated with climate change (Li et al. 2011). In conducting such analyses, it must be recognized that species will experience a gradual shift from current to future conditions rather than simply experiencing a new set of average conditions (Early and Sax 2011). Wetlands represent an ideal system in which to examine climate change effects on populations because the hydrology of wetlands depends upon patterns of both temperature and precipitation. Data for future climate scenarios are of adequate resolution to be incorporated into models of wetland hydrology, so it is possible to characterize how wetland hydrology might shift under different climate scenarios (Lu et al. 2009).

Amphibians provide a strong model system for studying the effects of climate change on biodiversity. Worldwide declines in amphibian populations are among the starkest examples of biodiversity loss (Lips et al. 2006). Declines may result from a variety of factors including introduced species, overexploitation, changes in land use,

emerging diseases, and climate change (Houlahan *et al.* 2000, Collins and Storfer 2003). Among all amphibians, those breeding in wetlands provide an ideal system in which to assess the effects of climate change on population viability, as complete development of their larval stage depends upon wetlands remaining inundated for a certain period of time (typically several months), and wetland hydrology can be linked directly to projected climate scenarios. In addition to this, many amphibian species can be long-lived, which makes them more suitable subjects for evaluating the effects of climate change. A short-lived species might suffer local extinctions when climatic conditions first become stressful, but populations of longer-lived species would track longer-term shifts in the environment, as has been demonstrated in a number of studies. Church *et al.* (2007) demonstrated that some tiger salamanders (*Ambystoma tigrinum*) may live a relatively long time for a small vertebrate species, and adults may choose to avoid breeding during dry years. Griffiths *et al.* (2010) showed that survival of adult newts was affected by weather conditions during the time of year when newts were not in breeding ponds and used closed population mark-recapture models to assess demographic processes associated with local extinctions in a metapopulation. McMenamin *et al.* (2008) linked declines in rates of pond occupancy to shortened hydroperiods in amphibian breeding wetlands. Although these studies have shown how changes in vital rates or occupancy patterns of amphibians may respond to fluctuations in climate, the relative importance of different vital rates and the viability of amphibian populations under different climate scenarios is poorly studied.

We incorporated a long-term climate data set into population models for an amphibian to examine how fluctuations in weather patterns may interact with amphibian

demographic rates to affect the viability of amphibian populations through time. We address these complex issues through a series of analyses designed to determine the effects of climate change and demographic processes on the population viability of a rare amphibian, the tiger salamander. First, we analyzed a deterministic model of a tiger salamander population to determine the relative importance of larval recruitment, subadult survival, and adult survival for population growth. We did this by conducting standard sensitivity and elasticity analyses on 5 years of tiger salamander demographic data. Second, we examined the effects of temporal variation in pond hydroperiod by combining empirical data from a tiger salamander population with models predicting the hydrology of their breeding sites based on temperature and rainfall data from past climates, and future climates with low, medium, or high emissions. To determine how climate change may affect amphibian demography, we compared the relative importance of different demographic rates to population growth in stochastic population models that include pond hydroperiod as an independent random or autocorrelated variable. These analyses reveal whether different climate scenarios might result in wetland conditions that differ from what this population has recently experienced, and whether wetland conditions could affect the relative importance of different life stages in limiting population growth.

Methods

Study site

We collected field data on tiger salamanders at the Fort Bragg Military Reservation, North Carolina, USA. Fort Bragg is a 72,000-ha military installation

located in the sandhills region of North Carolina. Tiger salamanders are rare in North Carolina; the best available data suggest that there are less than 20 extant populations (breeding ponds) in the state (NatureServe 2010), of which six are known to occur at Ft. Bragg. Much of the study area is covered in pine forest, with active management aimed at promoting regeneration of longleaf pine woodlands (*Pinus palustris*). We intensively surveyed three wetlands that were ephemeral, contained tiger salamander populations, and were consistently accessible to collect demographic data.

To measure demographic rates, we completely encircled each wetland with a drift fence. Five gallon buckets were buried every 4 – 5 meters on both sides of the fence so that the rim was flush with the ground. We placed a total of 14 – 16 pairs of buckets at each wetland. We initiated drift fence surveys each November, from 2005 – 2009, before adult tiger salamanders entered wetlands to breed. Drift fences were maintained open and checked daily during periods of peak migration in November-January, and during and after periods of rain. During dry periods, gates were opened in the fence every 10 m to allow free passage in the case of rare migrants. We continued to check fences through the winter and spring (approximately 6 months each year) until the wetlands dried and juveniles finished leaving wetlands. To obtain estimates of adult survival, we marked male tiger salamanders with PIT tags every year. In order to minimize stress on gravid females and small individuals in the population, we marked them with photographs, identifying individuals based on their spot patterns. We have shown that spots are reliable markers of individuals (M. Chesser and S. Hotaling, unpublished data). To obtain estimates for the fecundity of female salamanders, we counted egg masses following breeding migrations along transects in wetlands with spotlights during the first

two breeding seasons (Hudgens et al. 2005). Finally, to obtain estimates of juvenile recruitment and larval growth rates, we counted and measured all juveniles leaving ponds in late spring.

Wetland Hydrology

We predicted daily pond depth in the ephemeral wetlands we studied during the 2004 – 2005 and 2005 – 2006 field seasons using generalized linear models. Pond depth was measured following rain events at 4 sites within a wetland, and the average depth of these four measurements was used as the response variable in statistical models. We predicted pond depth based on the temperature and precipitation recorded at the weather station on Fort Bragg (NOAA 2011), which was less than 10 km from our study wetlands and was the closest available weather station. We developed a set of candidate models to predict water depth in wetlands based on the cumulative amount of precipitation and cooling degree days over 3-, 7-, 14-, and 30-day periods. Cooling degree days were set with a baseline of 50 F rather than 65 F because wetlands showed a tendency to dry rapidly when average daily temperatures exceeded 60 F during late spring (unpublished data). We assessed the relative support our data had for these different models during the 2005 – 2006 season by using Akaike's Information Criterion (Burnham and Anderson 2002). We then validated our best supported model with the data from the 2004 – 2005 season. Finally, we used the best model to predict pond depth for past and future climate conditions. We based predictions for past climate conditions on a 50-year record of climate data from the weather station closest to our study sites. Climate change has already caused precipitation in the southeastern U.S. to become more variable (Li et al.

2009). To predict pond hydrology under future climate scenarios, we used climate data that had been downscaled to a monthly timespan with an average daily temperature and precipitation for each month over our study area based on climate models that assumed low, medium, and high carbon emissions scenarios (B1, A1b, and A2, respectively) provided by the Intergovernmental Panel on Climate Change (IPCC 2007, William et al. 2006). We used output for these scenarios from the Community Climate System Model Version 3, which is a refined climate model that reduces bias from previous models by incorporating new methods to account for various factors that affect climate (Williams et al. 2006). We then applied the past and future climate data to the best statistical model we developed to predict pond depth, and we used our predictions to determine the length of time the wetlands were flooded during the tiger salamander breeding season each year.

Population Modeling

We conducted three analyses to assess population viability of tiger salamanders. We first used a deterministic model of tiger salamander populations to determine how important different vital rates were to population growth, and then used stochastic models to examine population dynamics over a longer time period. We constructed a 2 x 2 population projection matrix that allowed for delayed maturation of subadult tiger salamanders (Figure 1):

$$\begin{bmatrix} 0 & F \\ g & S \end{bmatrix}$$

We parameterized this projection matrix with vital rates that were calculated to coincide with an annual prebreeding census of the salamander population (Figure 1). This projection matrix included terms for adult survival (S), subadult survival and maturation

(g), and effective fecundity (F), which tracks a year's cohort from the point at which individual eggs are laid in wetland breeding sites to the time when young of the year have reached the subadult stage at the time of the next breeding season. These stages capture the important vital rates within this population from the time when breeding creates a new cohort to the time when that new cohort first returns to a pond to breed two years later.

The population model begins with a prebreeding census that measures the number of adult females entering the breeding wetland (Figure 1). Fecundity for each adult female is obtained by selecting a number at random from a normal distribution with published values for the mean and standard deviation of fecundity (Table 1). Although I made an effort to count egg masses within breeding wetlands, I did not account for the variation in water depth and clarity on the detectability of egg masses, so I used a published range of fecundity (Petranka 1998). The observed range of egg masses for the number of breeding females that we observed appears consistent with previously published values of fecundity (Thurgate et al. 2008, Petranka 1998). After obtaining the number of eggs produced by female salamanders, we determined the number of eggs expected to hatch into larvae.

In order to provide a mechanistic link between climate change and salamander demography, we constrained larval recruitment by pond hydroperiod. First, we assumed the size of larval salamanders upon hatching was 9 mm, which is consistent with field observations and published data on this species (Petranka 1998, personal observation). We used this initial size with the data on the size of young salamanders captured leaving the ponds after completing metamorphosis to determine the average growth of larval

salamanders. To determine the average daily growth rate of larval salamanders, we then divided the average growth of larval salamanders by the period of time the pond was flooded after adult salamanders entered to breed. We assumed larval salamanders must reach a minimum size in order to successfully complete metamorphosis, and we set this parameter at 54 mm, which was 5% less than the smallest juvenile tiger salamander that was captured over the course of our study. Finally, we compared the average number of eggs laid to juveniles produced to account for various sources of mortality during the larval stage. This ratio averaged 480:1, and we used this ratio to reduce the number of juveniles that were predicted to complete metamorphosis by the larval growth rate and the period of inundation for the wetland.

When the number of juvenile or subadult salamanders that successfully emerged from the breeding wetland had been calculated, I then calculated the survival of these individuals in the terrestrial environment from the time they emerged from the breeding pond until the onset of the next breeding season to complete my accounting for the production of a new juvenile cohort (Figure 1). Survival estimates for salamanders that have not yet reached reproductive maturity are difficult to obtain. Individuals typically delay reproduction until their second year, and it is difficult to safely mark small juvenile salamanders. Some experimental studies have examined the proportion of juveniles known to be alive within enclosures after a set period of time, but these data are difficult to convert into estimates of survival. Rates of survival can also vary between experimental treatments depending on the presence of cover objects or refugia (Rothermel and Luhring 2005, Rothermel and Semlitsch 2006). Because of these difficulties, I set the annual survival rate of juvenile salamanders to 0.5 (Table 4.1,

Appendix B). This rate is less than the estimated adult survival, and given that juveniles face a higher risk of desiccation than adults and have no prior knowledge of burrow locations or other refugia in the terrestrial environment that adults use during the nonbreeding season, it is reasonable to assume that juvenile survival would not exceed adult survival. I adjusted the annual rate to a daily rate by taking the 365th root of the annual survival rate and applied this to the period of time from which juvenile salamanders emerged from the wetlands until the start of beginning of the next breeding season. Together these calculations provided a measure of the effective fecundity, F , which represented the average number of new juveniles alive at the start of the next breeding season that were produced by an adult female in the preceding breeding season.

