

CONNECTIVITY, METAPOPOPULATION DYNAMICS, AND GENETIC STRUCTURE OF
TIGER SALAMANDERS IN A HETEROGENEOUS LANDSCAPE

BY

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DISSERTATION

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ABSTRACT

Metapopulation biology has been integral for understanding the impact of spatial habitat structure on ecological and evolutionary processes. In fragmented landscapes, theory predicts that species occupancy and turnover dynamics depend on habitat area and isolation, and isolation has historically been an important predictor of gene flow. However, metapopulation theory is neutral with respect to the effects of habitat heterogeneity on population processes. Landscape ecology approaches have begun to account for effects of habitat quality and matrix structure on occupancy and gene flow, but few empirical studies have integrated the area-isolation and habitat paradigms to understand metapopulation dynamics and genetic structure in the same system. Here, I employ both approaches to understand the spatial population dynamics and genetic structure of tiger salamanders (*Ambystoma tigrinum tigrinum*) in an agricultural landscape in Illinois.

First, I assessed the degree to which matrix heterogeneity influences *A. tigrinum* movement behavior. Using a field experiment, I showed that a physiological constraint, desiccation risk, varied significantly among matrix habitats (corn, soybean, forest, prairie). Water loss was greater in corn and prairie than in forest and soybean, indicating that dispersal costs can vary among agricultural crops. To assess whether movement decisions were influenced by desiccation risk, I tracked the movements of individuals released on habitat boundaries for two treatment combinations: soybean-corn, soybean-prairie. I observed that movements were oriented towards soybean in both cases, suggesting that variation in desiccation risk among matrix habitats influenced salamander movement decisions.

Next, I examined the effects of area, isolation, and habitat heterogeneity on metapopulation dynamics of *A. tigrinum*. Emphasis was placed on understanding the role of connectivity in moderating interactions between *A. tigrinum* and predatory fish. Occupancy and turnover of *A. tigrinum* were documented in 90 wetlands for three years. Since desiccation risk influenced *A. tigrinum* movements, I tested whether a connectivity metric that accounted for desiccation was a better predictor of occupancy and turnover than metrics based on Euclidean distance or expert opinion. Occupancy and colonization probabilities were related positively to connectivity and negatively to fish presence. Extinction probability was related positively to fish presence, but extinction risk was low in connected networks, suggesting a rescue effect. A desiccation-informed connectivity metric was a better predictor of colonization probability than alternative metrics, whereas a Euclidean model was the best predictor of occupancy and extinction probabilities. The results indicated that the effect of desiccation risk on individual movement can scale up to influence metapopulation processes, and that the effects of predatory fish on metapopulation dynamics depended on spatial connectivity.

Finally, I evaluated whether ecological factors underlying occupancy and turnover were also important predictors of metapopulation genetic structure. Newly colonized populations were more genetically differentiated than established populations, indicating that founder effects influenced genetic structure. However, the degree of genetic differentiation varied spatially. Genetic differentiation was related negatively to both wetland area and spatial connectivity. Differentiation was not strongly related to habitat quality, suggesting that metapopulation factors were more effective at reflecting the historical strength of genetic drift and gene flow than current habitat suitability.

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TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION.....	1
LITERATURE CITED	5
CHAPTER 2: CONNECTIVITY OF AGROECOSYSTEMS: DISPERSAL COSTS CAN VARY AMONG CROPS	8
ABSTRACT.....	8
INTRODUCTION	9
METHODS	11
RESULTS	16
DISCUSSION.....	18
ACKNOWLEDGMENTS	22
FIGURES.....	23
LITERATURE CITED.....	26
CHAPTER 3: SPATIAL CONNECTIVITY MODERATES THE EFFECT OF PREDATORY FISH ON SALAMANDER METAPOPOPULATION DYNAMICS	31
ABSTRACT.....	31
INTRODUCTION	32
METHODS	34
RESULTS	41
DISCUSSION.....	43
ACKNOWLEDGMENTS	49

TABLES	50
FIGURES	51
LITERATURE CITED	55

CHAPTER 4: AREA AND ISOLATION PREDICT METAPOPULATION GENETIC

STRUCTURE OF A POND-BREEDING SALAMANDER62

ABSTRACT	62
INTRODUCTION	63
METHODS	66
RESULTS	71
DISCUSSION	73
ACKNOWLEDGMENTS	77
TABLES	78
FIGURES	79
LITERATURE CITED	81

APPENDIX A89

APPENDIX B90

APPENDIX C91

APPENDIX D93

APPENDIX E95

APPENDIX F96

APPENDIX G99

APPENDIX H	100
CURRICULUM VITAE.....	102

CHAPTER 1

INTRODUCTION

The theoretical framework of metapopulation biology highlights the dependence of ecological and evolutionary processes on spatial habitat structure (Hanski and Gilpin 1997, Hanski and Gaggiotti 2004). Levins (1969) originally coined the term “metapopulation” to describe a network of populations in which local populations go extinct and become recolonized through dispersal. While the significance of local extinction for population dynamics and evolution was recognized before 1969 (e.g., Wright 1931, Andrewartha and Birch 1954, reviewed in Hanski and Simberloff 1997), Levins was the first to demonstrate the main tenet of metapopulation dynamics. In a network of habitat patches, he showed that the long-term persistence of a species can occur at the metapopulation level through a balance of extinction and recolonization at the patch level.

Due to its emphasis on spatial structure, the metapopulation concept has become a central element of conservation biology in fragmented landscapes. Habitat fragmentation typically results in a network of habitat patches that vary in size and physical isolation. While Levins’ (1969) original model was spatially-implicit, Hanski (1994) recognized that spatial heterogeneity in patch extinction and colonization probabilities can emerge from variation in patch geometry. Hanski’s spatially-realistic metapopulation model (e.g., incidence function model, IFM; Hanski 1994) makes two key predictions, both rooted in island biogeography theory (MacArthur and Wilson 1967): 1) patch extinction probability is related negatively to patch area, and 2) patch colonization probability is related negatively to isolation (i.e., Euclidean distance between

patches). The IFM assumes that population size increases with patch area, resulting in low probability of stochastic extinction in large patches. Similarly, dispersal probability is assumed to decrease with increasing patch isolation, resulting in high colonization probability in connected patches. While metapopulation dynamics have been successfully described by area and isolation for a number of species and systems (e.g., Hanski et al. 1994, Sjögren-Gulve and Ray 1996, Moilanen et al. 1998), recent analyses suggest that area and isolation alone can often be poor predictors of occupancy and turnover dynamics (Baguette 2004, Pellet et al. 2007, Prugh et al. 2008).

Landscape ecologists have emphasized two aspects of habitat heterogeneity that may improve predictions of occupancy and turnover dynamics in systems where area and isolation are inadequate. First, habitat quality can affect local extinction risk deterministically because within-patch factors such as predation, competition, and disturbance can directly influence individual survival, reproductive success, and ultimately population size (Thomas 1994, Fleishman et al. 2002, Armstrong 2005). Habitat quality can also influence colonization probability for species that actively select habitat during dispersal (Bélisle 2005, Schooley and Branch 2009). Thus, spatial variation in habitat suitability can generate spatial variation in extinction risk and colonization probability. Second, matrix heterogeneity can affect colonization probability due to variation in dispersal costs among matrix habitats (Taylor et al. 1993, Wiens 1997, Ricketts 2001). Whereas the IFM represents a neutral view of matrix structure, landscape ecology approaches have accounted for matrix heterogeneity by modeling dispersal paths that vary depending on the degree to which habitats facilitate or impede movement (e.g., Adriaensen et al. 2003). Thus, colonization probability at the patch-level can depend on the proximate effects of matrix structure on movement behavior. If the persistence of

local populations depends on dispersal (i.e., rescue effect; Brown and Kodric-Brown 1977), then matrix heterogeneity can influence local extinction risk as well.

An integration of metapopulation and landscape ecology approaches is becoming more common in empirical studies, particularly for prediction of species occupancy. However, relatively few studies are available that account for the effects of metapopulation factors, habitat suitability, and matrix structure on turnover dynamics (e.g., Schooley and Branch 2009). Furthermore, I am not aware of empirical studies that have applied the area-isolation and habitat paradigms to understand genetic structure in a metapopulation context. If area, isolation, and habitat factors are related to population size and dispersal, then ecological factors driving metapopulation dynamics may be critical determinants of genetic drift, gene flow, and spatial genetic structure as well. In this dissertation, I combine the metapopulation and habitat heterogeneity approaches to understand occupancy, turnover dynamics, and spatial genetic structure of the eastern tiger salamander (*Ambystoma tigrinum*) in an agricultural landscape in northern Illinois.

In chapter 2, I evaluate the degree to which matrix heterogeneity influences *A. tigrinum* movement behavior. Water economy is a critical physiological and behavioral constraint on the life history of terrestrial amphibians (Jørgensen 1997). Using field experiments I test whether 1) desiccation risk varies among matrix habitats experienced by *A. tigrinum* during overland movement, and 2) individual movement decisions are influenced by desiccation risk. I show that water loss varies significantly among matrix habitats, including agricultural crops, and that desiccation risk likely influences movement decisions. I discuss the implications of variation in dispersal costs among crops on the way landscape ecologists conceptualize population

connectivity in agroecosystems. I also discuss how the effects of desiccation on amphibian movement may scale up to influence spatial population dynamics.

In chapter 3, I examine the effects of wetland area, isolation, and habitat heterogeneity on the metapopulation dynamics of *A. tigrinum*. I explicitly test whether occupancy and turnover dynamics depend on the combined effects of predatory fish presence and spatial connectivity. Since desiccation risk was previously shown to influence *A. tigrinum* movements (Chapter 2), I test whether a connectivity metric that accounts for desiccation is a better predictor of occupancy and turnover than metrics based on Euclidean distance or expert opinion. My results indicated the distribution of *A. tigrinum* is strongly limited by fish predators, but that spatial connectivity can moderate the effects of fish on extinction and colonization dynamics. The results also suggested that the effect of desiccation risk on individual movement scales up to influence metapopulation processes. I stress that the population-level outcomes of fish-amphibian interactions can strongly depend on spatial connectivity.

In chapter 4, I evaluate whether metapopulation and habitat factors underlying metapopulation dynamics for *A. tigrinum* are also important predictors of metapopulation genetic structure. Unlike theory in metapopulation ecology, models of metapopulation genetics (e.g., island model; Slatkin 1977) are spatially implicit and assume that habitat patches do not vary in size or quality. My results indicate that genetic differentiation within an *A. tigrinum* metapopulation is related to area and connectivity, but not to habitat quality. I discuss the degree to which metapopulation factors and habitat heterogeneity reflect the historical strength of genetic drift and gene flow within local populations. I also emphasize that more empirical studies are needed to evaluate the relative degree to which spatial genetic structure is shaped by metapopulation factors and habitat heterogeneity.

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CHAPTER 2

CONNECTIVITY OF AGROECOSYSTEMS: DISPERSAL COSTS CAN VARY AMONG CROPS¹

ABSTRACT

Knowledge of how habitat heterogeneity affects dispersal is critical for conserving connectivity in current and changing landscapes. However, we generally lack an understanding of how dispersal costs and animal movements vary among crops characteristic of agroecosystems. I hypothesized that a physiological constraint, desiccation risk, influences movement behavior among crops and other matrix habitats (corn, soybean, forest, prairie) in *Ambystoma tigrinum* (tiger salamander) in Illinois, USA. In a desiccation experiment, salamanders were added to enclosures in four replicate plots of each matrix habitat, and water loss was measured every 12 hrs for 48 hrs. Changes in water loss were examined using a linear mixed model. Water loss varied among treatments, over time, and there was a significant treatment-time interaction. Water loss was greater in corn and prairie than in forest and soybean.

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To assess whether salamanders move through matrix habitats that minimize desiccation, I tracked movements of individuals released on edges between habitats for two treatment combinations: soybean-corn, and soybean-prairie. As predicted based on my desiccation experiment, movements were oriented towards soybean in both cases. Thus, variation in desiccation risk among matrix habitats likely influenced movement decisions by salamanders, although other factors such as predation risk could have contributed to habitat choice. I argue that conceptualizing dispersal cost as uniformly high in all crop types is too simplistic. Estimating crop-specific dispersal costs and movement patterns may be necessary for constructing effective measures of landscape connectivity in agroecosystems.

INTRODUCTION

Dispersal is an important life-history trait with consequences for individual fitness, population dynamics, and evolution (Clobert et al. 2001). Dispersal is also a key determinant of spatial population structure (Harrison and Taylor 1997), species persistence (Lande 1988), and potential distributional shifts in response to climate change (Opdam and Wascher 2004). Metapopulation biology has become a dominant conservation paradigm for understanding the influence of dispersal on population processes in fragmented landscapes (Hanski and Gilpin 1997). Although metapopulation theory was historically neutral with respect to dispersal and matrix habitats (i.e., habitats between suitable patches), matrix heterogeneity is becoming an important component of metapopulation approaches (Wiens 1997, Ricketts 2001, Schooley and Wiens 2005, Prugh et al. 2008).

Despite recent integration of matrix heterogeneity into metapopulation models, we have a

limited understanding of how matrix habitats influence dispersal and connectivity in agroecosystems. In many systems, models of landscape connectivity (e.g., least-cost models; Adriaensen et al. 2003) are based on expert opinion to estimate the resistance of matrix habitats to dispersal (Baguette and Van Dyck 2007, Beier et al. 2009, Janin et al. 2009). In agricultural systems, reliance on expert opinion often results in the assumption that all crops impose a uniformly high cost on dispersal (e.g., Schadt et al. 2002, Compton et al. 2007, Magle et al. 2009). Yet, agricultural crops can vary tremendously in vegetation structure and cover, associated predation risk, and resources such as food or refuge availability. Patterns of animal movement can vary among agricultural crops as well (Rizkalla and Swihart 2007), suggesting that a single, high dispersal cost does not apply equally to all crops. If crops differentially influence animal movement patterns, an evaluation of how dispersal costs vary among crops can inform models of landscape connectivity in agricultural systems.

Insight into how dispersal costs vary among agricultural crops and other matrix habitats may be gained by understanding the proximate physiological and behavioral factors that influence movement costs and decisions. In particular, pond-breeding amphibians are excellent model organisms to address how dispersers interact with matrix habitats within a physiological context. Risk of water loss should impose strong physiological constraints on juvenile dispersers due to their small bodies, permeable skin, and high surface area to volume ratio (Sinsch 1990, Rothermel and Semlitsch 2002, Chan-McLeod 2003, Mazerolle and Desrochers 2005, Semlitsch 2008). Using a field experiment, I tested the hypothesis that desiccation risk varies among agricultural crops and matrix habitats that differ in canopy coverage, air temperature, and relative humidity for *Ambystoma tigrinum tigrinum* (eastern tiger salamander, Ambystomatidae) in northern Illinois. I predicted that desiccation risk would be greater in matrix habitats with less

canopy coverage, higher air temperatures, and lower humidities at the soil surface. Next, I conducted a second experiment to test the hypothesis that matrix habitat influences movement decisions by juvenile dispersers. I predicted that salamanders would select habitats that minimize desiccation risk when given a choice, although other factors could contribute to movement decisions (e.g., predation risk). I discuss how an empirical, mechanistic understanding of dispersal costs and movement behavior may advance our conceptualization of landscape connectivity and enhance conservation efforts for species in agricultural ecosystems.

METHODS

Study species

Ambystoma tigrinum is subterranean, using mammal burrows and excavated burrows in upland forests and prairies for refuge during most of the year. In Illinois, adults breed primarily in fishless ponds from February to April. Juveniles emigrate from ponds into upland habitats between July and September and become sexually mature within two years (Petranka 1998). Consistent with other pond-breeding amphibians (e.g., Phillips 1989), interpond dispersal for this species is greater for juveniles than adults (Church et al. 2007). Thus, I used juveniles in my desiccation and movement experiments.

I collected 78 *A. tigrinum* larvae for both experiments from 4 spatially independent wetlands in Lee County, IL. Individuals were collected and stored individually in plastic containers filled with 4-cm of well water between 22 June and 2 July 2009. To avoid capturing siblings within wetlands, I collected individuals of varying size classes from spatially segregated locations. Larvae were fed mealworms *ad libitum* until the start of metamorphosis. After metamorphosis, I

stored salamanders individually in plastic containers lined with moist paper towels, and metamorphs were fed mealworms *ad libitum*.

Desiccation experiment

I conducted the desiccation experiment at a 9300-ha area in northern Illinois centered on the Richardson Wildlife Foundation property (West Brooklyn, IL; 41° 42' 26.6" N, 89° 11' 25.0" W). To address whether desiccation risk varies among crops and other matrix habitats, I subjected individuals to water loss in one of four treatments: corn, soybean, forest, and prairie. Treatments were chosen to represent the dominant habitats experienced by juvenile dispersers throughout the region. I used four replicate plots of each habitat. Experimental units were located in four spatially-disjunct blocks (average distance between blocks = 1260 m). Blocks were not chosen randomly, as I selected areas to minimize variation in soil characteristics. Treatments were assigned to a single experimental unit within blocks (4 treatments x 4 blocks = 16 total plots). Prairie vegetation was dominated by *Coreopsis lanceolata*, *Schizachyrium scoparium*, and *Sorghastrum nutans*, whereas forest plots were dominated by *Acer negundo*, *Prunus serotina*, *Quercus velutina*, and *Robinia pseudoacacia*.

I used 64 individuals in the desiccation experiment. Within each replicate plot, I installed four dehydration enclosures (modified from Rothermel and Luhring 2005). Each enclosure contained one salamander. I attached a 51 x 57-cm cylinder sleeve of fiberglass screening to a 25-cm section of 15-cm diameter polyvinyl chloride (PVC) pipe. I wrapped the fiberglass screening around the outside edge of each PVC pipe such that a 30-cm tall section of screening extended beyond the end of the pipe. Duct tape was used to fasten the fiberglass screening to the outside edge of each PVC pipe. I used 9.1-kg fishing line to sew together the ends of each

section of cylindrical screening. The PVC was buried so that the top end of the PVC was at the soil surface, and only the 30-cm tall section of the screening was above ground. Enclosures were placed 2 m apart in a 2 x 2-m grid. Care was taken to minimize disturbance to the soil surface within each enclosure during installation.

The experiment was conducted between 12 August and 14 August 2009. I stopped feeding salamanders two days before the start of the experiment. On the first day of the experiment, individuals were placed in containers with 1-cm well water to fully hydrate for a minimum of 1.5 hrs. Before transferring salamanders to enclosures, I gently blotted individuals with a paper towel, and I measured their snout-vent-length (SVL) and mass to the nearest 0.01 g using a portable electronic scale (Ohaus Scout Pro Balance, Pine Grove, New Jersey, USA). I randomly assigned salamanders to enclosures. Individuals were placed on the soil surface within enclosures on 12 August between 1700 and 2100. I returned every 12 hrs for 48 hrs to measure salamander mass. Weight loss during this time was assumed to be due to water loss (Pough and Wilson 1970, Rothermel and Luhring 2005). I also measured air temperature and relative humidity at 10-min intervals throughout the experiment using a HOBO Pro v2 logger (Onset Computer Corp., Bourne, Massachusetts, USA). A single data logger was mounted 1-2 cm above the ground in the center of each 2 x 2-m experimental plot. Canopy cover was measured as % closed canopy at the soil surface in each enclosure using a spherical densiometer.

I used a linear mixed model using restricted maximum likelihood estimation (PROC MIXED—SAS version 9.1; SAS Institution Inc., Cary, North Carolina, USA) to test for effects of treatment, block, time, and all two-way interactions on water loss. Individual was used as a random effect. I chose the first-order autoregressive covariance structure, which assumes that observations on a given individual closer in time are more correlated than are observations

separated by longer times. Individuals were nested within the treatment-block interaction. Mass at each time interval was used as the response variable, and initial mass was used as a covariate. In eight cases, fewer than four subsamples were available within experimental units due to escape (1 individual each missing after 12 and 24 hours), mortality (2 individuals at 48 hrs), and an erroneous data record (1 individual at 48 hrs).

Finally, I used ANOVA to evaluate the effect of matrix habitat on canopy cover at the soil surface using PROC GLM in SAS. Canopy cover estimates were averaged across subsamples at the soil surface (Gotelli and Ellison 2004) and arcsin-transformed to reduce heteroscedasticity.

Movement orientation experiment

To evaluate the prediction that salamanders choose to move through matrix habitats that minimize desiccation risk, I released individuals on edges between habitats used in my desiccation experiment. Short-term movements (<16 hrs) were recorded using radiotelemetry. Because I had a limited number of salamanders and radiotransmitters, I only assessed movement decisions for individuals released at two treatment combinations, soybean-prairie and soybean-corn, which provided clear expectations based on results of the desiccation experiment. The soybean-prairie plot was located at the Phillips Tract natural area in Urbana, IL (40° 7' 59.3" N, 88° 8' 56.9" W) and the soybean-corn plot was located at the South Farms research area in Champaign, IL (40° 2' 38.1" N, 88° 14' 5.8" W). The University of Illinois owns both sites. Treatment combinations and locations were chosen due to 1) presence of sharp, narrow (<1.5 m) boundaries with bare soil between habitats to motivate movement, and 2) absence of a visible elevation gradient, which could potentially bias movement decisions.

The experiment was conducted between 3 September and 27 September 2009. I

established four 1 x 1-m release locations along edges at the soybean-prairie plot, and five 1 x 1-m release locations along edges at the soybean-corn plot. My generalizations are restricted because there was only one plot per each treatment combination. However, the releases within a plot were considered independent, and release locations were ≥ 20 m from each other and established along boundaries with varying aspect orientations (i.e. north-south vs. east-west). I used 49 salamanders for this experiment, 40 of which were also used in the desiccation experiment. Juvenile salamanders were randomly assigned to treatments, release dates, and release locations within treatments, with the exception that each treatment combination received an equal number of individuals originally used in the desiccation experiment ($n = 20$). I released individuals only on days without measurable precipitation to avoid soil-surface temperature and humidity conditions being homogenized among matrix habitats by rain. Salamanders were fitted with radiotransmitters (Models A1015, A1025, and A1036, ATS, Inc., Isanti, Minnesota, USA) that weighed $\leq 8\%$ body mass. Because I was primarily interested in short-term movements (< 16 hrs), I affixed transmitters directly to the dorsal surface of each individual with cyanoacrylate (SuperGlue). Cyanoacrylate is commonly used to close skin incisions in amphibians (Gentz 2007), and it has been used to affix passive integrated transponder tags externally to ambystomatid salamanders (Charney et al. 2009). On the day of releases, I affixed transmitters to individuals between 1400 and 1600 in the laboratory. Individuals were then transported to treatment plots and released between 1700 and 2000. I placed each salamander under a black bucket on a randomly assigned release location for two min of acclimation, and the bucket was removed with a 4-m rope. Salamanders were released at both plots on 6 of 11 release nights, and the average number of individuals released on any given night was 3. The time interval between releases at a given release location ranged from 1–10 days (median = 2). I released a total of 24

individuals in the soybean-prairie plot and 25 individuals in the soybean-corn plot.

I relocated and recovered radiomarked salamanders using an ATS R410 receiver (Isanti, Minnesota, USA) 12-16 hrs after release. Individuals were recovered with transmitters still affixed 82% of the time ($n = 40$ individuals). For each salamander that moved ≥ 1 m, I recorded total distance moved from the release location and the angle of movement (0° defined movement directly into soybean, 90° and 270° represented movement along ecotone). I included angles of movement for nine individuals for which only the transmitter was recovered, assuming that the transmitter location was representative of the individual's short-term movement orientation. Based on the desiccation experiment (see Results), my *a priori* prediction was that the mean direction of movement would be oriented towards soybean in both treatments. A V-test was used to test the null hypothesis that the distribution of angles was randomly distributed against the alternative that angles were clustered around 0° (Zar 1984). Statistical analyses were conducted in Oriana (version 3.13, Kovach Computing Services, Anglesey, Wales).

RESULTS

Desiccation experiment

Individual mass varied among treatments and over time, and there was an interaction between treatment and time (Treatment: $F = 8.61$, $P = 0.0001$, $df = 3, 47$; Time: $F = 83.12$, $P < 0.0001$, $df = 3, 163$; Treatment*Time: $F = 18.86$, $P < 0.0001$, $df = 9, 163$). Individual mass at each time period also depended on initial mass ($F = 456.81$, $P < 0.0001$, $df = 1, 47$). There were no significant block effects, either alone or in interaction with treatment or time (Block: $F = 1.09$, $P = 0.36$, $df = 3, 47$; Block*Treatment: $F = 0.94$, $P = 0.50$, $df = 9, 47$; Block*Time: $F =$

0.94, $P = 0.49$, $df = 9, 163$). Water loss was consistently low in forest and soybean plots and greatest in corn and prairie plots (Fig. 2.1A). Mass decreased over time in all habitats, with the exception of a slight increase in mass in soybean and prairie plots between 24 and 36 hrs. Overall, mass decreased faster in corn and prairie plots compared to soybean and forest plots. Two mortalities occurred in the prairie treatment between 36 and 48 hrs.

Differences in mass among treatments corresponded to variation in daytime air temperature (Fig. 2.1B) and humidity levels at the soil surface (Fig. 2.1C). Forest and soybean plots had lower daytime air temperatures and greater daytime humidities compared to corn and prairie plots. Variation in soil-surface air temperature and relative humidity among treatments was less pronounced at night than during the day. Canopy cover at the soil surface also varied significantly among treatments (ANOVA, $F = 25.43$, $P < 0.0001$, $df = 3, 12$; mean % closed canopy ± 1 SE: corn = 83.56 ± 3.60 , forest = 88.19 ± 5.63 , prairie = 34.63 ± 17.52 , soybean = 87.25 ± 2.52).

Movement orientation experiment

Of individuals moving ≥ 1 m after release (soybean-prairie: $n = 16$; soybean-corn: $n = 23$), the total distance moved averaged 16.7 m (range = 1.5 – 91.1 m; SD = 21.8 m) in the soybean-prairie treatment and 7.9 m (range = 1.3 – 40.0 m; SD = 8.0 m) in the soybean-corn treatment. Salamander movement directions were not randomly distributed in either treatment (V-test; soybean-prairie: $u = 1.61$, $P = 0.054$; soybean-corn: $u = 1.79$, $P = 0.037$), and movements were oriented towards soybean in both treatments (Fig. 2.2).

DISCUSSION

Desiccation risk for *A. tigrinum* juveniles varied substantially among matrix habitats. Water loss was greater in open prairies than closed-canopy forests, supporting results from a previous desiccation study on pond-breeding amphibians (Rothermel and Semlitsch 2002). However, the two row crops dominating agricultural landscapes in the midwestern USA – corn and soybean – had different effects on desiccation. Water loss was equally low in forest and soybean, whereas it was high in corn and prairie. When individuals were given a choice to move between matrix habitats with variable desiccation regimes (soybean-prairie and soybean-corn), movements were oriented towards soybean, suggesting that 1) a physiological constraint influenced movement decisions, and 2) dispersal costs can vary significantly among crops in agricultural landscapes.

Dehydrated amphibians can be subject to greater predation risk (Rohr and Madison 2003) and lower survival (Rothermel and Luhring 2005, Rittenhouse et al. 2008, Rittenhouse et al. 2009) than hydrated animals. Negative consequences of dehydration on locomotor performance (Prest and Pough 1989) and habitat permeability during movement (Rothermel and Semlitsch 2002, Mazerolle and Desrocher 2005) have suggested that desiccation risk influences dispersal as well. My results expand on this work by showing that *A. tigrinum* desiccation risk varies among common upland matrix habitats, and that juvenile salamanders orient movements toward low-risk habitat where dehydration should be reduced. Previous experimental studies on habitat choice at forest-clearcut boundaries indicate that many species prefer forested habitats, but these studies do not link movement decisions to measured desiccation risk (Chan-McLeod 2003, Rittenhouse and Semlitsch 2006, Stevens et al. 2006, Graeter et al. 2009). In my system, even

when given a choice between prairie and an agricultural crop, salamanders oriented towards soybean, which represented low desiccation-risk habitat. I cannot completely rule out the possibility that other factors confounded with matrix habitat (e.g., predation risk) influenced movement decisions, although I note that the only predation event during my experiment took place in soybean.

Variation in desiccation risk among habitats appears to be related to differences in air temperature and relative humidity levels at the soil surface, especially during the day (Fig. 2.1). Furthermore, these differences in microclimatic conditions may be related to canopy coverage at the soil surface, which varied significantly among treatments. Average canopy cover was greatest in corn, soybean, and forest, and lowest in prairie. Temperature and humidity differences between corn and soybean may be related to vegetation structure as well. In contrast to corn, soybean has dense, shrub-like foliage near the soil surface. Morning dew formation on soybean foliage was substantial, whereas dew formation was minimal in corn plots (B.J. Cosentino, *personal observation*). Dew formation on low-lying foliage may have kept daytime humidity levels high at the soil surface in soybean plots. Previous studies in forest-clearcut systems have shown that desiccation rate covaries with daytime air temperature among habitats, but not with relative humidity (Rothermel and Semlitsch 2002, Rothermel and Luhring 2005). Soil moisture has also been correlated with amphibian desiccation in some cases (Rothermel and Semlitsch 2002), but not in others (Rothermel and Luhring 2005). Although surface movement occurs mainly at night when environmental conditions are relatively uniform, *A. tigrinum* movement can occur during the day (B. J. Cosentino, *personal observation*), and individuals using refuges are still exposed to variable daytime temperature and humidity conditions among habitats.

Of broad significance is the difference in *A. tigrinum* desiccation between corn and soybean, and the corresponding orientation of movements towards soybean when individuals were given a choice between corn and soybean. Agricultural landscapes represent 40.8% of land in the United States (USDA NASS 2007) and are composed of numerous crop types, but modeling and empirical studies of landscape connectivity have commonly treated agricultural land as a single, homogeneous land cover that is highly resistant to animal movement. I argue that this assumption can be too simplistic. Given previous work on effects of desiccation risk on movement rates and survival in amphibians (Preest and Pough 1989, Rothermel and Semlitsch 2002, Rothermel and Luhring 2005, Rittenhouse et al. 2008, Rittenhouse et al. 2009), my results strongly suggest that crops can differentially influence movement decisions, habitat permeability, and individual survival. Such variation in dispersal costs among crops creates the potential for the spatial distribution and temporal rotation of crops to influence population processes.

When quantifying landscape connectivity, data on desiccation risk can inform the rank and magnitude of movement resistances for matrix habitats in least-cost (Adriaensen et al. 2003) or circuit theory (McRae et al. 2008) frameworks (Stevens et al. 2004, Rayfield et al. 2010). In my study area, a cost surface accounting for crop-specific desiccation risk varies greatly from a surface informed by expert opinion (Fig. 2.3). These surfaces represent alternative hypotheses on how landscape structure influences dispersal, and the relative support of connectivity metrics based on each cost surface can be evaluated using data on interpond movement, occupancy dynamics, or gene flow. Such an analysis would provide insight into how a key physiological constraint on amphibian movement – desiccation risk – scales up to influence metapopulation dynamics and population genetic structure.

Importantly, dispersal costs associated with desiccation risk in agricultural crops will

vary temporally (Mazerolle and Vos 2006). Before planting, agricultural fields are open and bare during spring in many parts of the United States. Thus, adults of spring-breeding amphibians may face a uniformly high risk of movement when migrating across agricultural fields. However, field-level tillage practices may influence desiccation risk. For example, the presence of old plant material in no-till fields may moderate desiccation risk by functioning as refuges, whereas tilled fields would be relatively barren at the soil surface. In a forested ecosystem, Rittenhouse et al. (2008) found that the presence of coarse woody debris in clearcuts moderates desiccation risk for anurans. In agricultural fields, desiccation risk likely declines as plant cover increases through the growing season, but I would expect greater among-crop variation in risk late in the growing season (July – September) when juveniles emigrate from ponds after metamorphosis. Finally, although crops such as soybean provide low desiccation risk-habitat, individuals emigrating during harvest may be susceptible to disturbance from agricultural machinery (Saumure et al. 2007).

When possible, I stress the utility of using experiments to understand how movement behaviors and decisions vary among matrix habitats encountered during dispersal. In this study, an experimental approach improved our understanding of how a physiological constraint was related to dispersal cost for *A. tigrinum* among matrix habitats, including agricultural crops. These results can inform resistance values in studies of landscape connectivity to assess how specific, proximate factors driving the disperser-matrix interaction scale up to influence landscape-ecological and evolutionary processes. Effective measures of spatial connectivity are needed to understand current distributions of species in agroecosystems and to predict responses to land-use change and climate shifts.

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FIGURES

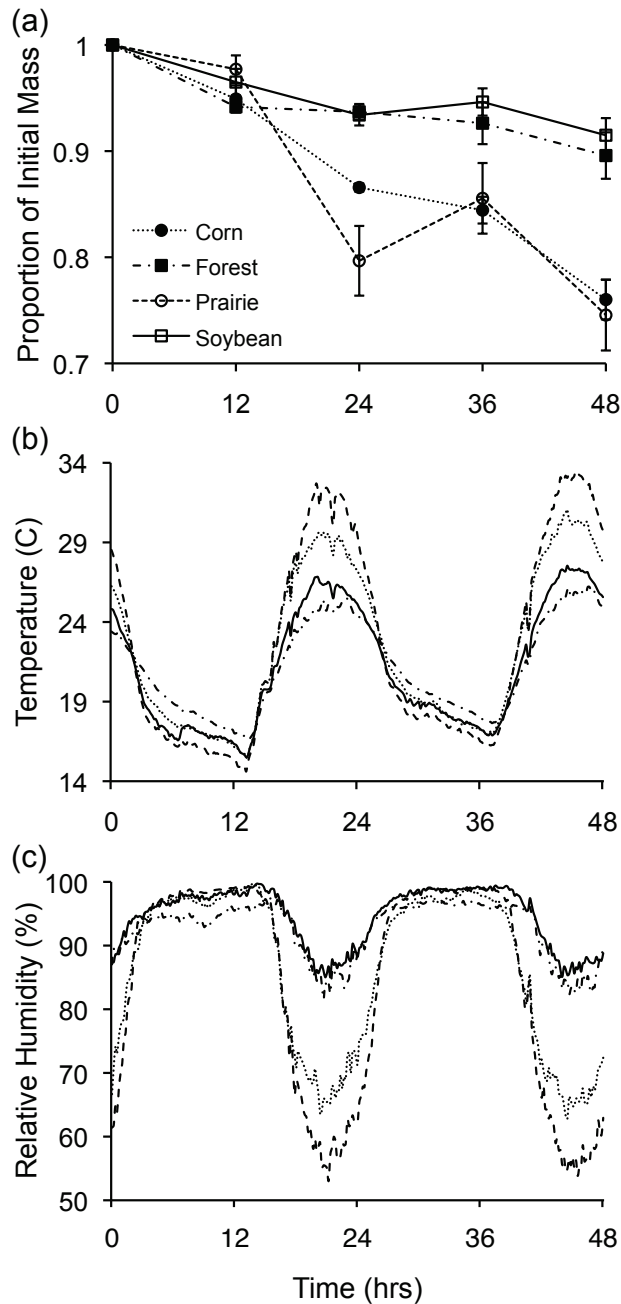


Figure 2.1 Temporal patterns for (A) water loss (mean proportion of initial mass \pm 1 SE) for juvenile *Ambystoma tigrinum*, (B) air temperature, and (C) relative humidity at the soil-surface among corn, forest, prairie, and soybean treatments during a desiccation experiment in Illinois. Night intervals (1700 – 500) are 0-12 and 24-36 hrs, and day intervals (500 – 1700) are 12-24 and 36-48 hrs. Note that individual mass was used as the response variable in my analysis of water loss. Proportion of initial mass is presented for display purposes only.