Calculation of the growth and maturation of subadult salamanders to adult salamanders, g , and the survival of adult salamanders, S , was more straightforward than the methods used to derive the effective fecundity. As mentioned above, an annual survival rate of juvenile or subadult salamanders was set at an annual rate of 0.5. I assumed that all juvenile salamanders that survived their second year also matured and were able to enter the breeding population as new adults during their second breeding season (Figure 1). Adult survival was estimated using standard open population mark-recapture models with five years of mark-recapture data. This analysis accounted for the process of temporary emigration, which, in the case of breeding amphibians, represents the probability that individuals do not return to a pond to breed (Williams *et al.* 2002, Thurgate *et al.* 2007). Including temporary emigration and modifying the population model to include a stage for nonbreeding adults did not change the relative importance of different parameters in the population models presented here (Appendices A and B).

We then constructed two types of stochastic population models to examine how variation in past and future climate conditions might affect population growth. These models differed in how they accounted for variation in pond hydroperiod. The first model included pond hydroperiod as an independent random variable that was calculated with the mean and standard deviation of the hydroperiod for past or future climate scenarios. The second stochastic model accounted for correlation in successive years of pond hydroperiod. For each model, we ran 1000 simulations that were 50 years in duration. We calculated year-to-year correlation in pond hydroperiod and then incorporated it into stochastic models by using the equation:

$$\varepsilon_t = \rho\varepsilon_{t-1} + \sqrt{\sigma^2 - \rho^2} z_t$$

where ε_t is the environmental deviation in pond hydroperiod at time t , ρ is the correlation coefficient between pond hydroperiods in consecutive years, and z_t is a random number selected from a distribution with a mean of 0 and variance of 1 (Morris and Doak 2002).

We analyzed both population viability and the relative importance of different demographic rates to population growth in the deterministic and stochastic models. First, we conducted standard sensitivity and elasticity analyses on the parameters in the deterministic model to determine the absolute and relative effects, respectively, of changes in vital rates on population growth (Morris and Doak 2002). Although elasticity values assess the proportional changes in parameter values, mathematical properties of elasticities are such that vital rates tend to have smaller elasticities if they are more variable. Thus, while sensitivities and elasticities are informative they may not provide a full picture of the effects of different vital rates on population growth, and their

calculation is less straightforward for stochastic models. For these reasons, we also used life stage simulation analysis (LSA) to assess how strongly variation in vital rates correlates with population growth and what effects changes in vital rates would have on population growth in our stochastic population models (Wisdom *et al.* 2000). Although this approach differs somewhat from traditional sensitivity and elasticity analyses, it still allows for comparisons to be made between deterministic and stochastic population models. A parameter identified as being important to population growth in sensitivity or elasticity analyses would show a strong correlation with population growth in LSA. We compared the sensitivity and elasticity of the effective fecundity (F) from the deterministic model with the correlation between pond hydroperiod and population growth in LSA because pond hydroperiod was the parameter that constrained larval recruitment in our stochastic models. Finally, we created cumulative distribution functions to compare the probability of extinction in simulations where pond hydroperiod was an independent random or autocorrelated variable. Stochastic models used an initial population vector with 25 subadult salamanders and 50 adult salamanders, which are within the range of sizes we have observed at our ponds.

Results

Wetland Hydrology

A model predicting pond depth on a 14-day running total of precipitation and temperature provided the best fit to the data (Table 4.2). The predicted pond depth from the best supported model was strongly correlated with actual pond depth from both the data used to create the model ($r^2 = 0.90$, $p < 0.001$) and with the pond depth data from the

previous year ($r^2 = 0.65$, $p < 0.05$, Figure 4.2). The predicted period of pond inundation each winter for the 58-year period for which we had climate data varied considerably (Figure 4.3). We detected slight first order autocorrelation in the predicted period of inundation for the 58-year period of past climate data ($r^2 = 0.10$), and we used this correlation to account for year-to-year correlation in pond hydrology when simulating wetland dynamics under future climate scenarios.

Projections for pond hydroperiod under future climate scenarios were similar regardless of emissions levels when year-to-year correlation in pond hydroperiod was not incorporated into the model (Figure 4.4). All three climate scenarios showed a similar frequency of pond hydroperiods when pond hydrology was treated as an independent random variable with a mode near 200 days. Years in which pond hydroperiod lasted in excess of 250 days were binned with years that had 250-day pond hydroperiods because salamanders are not paedomorphic in the study population and do not require more than 6 months to complete development.

Year-to-year correlation in pond hydrology had varying effects on pond hydrology under different climate scenarios. Accounting for year-to-year variation in the low emissions (B1) scenario reduced the variance in the frequency distribution of pond hydrologies. Although the mode was still near 200 days, the frequency of 200-day hydroperiods was approximately four times greater than it had been in the model for this climate scenario that did not account for interannual variation in wetland conditions. In contrast to the low emissions scenario, the variation in the pond hydrology under the moderate (A1b) and high (A2) emissions scenarios increased. The moderate emissions scenario showed a bimodal distribution of pond hydrology with dry winters and very wet

winters (>240-day) being most frequent and intermediate pond hydrologies being rare. In contrast to this, the high emissions scenario had moderate peaks in its frequency distribution for winters that were dry or near the 200-day mark, but a higher peak in frequency occurred with very wet (>240-day) hydrologies.

Population modeling

Model parameters used for the deterministic and stochastic population models are shown in Table 4.1. I estimated the annual adult survival rate to be 0.60 (95% confidence interval: 0.49 – 0.71) from an open population mark-recapture model. The deterministic model of tiger salamander population growth showed a population that was in significant decline ($\lambda = 0.84$). Sensitivity analysis indicated that changes in adult survival resulted in larger changes in population growth than changes in larval recruitment or juvenile survival (Table 4.3). Elasticity analysis revealed that proportional changes in larval recruitment and juvenile survival caused similar changes in population growth, but elasticities for both of these parameters were less than half of the elasticity values for adult survival (Table 4.3).

In contrast to the deterministic model, results from stochastic models showed a strong association between pond hydroperiod and population growth in stochastic models, but weak correlations between population growth and other model parameters (Table 4.4). Results from stochastic simulations of populations in past and future climate scenarios were relatively consistent. Population growth was most strongly correlated with pond hydroperiod, and this effect was more pronounced in models that accounted for year-to-year correlation in pond hydroperiod (Table 4.4). However, reduced variance

in the frequency of pond hydroperiod under the low emissions scenario (B1) was associated with a slightly lower correlation between pond hydrology and population growth. The moderate (A1b) and high (A2) emissions scenarios showed the strongest correlation between pond hydrology and population growth (Table 4). Population viability was similar in stochastic models with pond hydroperiod as an independent random and autocorrelated variable. For all stochastic models, populations had a 50% chance of extinction after approximately 15 years, which is likely due in part to the relatively low adult survival rates.

Discussion

The viability of this tiger salamander population is low, and, if emissions increases maintain their present course, will decrease in the future. Under current conditions, tiger salamander viability is already low because of low adult survival. Climate projections suggest that precipitation may decrease over the southeastern U.S. in both summer and winter (Mearns et al. 2003). Under climate scenarios with increased frequencies of dry breeding seasons, high correlation between pond hydrology and population growth makes this amphibian even more vulnerable.

This increased risk of extinction is driven by year-to-year variation in wetland conditions rather than the overall average change in precipitation and temperature, as changes to wetland hydrology constrains larval recruitment (Figure 4.5). When exposed to variation in hydrology associated with climate change, the relative importance of different demographic rates to population growth shifts. Although life history theory predicts that adult survival is more critical for the viability of long-lived species than

juvenile recruitment (Crouse et al. 1987), we find that climate-mediated variation in environmental conditions enhances the importance of juvenile recruitment to salamander population growth (Table 4.4).

Our findings should apply more generally to species in variable environments: if a life stage is strongly associated with environmental variation, then a reduction in the frequency of favorable environmental conditions should make that life stage more critical to population growth. In the case of amphibian demography, an increased frequency of shorter hydroperiods, which could occur from either shorter pond hydroperiods becoming more frequent or from stronger correlation in pond hydrology from one year to the next, causes larval recruitment to have a stronger effect on population growth. This property of populations in variable environments is corroborated by theoretical studies that have examined selection pressures in variable environments (Orzack and Tjulakapar 1989). Low population viability in all stochastic population models is due to the correlation in the model of pond hydroperiod from climate data and the relatively low survival estimates for adult tiger salamanders, and highlights the sensitivity of amphibians to climate-mediated shifts in wetland hydrology.

Our results reinforce the need for caution when interpreting sensitivity and elasticity analyses from deterministic models of population growth (Wisdom et al. 2000, Mills et al. 1999, Wisdom and Mills 1997). Adult survival had the highest sensitivity and elasticity values of any parameter in our deterministic model, but stochastic simulations revealed that population growth was more strongly associated with pond hydroperiod, and thus effective fecundity, than adult survival. This apparent contradiction between the models is caused by the low parameter estimate for larval recruitment used in our

deterministic model. We never observed high levels of recruitment in our study population, so the range of variation in this parameter was lower for the deterministic model than it was in the stochastic models. We caution against discounting the importance of adult survival too much because correlation between adult survival and weather conditions affecting pond hydroperiod could increase the relative importance of adult survival to population growth.

Conservation of wetland-breeding amphibians like the tiger salamander depends upon maintaining wetland hydrology, which may be subject to threats from both shifts in the timing of precipitation and increases in the year-to-year variability of precipitation. Like many amphibians, tiger salamanders respond to environmental cues to initiate breeding during the late fall and early winter months (Petranka 1998). This means that the seasonal component of when wetlands become inundated is as important as the period of time they remain inundated (Todd et al. 2010). In addition, if wetlands become flooded too far in advance of the onset of the breeding season, then predatory aquatic invertebrates like odonate larvae or aquatic beetles could become established in wetlands, and this might result in reduced survival rates for amphibian larvae (Wilbur 1997). Our models of pond hydrology did not address the potential for wetlands to remain flooded from one year to the next because low temperatures during the summer in our study area generally exceed highest temperatures we recorded during winter and late spring. Attempts to extrapolate pond depths would be challenging as we lack field data documenting wetland hydrology during such high temperatures, but additional field data could be collected to address this issue.