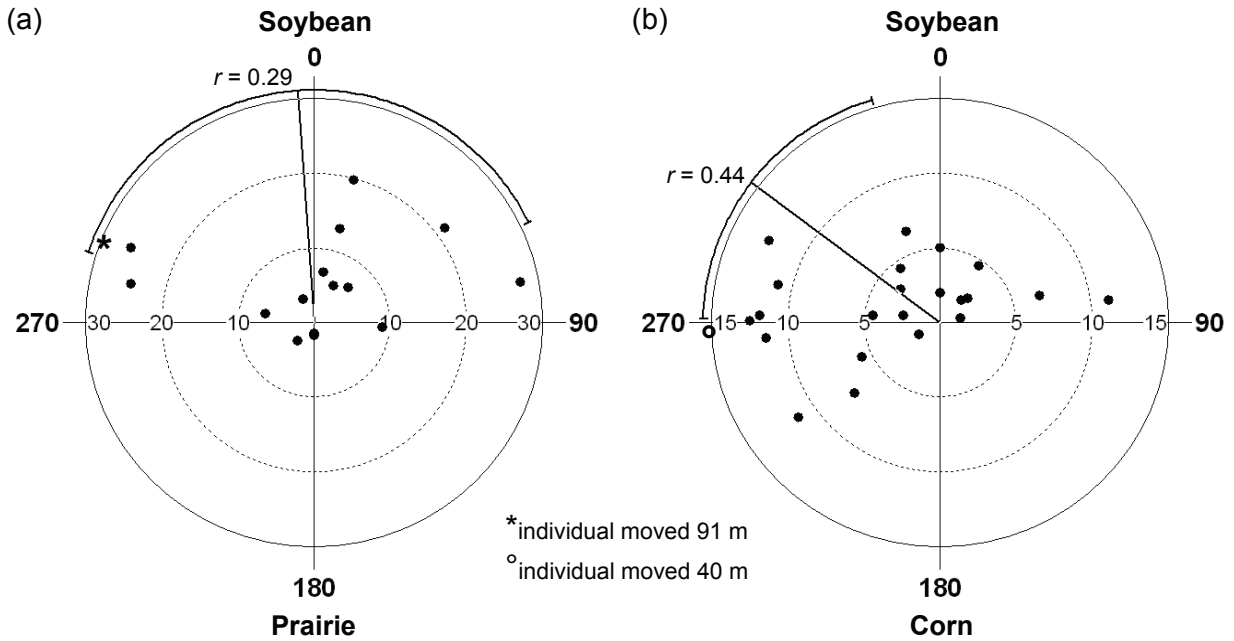


Figure 2.2 Short-term (<16 hrs) angular orientations and linear distances moved for juvenile *Ambystoma tigrinum* released at edges between (A) soybean and prairie ($n = 16$), and (B) soybean and corn ($n = 23$) in Illinois. Orientation towards soybean was the *a priori* expectation based on a desiccation experiment (Fig. 2.1A). Direct movement into soybean was defined as 0° . Black circles represent both orientation and distance moved (m, represented by concentric circles) for individual salamanders. Mean vector and 95% confidence intervals are represented by bold black lines. Length of the mean vector (r) is also indicated.

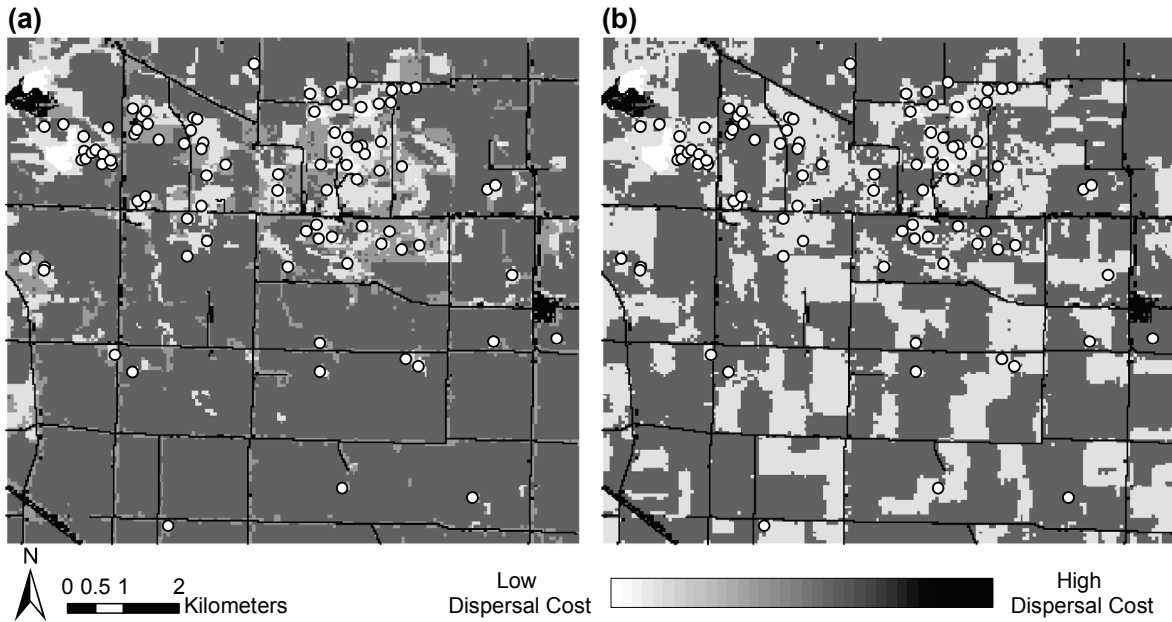


Figure 2.3 Dispersal cost surfaces for *Ambystoma tigrinum* (A) representative of expert opinion and (B) based on empirical data on desiccation risk (Fig. 2.1A) for an agricultural landscape in northern Illinois, USA. The landscape is dominated by corn, soybean, forest, prairie, and developed areas. In the expert opinion surface, forest was assigned a lower cost than prairie, and costs were uniformly high among crops. In the surface based on empirical data, soybean and forest had lower costs than corn and prairie. Developed areas were assigned the highest cost in both surfaces. Cost values were fixed for each cover type. Open circles represent potential breeding wetlands used by *A. tigrinum*.

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CHAPTER 3

SPATIAL CONNECTIVITY MODERATES THE EFFECT OF PREDATORY FISH ON SALAMANDER METAPOPULATION DYNAMICS

ABSTRACT

In predator-prey metapopulations, persistence of prey in patches with predators may depend on the rescue effect in which immigration from nearby sources prevents local extinction. Thus, constraints on spatial connectivity may have important implications for predator-prey coexistence. I tested the hypothesis that metapopulation dynamics of *Ambystoma tigrinum* (tiger salamander) depend on combined effects of predatory fish and spatial connectivity. Because matrix heterogeneity can influence dispersal, I also considered how a proximate constraint on amphibian dispersal – desiccation risk – scales up to influence metapopulation dynamics for *A. tigrinum*. Initial occupancy and subsequent turnover patterns were quantified in a network of 90 wetlands for three years. My previous field experiments demonstrated that desiccation risk varies among matrix habitats, and that individuals orient movements towards habitat with low desiccation risk. I used cost-distance modeling to generate a connectivity metric that accounted for desiccation risk. Initial occupancy and colonization probabilities were related positively to connectivity. Matrix structure had a strong influence on colonization, and the connectivity metric based on desiccation risk was a better predictor of colonization than metrics representing Euclidean distance or expert opinion. The effect of desiccation-informed connectivity on colonization was strongest in wetlands with fish, indicating matrix composition can moderate the

effects of predation on amphibians. I detected a rescue effect in which extinction probability was related negatively to connectivity, and this effect was strongest in sites with fish. Initial occupancy and extinction probabilities were best explained by Euclidean distance, and I discuss why matrix effects may vary for different aspects of population turnover. Overall, my results suggest effects of fish predators on metapopulation dynamics of amphibians depend on spatial connectivity, and the mechanisms underlying dispersal limitation for *A. tigrinum* may include desiccation risk.

INTRODUCTION

Metapopulation theory predicts a balance between stochastic extinction and subsequent recolonization, underscoring the importance of dispersal for regional persistence (Hanski and Gaggiotti 2004). In systems in which patch area and isolation are poor predictors of extinction and colonization (e.g., Baguette 2004, Pellet et al. 2007, Prugh et al. 2008), habitat heterogeneity may be a primary factor driving observed turnover dynamics (With 2004, Schooley and Branch 2009, Cosentino et al. 2010). For example, extinction can be deterministic in patches with poor habitat quality (Thomas 1994), and recolonization and immigration can depend on the effects of matrix heterogeneity on dispersal (Ricketts 2001). For species with patchily-distributed predators, both local habitat suitability (i.e., predator presence or abundance) and landscape connectivity are likely important for predicting occupancy and turnover dynamics.

In predator-prey metapopulations, the patchy occurrence of predators can create strong spatial variation in survival and reproductive success for prey. In these systems, the persistence of prey in patches with predators can depend on the rescue effect (Brown and Kodric-Brown

1977) or source-sink dynamics (Pulliam 1988) in which immigration from predator-free sources prevents local extinction (Amezcuca and Holyoak 2000, Caudill 2003, 2005, Woodford and McIntosh 2010). Thus, the degree to which patches are connected through dispersal is likely to have implications for predator-prey coexistence. Prey populations in isolated sites should be more susceptible to deterministic extinction by predators than populations in connected sites. Furthermore, rescue effects may be reinforced or inhibited in complex landscapes depending on the degree to which matrix structure facilitates or impedes movement (e.g., Cronin and Haynes 2004).

Fish predation is an important source of mortality for pond-breeding amphibians in permanent or semi-permanent wetlands (Wellborn et al. 1996). Predatory fish consume the eggs and larvae of many pond-breeding amphibians, and fish negatively influence amphibian reproductive behavior, survival, abundance, and species richness (e.g., Sexton et al. 1994, Hecnar and McCloskey 1997, Werner et al. 2007, Pope 2008). Although predatory fish can strongly limit the spatial distribution of amphibians (Pilliod et al. 2010), the rescue hypothesis may explain the persistence of amphibians in wetlands with fish (Pilliod and Peterson 2001). However, empirical evidence is rare (Sjögren Gulve 1994), and I am unaware of studies that include a spatial perspective on fish-amphibian interactions within the context of both extinction and colonization dynamics.

I collected three years of data on wetland occupancy and spatial turnover for *Ambystoma tigrinum tigrinum* (eastern tiger salamander, Ambystomatidae) to address the hypothesis that spatial population dynamics depend on the combined effects of predatory fish presence and connectivity. Like many pond-breeding amphibians, *A. tigrinum* is susceptible to predatory fish and can be excluded from sites occupied by fish (Sexton and Phillips 1986). I considered how

connectivity interacts with the spatial distribution of predators to influence occupancy, colonization, and extinction probabilities of *A. tigrinum*.

Because the distribution and movement patterns of amphibians can depend on matrix heterogeneity (e.g., Joly et al. 2001, Stevens et al. 2004, Mazerolle and Desrochers 2005, Rittenhouse and Semlitsch 2006), I also evaluated support for different models of connectivity. Desiccation risk has been proposed as an important cost of movement for juvenile dispersers due to their small bodies, permeable skin, and high surface-area-to-volume ratio compared to adults (Spight 1968, Rothermel and Semlitsch 2002). In a previous field experiment on *A. tigrinum*, desiccation rates varied significantly among the dominant matrix habitats in my study area in Illinois, USA (Chapter 2). Desiccation was greatest in corn and grasslands and lowest in forest and soybean. I then used a movement experiment to evaluate whether salamanders choose habitats that minimize desiccation risk when released at habitat boundaries. Movements were consistently oriented toward habitat with low desiccation risk (Chapter 2). Together, these results indicate desiccation for *A. tigrinum* varies among matrix habitats, and that movement decisions of individuals are influenced by desiccation risk. To evaluate the consequences of this physiological constraint at the population-level, I used cost-distance modeling to examine how a connectivity metric based on habitat-specific desiccation risk explained occupancy, colonization, and extinction compared to metrics representing Euclidean distance and expert opinion.

METHODS

Study species and site

Ambystoma tigrinum is frequently subterranean, using mammal burrows and self-

excavated burrows in upland forests and grasslands for refuge during most of the year. Breeding migrations occur between late fall and early spring, and adults breed primarily in fishless ponds from February to April. Juveniles emigrate from ponds between July and September and can become sexually mature within two years (Petranka 1998). Consistent with other pond-breeding amphibians (Semlitsch 2008), interpond dispersal for this species is common for juveniles and rare for adults (Church et al. 2007).

My study was conducted at a 9300-ha area in northern Illinois centered at the Richardson Wildlife Foundation property (West Brooklyn, IL; 41° 42' 26.6" N, 89° 11' 25.0" W). The landscape is dominated by row-crop agriculture (corn, soybean) and patches of grassland and forest (Fig. 3.1). Yearly crop rotation between corn and soybean is common, but corn cover increased while soybean cover declined between 1999 and 2008 (B. J. Cosentino, *unpublished data*). In 2008, cover by corn was 50% and cover by soybean was 21%. Suitable breeding habitat for *A. tigrinum* in this landscape consisted of freshwater wetlands with variable hydroperiods, which represented only 0.8% of the landscape.

I documented the occupancy status of *A. tigrinum* in 90 wetlands (median area = 0.56 ha; range = 0.01 – 5.29 ha) in 2007, 2008, and 2009. The median nearest-neighbor distance between wetlands was 245 m (range = 36 – 2830 m). Wetlands were identified using 1:24000 National Wetland Inventory quadrangles and aerial photographs, and all temporary pools (i.e., those that held water only after heavy rains) were excluded from sampling. Wetland emergent vegetation was dominated by *Alisma subcordatum*, *Eleocharis* spp., *Phalaris arundinacea*, *Polygonum* spp., *Pontederia cordata*, *Sagittaria* spp., *Scirpus* spp., and *Typha* spp. Other amphibians encountered during surveys included *Acris crepitans*, *Bufo americanus*, *Hyla chrysoscelis*, *Pseudacris crucifer*, *Rana catesbiana*, *Rana clamitans*, and *Rana pipiens*.

Wetland surveys: salamanders and predatory fish

I surveyed each wetland a single time in sampling sessions of 1–4 consecutive days between late May and early August in each year. Sites were surveyed for ≥ 3 consecutive days in 97% of sampling sessions across seasons. Sites were not sampled randomly due to logistical constraints. Instead, wetlands were grouped by spatial proximity, and I randomized the sequence in which groups were surveyed in each year. Minnow traps were used to detect the presence of *A. tigrinum* larvae at each wetland. I set traps within 10 m of the shoreline, and sampling effort was standardized by wetland area.

I documented adult and juvenile fish at each wetland using minnow traps and collapsible hoop traps. The most common fish encountered were yellow bullhead (*Ameiurus natalis*), green sunfish (*Lepomis cyanellus*), and bluegill (*Lepomis macrochirus*). *Ameiurus* sp. and *Lepomis* sp. are both documented predators of pond-breeding amphibians (e.g., Sexton and Phillips 1986, Hecnar and M'Closkey 1997, Babbitt et al. 2003). I used occupancy models that account for imperfect detection (MacKenzie et al. 2006) to estimate the probability of fish predators occupying a wetland. Program PRESENCE v3.1 was used to build single-season occupancy models (MacKenzie et al. 2006) to estimate wetland occupancy probability given a site's detection history for fish in each year (Appendix A). The conditional occupancy probability (ψ_{fish}) for wetlands in which fish were detected was 1. When fish were not detected, conditional occupancy probabilities were $0 \leq \psi_{\text{fish}} < 1$. Predatory fish occurred in $\geq 31\%$ of wetlands each year, and fish occupancy was temporally dynamic (27 observed turnover events).

Wetland area and connectivity

Patch area and connectivity metrics were measured with ArcMap v9.3 (ESRI, Redlands,

California, USA) after digitizing wetlands using aerial photographs from 2007. To measure connectivity of each wetland, I used a metric that includes a negative exponential dispersal kernel and accounts for distances to potential source wetlands (Hanski 1994, Moilanen and Nieminen 2002). The connectivity (C_i) of wetland i was defined as

$$C_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij})$$

where p_j is the probability of occupancy of source wetland j , α is a parameter scaling the effect of distance on dispersal ($1/\alpha$ is the mean dispersal distance), and d_{ij} is the distance between target wetland i and source wetland j .

Observed colonizations were used to estimate the mean dispersal distance ($1/\alpha$) for *A. tigrinum* (Prugh 2009). The ability of three connectivity metrics to explain extinction and colonization dynamics was assessed when α was set to represent the mean distance ± 1 SE (550 \pm 99 m) between colonized wetlands and the nearest occupied source (451, 550, and 649 m). A metric with $\alpha = 0.0022$ (mean dispersal distance = 451 m) was a better predictor of turnover than alternative metrics (Appendix B), so I specified α as 0.0022 in subsequent analyses.

Connectivity was calculated separately for each transition period between years: 2007-2008 and 2008-2009. I calculated C_i by setting p_j equal to 0 for source wetlands in which *A. tigrinum* was undetected in all three years, 0.33 for source wetlands occupied in one year, 0.67 for source wetlands occupied in two years, and 1 for source wetlands occupied in all three years.

Cost-distance modeling

I used cost-distance modeling to incorporate matrix heterogeneity into my connectivity metric (Adriaensen et al. 2003). To account for variation in dispersal cost among matrix

habitats, cost surfaces were created in ArcMap v9.3 by assigning movement resistances to each habitat in the landscape. Then, distances along paths between source and target wetlands that minimize cost were estimated (i.e., effective distances) using PATHMATRIX in ArcView v3.2 (Ray 2005). Finally, effective distances were substituted for Euclidean distances (d_{ij}) in the formula for C_i to generate a connectivity measure that accounted for matrix heterogeneity.

I used USDA Cropland Data Layer Maps to generate cost surfaces (www.nass.usda.gov/research/Cropland/SARS1a.htm). I collapsed land-cover types into seven categories: corn, soybean, other crop (mainly alfalfa and winter wheat; <1% of landscape), forest, grassland, developed or road, and water. I developed three resistance sets that represented different hypotheses about how the landscape influences movement. In all resistance sets, I assigned the value of 1.0 to water, assuming that wetlands function as stepping stones for dispersal. For set R_{EUC} (Euclidean), resistances were set as 1.0 for each habitat to represent a homogeneous matrix. For set R_{EXP} (Expert Opinion), I assigned resistances to reflect expert opinion for agricultural landscapes in which the common assumption is that all crops impose a uniformly high cost on dispersal (e.g., Compton et al. 2007, Greenwald et al. 2009). Thus, I assigned an equally high resistance value of 500 to all agricultural crops, and forested habitats were assigned a lower resistance value than grassland habitats (Fig. 3.2; forest = 100, grassland = 200; e.g., Rothermel and Semlitsch 2002). For set R_{DES} (Desiccation), the relative rankings of movement resistances were directly informed by experimental data on *A. tigrinum* desiccation risk and movement behavior (Chapter 2). Soybean and forested areas received equally low resistances of 100, and corn and grassland areas received equally high resistances of 500 (Fig. 3.2). I assigned a resistance value of 500 to crops other than corn and soybean and a value of 1000 to roads and developed areas in all sets. The three resistance sets were used to generate

three measures of connectivity: C_{EUC} , C_{EXP} , and C_{DES} . Resistance values for each set are relative values (Adriaensen et al. 2003), and my results were not sensitive to changes in absolute cost values when the relative rankings remained the same (B. J. Cosentino, *unpublished data*).

Due to temporal variation in crop cover associated with crop rotations, I created year-specific cost surfaces for sets R_{EXP} and R_{DES} (Fig. 3.2). When evaluating the effect of connectivity on demographic parameters, I used connectivity metrics generated from cost surfaces in the year previous to the parameter-year combination being modeled. For example, the 2007 cost surfaces were used to generate connectivity metrics to explain colonization patterns in 2008. That is, I assumed most dispersal contributing to spring colonization occurs during the previous growing season when agricultural crops are on the landscape. However, I note that cost surfaces based on R_{EXP} exhibited minimal yearly variation because corn and soybean were assigned equally high resistance values (Fig. 3.2). If most dispersal contributing to colonization occurs in spring when agricultural landscapes are barren, R_{EXP} may be a good representation of dispersal cost because amphibians avoid moving in barren areas associated with high desiccation (e.g., Mazerolle and Desrochers 2005).