Finally, the increased use of water resources associated with human development could be an important issue for amphibian conservation. Our study sites were artificial wetlands that typically dried completely at least once during a year. Natural wetlands may also be ephemeral, but unlike artificial wetlands, the hydrology of natural wetlands is often buffered by groundwater. Following wet periods, natural wetlands may remain inundated longer than artificial wetlands. Conversely, artificial wetlands fill more quickly than natural wetlands during droughts. This is significant because if water use increases enough to depress groundwater levels, then natural wetlands may experience a shift in their hydrology, functioning more like artificial wetlands that lack a source of groundwater to buffer against pond drying. Reductions in groundwater levels could cause natural wetlands to dry more rapidly and prevent amphibian recruitment from occurring. Our predictive model for pond depth at an artificial wetland was simpler than models for natural ponds because we assumed that pond depth depended solely on precipitation and evaporation and that there was no link between pond level and groundwater levels. Natural wetlands are more likely to vary in their hydroperiod than artificial wetlands because of localized differences in soil composition and groundwater flows (Sun et al. 2000). This natural variation in wetland hydrology could potentially benefit amphibians, but only if groundwater levels are not depressed to the point that wetlands flood less frequently.

Conservation of amphibian species is a challenging endeavor, and a diverse group of factors has been tied to amphibian declines around the globe. Our research highlights how different vital rates act to limit population growth under changing climate conditions. For wetland-breeding species like the tiger salamander, conservation of both

breeding wetlands and upland forest is essential to the maintenance of viable populations, but when adult populations are low or wetland conditions become more variable, larval recruitment becomes more critical. Climate change may complicate matters by altering wetland hydrology in different ways depending upon the emissions scenario in question and other factors like the demand for water resources. We suggest that conservation efforts for these species should focus on protecting natural landscapes that contain wetlands that vary in their hydrology. Protecting natural variation in wetland hydrology now may increase the likelihood that there will be at least some wetlands with suitable hydrology for amphibian breeding under future climate regimes. Protecting landscapes of wetlands may allow different subpopulations to enhance the overall viability of a species in an area through rescue effects (Brown and Kodric Brown 1977, Petranka 1998).

Recent research has demonstrated that variability in weather patterns in the southeastern U.S. has already changed, likely as a result of human-caused climate change (Li et al. 2011). I show that variability that results from climate change can have strong impacts on species. The tiger salamander population I studied appears to be in decline and would be at great risk of extinction under moderate or high emissions scenarios when year-to-year variation in wetland conditions is accounted for. Effective conservation strategies for species that are sensitive to increased variability in climate must focus on mitigating the negative effects of this variation on critical life stages.

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1 **Table 4.1.** Parameters used in deterministic and stochastic population models of tiger salamanders.

2

<i>Deterministic model</i>	<i>Parameter estimate</i>	<i>Data Source</i>
Effective fecundity	0.40	This study and Petranka (1998)
Subadult survival	0.50	Petranka (1998)
Adult survival	0.60	This study
<i>Stochastic models</i>		
Fecundity	200 eggs/female (st. dev = 10)	Petranka (1998)
Larval growth rate	0.35 mm/day (st. dev = 0.03)	This study
Subadult survival	0.50 (st. dev = 0.05)	Petranka (1998)
Adult survival	0.60 (st. dev = 0.05)	This study

Table 4.2. Linear models predicting pond depth as a function of cumulative precipitation and cooling degree days over varying time periods.

Model	β_{rainfall} (SE)	$\beta_{\text{temperature}}$ (SE)	AIC
14-day running total	6.42 (3.04)	-0.05 (0.02)	290.2
7-day running total	13.41 (3.91)	8.49 (2.80)	293.0
3-day running total	17.46 (5.40)	10.44 (2.51)	294.1
30-day running total	4.87 (3.29)	0.01 (0.02)	301.7

Table 4.3. Elasticity and sensitivity values for parameters in a deterministic model of tiger salamander population growth.

Parameter	Sensitivity	Elasticity
Larval Recruitment	0.464	0.222
Juvenile Survival	0.371	0.222
Adult Survival	0.778	0.557

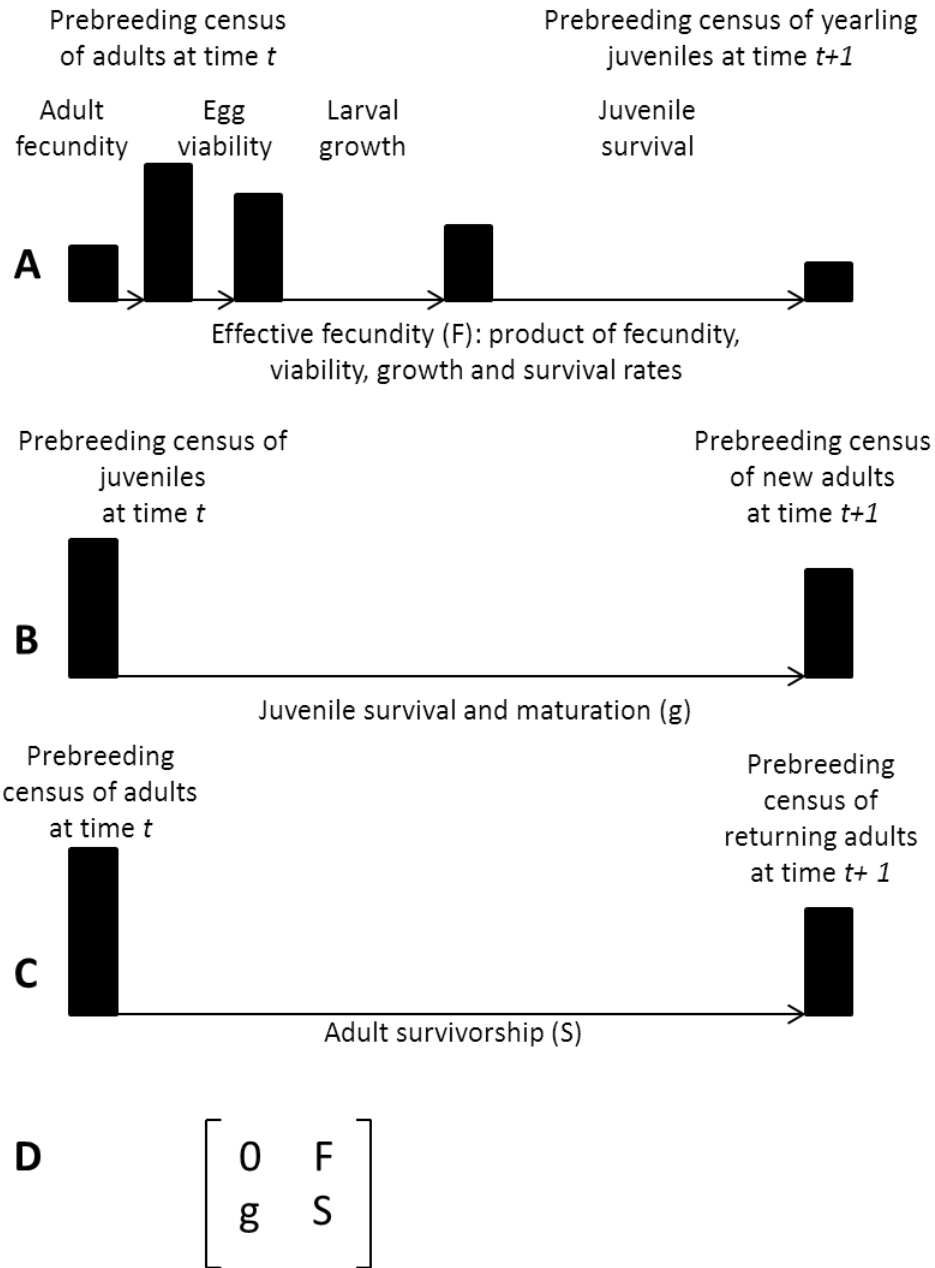


Figure 4.1. Graphical representation of vital rates incorporated into projection matrix for a tiger salamander population with a prebreeding census of the population (modeled after Morris and Doak [2002]). Height of bars is not to scale, but represents relative increases or decreases in number of individuals between successive censuses of the population.

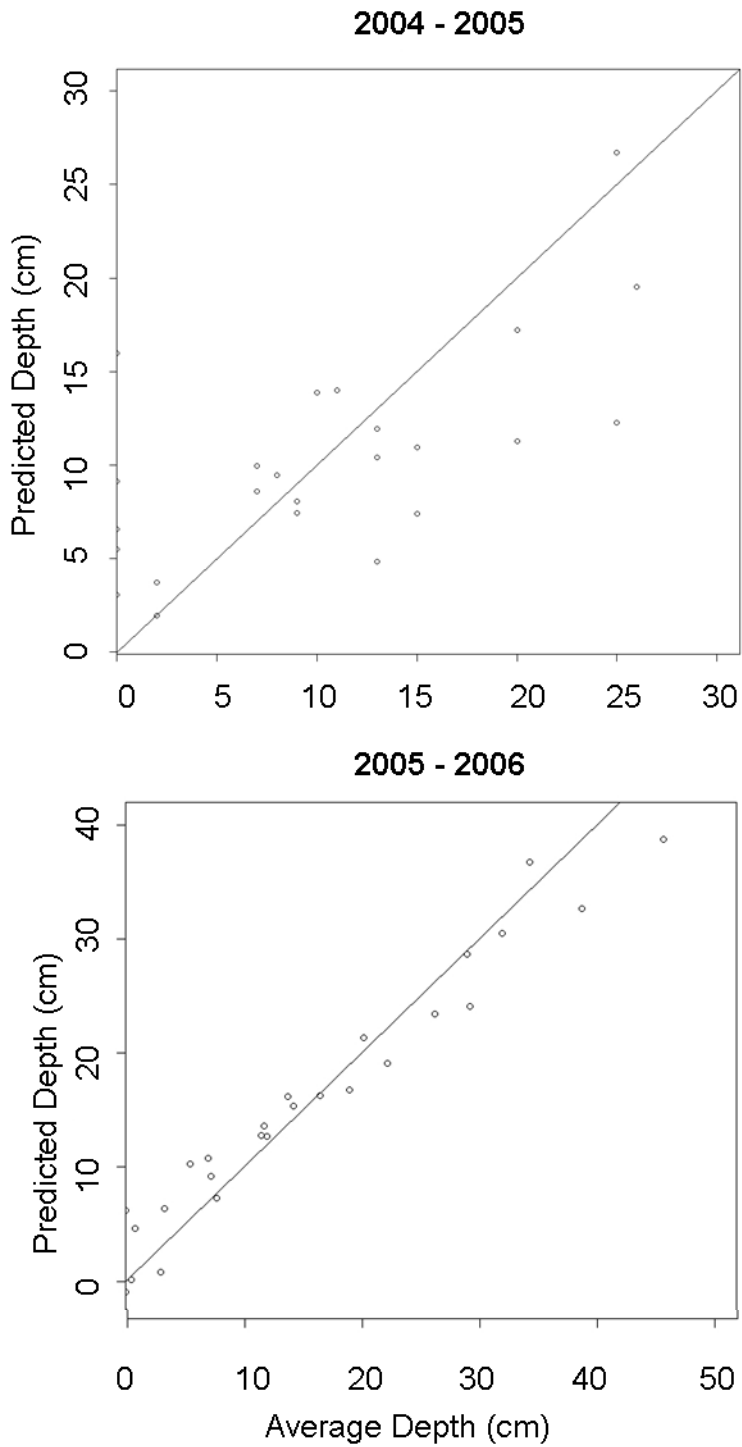


Figure 4.2. Predicted and average actual depth measured at reference points within artificial wetlands based on a linear model.