Data analysis

A multiple-season occupancy model that accounts for imperfect detection probability (ρ) was used to assess how metapopulation factors (i.e., area and connectivity) and fish presence influenced initial occupancy probability (ψ_{2007}), colonization probability (γ), and extinction probability (ϵ) for *A. tigrinum*. I considered using a two-species parameterization to model the co-occurrence of fish and *A. tigrinum*, but that parameterization was not available in a multiple-season framework (MacKenzie et al. 2006). I conducted all analyses in program PRESENCE

v3.1 using a logit link function to model effects of covariates on among-wetland variation for each rate parameter. Initial analyses were conducted to select a model accounting for variation in ρ while holding ψ_{2007} , γ , and ε constant. Potential detection covariates included survey day within sampling session (1-4), Julian date, and year. I then modeled ψ_{2007} , γ , and ε sequentially, starting with ψ_{2007} and ending with ε . The most supported model for each rate parameter was used in subsequent model sets for the remaining parameters.

The Akaike Information Criterion corrected for small sample size (AIC_C) was used to rank the support of 31 candidate models representing the effect of different combinations of metapopulation factors and fish occupancy on ψ_{2007} , γ , and ε . The candidate set was the same for each rate parameter. The first model constrained the parameter of interest to be equal among sites (constant). The next 3 models included the effects of fish occupancy (F) and metapopulation factors (A = area, C = connectivity) individually (F, A, C). The next 4 models included additive effects of metapopulation factors and fish occupancy (A+C, F+A, F+C, F+A+C). Because the importance of connectivity may vary between sites with and without fish, I then added a fish \times connectivity interaction effect (F*C) to models that contained fish presence and connectivity (F+C+F*C, F+A+C+F*C). Finally, I added an area \times connectivity interaction effect (A*C) to models that contained wetland area and connectivity (A+C+A*C, F+A+C+A*C, F+A+C+F*C+A*C). Importantly, models including connectivity were constructed separately using each metric: C_{EUC} , C_{EXP} , or C_{DES} .

Akaike weights (w_i) were estimated for each model, and model-averaged estimates of ψ_{2007} , γ , and ε were calculated for each wetland using all models from each candidate set (Burnham and Anderson 2002). To evaluate the hypothesis that desiccation risk scales up to influence *A. tigrinum* occupancy dynamics, I compared the relative support of C_{EUC} , C_{EXP} , and

C_{DES} in explaining ψ_{2007} , γ , and ϵ . Each connectivity metric was in nine models for each candidate set, and Akaike weights were summed across models within each set to generate parameter importance values (Burnham and Anderson 2002).

RESULTS

Ambystoma tigrinum was detected at 29 wetlands (naïve occupancy probability = 0.32) in 2007, 43 wetlands (0.48) in 2008, and 45 wetlands (0.50) in 2009. Using a constant model of ψ in single-season occupancy models, yearly occupancy probabilities after accounting for imperfect detection were 0.42 (SE = 0.06) in 2007, 0.55 (SE = 0.06) in 2008, and 0.51 (SE = 0.05) in 2009. Of the 90 sites, 35 sites (38.9%) were never occupied, 12 sites (13.3%) were occupied once, 23 sites (25.6%) were occupied twice, and 20 sites (22.2%) were occupied during all three years (Fig. 3.1). Turnover was common in both transition periods. Observed local colonizations outnumbered local extinctions between 2007 and 2008 ($N_C = 20$, $N_E = 6$) and between 2008 and 2009 ($N_C = 9$, $N_E = 7$).

Multiseason occupancy and turnover models

The average daily detection probability in each year was high (2007 = 0.74, 2008 = 0.74, 2009 = 0.82; range = 0.43 – 0.95). The most supported model of detection probability in my multiseason models included effects of Julian date in 2007 and 2008, and survey day in 2009 (accounting for 3 parameters). Specifically, Julian date had a negative effect on detection probability in 2007 and 2008. In 2009, detection was greatest on the second day of each sampling session.

The top model of initial occupancy probability for salamanders included additive effects of fish occupancy, wetland area, and Euclidean connectivity (Table 3.1). Initial occupancy was related negatively to fish occupancy and positively to wetland area and connectivity (beta estimate \pm 1 SE for the top model, $F = -1.63 \pm 0.43$, $A = 0.78 \pm 0.36$, $C_{EUC} = 0.67 \pm 0.40$). A competing model ($\Delta AIC_C \leq 2$) included only effects of fish and wetland area (Table 3.1).

The top model of colonization probability included effects of fish occupancy and connectivity accounting for desiccation risk (C_{DES} ; Table 3.1). In general, colonization probability was greatest in fishless sites and lowest in sites with fish, and colonization increased with connectivity (Fig. 3.3A-B; beta estimate \pm 1 SE for the top model without interaction effects, $F = -1.30 \pm 0.37$, $C_{DES} = 0.76 \pm 0.43$). However, connectivity interacted with both fish occupancy and wetland area (Table 3.1). Connectivity interacted positively with fish occupancy (beta estimate \pm 1 SE, $F * C_{DES} = 3.90 \pm 1.95$) indicating the positive effect of connectivity on colonization was strongest in wetlands with fish. Connectivity interacted negatively with wetland area (beta estimate \pm 1 SE, $A * C_{DES} = -4.14 \pm 1.80$) indicating the positive effect of connectivity on colonization was strongest in small wetlands. Colonization probability also increased with wetland area in fishless sites with low to moderate connectivity (Fig. 3.3A).

The most supported model of extinction probability included additive effects of fish and connectivity based on Euclidean distance (Table 3.1). Local extinctions were most common in wetlands with fish and low connectivity (Fig. 3.3C; beta estimate \pm 1 SE for the top model, $F = 0.80 \pm 0.35$, $C_{EUC} = -0.84 \pm 0.44$). There was marginal support for a positive interaction between fish occupancy and connectivity ($-2 * \log$ -likelihood estimates: $F + C_{EUC} = 590.95$, $F + C_{EUC} + F * C_{EUC} = 589.7$), suggesting the effect of connectivity on extinction probability was strongest in wetlands with fish.

Cost-distance connectivity metrics: summed Akaike weights

Given model selection uncertainty (Table 3.1), the summed Akaike weights were the most effective way to assess relative support for the three connectivity metrics. Cost-distance models accounting for matrix heterogeneity (C_{EXP} , C_{DES}) did not have more support than Euclidean connectivity (C_{EUC}) for predicting initial occupancy and extinction probabilities (Fig. 3.4). In contrast, a connectivity metric accounting for upland desiccation risk was more supported than Euclidean and expert opinion models for predicting colonization probability (Fig. 3.4).

DISCUSSION

My results support the hypothesis that metapopulation dynamics of *A. tigrinum* depend on both the spatial distribution of fish predators and the degree to which wetlands are connected through dispersal. Initial occupancy and colonization probabilities were related negatively to fish occupancy, whereas extinction probability was related positively to fish occupancy. However, my results demonstrated that spatial connectivity can moderate the effects of fish on colonization and extinction. Initial occupancy and colonization probabilities both increased with connectivity, and an interaction between fish occupancy and connectivity indicated that the positive effect of connectivity on colonization was strongest in sites with fish. Extinction probability was related negatively to connectivity, suggesting a rescue effect in both fish and fishless sites. Importantly, I also found that desiccation risk for dispersing individuals of *A. tigrinum* scales up to influence metapopulation dynamics. As predicted, a cost-distance model based on desiccation risk was a better predictor of colonization probability than alternative

models, thereby linking isolation effects to a physiological constraint on dispersal. In contrast, initial occupancy and extinction probabilities were best explained by Euclidean connectivity.

Fish predators and spatial connectivity

The positive effect of desiccation-informed connectivity on colonization was strongest for sites with fish predators, which demonstrates that matrix composition can moderate predation effects on metapopulation dynamics. Simple habitat geometry also appeared to counteract the effects of fish because extinction probability was related negatively to Euclidean connectivity. Fish predators reduce amphibian survival and population growth (e.g., Pope 2008), and individuals have made wholesale shifts to new breeding ponds in response to fish invasions (Petranka et al. 2004). My results indicate that both structural and functional connectivity are important in determining the population-level outcomes of fish-amphibian interactions, which have implications for resulting patterns of community composition and species diversity (e.g., Chase et al. 2009).

If fish typically have strong deterministic effects on pond-breeding amphibians, what explains the pattern of co-occurrence between *A. tigrinum* and fish predators in highly connected wetlands? One hypothesis is that source-sink dynamics could generate this pattern (Pulliam 1988). In connected networks, the persistence of *A. tigrinum* at sites with fish may be dependent on continual dispersal from nearby sources without fish (e.g., Caudill 2003, 2005). If resources are limited in fishless sites because of large population sizes, intense competition for resources may force some individuals to colonize low-quality sites with fish.

However, source-sink dynamics partly depend on the ability of individuals to assess habitat quality (Schooley and Branch 2007). For amphibians, juvenile dispersers have limited

perceptual range (e.g., <50 m; Rothermel 2004) and are not known to exhibit sophisticated searching strategies. Moreover, some ambystomatids are unable to detect fish predators using olfaction (Sexton et al. 1994). If individuals disperse and select habitat randomly (Semlitsch 2008), an expected strategy when the direction of suitable habitat is unpredictable (Hawkes 2009), then colonization probability at sites with fish may be a simple function of the total number of dispersers moving through an area. Connected networks may generate a rescue effect in which a large number of colonizers reduces the overall chance of local extinction (Fig. 3.3; Brown and Kodric-Brown 1977). If isolated sites are colonized by fewer individuals than connected sites, isolated sites may be more susceptible to extinction due to the combined effects of fish predation and demographic stochasticity. In contrast, colonization of connected wetlands without fish may be less dependent on high propagule size, which would explain why the effect of connectivity on colonization was strongest for sites with fish. Although oviposition by a single female may result in successful colonization in fishless sites (Trenham et al. 2001), a greater breeding effort is likely required in sites with fish predators.

Interestingly, colonization probability was related positively to wetland area when wetland connectivity was low, suggesting a target effect for isolated sites (Lomolino 1990, Cosentino et al. 2010). The target effect is expected for species whose dispersal systems can be described by a diffusion model, where individual movement patterns exhibit a random walk (Kareiva 1985). However, the effect of area on colonization was substantial only among fishless wetlands (Fig. 3.3A-B). In isolated sites, the deterministic effects of fish on *A. tigrinum* may overwhelm the structural effect of large area on colonization, particularly if population sizes of fish increase with wetland area. In my study area, some permanent, large wetlands were stocked with large numbers of fish, whereas small wetlands were often colonized naturally by relatively

few individuals (B. J. Cosentino, *personal observation*). In connected sites, a target effect for colonization (as opposed to immigration) may not occur if the density of dispersers is high. In this case, the probability of at least one propagule intercepting a patch is not strongly related to area in connected networks, whereas patch area may be more important in isolated locations where the density of dispersers is low.

In my system, fish occupancy was related positively to wetland hydroperiod and negatively to both emergent vegetation cover and canopy cover (Appendix A). Thus, one possible interpretation is that *A. tigrinum* turnover dynamics can be explained by habitat variables as opposed to fish presence. However, occupancy modeling of fish and habitat variables indicated that hydroperiod, emergent vegetation, and canopy cover are not strong predictors of *A. tigrinum* turnover compared to fish presence (Appendix C). Thus, I am confident that fish predation is a major factor driving *A. tigrinum* colonization and extinction dynamics.

Dispersal costs and functional connectivity

My results indicate that the mechanistic basis of dispersal limitation for *A. tigrinum* likely involves the physiological risk of desiccation. Wetlands separated by matrix habitats with a low risk of desiccation (forest and soybean) were more likely to be colonized than wetlands separated by high-risk habitat (corn and grassland). Although a connectivity model based on expert opinion had competitive support (Table 3.1), summed Akaike weights across all models indicated that desiccation-informed connectivity had more overall weight for predicting colonization (Fig. 3.4). Given the limited timeframe of my study and the similarity in most cost values between models C_{DES} and C_{EXP} (Fig. 3.2), the power to detect strong differences in

support between C_{DES} and C_{EXP} was likely low. However, there was little support for a Euclidean model of connectivity (Fig. 3.4), which indicated that matrix heterogeneity in general had a strong effect on wetland colonization.

Previous cost-distance studies have used model-fitting techniques (e.g., Sutcliffe et al. 2003) and expert opinion to estimate habitat-specific movement resistances. Less frequently, experimental data have been used to inform resistances by assessing movement rates in matrix habitats and movement decisions at habitat boundaries (Schooley and Wiens 2004, Stevens et al. 2004, 2006, Castellon and Sieving 2006, Desrochers et al. 2011). My study extends this approach by mechanistically linking a physiological constraint on small-scale movement decisions to landscape-scale population dynamics (Lima and Zollner 1996).

In spatially structured systems, population dynamics can be strongly dependent on the ability of animals to disperse among habitat patches (Bowler and Benton 2005). For pond-breeding amphibians, water economy plays an essential role in determining mortality risk and overall resistance to dispersal in matrix habitats. Desiccation can decrease locomotor performance (Preest and Pough 1989), habitat permeability (Rothermel and Semlitsch 2002, Mazzerolle and Desrochers 2005), and survival (e.g., Rittenhouse et al. 2009) in amphibians. Additionally, habitat choices at forest-clearcut edges are commonly biased towards forest, where desiccation risk is presumed to be low (Chan-McLeod 2003, Rittenhouse and Semlitsch 2006, Chapter 2). Taken together, these studies indicate physiology can be a major constraint on dispersal, and my results reveal the consequences of that constraint for wetland colonization.

Matrix effects on occupancy dynamics

Few empirical studies have assessed how matrix effects vary among occupancy,

colonization, and extinction (e.g., Schooley and Branch 2009). The absence of matrix effects on initial occupancy and extinction for *A. tigrinum* may be related to the dynamic nature of landscape structure in agricultural systems dominated by annual row crops. Matrix habitats in agroecosystems are temporally dynamic due to yearly crop rotations and long-term trends in crop-plantings. However, habitat maps in ecological studies generally represent a snapshot of landscape structure. When dispersal costs vary among agricultural crops, snapshot maps may have important limitations. For example, occupancy and extinction patterns in a given year may reflect long-term stochastic processes, delayed responses to deterministic factors, or immigration patterns over multiple years. Therefore, historical effects of matrix structure on immigration may go undetected by using a snapshot of landscape structure. In contrast, matrix effects on colonization should be easier to detect with snapshot maps if the timing of colonization aligns with the period for which land cover is represented. For pond-breeding amphibians like *A. tigrinum*, wetland colonizations are likely punctuated events resulting from recent dispersal across matrix habitats (Semlitsch 2008). To account for historical effects in cost-distance modeling, cost surfaces for different years may be merged using GIS methods. However, such an approach is difficult due to uncertainties about the timeframe for ecological processes and the appropriate scheme for weighting resistance values over time.

Conclusion

The distribution and turnover of predatory fish in my system was mostly the result of natural processes (e.g., colonization via drainage ditches during high water events, extinction due to pond drying). In other systems, the introduction of non-native fish predators is a well-documented cause of amphibian declines and local extinction (e.g., Kats and Ferrer 2003, Pilliod

et al. 2010). In systems with anthropogenic introductions, my data suggest that extinction risk may be greatest for amphibians when fish are introduced to isolated sites, where the potential for a rescue effect is low. I also demonstrate how spatial connectivity and matrix structure interact to influence the potential for recolonization after extinction, and my approach illustrates how empirical data on movement costs can be used to understand the proximate source of matrix effects on population processes. Overall, my results indicate that a more complete understanding of effects of fish predators on the distribution of pond-breeding amphibians requires a spatial perspective on turnover dynamics.

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TABLES

Table 3.1 Model selection statistics for initial occupancy, colonization, and extinction probabilities of *Ambystoma tigrinum* from 90 wetlands in northern Illinois.

Rate Parameter	Model	ΔAIC_c	ω_i	$-2l$	K
Occupancy ₂₀₀₇	F+A+C _{EUC}	0.00	0.19	634.51	9
	F+A+C _{DES}	0.95	0.12	635.46	9
	F+A+C _{EXP}	0.96	0.12	635.47	9
	F+A	1.31	0.10	637.96	8
Colonization _{2008,2009}	F+C _{DES} +F*C _{DES} +A+A*C _{DES}	0.00	0.45	602.61	14
	F+C _{EXP} +F*C _{EXP} +A+A*C _{EXP}	0.79	0.30	603.4	14
Extinction _{2008,2009}	F+C _{EUC}	0.00	0.10	590.95	16
	F+C _{EUC} +F*C _{EUC} +A	0.18	0.09	586.55	18
	F+C _{EXP}	0.21	0.09	591.16	16
	F+C _{EUC} +A	0.64	0.07	589.31	17
	F+C _{DES}	0.77	0.07	591.72	16
	F+C _{EXP} +A	0.92	0.06	589.59	17

Years are indicated as subscripts for each rate parameter. Main effects include fish occupancy probability (F), wetland area (A), Euclidean connectivity (C_{EUC}), expert opinion connectivity (C_{EXP}), and desiccation risk connectivity (C_{DES}). Summary includes relative difference between model AIC_C and AIC_C for the best model (ΔAIC_c), Akaike weights (ω_i), twice the negative log-likelihood ($-2l$), and number of parameters (K). Effects of Julian date and survey day on detection probability were included in all models (3 parameters). Only models with $\Delta AIC_c \leq 2$ are presented for occupancy and colonization and $\Delta AIC_c \leq 1$ for extinction.