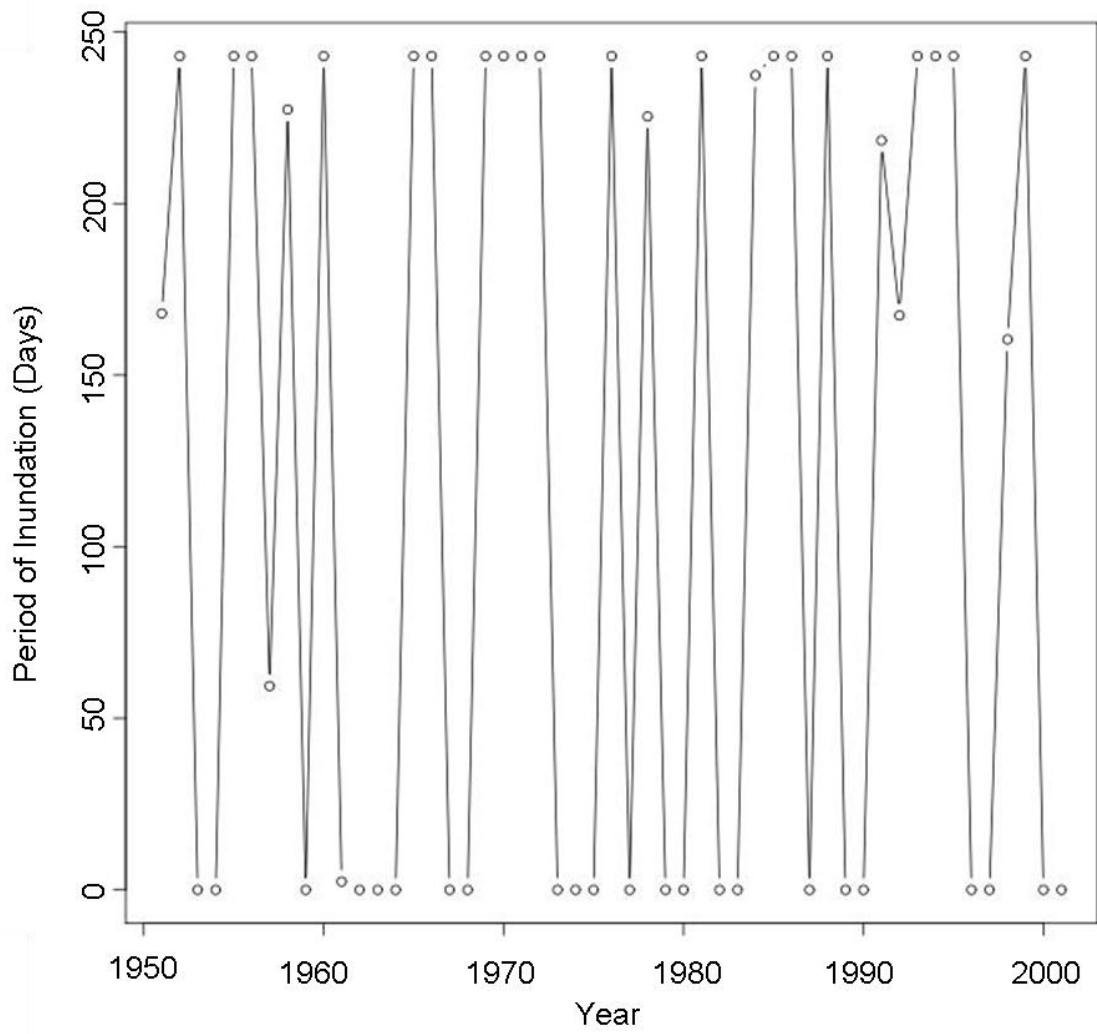


Figure 4.3. Predicted wetland hydrology for the study area from 1950 – 2000.

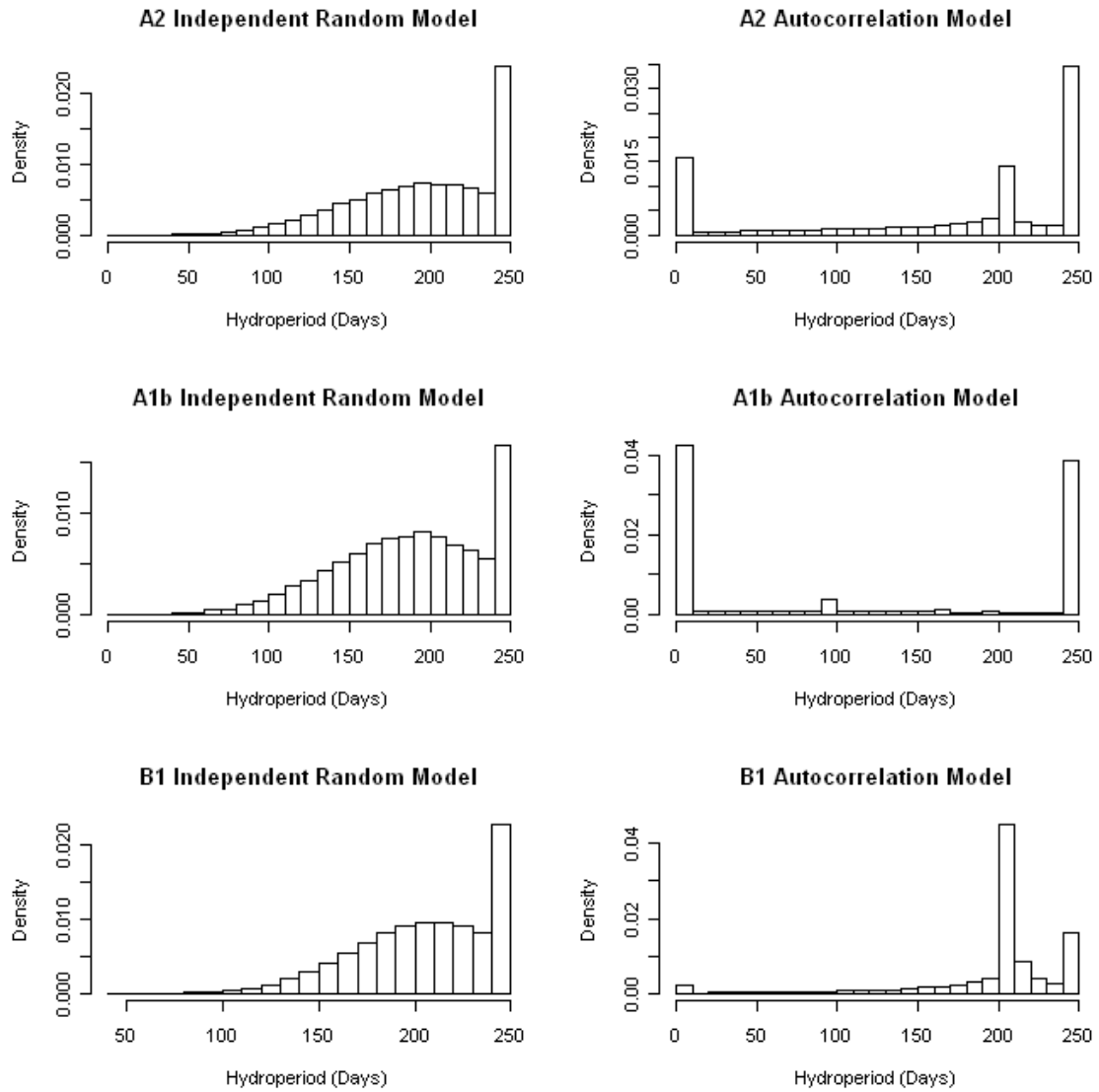


Figure 4.4. Frequency distributions of wetland hydroperiods under different climate scenarios that treat wetland hydrology as an independent random or autocorrelated variable.

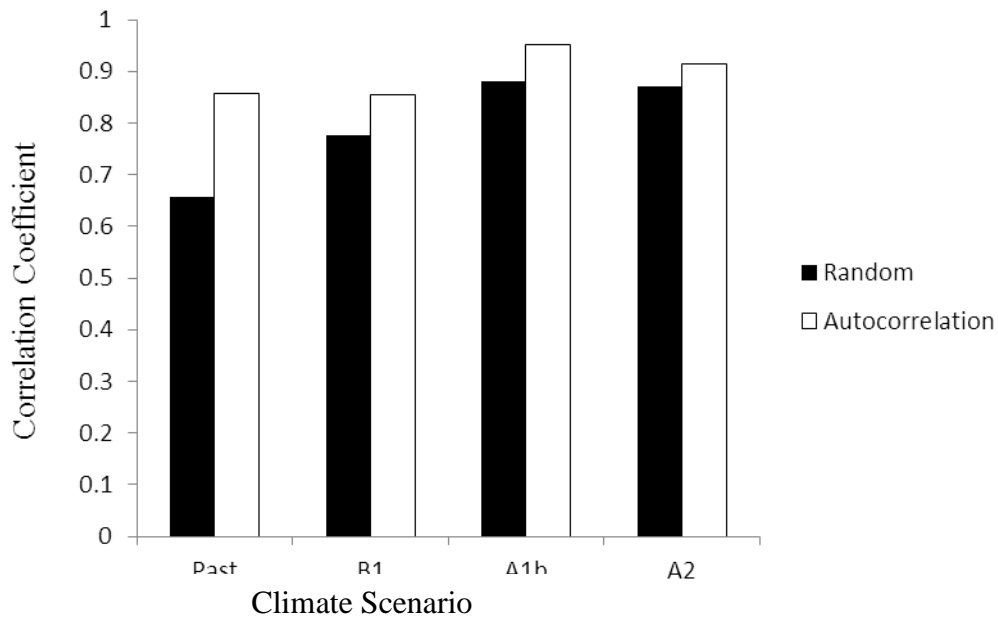


Figure 4.5. Correlation between wetland hydroperiod and population growth for stochastic population models with wetland hydroperiod included as an independent random or autocorrelated variable under past climate (1950 – 2000), low (B1), moderate (A1b), and high (A2) emissions scenarios. Correlations between population growth and adult survival, subadult survival, adult fecundity, and larval growth rates were not significant ($r^2 < 0.001$, $p\text{-value} > 0.05$).