FIGURES

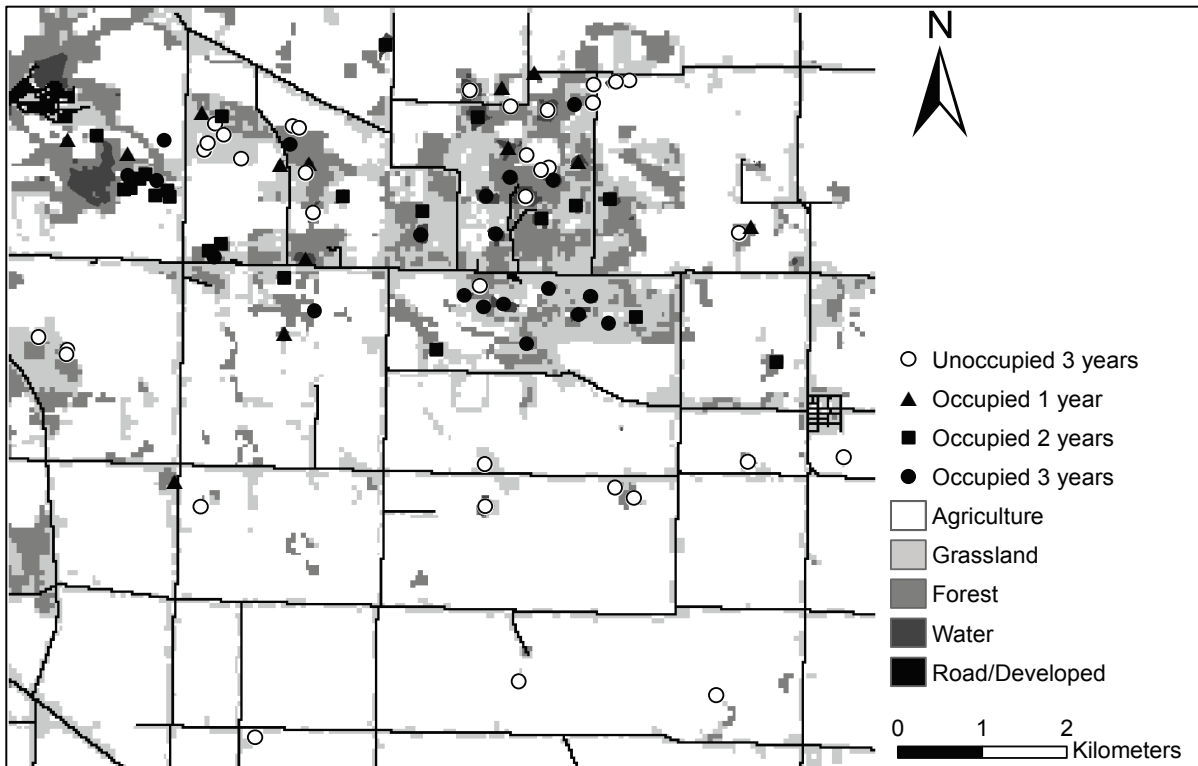


Figure 3.1 Naïve occupancy pattern of *Ambystoma tigrinum* among 90 wetlands surveyed for three years (2007-2009) in northern Illinois. Wetlands were unoccupied by salamanders in all years (open circles), occupied in one year (closed triangles), occupied in two years (closed squares), or occupied in all three years (closed circles).

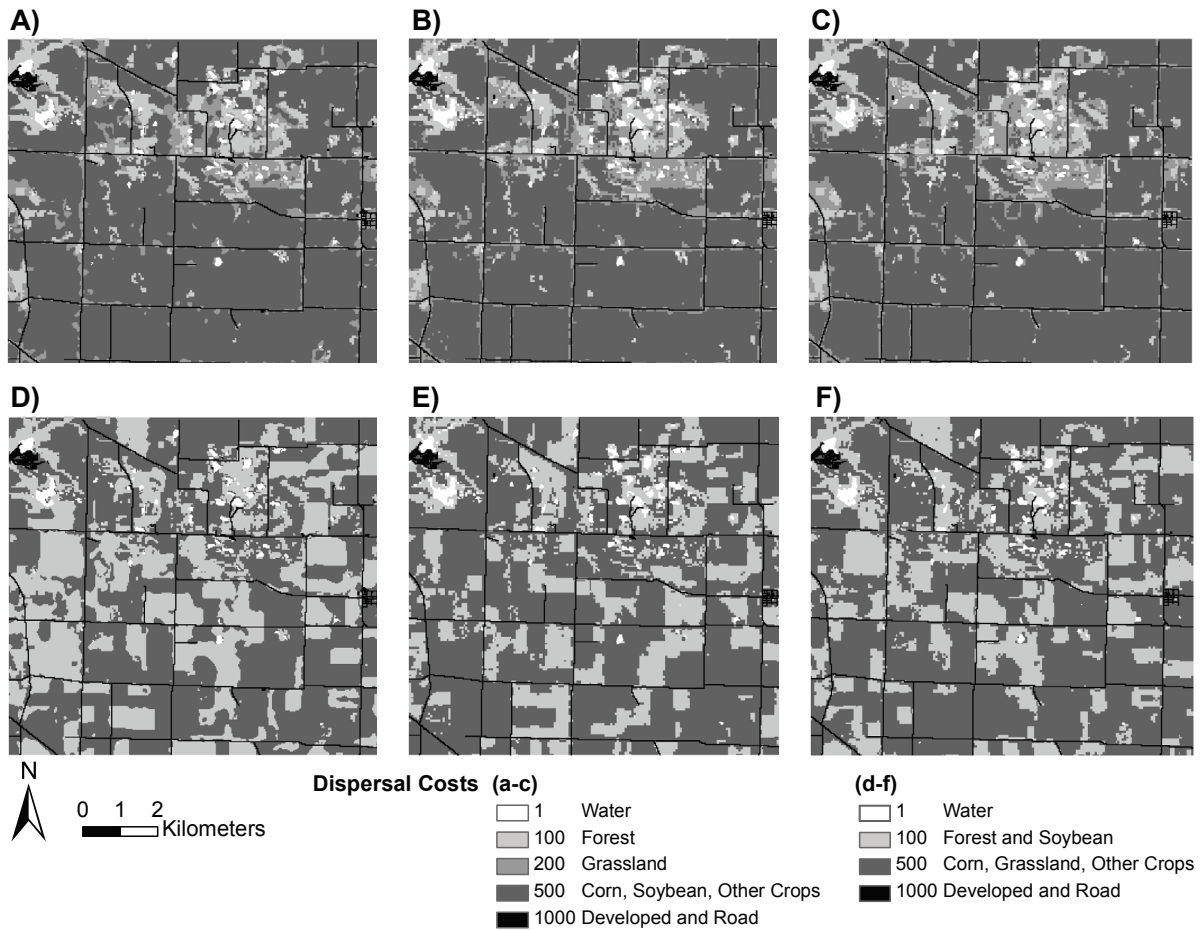


Figure 3.2 Dispersal cost surfaces for *Ambystoma tigrinum* in a northern Illinois landscape for 2006, 2007, and 2008. Movement resistances were either representative of expert opinion in agricultural landscapes (A-C) or based on empirical data on desiccation risk and movement behavior (D-F).

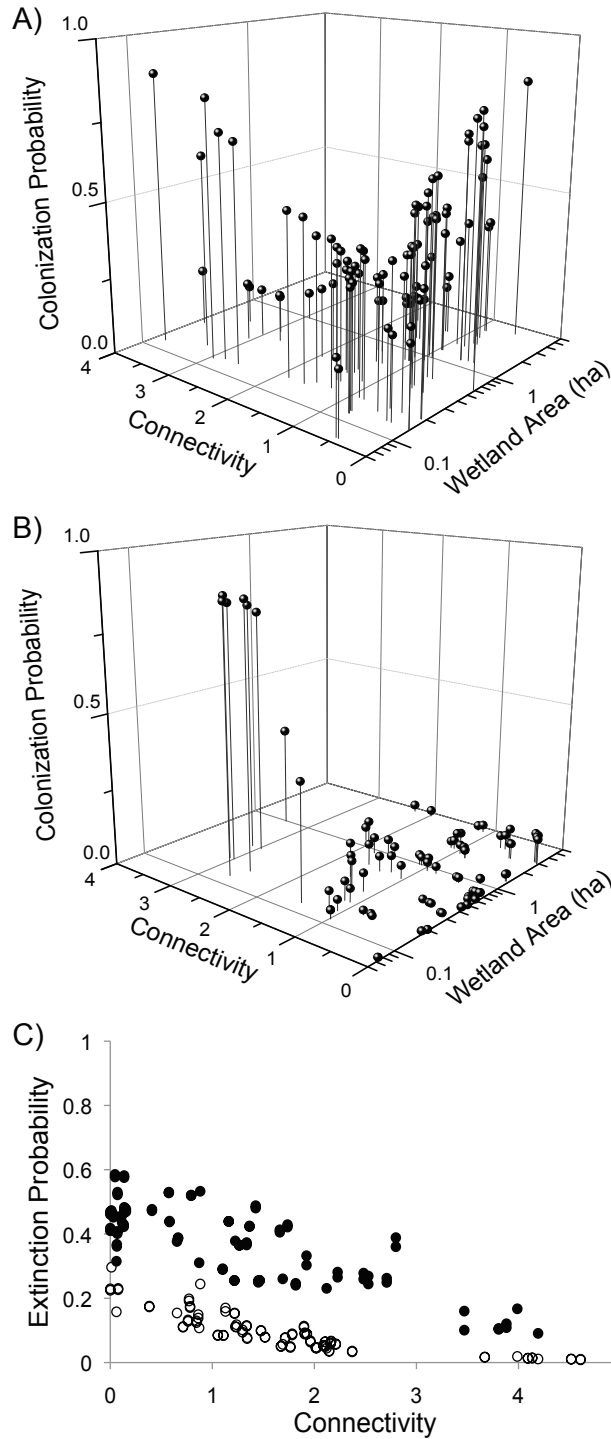


Figure 3.3 Relationships of predicted colonization probability of *Ambystoma tigrinum* to desiccation connectivity and wetland area in sites (A) without and (B) with fish, and (C) relationship of predicted extinction probability to Euclidean connectivity in sites without (open circles) and with (closed circles) fish. For display purposes, sites with fish occupancy probabilities > 0.85 were defined as present, and sites with < 0.15 were defined as absent.

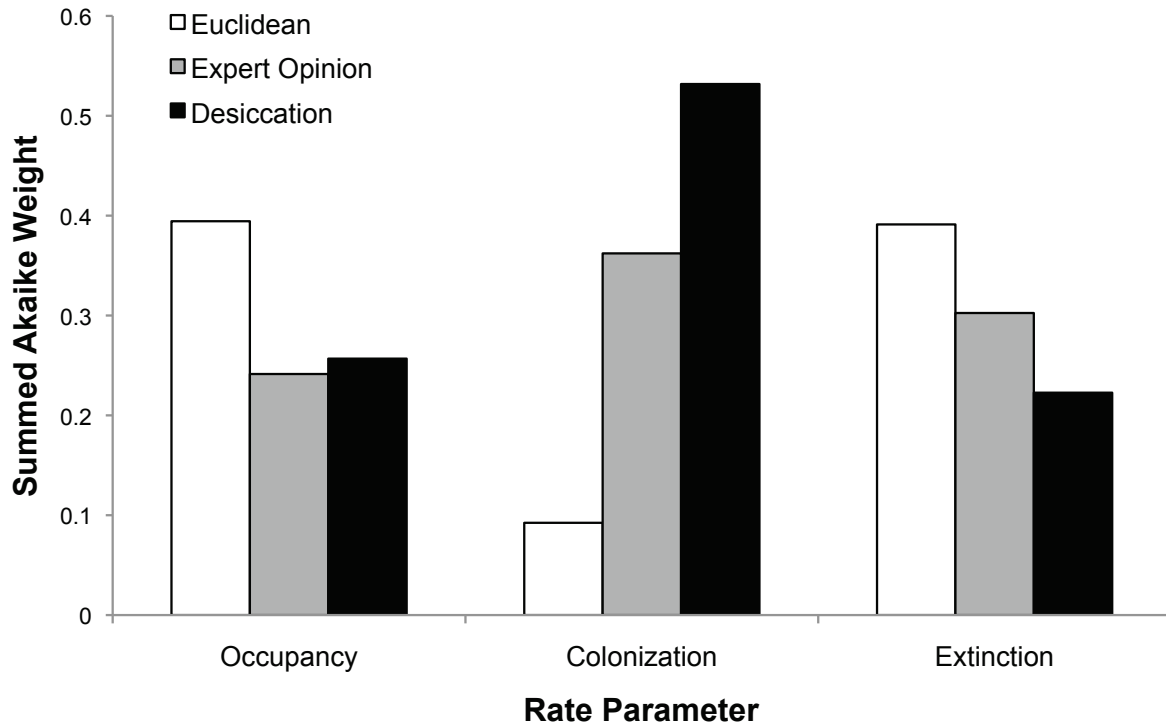


Figure 3.4 Relative support of cost-distance connectivity metrics based on summed Akaike weights for models of initial occupancy probability, colonization probability, and extinction probability of *Ambystoma tigrinum*. Cost-distance models represented Euclidean distance (white bars), expert opinion (gray bars), and desiccation risk in matrix habitats (black bars).

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CHAPTER 4

AREA AND ISOLATION PREDICT METAPOPOPULATION GENETIC STRUCTURE OF A POND-BREEDING SALAMANDER

ABSTRACT

In metapopulations with demographic turnover, theory predicts that founder effects have an important role in determining spatial genetic structure. However, among-patch heterogeneity in ecological factors (e.g., area, isolation, habitat quality) that affect extinction and colonization probabilities may create spatial variation in the strength of genetic drift and gene flow. I used microsatellite markers to test the hypothesis that ecological factors underlying extinction-colonization dynamics were also determinants of spatial genetic structure in a tiger salamander (*Ambystoma tigrinum*) metapopulation. My previous research demonstrated that metapopulation dynamics of *A. tigrinum* were influenced by metapopulation (wetland area, spatial connectivity) and habitat factors (predatory fish presence, wetland hydroperiod). I used a hierarchical Bayesian approach to evaluate how population age (newly colonized vs. established) and both metapopulation and habitat factors influenced the degree of genetic differentiation of 41 local populations. Newly colonized populations were more differentiated than established populations, suggesting founder effects had a role in generating population genetic structure. However, ecological variables related to metapopulation dynamics were more important than age in predicting genetic differentiation. Genetic differentiation was related negatively to wetland area and spatial connectivity, indicating metapopulation factors had significant roles in

generating spatial genetic structure. Genetic differentiation was not strongly related to fish presence or wetland hydroperiod, and I discuss why these habitat quality factors may not be good predictors of genetic structure. Overall, my results demonstrate that ecological factors driving metapopulation dynamics can be key predictors of spatial genetic structure, and that habitat area and isolation may reflect the relative importance of genetic drift and migration in shaping patterns of genetic differentiation within a metapopulation.

INTRODUCTION

A major goal of population genetics is to understand the ecological and evolutionary drivers of spatial genetic structure, which can provide insight into the demographic history and evolutionary potential of populations (Manier and Arnold 2006, Gaggiotti et al. 2009). From an evolutionary perspective, the degree of neutral genetic differentiation (e.g., F_{ST}) among populations depends mainly on the relative forces of genetic drift and migration (Wright 1931, 1951). Whereas genetic drift increases differentiation among populations, migration opposes drift by genetically homogenizing populations. Importantly, the strength of genetic drift is related negatively to population size, and migration is related positively to the frequency of dispersal. Thus, environmental factors associated with population size and dispersal patterns should have essential roles in shaping both demographic patterns and spatial genetic structure (Whiteley et al. 2004, Manier and Arnold 2006, Kittlein and Gaggiotti 2008, Gaggiotti et al. 2009, Alberto et al. 2010).

For species in fragmented landscapes, population size and dispersal probabilities can vary substantially among habitat patches, and species can exhibit local extinction and colonization

dynamics while persisting at a regional scale (Hanski 1999). In systems with turnover, spatially-realistic metapopulation theory predicts that extinction probability is related negatively to patch area, and colonization probability is related negatively to patch isolation (Hanski 1994, Hanski and Gaggiotti 2004). Habitat heterogeneity is also predicted to influence turnover dynamics because habitat quality can affect populations deterministically (Thomas 1994, Fleishman et al. 2002, Armstrong 2005), and landscape structure can affect the likelihood of dispersal (Wiens 1997). Both metapopulation factors (i.e., area and isolation) and habitat heterogeneity have been critical predictors of turnover dynamics in a wide array of systems (e.g., Hanski et al. 1994, Sjögren-Gulve and Ray 1996, Hokit et al. 1999, Schooley and Branch 2009, Cosentino et al. 2010).

Contrary to spatially-realistic metapopulation theory, most metapopulation genetic models are spatially-implicit and assume that patches are identical with respect to ecological characteristics. Under an island model, metapopulation genetic theory predicts that the main influence of turnover on genetic differentiation involves founder effects associated with patch recolonization (Slatkin 1977, Wade and McCauley 1988, Pannell and Charlesworth 2000). Differentiation among local populations is predicted to increase as a result of founder effects when colonization and migration are similar processes (i.e., the number of colonists is similar to the average number of migrants among extant populations) and colonists are derived from a small number of source populations (Whitlock and McCauley 1990). Empirical studies of some metapopulations have supported these predictions by demonstrating F_{ST} among newly colonized populations is greater than F_{ST} among established populations (Whitlock 1992a, Giles and Goudet 1997, Haag et al. 2005, but see Dybdahl 1994, Jacquemyn et al. 2006, Vandepitte et al. 2007).

Although population age can be a useful predictor of genetic differentiation in metapopulations, age does not provide insight into the underlying spatial and ecological factors driving turnover dynamics, or the effects of spatial heterogeneity on microevolutionary processes. Extinction and colonization are driven by factors (area, isolation, habitat quality) that have assumed relationships with population size and dispersal probability (Hanski 1994, Thomas 1994). Because genetic drift and migration also depend on population size and dispersal, ecological factors related to demographic turnover should affect spatial patterns of genetic differentiation. For example, extinction-prone patches characterized by small area or poor quality may have high rates of genetic drift due to low population size or recurring founder events, resulting in high differentiation. In contrast, patches spatially connected to other patches via dispersal may have high colonization probability, leading to gene flow and low differentiation. Over time, strong migration may even counteract the influence of drift in patches where local extinction is common (Whitlock 1992b, Pannell and Charlesworth 2000, Richards 2000).

The area-isolation and habitat paradigms have been critical approaches for understanding metapopulation dynamics (Armstrong 2005), but these approaches are rarely employed to predict metapopulation genetic structure. I hypothesized that the ecological factors underlying metapopulation dynamics of the eastern tiger salamander (*Ambystoma tigrinum tigrinum*, Ambystomatidae) were also important predictors of metapopulation genetic structure. *Ambystoma tigrinum* is a pond-breeding amphibian that prefers breeding in fishless ponds with a hydroperiod long enough to ensure larval development and metamorphosis (development time typically >3 months; B.J. Cosentino, *personal observation*). Juveniles become sexually mature within two years and are the primary contributors to among-pond dispersal (Church et al. 2007).