CHAPTER 5: LARVAL CONDITIONS DETERMINE JUVENILE DISPERSAL BEHAVIOR IN ORNATE CHORUS FROGS

Abstract

Dispersal behavior is an important process that affects landscape connectivity for species, and studies of landscape connectivity are increasingly common as researchers seek to better understand how species are affected by habitat loss and fragmentation. However, many studies of landscape connectivity ignore implicit assumptions about dispersal behavior that might be violated. I examined the effects of larval conditions on the dispersal behavior of juvenile ornate chorus frogs with two experiments to test the assumption that individuals at similar life stages within a species exhibit similar dispersal behaviors. I reared ornate chorus frog tadpoles in cattle tanks at high and low densities to produce juvenile frogs that were then released in two experiments: one experiment to examine how larval conditions affected behavior in forest and open habitats, and a second experiment to test how larval conditions affected behavior within forest habitats where groundcover had been removed. In the first experiment, I found that juvenile frogs reared at low densities moved faster in open habitats than they did in forested habitats, but larval density did not affect movement rates of frogs in forest habitats. In the second experiment, I found that movement rates of juvenile frogs reared at different densities were similar in forest habitats where ground cover had been removed. The body size of frogs reared in low density tanks was significantly greater than that of frogs reared in high density tanks in the first experiment, but this size difference disappeared over time, and frogs from the two larval treatments were of a similar size in the second experiment. Increased body size may reduce desiccation risk, and this could be the mechanism

responsible for the observed differences in dispersal behavior in the first experiment. These findings suggest that landscape connectivity studies should carefully test the assumption that individuals within a population exhibit similar dispersal behaviors, especially if certain traits are known to be related to fitness, as is the case with amphibians. The variable nature of amphibian breeding sites may produce individuals with different dispersal capabilities in different years, so knowledge of larval conditions could be as important as mapping dispersal habitat for assessing landscape connectivity.

Introduction

Landscape connectivity is considered an important process that could mitigate the negative effects of habitat loss and fragmentation on populations (Gilbert-Norton et al. 2010). In spite of the increasingly prominent role of landscape connectivity research, many studies fail to address underlying assumptions regarding landscape connectivity (Beier et al. 2008). Researchers commonly employ a spatially explicit assessment of landscape connectivity where discrete habitat types are mapped, and individuals are assumed to follow different movement rules in these habitat types. In order to simplify analyses, it is often assumed that all individuals within a population exhibit similar movement behavior. However, individual variation is known to be important for reproduction and dispersal behavior, so it is likely to play an important role in movement behavior as well. To test these assumptions about the underlying mechanisms that affect landscape connectivity I designed a series of field experiments to examine the effects of individual variation on the movement behavior of ornate chorus frogs (*Pseudacris ornata*).

Amphibians are especially useful for examining the role of individual variation in movement behavior and connectivity for several reasons. First, there is considerable knowledge about the effects of phenotypic plasticity in amphibians on a variety of life history traits, and it is easy to manipulate experimental conditions to induce phenotypic plasticity in amphibian larvae (Wilbur 1997). The condition of amphibians at the time of metamorphosis is related to survivorship and fecundity of individuals later in life (Chelgren *et al.* 2006, Goater 1994), and a variety of factors from predation to competition and environmental contaminants may interact in complicated ways to affect the condition of juveniles at metamorphosis (Miner *et al.* 2005, Wilbur 1997). Second, the very nature of temporary wetlands where many amphibian species breed makes dispersal an important ecological process for amphibian populations. The natural drying of temporary wetlands where many amphibian larvae develop forces individuals to move away from their larval habitat. Moreover, adult amphibians often exhibit high rates of philopatry to breeding wetlands, so dispersal of juveniles is likely to play an important role in maintaining amphibian populations in fragmented landscapes (Cushman 2006). Third, amphibians as a group are currently in decline, and many species are vulnerable (Beebee and Griffiths 2005). Several studies have documented how far amphibians move from breeding wetlands and how these movements are affected by forest management practices (Todd *et al.* 2009, Semlitsch 2008), but research on how individual variation and small scale changes in habitat structure affect dispersal will provide broader lessons for conserving species in fragmented landscapes while simultaneously resulting in specific lessons for amphibians undergoing population declines.

I conducted experiments to examine factors associated with the movement ecology of amphibians as they leave breeding ponds. First, I manipulated larval density of ornate chorus frogs to determine how variation in larval conditions affects movement behavior in forest and field habitats. Although the dispersal of juvenile amphibians has been studied by others, important questions remain unresolved. Chelgren *et al.* (2006) observed juvenile red-legged frogs (*Rana aurora aurora*) leaving natal ponds and found that smaller body size and delayed timing of metamorphosis resulted in slower dispersal rates. Patrick *et al.* (2008) examined patterns of habitat selection and mortality for juvenile wood frogs (*Rana sylvatica*) and found that habitat selection was affected by coarse-scale rather than fine-scale variation in habitats, which resulted in high densities of juveniles in suitable habitats that were associated with higher density-dependent mortality. However, experiments examining the effects of larval conditions on juvenile movement behavior in habitats that vary in suitability are lacking. Here I manipulate larval density of ornate chorus frog tadpoles to test for the effects of variation in body condition on movement behavior in high and low quality habitats where low quality habitat reflects common management practices. I initially compared movement behavior of frogs reared at different densities in forest and field habitats. Previous experiments have demonstrated that dispersing amphibians are at greater risk of desiccation in field habitats than in forested habitats (Rothermel and Semlitsch 2002). I predicted that frogs raised at low densities would be larger and move more rapidly than frogs reared at high densities regardless of the habitat in which they are released following the pattern observed by Chelgren *et al.* (2006).

Whereas my first experiment tested for density-dependent effects on individual behavior in different habitats, my second experiment tested for individual variation in response to microhabitat variation within the dominant, woodland habitat. I manipulated microhabitats by raking pine straw because this has been linked to changes in amphibian behavior (Moseley et al. 2004), it is a common forestry practice in the southeastern U.S., and it is also reduced by both natural and prescribed fires. Because amphibians are expected to move faster through lower quality habitats (Rosenberg et al. 1997), I expected that both of our study species would move faster through areas in which pine straw had been harvested. I also hypothesized that, in their escape from unfavorable habitats, amphibians would move in more direct paths in order to minimize their time spent in those habitats (Rosenberg et al. 1997). Through this experiment, I assessed how variation in microhabitat structure heterogeneity affects amphibian movement rates and behavior, (see Roznik and Johnson 2010). These experiments provide important insights into our understanding of movement ecology, dispersal behavior, and landscape connectivity by providing information on the underlying mechanisms that determine dispersal behavior to test assumptions regarding landscape connectivity.

Methods

Study area

I conducted my field experiments with ornate chorus frogs at Fort Bragg, North Carolina, a 65,000-ha military installation located within the sandhills region of southern North Carolina. Ornate chorus frogs breed in ephemeral wetlands that typically remain flooded for a period of several months between November and May. These breeding

sites are surrounded by longleaf pine (*Pinus palustris*) woodlands in upland areas, riparian forest that is dominated by hardwood species, open fields, and developed areas. Microhabitat structure within each of these broad habitat types varies due to both natural and anthropogenic disturbances. Ground cover, for example, includes a variety of elements from coarse woody debris to pine straw and grasses. These elements are manipulated by humans through management activities such as prescribed burning, removal of pine straw for mulch, and mowing. These activities modify the surface upon which pond-breeding amphibians travel during breeding migrations. Fort Bragg hosts multiple rare species of pond-breeding amphibians of conservation concern, including the ornate chorus frog, as well as the gopher frog (*Rana capito*) and the tiger salamander (*Ambystoma tigrinum*).

Tadpole Rearing

I selected the ornate chorus frog as a model species because it is more abundant than other rare amphibians and it is easier to rear in cattle tanks. Because few areas are known to support ornate chorus frog populations within the sandhills region of North Carolina, I collected 24 ornate chorus frog egg masses from one wetland on 2 February 2010, when ornate chorus frogs were most abundant. Egg masses were held in containers filled with pond water at room temperature for 7 days until the eggs hatched. After larvae became free swimming, they were randomly assigned to 20 500-L cattle tanks. These cattle tanks had been fitted with screened standpipes and allowed to fill naturally with rainwater over a 3-month period prior to the collection of tadpoles. I added window screen covers to cattle tanks in mid-January and examined tanks carefully to verify that

aquatic invertebrates had not colonized tanks. Three days prior to the introduction of tadpoles to the tanks, I added 100 L of dry longleaf pine needles collected from Fort Bragg. I also collected phytoplankton and algae from the pond where egg masses were collected with a 80-micron plankton net, and I added 500mL of pond water containing plankton and algae to each tank. Each tank was randomly assigned a high or low density of tadpoles (40 or 20, respectively). Densities were selected based upon densities commonly used in other amphibian experiments to produce effects of intraspecific competition (N. Y. Thurgate, personal communication).