I used microsatellite markers to evaluate the pattern of genetic differentiation among 41 populations in an *A. tigrinum* metapopulation in northern Illinois, USA. A three-year study on metapopulation dynamics in my study area indicated that extinction and colonization events were common (Chapter 3). First, to test whether founder effects associated with turnover influenced metapopulation genetic structure, I evaluated whether F_{ST} differed between newly colonized and established populations. Next, I assessed whether genetic differentiation depended on ecological factors that were predictive of *A. tigrinum* metapopulation dynamics. Occupancy probability of *A. tigrinum* was related negatively to fish presence and positively to area and connectivity (Chapter 3), and occupancy was low in wetlands with short hydroperiods (B. J. Cosentino, *unpublished data*). Colonization probability was related negatively to fish presence and positively to area and connectivity, whereas extinction probability was related positively to fish presence and negatively to connectivity (Chapter 3). These results suggest genetic drift should be strongest in wetlands with predatory fish, short hydroperiod, small area, and low connectivity, whereas migration should be strongest in fishless wetlands with large area and high connectivity. Thus, I predicted that genetic differentiation would be related positively to fish presence and negatively to area, connectivity, and hydroperiod.

METHODS

Study sites and tissue collection

This study was conducted in a 9300-ha area in northern Illinois centered at the Richardson Wildlife Foundation property (West Brooklyn, IL; 41° 42' 26.6" N, 89° 11' 25.0" W). The landscape is dominated by row-crop agriculture with fragmented patches of forest,

wetland, and sand prairie. Marsh wetlands and open ponds with variable hydroperiods make up 0.8% of the landscape. I collected tissues samples from *A. tigrinum* individuals at 41 wetlands (Fig. 4.1) that were part of a study on metapopulation dynamics conducted between 2007 and 2009 (Chapter 3). The median wetland area was 0.97 ha (range = 0.07 – 3.8 ha), and the median Euclidean distance between wetlands was 2861 m (range = 82 – 8487 m).

Minnow traps were used to capture *A. tigrinum* individuals at wetlands for four consecutive days between May and early August during 2008 and 2009. I collected an average of 18 tissue samples per site (range = 14 – 27, Appendix D) from larvae by removing a small (< 5 mm) piece of the tail. I collected samples from 37 sites in 2008 and 4 sites in 2009. Tissues samples were preserved in 95% ethanol and stored at -80° C before DNA extraction.

Microsatellite amplification and scoring

Total genomic DNA was extracted from tissues using the Qiagen DNeasy Blood and Tissue kit (Qiagen, Inc., Valencia, California). I genotyped individuals at 13 microsatellite loci developed for other *Ambystoma* species and subspecies: *AcalD001*, *AcalD021*, *AcalD031*, *AcalD032*, *AcalD088*, *AcalD098*, *AcalD108*, and *AcalB142* (Savage 2008), *AmaD321* (Julian et al. 2003a), *AjeD23* and *AjeD422* (Julian et al. 2003b), *At52.6* (Parra-Olea et al. 2007), and *ATS5-7* (Mech et al. 2003; see Appendix E for PCR conditions). PCR products were visualized using an ABI Prism 3730xl Analyzer, and alleles were scored manually with GENEMAPPER v3.7 software (Applied Biosystems, Foster City, California).

I used MICROCHECKER v2.2.3 to identify genotyping errors and assess whether null alleles were present (van Oosterhout et al. 2004). MICROCHECKER indicated that null alleles were present for three loci across sites: *AcalB142*, *AjeD23*, and *AjeD422*, so I excluded those loci

from the analyses. Because the presence of full siblings in larval samples may bias allele frequencies (Goldberg and Waits 2010), I used the program COLONY v2.0 to identify full-siblings within each population (Wang 2004). One individual of each full-sibling pair was randomly removed from the dataset. There was an average of 17 individuals per site (range = 13 – 26) after exclusion of full-siblings (Appendix D).

Standard Genetic Analyses

I calculated the number of alleles per locus (N_A) and average observed (H_O) and expected heterozygosities (H_E) across loci for each population using GENALEX v6.41 (Peakall and Smouse 2006). Allelic richness corrected for sample size was calculated using FSTAT v2.9.3 (Goudet 1995). I tested for departures from Hardy-Weinberg and linkage equilibrium within populations using exact tests in GENEPOP v4.0 (Markov chain method, 10000 dememorization steps, 1000 batches, 10000 iterations per batch; Raymond and Rousset 1995). To evaluate genetic differentiation among sites, I used FSTAT v2.9.3 to calculate mean F_{IS} and F_{ST} (Weir and Cockerham 1984) across all populations by jackknifing across loci (Goudet 1995). I also calculated F_{ST} between all population pairs, and the significance of pairwise F_{ST} values was calculated using a permutation test (16400 permutations, Goudet 1995). In cases where multiple statistical tests were performed, I applied a sequential Bonferroni correction to P -values for a familywise error rate of $\alpha=0.05$ (Rice 1989).

Effect of metapopulation and habitat factors on genetic structure

First, to evaluate whether population turnover affected genetic differentiation, I tested the prediction that F_{ST} among newly colonized populations was greater than F_{ST} among established

populations. Data on wetland occupancy from 2007 to 2009 allowed me to distinguish newly colonized and established populations (Chapter 3). Newly colonized populations were defined as sites at which tissues were collected in the year in which a site was colonized by *A. tigrinum* (i.e., the wetland was vacant the previous year). In contrast, established populations had been occupied for ≥ 1 year when tissues were collected. My classification of population age was based on naïve occupancy, which was reliable given my detection rates. The average daily detection probability of *A. tigrinum* using minnow traps was 0.77 (Chapter 3). Because sites were surveyed for four consecutive days each year, the cumulative probability of detecting *A. tigrinum* at a wetland each year (p_c) was 0.997 using the equation

$$p_c = 1 - (1 - \bar{p})^n$$

where \bar{p} is the average daily detection probability and n is the number of surveys (Schmidt and Pellet 2009). I used FSTAT v2.9.3 to separately calculate F_{ST} among newly colonized and established populations, and a permutation test (10000 permutations) to examine whether F_{ST} was greater among newly colonized populations than among established populations.

Next, I tested the hypothesis that the genetic differentiation of populations was influenced by ecological factors driving extinction-colonization dynamics for *A. tigrinum*. I used the program GESTE v2.0 to implement a hierarchical Bayesian method that estimates population-specific F_{ST} 's (hereafter "local F_{ST} 's") and relates F_{ST} 's to environmental factors using a generalized linear model (Foll and Gaggiotti 2006). Local F_{ST} 's represent the degree to which populations are genetically differentiated from the metapopulation as a whole (Balding and Nichols 1995, Foll and Gaggiotti 2006). Although the GESTE method assumes equilibrium between migration and genetic drift, it is more realistic than the island model (Wright 1931) in that it allows for variation in rates of migration and drift among populations. Environmental

factors are used to explain variation in F_{ST} resulting from different rates of migration and drift among populations. Notably, the method is robust to deviations from migration-drift equilibrium, particularly when there is a large sample of populations (Gaggiotti and Foll 2010)

I evaluated effects of five factors on local F_{ST} 's: 1) wetland area, 2) connectivity, 3) fish presence, 4) wetland hydroperiod, and 5) population age (newly colonized vs. established). Wetland area and connectivity metrics were measured using ArcMap v9.3 (ESRI, Redlands, California). To measure wetland connectivity, I used a metric that includes a negative exponential dispersal kernel and accounts for distances to potential source wetlands (Hanski 1994, Moilanen and Nieminen 2002). The connectivity (C_i) of wetland i was measured as

$$C_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij})$$

where p_j is the probability of occupancy of source wetland j , α is a parameter scaling the effect of distance on dispersal ($1/\alpha$ is the average dispersal distance), and d_{ij} is the Euclidean distance between target wetland i and source wetland j . Euclidean distance was a better predictor of occupancy and extinction probabilities compared to distances that account for matrix structure (Chapter 3). I calculated C_i by setting α equal to 0.0022 (see Chapter 3 for justification), and p_j depended on wetland occupancy for *A. tigrinum* between 2007 and 2009. I set p_j equal to 0 for source wetlands in which *A. tigrinum* was undetected in all three years, 0.33 for source wetlands occupied in one year, 0.67 for source wetlands occupied in two years, and 1 for source wetlands occupied in all three years. Fish presence represented whether or not a site was occupied by predatory fish at least once between 2007 and 2009. I documented predatory fish in ten of the 41 sites over the three-year period (see Chapter 3 for survey methods). The most common predatory fish encountered were yellow bullhead (*Ameiurus natalis*), green sunfish (*Lepomis*

cyanellus), and bluegill (*Leopomis macrochirus*). Finally, I used an ordinal rank ranging from one to four to record hydroperiod for each wetland (1 = most ephemeral, 4 = most permanent). Hydroperiod ranks were based on observations during repeated occupancy surveys for *A. tigrinum* at each site between 2007 and 2009.

GESTE builds regression models using a constant term and parameters representing the effect of environmental factors on local F_{ST} (α_i = regression coefficient for factor i). An error term (σ^2) is estimated for each model as well. The model set consists of a single model with constant and error terms only, and additional models representing all possible combinations of environmental factors to explain variation in F_{ST} . With five factors, the model set consisted of 32 total models. A reversible jump Markov chain Monte Carlo approach was used to estimate the model-averaged posterior means of local F_{ST} 's and the posterior probability and parameters for each model. The model with the highest posterior probability is most supported. Overall support of individual factors was evaluated by summing posterior probabilities across models including a given factor. I used the following parameter settings: 10 pilot runs of 5000 iterations to estimate parameters of the proposal distribution, 500000 iterations of additional burn-in, a thinning interval of 50, and a sample size of 30000 to obtain parameter estimates. I report the mean posterior parameter estimates for α_i 's, whereas I report the mode for σ^2 because its posterior distribution was highly asymmetric (Foll and Gaggiotti 2006).

RESULTS

I found no evidence of linkage disequilibrium between loci within populations after Bonferroni corrections. Furthermore, there were only five of 410 cases in which allele

frequencies at individual loci deviated from Hardy-Weinberg proportions. Because deviations were not consistent for individual loci across populations, I retained all ten loci for further analyses.

Genetic variation was generally high. Allelic richness, standardized for a sample size of 12 individuals, averaged 6.7 alleles per locus within populations (range = 4.3–7.8; Appendix D), and the average H_E was 0.73 (range = 0.63 – 0.77; Appendix D). Across all populations, the number of alleles per locus averaged 10.8 (range = 2–20; Appendix E). Although there was no evidence for nonrandom mating within populations (mean F_{IS} = 0.015, SE = 0.023), there was moderate genetic divergence between sites. Pairwise F_{ST} ranged from 0 to 0.16 (Appendix F). The mean F_{ST} among all sites was 0.036 (SE = 0.002). Genetic divergence was significantly greater among newly colonized populations than among established populations (newly colonized F_{ST} = 0.046, established F_{ST} = 0.025, P = 0.038).

The model of genetic differentiation with the highest posterior probability included effects of wetland area and connectivity (Table 4.1). Local F_{ST} was related negatively to both area and connectivity (Fig. 4.2; α estimate for the top model, Area = -0.40, Connectivity = -0.33; σ^2 = 0.48). Although there was clear support for the top model relative to other models, there was weak support for effects of hydroperiod and age on F_{ST} as well (Table 4.1). F_{ST} was related negatively to both hydroperiod and age (α for the most-supported models including each term, Hydroperiod = -0.21, Age = -0.16). The model including an intercept only had a low posterior probability (0.036), and models with fish presence were generally not supported (Table 4.1).

DISCUSSION

This is one of the few studies to apply the area-isolation and habitat paradigms of metapopulation ecology to understand metapopulation genetic structure. I found genetic differentiation was greater among newly colonized populations than among established populations, suggesting founder effects have influenced genetic structure in this *A. tigrinum* metapopulation. Furthermore, the degree of genetic differentiation of each population was influenced by wetland area and spatial connectivity, two factors also predictive of *A. tigrinum* metapopulation dynamics (Chapter 3). Thus, my results support the hypothesis that the ecological factors underlying metapopulation dynamics also have crucial roles in shaping spatial genetic structure. Genetic differentiation was related negatively to both wetland area and connectivity. Contrary to my prediction, wetland hydroperiod and presence of predatory fish were not strong predictors of genetic differentiation.

Greater genetic differentiation among newly colonized populations than established populations indicated that founder effects associated with turnover did have a role in generating spatial genetic structure. Previous studies have found a similar pattern in plants (e.g., McCauley et al. 1995, Giles and Goudet 1997), beetles (e.g., Whitlock 1992a, Ingvarsson et al. 1997), and copepods (Haag et al. 2005), but I am unaware of comparable studies on vertebrates in a metapopulation context. In metapopulations with demographic turnover, Whitlock and McCauley (1990) showed that F_{ST} increases among sites due to turnover when

$$k < \frac{2Nm}{1 - \phi} + \frac{1}{2}$$

where k is the number of colonists of newly established populations, Nm is the number of

migrants among extant populations, and ϕ is the probability that any two alleles among colonists have the same population of origin. In my system, sites were likely colonized by a small number of individuals ($k < 2Nm$), which resulted in low allelic diversity in colonized sites compared to established sites (Appendix G). Given that *A. tigrinum* is dispersal-limited (Chapter 3), my results suggest that, on average, newly colonized wetlands were founded by *A. tigrinum* dispersers from a small number of nearby source populations (i.e., high ϕ). Colonization by long-distance dispersers can increase F_{ST} within metapopulations with high extinction rates (Bohrer et al. 2005), but a stronger isolation by distance pattern for newly colonized populations than established populations suggested that colonization by long-distance dispersers is rare (Appendix H).

Although genetic differentiation varied between newly colonized and established populations, population age was not an important predictor of local F_{ST} 's compared to ecological variables underlying turnover dynamics. This outcome likely reflects the failure of population age to account for spatial heterogeneity in environmental factors related to genetic drift and migration (Giles and Goudet 1997). For example, wetlands with high spatial connectivity were less differentiated than isolated sites (Fig. 4.2), indicating that k and ϕ likely depend on spatial context. Genetic drift due to founder events may be buffered in sites with high connectivity due to a greater number of colonists or lower probability of common origin among colonists compared to isolated sites. Even in the case of extreme founder effects (i.e., very low k), F_{ST} may decrease over time in connected sites due to gene flow after initial colonization (Whitlock 1992b, Jacquemyn et al. 2004). The weaker pattern of isolation by distance for established populations than newly colonized populations indicated that occasional long-distance gene flow may decrease differentiation over time as well (Appendix H).

For *A. tigrinum*, wetland area may have affected both gene flow and genetic drift. My previous study supported a target effect for *A. tigrinum*, in which colonization probability was related positively to wetland area (Chapter 3). Thus, the negative effect of wetland area on genetic differentiation may be explained by a greater rate of gene flow at large wetlands than at small wetlands. Pond size also had a strong positive effect on immigration of marbled salamanders (*Ambystoma opacum*; Greenwald et al. 2009). However, if population size is related positively to wetland area, the strength of genetic drift could be reduced in large wetlands. Although wetland area did not explain variation in extinction risk for *A. tigrinum*, area had a positive effect on occupancy probability (Chapter 3). Big wetlands may support larger breeding populations and provide more substrate area (e.g., twigs, emergent vegetation) for egg deposition than do small wetlands, although local population size also likely depends on the amount of upland habitat available for terrestrial juveniles and adults (Semlitsch 1998).

Although habitat area is a focus of empirical studies on metapopulation ecology, relatively few metapopulation genetic studies have evaluated the relationship between habitat area and spatial genetic structure (e.g., Kittlein and Gaggiotti 2008). Spawning area had a negative effect on F_{ST} for Atlantic salmon (*Salmo salar*), and this effect was attributed to the limited impact of genetic drift when spawning area is large (Dillane et al. 2008). Genetic differentiation was also related negatively to pool volume for *Daphnia longispina*, which was suggested to be due to either weak genetic drift or strong gene flow in large populations (Haag et al. 2005). Interestingly, Vandepitte et al. (2007) found that the level of genetic diversity within populations of the herb *Geum urbanum* depended on an interaction between population size and connectivity, in which connectivity increased genetic diversity only in small populations. Similarly, I found marginal support for an interaction between area and connectivity when

explaining F_{ST} , in which the negative effect of connectivity on F_{ST} was strongest in small wetlands (B. J. Cosentino, *unpublished data*). Hence, large populations may have low genetic differentiation even when connectivity is low due to the weak effect of drift in large populations (Vandepitte et al. 2007). In isolated locations, small sites may also receive less gene flow than large sites due to a target effect. Samples from more populations are needed to confirm an interaction effect, however, because I had a limited number of large wetlands with high connectivity in my dataset (Fig. 4.2).

Whereas area and connectivity were important predictors of F_{ST} , fish presence and wetland hydroperiod were not. Predatory fish have negative effects on amphibian survival, abundance, and distribution (Hecnar and McCloskey 1997, Pope 2008, Pilliod et al. 2010), and wetlands with short hydroperiod can decrease adult survival and the probability of successful recruitment for *A. tigrinum* (Church et al. 2007). I predicted that sites with predatory fish and short hydroperiod would be subject to strong genetic drift associated with periodic decreases in population size and founder events, which should result in high local F_{ST} (e.g., Kittlein and Gaggiotti 2008, Murphy et al. 2010). Hydroperiod did have a weak negative effect on F_{ST} , suggesting long hydroperiod may partly limit the impact of genetic drift. However, fish presence was not predictive of F_{ST} . In my study system, *A. tigrinum* populations are maintained in sites with fish by a rescue effect (Chapter 3). Thus, gene flow from connected source populations may maintain genetic diversity in sites with predatory fish (i.e., genetic rescue; Richards 2000). Occupancy by predatory fish in my system was also highly dynamic over three years, suggesting impacts of predation on genetic differentiation may have been limited due to short persistence time or low population size of fish within wetlands.

Importantly, F_{ST} reflects the impacts of genetic drift and migration over many

generations. In systems where habitat quality is temporally dynamic, the predictive value of habitat heterogeneity may vary between demographic and genetic processes. Although deterministic effects of habitat heterogeneity can strongly influence short-term population dynamics, contemporary habitat quality or matrix structure may not reflect historical effects of habitat heterogeneity on genetic structure (Anderson et al. 2010). Area and connectivity – two factors that form the basis of spatially-realistic metapopulation theory – were clearly more effective than current habitat quality at reflecting the historical impacts of genetic drift and migration on metapopulation genetic structure for *A. tigrinum*. In general, this study highlights the utility of using demographic data to make specific predictions about genetic differentiation (Lowe et al. 2008, Lowe and Allendorf 2010). More empirical studies linking demographic and genetic data are needed to provide insight into the relative effects of area, isolation, and habitat heterogeneity on the evolutionary forces shaping metapopulation genetic structure.

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TABLES

Table 4.1 Posterior probabilities for the five most-supported models of genetic isolation (F_{ST}) of *Ambystoma tigrinum* populations from 41 wetlands in northern Illinois. The sum of posterior probabilities of models with a given factor are also included.

Most Probable Models		Sum of Posterior Probabilities	
Model	Posterior Probability	Factor	Sum
Area + Connectivity	0.57	Area	0.86
Area + Connectivity + Hydroperiod	0.09	Connectivity	0.84
Area	0.08	Hydroperiod	0.13
Area + Connectivity + Age	0.05	Age	0.12
Connectivity	0.04	Fish	0.06

FIGURES

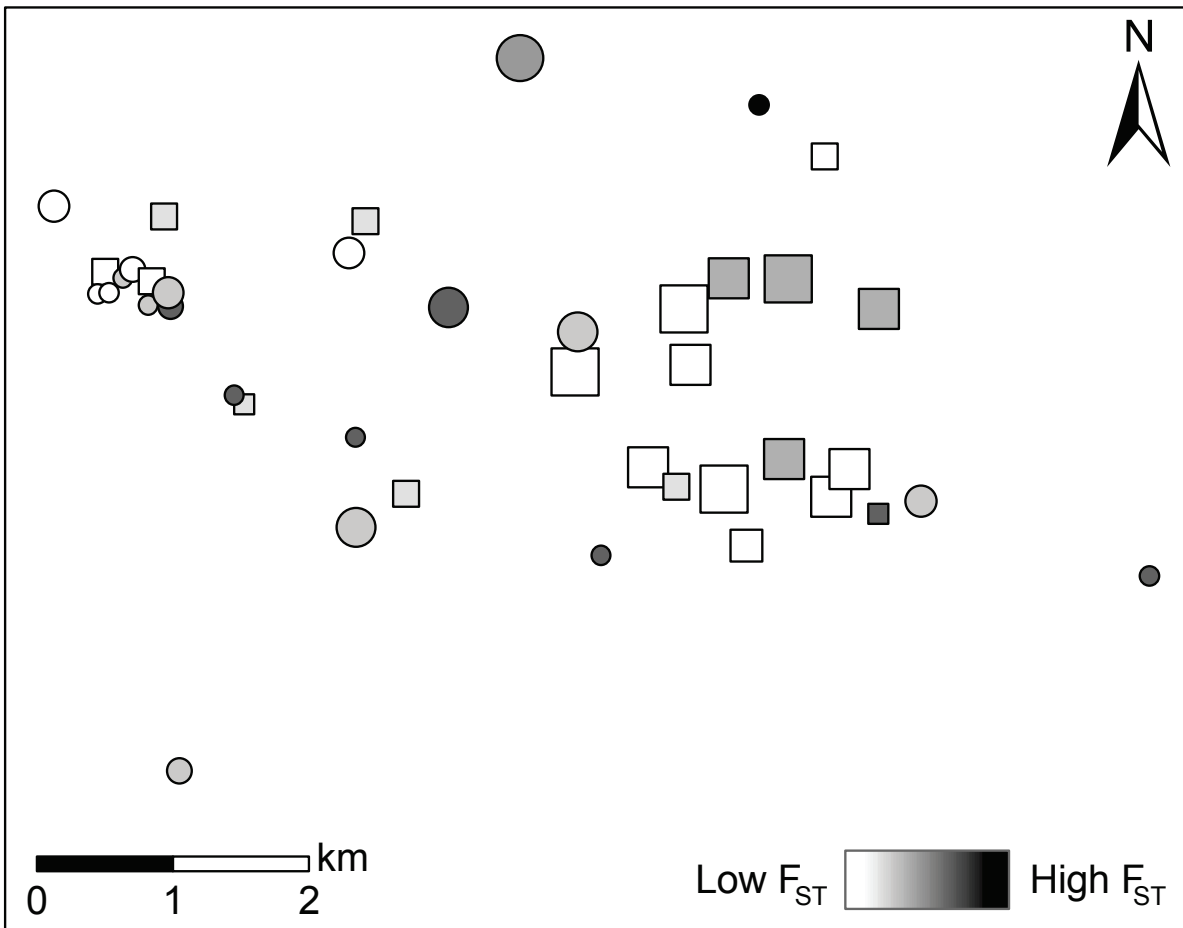


Figure 4.1 Patterns of age, area, connectivity, and genetic isolation (F_{ST}) of *Ambystoma tigrinum* populations from 41 wetlands in northern Illinois. Circles and squares represent locations of wetlands where *A. tigrinum* tissue samples were collected. Populations were classified as newly colonized (circles) or established (squares). Symbol size is proportional to wetland area.

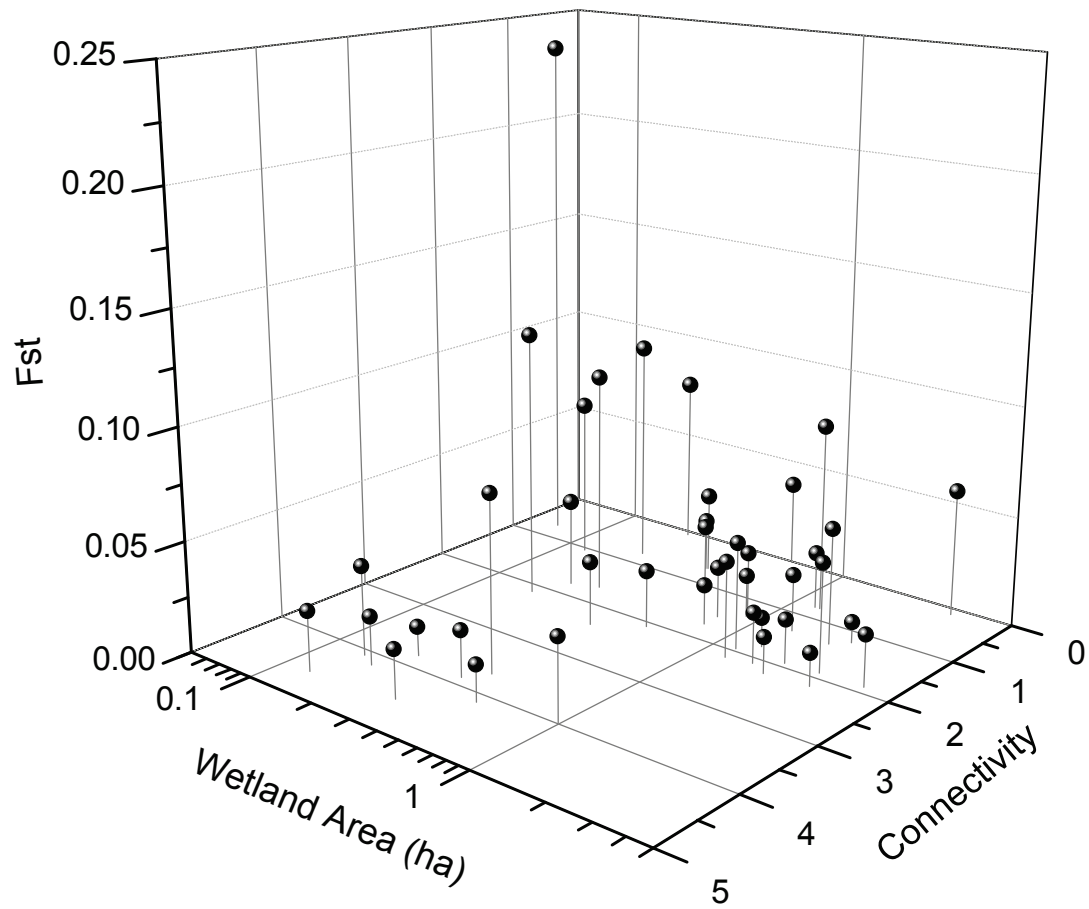


Figure 4.2 Relationships of genetic isolation (F_{ST}) of populations to wetland area and connectivity for an *Ambystoma tigrinum* metapopulation.

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APPENDIX A

Table A.1 Occupancy models for fish predators from 90 wetlands in northern Illinois in 2007, 2008, and 2009.

Year	Model	ΔAIC_c	ω_i	$-2l$	K
2007	L1+L2	0.00	0.97	80.63	5
	L1+A	7.96	0.02	88.59	5
2008	L1+L2	0.00	0.90	231.80	4
	L1+A	6.44	0.04	238.24	4
2009	L1+L2	0.00	0.78	266.22	5
	L1+S	4.48	0.08	270.70	5

Main effects include wetland area (A), the number of stream inlets/outlets at a wetland (S), and PCA scores for two axes that explained 91.8% of the variation in local habitat characteristics (canopy cover, emergent vegetation cover, and hydroperiod). The first PCA axis (L1) was positively correlated with emergent vegetation and negatively correlated with hydroperiod (factor loadings: canopy = 0.03, emergent vegetation = 0.95, hydroperiod = -0.79). The second axis (L2) was positively correlated with canopy cover and negatively correlated with hydroperiod (factor loadings: canopy = 0.98, emergent vegetation = -0.11, hydroperiod = -0.50). Models are presented with the relative difference between model AIC_C and AIC_C for the best model (ΔAIC_c), Akaike weights (ω_i), twice the negative log-likelihood ($-2l$), and the number of parameters (K). Effects of Julian date on detection probability were included in all models for 2007 and 2009 (accounting for 2 parameters). The average detection probability was 0.94 (SE = 0.01) in 2007, 0.82 (SE = 0.03) in 2008, and 0.73 (SE = 0.01) in 2009. The top two models are included for each year. Fish occupancy was related negatively to emergent vegetation and canopy cover and positively to hydroperiod in each year (beta estimates for top models ± 1 SE: $L1_{2007} = -2.51$, SE = 0.59; $L2_{2007} = -3.98$, SE = 1.59; $L1_{2008} = -1.11$, SE = 0.28; $L2_{2008} = -0.94$, SE = 0.38; $L1_{2009} = -1.12$, SE = 0.29, $L2_{2009} = -0.84$, SE = 0.35).

APPENDIX B

I assessed the ability of three connectivity metrics to explain colonization and extinction probabilities of *A. tigrinum* when α was set to 0.0015 (mean dispersal distance = 649 m), 0.0018 (mean dispersal distance = 550 m), or 0.0022 (mean dispersal distance = 451 m). I used a multiple-season occupancy model (MacKenzie et al. 2006, Program PRESENCE v3.3) to model initial occupancy (ψ), colonization (γ), and extinction probabilities (ϵ) as functions of covariates (Table B.1). Fish occupancy was always included as a covariate for each rate parameter. I included the additive effect of connectivity to model γ and ϵ . The relative support of connectivity metrics with different α values was evaluated using the Akaike Information Criterion corrected for small sample size (AIC_C).

Table B.1 Models of *Ambystoma tigrinum* occupancy dynamics using connectivity metrics with different values of α .

Model	ΔAIC_C	ω_i	$-2l$	K
$\psi(F), \gamma(F+C_{0.0022}), \epsilon(F+C_{0.0022})$	0.00	0.81	610.23	11
$\psi(F), \gamma(F+C_{0.0018}), \epsilon(F+C_{0.0018})$	3.31	0.15	613.54	11
$\psi(F), \gamma(F+C_{0.0015}), \epsilon(F+C_{0.0015})$	5.93	0.04	616.16	11

Parameters are initial occupancy (ψ), colonization (γ), and extinction (ϵ) probabilities. Main effects (F = fish occupancy, C = connectivity) for each parameter are included within parentheses. Subscripts indicate the value of α used to calculate connectivity. Models are presented with the relative difference between model AIC_C and AIC_C for the best model (ΔAIC_C), Akaike weights (ω_i), twice the negative log-likelihood ($-2l$), and the number of parameters (K). Effects of Julian date and survey day on detection probability were included in all models (3 parameters).

APPENDIX C

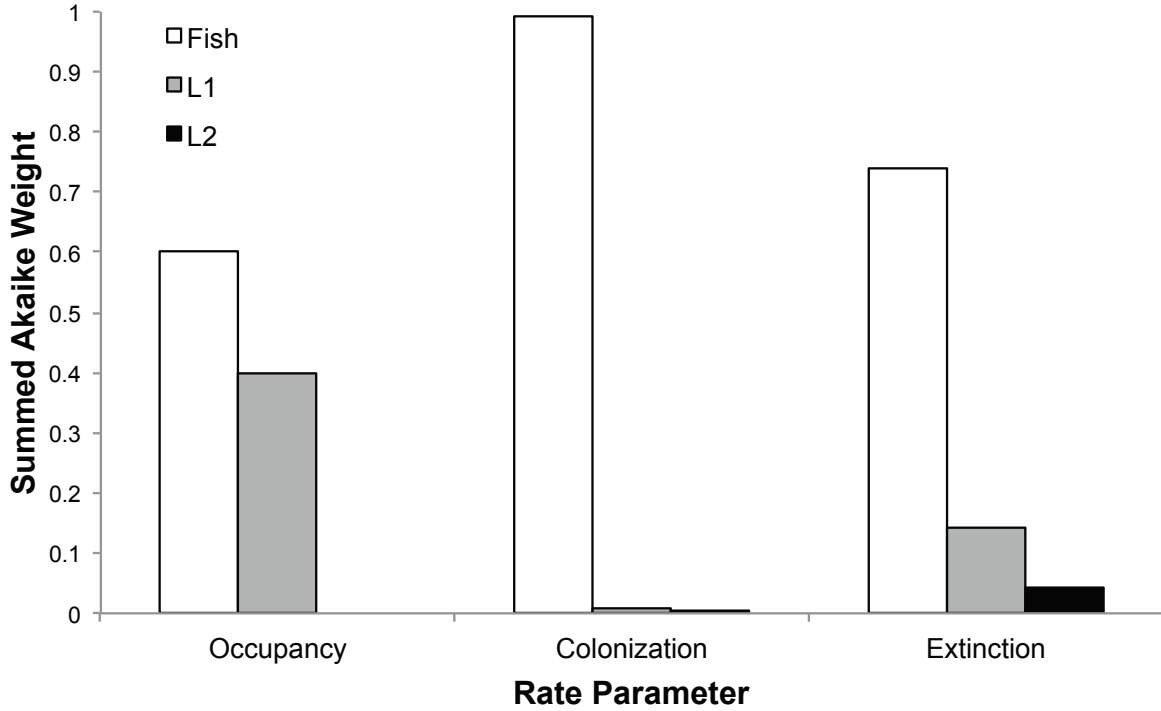
I evaluated how occupancy and turnover of *A. tigrinum* were related to habitat variables predictive of fish occupancy (Table C.1; see Appendix A for fish occupancy models). I analyzed the same set of multiple-season occupancy models presented in Chapter 3 with two exceptions. First, only Euclidean connectivity was used to predict occupancy and extinction probabilities, whereas I used desiccation connectivity to predict colonization probability. Second, in addition to analyzing models with fish occupancy as a covariate, I included models with PCA axes summarizing variation in hydroperiod, emergent vegetation cover, and canopy cover (L1 and L2; see Appendix A). I replaced fish occupancy with L1 or L2 for every model that included fish. I modeled initial occupancy, colonization, and extinction sequentially, starting with initial occupancy and ending with extinction. The most supported model for each rate parameter was used in subsequent model sets for remaining parameters. Fish, L1, and L2 were included in eight models in each model set. I compared the relative support of fish, L1, and L2 by summing Akaike weights across models within each model set (Fig. C.1; Burnham and Anderson 2002).

Table C.1 Occupancy models for *Amybstoma tigrinum* from 90 wetlands in northern Illinois in 2007, 2008, and 2009.

Rate Parameter	Model	ΔAIC_c	ω_i	$-2l$	K
Occupancy ₂₀₀₇	F+C _{EUC} +A	0.00	0.23	634.51	9
	F+A	1.31	0.12	637.96	8
	L1+C _{EUC}	1.45	0.11	638.10	8
	L1+C _{EUC} +L1*C _{EUC}	1.49	0.11	636.00	9
Colonization _{2008,2009}	F+C _{DES} +F*C _{DES} +A+A*C _{DES}	0.00	0.82	602.61	14
Extinction _{2008,2009}	F+C _{EUC}	0.00	0.16	590.95	16
	F+C _{EUC} +F*C _{EUC} +A	0.18	0.15	586.55	18
	F+A+C _{EUC}	0.64	0.12	589.31	17
	F+C+F*C _{EUC}	1.04	0.10	589.71	17
	F+A	1.34	0.08	592.29	16

Main effects include wetland area (A), connectivity (C_{EUC} = Euclidean connectivity, C_{DES} = desiccation connectivity), fish occupancy (F), and PCA axes summarizing variation in hydroperiod, emergent vegetation cover, and canopy cover (L1 and L2; see Appendix A for factor loadings). Models are presented with the relative difference between model AIC_C and AIC_C for the best model (ΔAIC_c), Akaike weights (ω_i), twice the negative log-likelihood ($-2l$), and the number of parameters (K). Effects of Julian date and survey day on detection probability were included in all models (3 parameters). Only models with $\Delta AIC_c \leq 2$ are presented.

Figure C.1 Relative support of fish occupancy, L1, and L2 based on summed Akaike weights for models of initial occupancy probability, colonization probability, and extinction probability of *Ambystoma tigrinum*. L1 and L2 are PCA axes summarizing variation in wetland hydroperiod, emergent vegetation cover, and canopy cover.



APPENDIX D

Table D.1 Wetland location, sample size, and genetic diversity indices for populations of *Ambystoma tigrinum* in northern Illinois.