I monitored the cattle tanks three to five times each week to check for leaks, ensure the screens covering tanks and standpipes remained in place, and to assess the status of the outflow of water through standpipes during and after periods of rain. This continued over a 12-week period, and I allowed the water levels in the cattle tanks to lower naturally in late April as tadpoles began to mature. Water levels declined 8 – 10 cm over this time period, and all tanks were lowered to a depth of 20 cm when tadpoles initiated metamorphosis. I collected juvenile frogs from cattle tanks as they completed metamorphosis, weighed them to the nearest 0.01 g, held them in controlled conditions in a laboratory, and fed them wingless fruit flies *ad libitum* until they were used in field experiments. I initially collected data on hind leg and body length for frogs as well, but I discontinued this after finding no difference between frogs from high and low density tanks. Frogs that completed metamorphosis more quickly were used in the first experiment to examine the effects of larval density and habitat type on movement behavior. When this experiment was completed, the remaining frogs were used in a

second experiment that examined the effects of larval density and microhabitat type on movement behavior.

Experiment 1

To test the effects of larval density and habitat structure on movement behavior of juvenile frogs, I established two 20 x 20m release plots at each of 4 sites (n = 8 plots) in areas of pine forest and open fields. I randomly assigned one frog reared in a high density tank and one frog reared in a low density tank to each plot during each bout of releases. Each night of field trials involved a set of releases at a randomly selected field and forest site in order to control for potentially confounding variables that might have varied by night. Releases were conducted on nights that were overcast and humid or rainy because frogs tend to shelter in place rather than moving on dry nights (Frock unpublished data). I conducted releases at night between 2100 and 0300, and I randomly selected the order of plots used for releases on each night.

I released juvenile frogs one at a time in plots until 4 – 6 frogs had been tracked on all plots. I marked frogs with DayGlo dye powder along their ventral surface, placed them in the center of the plot facing a randomly determined cardinal direction, and then left the vicinity for 3 minutes to allow them to move. After 3 minutes, I returned to the plot with a UV light and followed the trail of dye powder from the release point to the frog. I carefully delineated the trail of dye powder deposited by the frog with pin flags. Juvenile frogs moved primarily by hopping rather than crawling, and they deposited small clusters of dye powder where they landed. Thus, the trail of dye powder consisted of a series of clusters rather than a continuous track of powder. I assumed that frogs

moved from one cluster of powder to the nearest point of powder rather than jumping to a point farther away and then turning around and jumping back. This was a reasonable assumption because frogs were generally found facing the direction in which they were traveling. After following frogs for nine to twelve minutes, I recaptured the frog and rinsed any remaining dye powder off its ventral surface. The duration of time that frogs were allowed to move was determined by the rate of rainfall. Moderate rainfall washed away most dye powder after twelve minutes, so it was not feasible to track frogs for longer periods of time. Releases were sometimes shortened to avoid losing individuals during heavy rain. Initially, each step of a movement path was measured to the nearest centimeter, and the sum of these steps was used to calculate the total distance frogs moved. I also measured the straight-line distance from the release point to the final point where the frog was observed to obtain a net distance moved by each frog during its movement bout, and I recorded the total time frogs had to move so that movement rates could be calculated for all individuals. Frogs were released in the vicinity of their natal pond after being used in release experiments.

Experiment 2

In a second experiment, I compared the movement behavior of juvenile ornate chorus frogs in forest plots from the first experiment with forest plots where pine straw had been removed to examine the effects of microhabitat structure and larval density on movement behavior. I selected 3 additional 20 x 20-m forest plots where pine straw had been previously raked in January (4 months prior to releases) for another experiment that evaluated the effects of microhabitat manipulation on the movement behavior of ornate

chorus frogs and eastern newts. The effect of raking on ground cover was still apparent because no significant amount of new pine litter accumulated in late winter and early spring and the growing season for herbaceous plants had just begun. I randomly assigned pairs of frogs from high and low density tanks to be used in releases in raked plots. I marked frogs and measured movement paths as described above. Each night of releases included a pair of releases at each of the three plots, and the order of plots used in releases was randomly assigned.

Data Analysis

I compared the weight, body length, and hind leg length of juvenile frogs in the first experiment with t-tests. I examined the effects of larval density and habitat type on movement behavior in each experiment with a two-way ANOVA. I used two measures of movement behavior as response variables: the net distance moved (cm) and the linearity of movement paths, which was determined by dividing the net distance of a path by the total distance moved along each segment of a path. I tested movement rates and path linearity for normality with a Kilmogorov-Smirnov test, and I log-transformed data when necessary.

Results

Experiment 1

In experiment 1, I released 19 juvenile ornate chorus frogs in 4 forest plots and 19 juvenile ornate chorus frogs in 4 field plots between 17 May 2010 and 27 May 2010. I recorded data on both body length and hind leg length for the first 12 frogs that I used in

release experiments. Mean body length of low density frogs (11.8mm, standard deviation = 0.51mm) was similar to the mean body length of high density frogs (11.9, standard deviation=0.49mm). Hind leg length was also very similar between frogs from low density tanks (mean = 16.0mm, standard deviation = 0.26mm) and high density tanks (mean = 15.9, standard deviation = 0.36mm). I did not continue to record data on leg length and body length for other frogs used in the release experiments. The average weight of frogs from high density tanks was initially lower than that of frogs from low density tanks, but this difference disappeared over time (Figure 5.1). However, when all the frogs used in the releases for the first experiment were compared, the frogs from low density tanks were significantly heavier than frogs from high density tanks (mean(low density)=0.57g, mean(high density)=0.47g, $t = 3.07$, $p=0.004$).

The main effects of larval density and habitat type did not have a significant effect on the distance moved by juvenile frogs (Table 5.1). However, I found a significant interaction between larval density and habitat type; frogs from low density tanks moved farther in field habitats than frogs from high density tanks. Juvenile frogs reared at low densities traveled farther in fields than in forests, but there was no effect of larval density on the distance moved in forest plots (Table 5.1, Figure 5.2). Juvenile frogs from low density tanks moved an average of 229.4 cm (standard deviation = 139.4cm) in field plots and an average of 189.6 cm (standard deviation = 75.6 cm) in forest plots, while juvenile frogs from high density tanks moved an average of 136.1 cm (standard deviation =93.5cm) in field plots and an average of 159.3 cm (standard deviation = 139.3 cm) in forest plots. The linearity of movement paths was similar in forest and field plots regardless of larval density (Table 5.1).

Experiment 2

In experiment 2, an additional 18 juvenile ornate chorus frogs were released in raked plots within forested areas between 27 May 2010 and 29 May 2010. I was unable to collect data on the movement path of one frog due to rain washing away dye powder, so that frog was excluded from the analyses. The mean weight of low density frogs (0.47g, standard deviation = 0.07) was similar to the mean weight of high density frogs (0.45g, standard deviation = 0.05) used in these releases ($t=0.08$, $p=0.94$). In contrast to the first experiment, I found no effect of raking, larval density, or an interaction between raking and larval density on either the distance moved or the linearity of movement paths (Table 5.1). Frogs from low density tanks that were released in raked plots moved an average of 158.4 cm (standard deviation = 73.8 cm), while frogs from high density tanks released in these plots moved an average of 113.0 cm (standard deviation = 95.1 cm).

Discussion

My results provide strong evidence that larval conditions affect the habitat-specific movement behavior of juvenile frogs (Figure 1, Table 1). The pattern I observed of frogs reared at low density moving faster in field habitats could be explained by tradeoffs in risks associated with moving through novel environments. Juvenile frogs might seek to minimize the risk of desiccation by either moving faster to find refugia, or by staying in place and adopting a body posture that minimizes their rate of water loss. Studies of adult wood frogs (*Rana sylvatica*) show that individuals that remain still retain water better than individuals that move short distances within leaf litter, and frogs tend to

remain at their current location rather than move during dry periods even if they have begun to desiccate (Rittenhouse et al. 2009). Frogs used in our first experiment were larger on average if they were raised at low densities, so this difference in body size should reduce their risk of desiccation and might increase the likelihood of movement in poor quality habitat. Elevated movement rates through poor quality habitat have also been found in studies of butterflies (Kuefler et al. 2010).

Although the movement of frogs in open habitats was dependent upon larval density, this pattern did not hold in forest plots. However, other studies have shown that density-dependent mortality in terrestrial habitats is an important factor for both larval and adult anurans (Harper and Semlitsch 2007, Patrick et al. 2008). Individuals that came from higher larval densities might move more in order to reduce the chance of settling in areas with high densities of conspecifics, which could increase their risk of mortality. However, our experimental releases consisted of individual frogs being released on their own. It is possible that the behavior of groups of frogs might differ from the behavior of individual frogs. While our experiments were not designed to examine the effect of frog density in the terrestrial environment on movement behavior, additional studies could easily be done to examine this issue for ornate chorus frogs. This could be done by using a drift fence to construct a long narrow enclosure and placing pitfall traps along the inner edge of the enclosure (Pechmann 1995, Rosenburg et al. 1997, Moody et al. 2011). This would provide frogs with an opportunity to move up or down a narrow linear enclosure away from a release point. Frogs could be individually marked to allow for calculation of movement rates based upon subsequent captures of individuals within pitfall traps, and capture data on individual frogs could be used to

estimate survival rates. Given the natural variation in the abundance of juvenile amphibians leaving breeding ponds (Wilbur 1997), it is not surprising that density-dependent mortality in terrestrial habitat might play a role in determining movement behavior of dispersing individuals.

Although I found strong evidence that larval conditions affect juvenile movement behavior in open habitats, I did not see an effect of larval conditions on ornate chorus frog movement in plots where ground cover had been removed by raking away pine straw. This could be due to the decline in the difference in body sizes over time of frogs from the two larval densities. I conducted this experiment later, and as a result the frogs that were used from low and high density tanks were of a similar size. If response to desiccation risk is important in determining movement behavior, then similarity in body sizes might account for the similar movement behavior. However, release experiments with other amphibians in these study plots produced conflicting results. Adult eastern newts moved farther in raked plots, and adult ornate chorus frogs showed no difference in movement behavior in raked and unraked plots (Moody et al. 2011). Repeating this experiment with juvenile frogs from different densities that exhibit differences in body size would help clarify these results.

My experiments illustrate an important lesson for studies that seek to assess landscape connectivity for species. It is frequently assumed that all individuals within a population exhibit similar movement behavior (Beier et al. 2008, Revilla and Wiegand 2008). I have shown that larval conditions may determine movement behavior in more stressful habitats for juvenile frogs (Figure 5.2, Table 5.1). In thinking about whether the assumption that individuals within a population exhibit similar behavior might be valid, it

may be helpful to consider whether there are traits within a population that are known to correlate well with fitness. In amphibians, body size is known to affect adult fitness in general (Semlitsch et al. 1988) as well as survivorship of juvenile amphibians (Patrick et al. 2006). Basing landscape connectivity studies on empirical movement data provides the clearest way to assess the potential effects of individual variation on dispersal behavior. However, it may not always be feasible to conduct multiple experiments to examine the effects of different factors on the movement ecology of a species. If empirical data are not obtained for landscape connectivity studies, then I echo the concerns of Beier et al. (2008): it becomes essential to conduct sensitivity analyses to determine how important violating the assumption that individuals within a population behave in a similar manner is. Finally, if dispersal behavior is determined by larval conditions, then knowledge about conditions within breeding ponds may be as important in assessing landscape connectivity as mapping dispersal habitat in upland areas.

These experiments also provide some intriguing insights into the population ecology of amphibian species. The conditions of amphibian breeding sites are variable over time, with the communities of predators and competitors shifting from one year to the next along with the duration of time that a site remains flooded (Wilbur 1997). These factors can have strong effects on the condition of amphibians at metamorphosis, which in turn influences the dispersal behavior of juvenile amphibians (Goater 1994, Chelgren et al. 2006). Ultimately, it is possible that amphibians might be subject to the “silver spoon effect” – that is, individuals that originate in better habitats as larvae could be more likely to settle in better quality habitat as adults (Stamps 2006). Body conditions that favor resistance to desiccation and faster movement rates in poor dispersal habitat could

result in individuals that emerge from better larval conditions being stronger dispersers. Since high rates of site fidelity have been reported for some amphibian species, juveniles likely play an important role in colonizing new breeding sites (Gamble et al. 2007). This is an intriguing area for further research on the link between wetland conditions, juvenile dispersal, and the spatial dynamics of amphibian populations. Further research on the factors affecting juvenile dispersal in amphibians will assist in conservation planning for these species as well as revealing new information about the underlying spatial dynamics in amphibian populations over time.

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1 **Table 1.** Two-way ANOVAs comparing the effects of larval density and habitat type on juvenile ornate chorus frog movement speed
 2 and path linearity.

3

Release Experiment	Effect	df	F	p-value
Forest vs. Field: Movement Speed				
	Larval Density	1	0.3803	0.5415
	Habitat Type	1	0.0048	0.9453
	Larval Density * Habitat Type	1	4.6712	0.0378
Forest vs. Field: Path Linearity				
	Larval Density	1	0.2594	0.6140
	Habitat Type	1	1.5019	0.2291
	Larval Density * Habitat Type	1	0.1197	0.7315
Raked vs. Unraked: Movement Speed				
	Larval Density	1	0.3550	0.5557
	Raking	1	1.4533	0.2374
	Larval Density * Raking	1	0.5850	0.4503
Raked vs. Unraked: Path Linearity				
	Larval Density	1	1.5540	0.2229
	Raking	1	0.1124	0.7399
	Larval Density * Raking	1	0.0335	0.8561

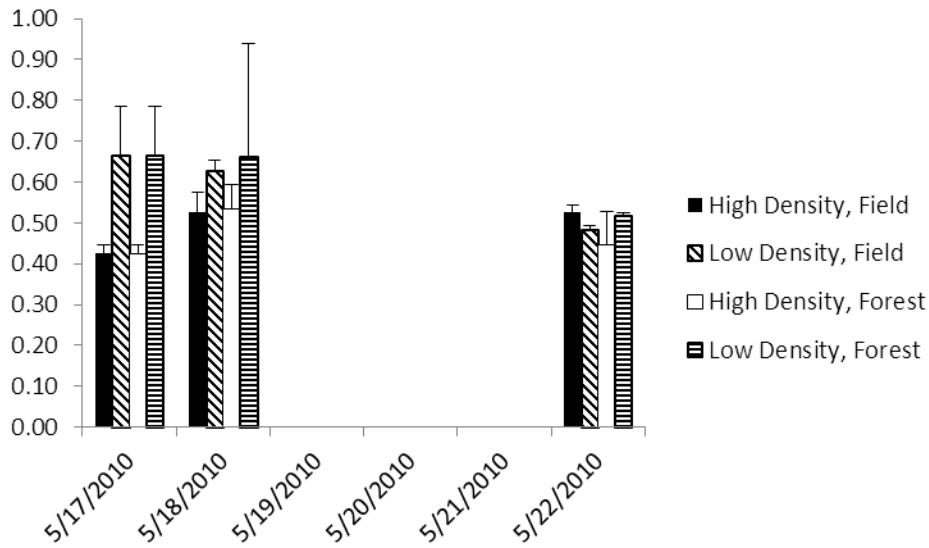


Figure 5.1. Average weight (g) of juvenile ornate chorus frogs used in experimental releases at forest and field sites on Fort Bragg, NC, for days in which at least two frogs from a density treatment were released in a given plot type. Frogs from low density tanks were heavier, on average, than frogs from high density tanks ($t=3.07$, $p=0.004$), even though the average weight of frogs from the two treatments began to converge over time.

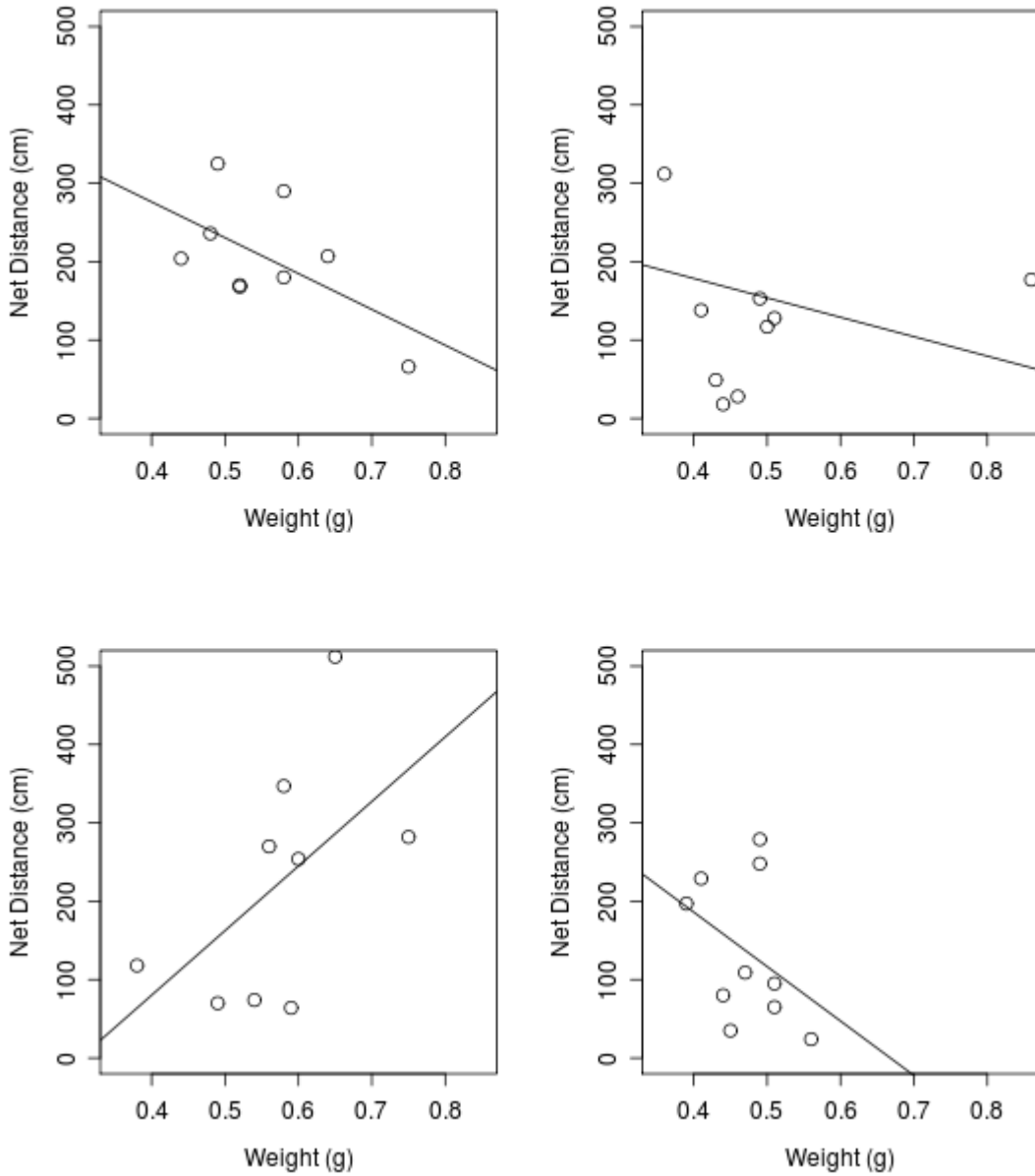


Figure 5.2. Net distances moved by frogs of varying weights that were released in field or forest sites on Fort Bragg, NC, and came from low or high density tanks.

APPENDICES

APPENDIX A. TEMPORARY EMIGRATION IN POPULATION MODELS.

I analyzed mark-recapture data from tiger salamanders with a modified robust design in Program MARK. I counted each breeding season as a primary sampling period, with captures of individuals entering and leaving the breeding pond as captures during a secondary sampling period. Accounting for temporary emigration in open populations should improve estimation of survival rates because the probability of temporary emigration can be estimated from data and reduce uncertainty about the fate of individuals that are not detected in subsequent sampling periods. In order to accommodate additional parameters in open population mark-recapture models, I modeled survival as a constant rate across the five breeding seasons and examined three competing models that assumed Markovian, random, or no temporary emigration. I found good support for a model that assumed Markovian temporary emigration (Table A1). Estimates of temporary emigration for the Markovian model varied across time, with the highest estimate for the second breeding season, and lower estimates for temporary emigration in the last two breeding seasons (Figure A1).

Table A1. Open population mark-recapture models for a tiger salamander population.

Model	Number of Parameters	ΔAIC_c	AIC Weight
Markovian Temporary Emigration	15	0.00	0.877
Random Temporary Emigration	18	3.92	0.123
No Temporary Emigration	11	27.25	0.000

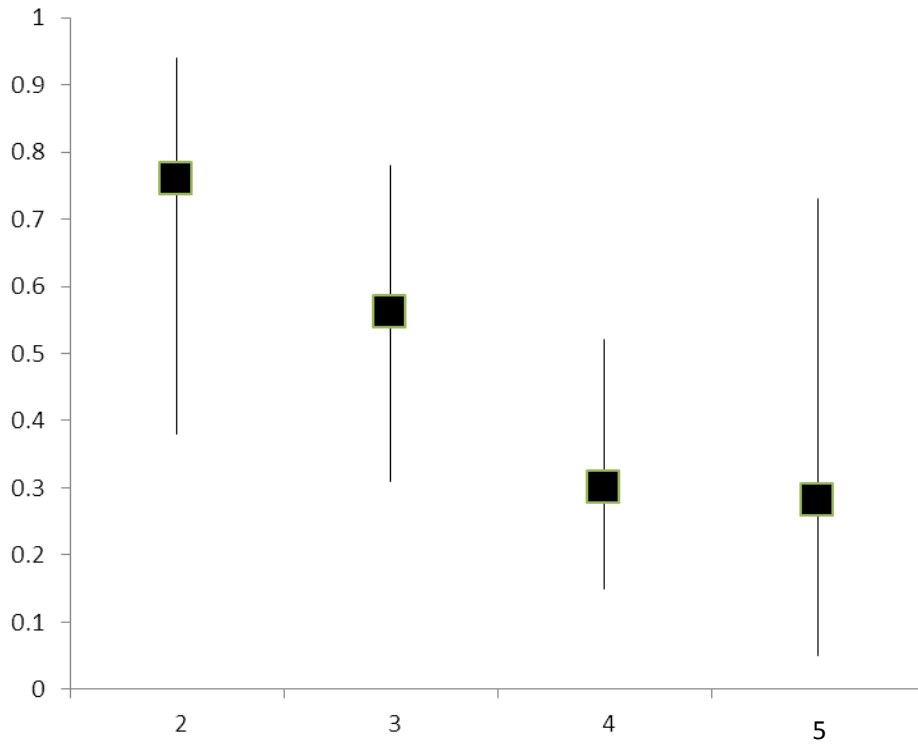


Figure A1. Estimates of temporary emigration with 95% confidence intervals from a model assuming Markovian temporary emigration in a tiger salamander population. Temporary emigration is estimated for the last four breeding seasons.

APPENDIX B. SENSITIVITIES AND ELASTICITIES OF DETERMINISTIC MODELS

In order to assess how robust the deterministic model of tiger salamander population growth was to variation in parameter values for effective fecundity, adult survival, and subadult survival, I systematically varied the values of these parameters one at a time and recalculated the sensitivities and elasticities for the new projection matrix while holding the other parameters constant.

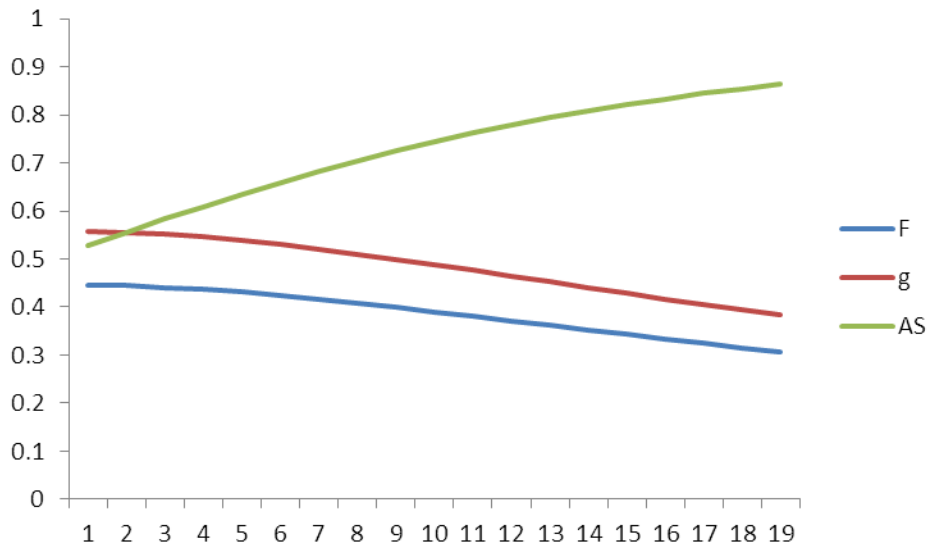


Figure B1. Sensitivities of adult survival (AS), effective fecundity (F), and subadult survival (g) over a range of values for adult survival. The value of 1 on the x-axis corresponds to 0.05, and the value of 19 corresponds to 0.95. Values for effective fecundity and subadult survival were fixed at 0.4 and 0.5, respectively.

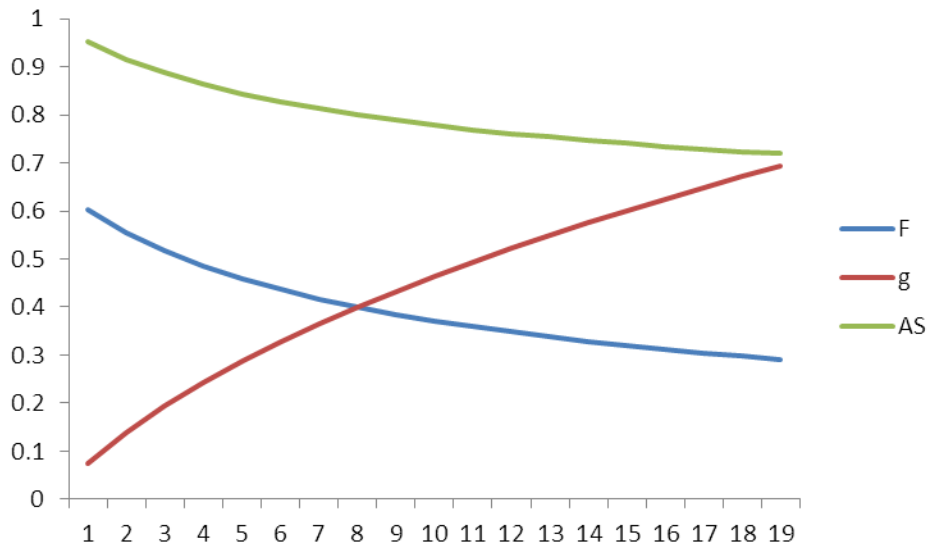


Figure B2. Sensitivities of adult survival (AS), effective fecundity (F), and subadult survival over a range of values for subadult survival. The value of 1 on the x-axis corresponds to 0.05, and the value of 19 corresponds to 0.95. Values for effective fecundity and adult survival were fixed at 0.4 and 0.6, respectively.

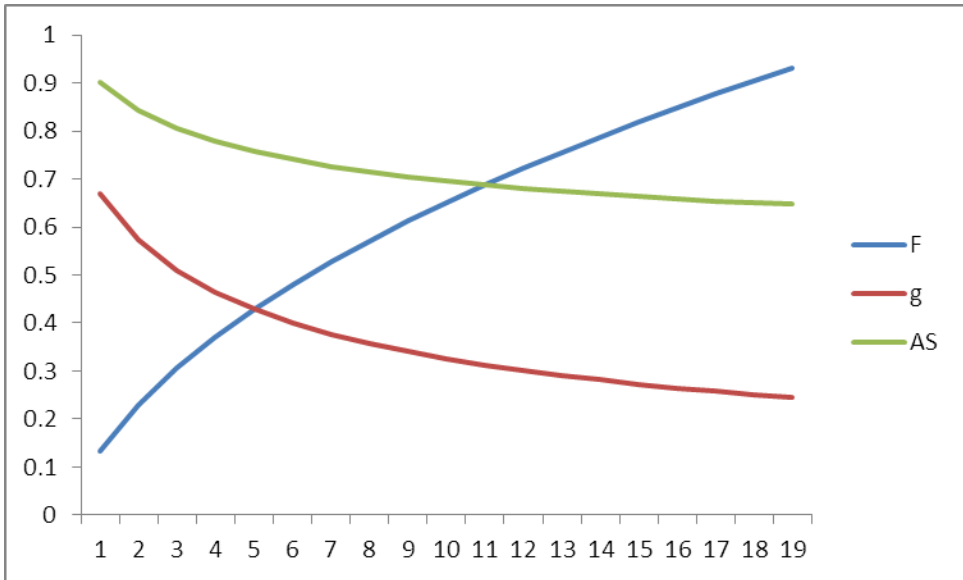


Figure B3. Sensitivities of adult survival (AS), effective fecundity (F), and subadult survival over a range of values for subadult survival. The value of 1 on the x-axis corresponds to 0.1, and the value of 19 corresponds to 1.9. Values for subadult survival and adult survival were fixed at 0.5 and 0.6, respectively.

APPENDIX C. MATLAB CODE USED IN POPULATION MODELS.

Function eigenall.m from Morris and Doak (2002):

```
function [lambdas,lambda1,W,w,V,v]=eigenall(A);  
  
% [lambdas,lambda1,W,w,V,v]=eigenall(A)  
  
% takes the projection matrix A as the argument of the function  
  
% eigenall and returns:  
  
%   lambdas, a vector containing the eigenvalues of A;  
  
%   lambda1, the dominant eigenvalue of A;  
  
%   W, a matrix with the right eigenvectors of A as its columns;  
  
%   w, the dominant right eigenvector of A (rescaled to proportions);  
  
%   V, a matrix with the left eigenvectors of A as its rows; and  
  
%   v, the dominant left eigenvector of A (rescaled as multiples of  
  
%           its first element).  
  
% Eigenvalues and eigenvectors are sorted from largest  
  
% to smallest.  
  
  
[W,lambdas]=eig(A);      % W=matrix with right eigenvectors of A as columns  
  
V=conj(inv(W));        % V=matrix with left eigenvectors of A as rows  
  
lambdas=diag(lambdas);  % lambdas=vector of eigenvalues  
  
[lambdas,I]=sort(lambdas); % sort eigenvalues from smallest to largest
```

```

lambdas=flipud(lambdas); % flip lambdas so that largest value comes first
lambda1=lambdas(1); % lambda1=dominant eigenvalue

I=flipud(I); % flip the index vector I
W=W(:,I); % sort right eigenvectors
V=V(I,:); % sort left eigenvectors
w=W(:,1); % w=stable distribution
w=w/sum(w); % rescale w to represent proportions
v=real(V(1,:))'; % v=vector of reproductive values
v=v/v(1); % rescale v relative to class 1

```

Modified code from Morris and Doak (2002) to calculate sensitivities and elasticities:

```

A=[.0 .4; .5 0.6]; % 2 x 2 population projection matrix
[lambdas,lambda1,W,w,V,v]=eigenall(A); % run eigenall.m function
lambda1 % print population growth
w
v
S=v*w'/(v'*w) % print sensitivities
E=A.*S/lambda1 %

```