Wetland	Easting	Northing	N _{Full}	N _{NoSib}	H _O	H _E	A _R
6	313121	4620773	27	26	0.78	0.77	7.17
32	313071	4620607	21	21	0.78	0.76	7.67
33	313152	4620618	17	16	0.74	0.72	7.23
34	313258	4620725	23	18	0.74	0.74	6.90
35	313325	4620787	18	17	0.79	0.74	6.91
36	313465	4620702	20	20	0.74	0.76	7.34
38	313608	4620516	20	17	0.65	0.70	5.71
41	317701	4620724	21	21	0.74	0.69	6.55
45	318404	4621618	18	18	0.82	0.75	6.91
49	318803	4620500	16	15	0.73	0.69	6.52
54	316573	4620039	15	15	0.67	0.75	7.34
55	314141	4619802	19	15	0.73	0.72	6.56
57	314076	4619865	15	15	0.76	0.71	5.38
58	317829	4618764	16	16	0.79	0.77	7.23
60	317107	4619336	18	18	0.76	0.77	7.58
61	317317	4619193	17	15	0.73	0.73	7.32
62	317668	4619175	15	15	0.81	0.77	7.84
63	318109	4619396	16	16	0.75	0.75	6.65
64	318452	4619122	15	15	0.72	0.75	7.03
65	318589	4619326	20	19	0.72	0.72	6.99
66	319116	4619085	18	18	0.75	0.75	7.23
67	318799	4618997	16	13	0.76	0.72	5.64
70	320791	4618538	14	14	0.78	0.69	5.77
125	316169	4622336	14	13	0.67	0.72	5.87
127	313670	4617106	21	18	0.78	0.74	6.41
222	317422	4620090	16	16	0.74	0.75	7.33
223	317373	4620500	25	25	0.74	0.76	7.11
224	316595	4620328	18	14	0.79	0.75	6.84
228	318136	4620720	15	14	0.76	0.73	6.66
278	315035	4621143	15	15	0.75	0.76	7.26
281	314963	4619552	20	13	0.72	0.72	6.07
283	314969	4618894	20	20	0.73	0.76	7.03
284	315332	4619144	16	15	0.80	0.74	6.50
285	316767	4618687	21	17	0.61	0.63	5.44
322	313554	4621178	16	15	0.74	0.74	6.83
332	315649	4620509	18	18	0.79	0.72	5.75

Table D.1 Continued

356	313588	4620617	20	20	0.73	0.73	6.42
777	312750	4621252	21	21	0.73	0.77	7.16
1002	314917	4620906	19	19	0.75	0.76	6.94
2016	313444	4620524	20	18	0.74	0.76	6.53
2022	317924	4621994	20	19	0.77	0.65	4.26

Easting and Northing are UTM coordinates for zone 16. N_{Full} is the total number individuals sampled from each wetland, and N_{NoSib} is the number of individuals per population after one individual of each full-sibling pair was removed from the dataset. Observed (H_O) and expected (H_E) heterozygosities and allelic richness (A_R) were calculated using N_{NoSib} and averaged across loci. Allelic richness was corrected for a minimum sample size of 12.

APPENDIX E

Table E.1 Polymerase chain reaction (PCR) conditions for microsatellite loci amplified in *Ambystoma tigrinum*.

Multiplex	Locus	Citation	Dye Label	T _A (°C)	[Primer] μM	N _A	Size Range (bp)
1	<i>AcalD021</i>	Savage 2008	NED	59	0.06	19	155–231
1	<i>AcalD088</i>	Savage 2008	6FAM	59	0.17	14	145–197
1	<i>AmaD321</i>	Julian et al. 2003a	VIC	59	0.15	13	159–215
1	<i>AjeD23</i>	Julian et al. 2003b	PET	59	0.14	2	163–167
2	<i>AcalD031</i>	Savage 2008	PET	60	0.09	8	81–109
2	<i>AcalD108</i>	Savage 2008	NED	60	0.10	13	113–162
3	<i>AcalD001</i>	Savage 2008	VIC	58	0.10	20	127–253
3	<i>AcalD032</i>	Savage 2008	PET	58	0.06	11	104–158
3	<i>AcalD098</i>	Savage 2008	NED	58	0.06	11	89–151
4	<i>AcalB142</i>	Savage 2008	NED	58	0.11	5	168–190
4	<i>AjeD422</i>	Julian et al. 2003b	PET	58	0.28	17	188–280
4	<i>At52.6</i>	Parra-Olea et al. 2007	6FAM	58	0.11	3	155–163
4	<i>ATS5-7</i>	Mech et al. 2003	VIC	58	0.09	4	238–248

All microsatellite loci were developed for other *Ambystoma* species and subspecies and cross-amplified in *A. tigrinum*. Loci were amplified in four multiplex reactions consisting of 2 – 4 loci each. Forward primers were labeled with 6FAM, VIC, NED, or PET fluorescent dyes for genotyping (Applied Biosystems, Foster City, California). All PCRs consisted of 10 μl volumes containing 1X buffer, 2.0 mM MgCl₂, 0.25 mM of each dNTP, 0.06 to 0.28 μM of forward and reverse primers, 0.5 units *Taq* DNA polymerase, and 1.0 μl template DNA (10-50 ng). The PCR profile for each multiplex reaction was initial denaturing at 94° C for 2 min, 40 cycles of 94° C for 45 s, annealing temperature (T_A) for 30 s, and 72° C for 1 min, followed by final extension at 72° C for 5 min. Primer concentration, number of alleles (N_A), and the allele size range is given for each locus. The repeat motif of *ATS5-7* was dinucleotide, and all other loci were tetranucleotides.

APPENDIX F

Table F.1 Pairwise F_{ST} estimates between *Ambystoma tigrinum* populations in Illinois. F_{ST} values significantly different from 0 after Bonferroni correction are in bold.

Wetland	6	32	33	34	35	36	38	41	45	49	54	55	57	58
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
33	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-
34	0.01	0.00	0.01	-	-	-	-	-	-	-	-	-	-	-
35	0.01	0.01	0.01	0.00	-	-	-	-	-	-	-	-	-	-
36	0.00	0.00	0.01	0.01	0.00	-	-	-	-	-	-	-	-	-
38	0.03	0.04	0.06	0.02	0.03	0.04	-	-	-	-	-	-	-	-
41	0.04	0.03	0.03	0.05	0.04	0.04	0.08	-	-	-	-	-	-	-
45	0.01	0.02	0.02	0.02	0.02	0.01	0.04	0.03	-	-	-	-	-	-
49	0.05	0.05	0.05	0.06	0.04	0.05	0.09	0.05	0.05	-	-	-	-	-
54	0.01	0.00	0.01	0.02	0.01	0.00	0.04	0.02	0.01	0.04	-	-	-	-
55	0.02	0.02	0.02	0.03	0.02	0.01	0.07	0.03	0.01	0.06	0.02	-	-	-
57	0.05	0.05	0.07	0.06	0.07	0.05	0.08	0.09	0.08	0.11	0.04	0.07	-	-
58	0.02	0.01	0.03	0.03	0.03	0.02	0.06	0.03	0.01	0.03	0.00	0.04	0.06	-
60	0.01	0.02	0.03	0.03	0.03	0.02	0.05	0.05	0.02	0.05	0.00	0.03	0.04	0.00
61	0.02	0.02	0.02	0.03	0.02	0.02	0.05	0.02	0.02	0.03	-0.01	0.01	0.08	0.01
62	0.01	0.01	0.02	0.03	0.02	0.01	0.06	0.03	0.01	0.03	-0.01	0.02	0.06	-0.01
63	0.02	0.03	0.05	0.04	0.04	0.03	0.06	0.05	0.02	0.04	0.01	0.04	0.07	0.01
64	0.02	0.03	0.02	0.03	0.02	0.02	0.06	0.03	0.02	0.03	0.00	0.03	0.05	0.01
65	0.03	0.01	0.02	0.04	0.02	0.02	0.08	0.03	0.03	0.02	0.00	0.04	0.07	0.01
66	0.03	0.03	0.04	0.05	0.04	0.02	0.07	0.04	0.03	0.04	0.01	0.06	0.07	0.01
67	0.06	0.05	0.08	0.08	0.07	0.06	0.10	0.09	0.07	0.06	0.04	0.10	0.09	0.02
70	0.05	0.06	0.07	0.08	0.06	0.05	0.10	0.05	0.04	0.04	0.04	0.07	0.10	0.03
125	0.02	0.03	0.05	0.03	0.03	0.02	0.04	0.04	0.02	0.06	0.02	0.04	0.06	0.03
127	0.02	0.02	0.04	0.02	0.01	0.01	0.03	0.07	0.02	0.05	0.01	0.04	0.07	0.03
222	0.02	0.02	0.02	0.04	0.02	0.02	0.06	0.03	0.02	0.02	0.01	0.04	0.07	0.00
223	0.02	0.02	0.02	0.03	0.03	0.02	0.06	0.02	0.01	0.04	0.01	0.02	0.06	0.02
224	0.02	0.02	0.04	0.03	0.03	0.02	0.04	0.04	0.01	0.06	0.01	0.03	0.06	0.02
228	0.04	0.05	0.08	0.07	0.07	0.04	0.08	0.08	0.04	0.05	0.03	0.05	0.07	0.04
278	0.01	0.01	0.03	0.02	0.01	0.01	0.04	0.06	0.02	0.05	0.00	0.03	0.05	0.02
281	0.03	0.02	0.04	0.03	0.04	0.03	0.06	0.06	0.04	0.08	0.02	0.04	0.07	0.04
283	0.01	0.02	0.04	0.03	0.03	0.02	0.04	0.05	0.02	0.06	0.00	0.02	0.04	0.02
284	0.01	0.01	0.04	0.02	0.03	0.01	0.04	0.04	0.03	0.06	0.01	0.02	0.06	0.02
285	0.06	0.04	0.06	0.06	0.05	0.06	0.09	0.04	0.06	0.07	0.03	0.06	0.13	0.06
322	0.02	0.01	0.03	0.01	0.02	0.01	0.04	0.04	0.01	0.05	0.02	0.02	0.07	0.02
332	0.04	0.04	0.07	0.06	0.05	0.04	0.07	0.06	0.04	0.08	0.02	0.04	0.09	0.03
356	0.02	0.02	0.01	0.02	0.00	0.00	0.04	0.06	0.04	0.05	0.01	0.04	0.04	0.04
777	0.00	-0.01	0.01	0.00	0.00	0.00	0.03	0.04	0.01	0.05	0.00	0.01	0.03	0.01
1002	0.01	0.01	0.01	0.02	0.01	0.01	0.04	0.03	0.00	0.03	0.00	0.01	0.06	0.01
2016	0.01	0.01	0.03	0.02	0.01	0.01	0.04	0.05	0.02	0.06	0.02	0.03	0.05	0.03
2022	0.10	0.11	0.12	0.12	0.13	0.10	0.14	0.13	0.08	0.15	0.07	0.12	0.14	0.09

Table F.1 Continued

Wetland	60	61	62	63	64	65	66	67	70	125	127	222	223	224
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	-	-	-	-	-	-	-	-	-
49	-	-	-	-	-	-	-	-	-	-	-	-	-	-
54	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	-	-	-	-	-	-	-	-
57	-	-	-	-	-	-	-	-	-	-	-	-	-	-
58	-	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	-	-	-	-	-	-	-
61	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-
62	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-
63	0.02	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-
64	0.02	0.01	0.00	0.01	-	-	-	-	-	-	-	-	-	-
65	0.02	0.01	0.00	0.03	0.01	-	-	-	-	-	-	-	-	-
66	0.02	0.02	0.01	0.03	0.01	0.02	-	-	-	-	-	-	-	-
67	0.04	0.05	0.04	0.05	0.04	0.04	0.02	-	-	-	-	-	-	-
70	0.04	0.04	0.03	0.04	0.02	0.03	0.01	0.07	-	-	-	-	-	-
125	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.08	0.05	-	-	-	-	-
127	0.02	0.03	0.02	0.03	0.04	0.04	0.04	0.07	0.05	0.02	-	-	-	-
222	0.02	0.01	0.00	0.01	0.00	0.00	0.01	0.04	0.03	0.03	0.03	-	-	-
223	0.02	0.01	0.01	0.02	0.01	0.03	0.02	0.06	0.04	0.02	0.04	0.02	-	-
224	0.03	0.02	0.01	0.03	0.02	0.04	0.03	0.07	0.05	0.01	0.03	0.02	0.00	-
228	0.02	0.04	0.04	0.03	0.05	0.06	0.04	0.06	0.06	0.04	0.04	0.05	0.03	0.04
278	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.05	0.05	0.02	0.02	0.02	0.03	0.02
281	0.04	0.03	0.04	0.05	0.05	0.04	0.05	0.09	0.08	0.04	0.04	0.03	0.04	0.03
283	0.02	0.01	0.01	0.02	0.02	0.04	0.04	0.07	0.06	0.03	0.02	0.02	0.02	0.01
284	0.02	0.01	0.02	0.02	0.02	0.03	0.03	0.06	0.05	0.03	0.02	0.01	0.02	0.01
285	0.07	0.03	0.05	0.06	0.07	0.04	0.07	0.11	0.07	0.08	0.07	0.06	0.05	0.06
322	0.03	0.02	0.02	0.03	0.03	0.03	0.04	0.08	0.05	0.01	0.03	0.02	0.03	0.01
332	0.03	0.04	0.03	0.04	0.05	0.04	0.05	0.07	0.07	0.04	0.04	0.04	0.04	0.03
356	0.03	0.04	0.03	0.04	0.03	0.03	0.04	0.07	0.06	0.03	0.02	0.04	0.04	0.03
777	0.02	0.02	0.01	0.03	0.02	0.02	0.04	0.06	0.06	0.02	0.01	0.02	0.02	0.02
1002	0.01	0.01	-0.01	0.01	0.01	0.01	0.01	0.05	0.03	0.03	0.03	0.00	0.00	0.01
2016	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.06	0.05	0.03	0.03	0.02	0.03	0.02
2022	0.08	0.10	0.08	0.09	0.11	0.12	0.11	0.12	0.15	0.11	0.11	0.11	0.09	0.10

Table F.1 Continued

Wetland	228	278	281	283	284	285	322	332	356	777	1002	2016	2022
6	-	-	-	-	-	-	-	-	-	-	-	-	-
32	-	-	-	-	-	-	-	-	-	-	-	-	-
33	-	-	-	-	-	-	-	-	-	-	-	-	-
34	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	-	-	-	-	-	-	-	-	-	-	-	-
36	-	-	-	-	-	-	-	-	-	-	-	-	-
38	-	-	-	-	-	-	-	-	-	-	-	-	-
41	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	-	-	-	-	-	-	-	-
49	-	-	-	-	-	-	-	-	-	-	-	-	-
54	-	-	-	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	-	-	-	-	-	-	-
57	-	-	-	-	-	-	-	-	-	-	-	-	-
58	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	-	-	-	-	-	-
61	-	-	-	-	-	-	-	-	-	-	-	-	-
62	-	-	-	-	-	-	-	-	-	-	-	-	-
63	-	-	-	-	-	-	-	-	-	-	-	-	-
64	-	-	-	-	-	-	-	-	-	-	-	-	-
65	-	-	-	-	-	-	-	-	-	-	-	-	-
66	-	-	-	-	-	-	-	-	-	-	-	-	-
67	-	-	-	-	-	-	-	-	-	-	-	-	-
70	-	-	-	-	-	-	-	-	-	-	-	-	-
125	-	-	-	-	-	-	-	-	-	-	-	-	-
127	-	-	-	-	-	-	-	-	-	-	-	-	-
222	-	-	-	-	-	-	-	-	-	-	-	-	-
223	-	-	-	-	-	-	-	-	-	-	-	-	-
224	-	-	-	-	-	-	-	-	-	-	-	-	-
228	-	-	-	-	-	-	-	-	-	-	-	-	-
278	0.05	-	-	-	-	-	-	-	-	-	-	-	-
281	0.07	0.04	-	-	-	-	-	-	-	-	-	-	-
283	0.04	0.02	0.02	-	-	-	-	-	-	-	-	-	-
284	0.05	0.02	0.01	0.00	-	-	-	-	-	-	-	-	-
285	0.10	0.07	0.07	0.06	0.06	-	-	-	-	-	-	-	-
322	0.05	0.02	0.04	0.03	0.02	0.05	-	-	-	-	-	-	-
332	0.06	0.03	0.04	0.04	0.03	0.08	0.05	-	-	-	-	-	-
356	0.06	0.01	0.05	0.03	0.04	0.07	0.02	0.06	-	-	-	-	-
777	0.06	0.00	0.03	0.01	0.01	0.05	0.00	0.03	0.01	-	-	-	-
1002	0.03	0.02	0.03	0.02	0.01	0.04	0.01	0.03	0.02	0.01	-	-	-
2016	0.05	0.01	0.04	0.03	0.02	0.08	0.03	0.04	0.02	0.00	0.01	-	-
2022	0.10	0.12	0.13	0.08	0.11	0.16	0.12	0.09	0.13	0.10	0.10	0.13	-

APPENDIX G

I used PROC GENMOD in SAS to build linear models of allelic richness in *A. tigrinum* populations with a normal probability distribution and an identity link function (Table G.1; SAS version 9.2; SAS Institution, Inc., Cary, North Carolina, USA). Allelic richness was corrected for a sample size of 12. Wetland area, connectivity, fish presence, hydroperiod, and population age (newly colonized vs. established) were used as predictor variables. I built 15 models that included additive effects of up to two predictor variables, and I included a model with an intercept only. Model support was evaluated using the Akaike Information Criterion corrected for small sample size (AICc).

Table G.1 Models of allelic richness for 41 *Ambystoma tigrinum* populations in northern Illinois.

Model	$\Delta AICc$	ω_i	Log-likelihood	K
Area + Connectivity	0.00	0.82	-35.76	4
Age + Connectivity	4.75	0.08	-38.13	4
Area + Age	6.37	0.03	-38.94	4
Area	7.61	0.02	-40.79	3
Age	8.22	0.01	-41.10	3
Area + Hydroperiod	9.55	0.01	-40.53	4
Age + Hydroperiod	9.79	0.01	-40.65	4
Area + Fish	9.81	0.01	-40.66	4
Age + Fish	9.96	0.01	-40.74	4
Connectivity + Hydroperiod	10.46	0.00	-40.99	4
Connectivity	11.59	0.00	-42.79	3
Intercept only	13.48	0.00	-44.90	2
Connectivity + Fish	13.87	0.00	-42.69	4
Hydroperiod	14.47	0.00	-44.22	3
Fish	15.63	0.00	-44.80	3
Fish + Hydroperiod	16.89	0.00	-44.20	4

Main effects are included for each model. Models are presented with the relative difference between model AIC_C and AIC_C for the best model ($\Delta AICc$), Akaike weights (ω_i), log-likelihood, and the number of parameters (K). A scale parameter to correct for dispersion was estimated using maximum likelihood for each model. Allelic richness was related positively to wetland area and connectivity (parameter estimates for top models ± 1 SE: Area = 0.37, SE = 0.09; Connectivity = 0.25, SE = 0.07).

APPENDIX H

Isolation by distance (IBD) was assessed by examining the relationship between pairwise genetic distances ($F_{ST} / (1 - F_{ST})$) and the natural logarithm of geographic distances between *A. tigrinum* populations (Rousset 1997). I used the Isolation By Distance Web Service (IBDWS v. 3.16; Jensen et al. 2005) to calculate Mantel tests for all populations (Fig. H.1) and separately for newly colonized and established populations (Fig. H.2). Reduced major axis (RMA) regression was used to calculate the slope and intercept of the IBD relationship. I used 10000 bootstrap randomizations to evaluate whether the slope was significantly greater than zero and to evaluate whether the 95% confidence intervals for slope overlapped between newly colonized and established populations.

Figure H.1 Relationship of pairwise genetic distances to pairwise geographic distances between 41 populations in an *Ambystoma tigrinum* metapopulation. The slope of the regression line was significantly greater than zero ($F_{ST} / (1 - F_{ST}) = -0.25 + 0.087 [\ln (\text{Geographic Distance})]$); $r = 0.29$, $P < 0.0001$).

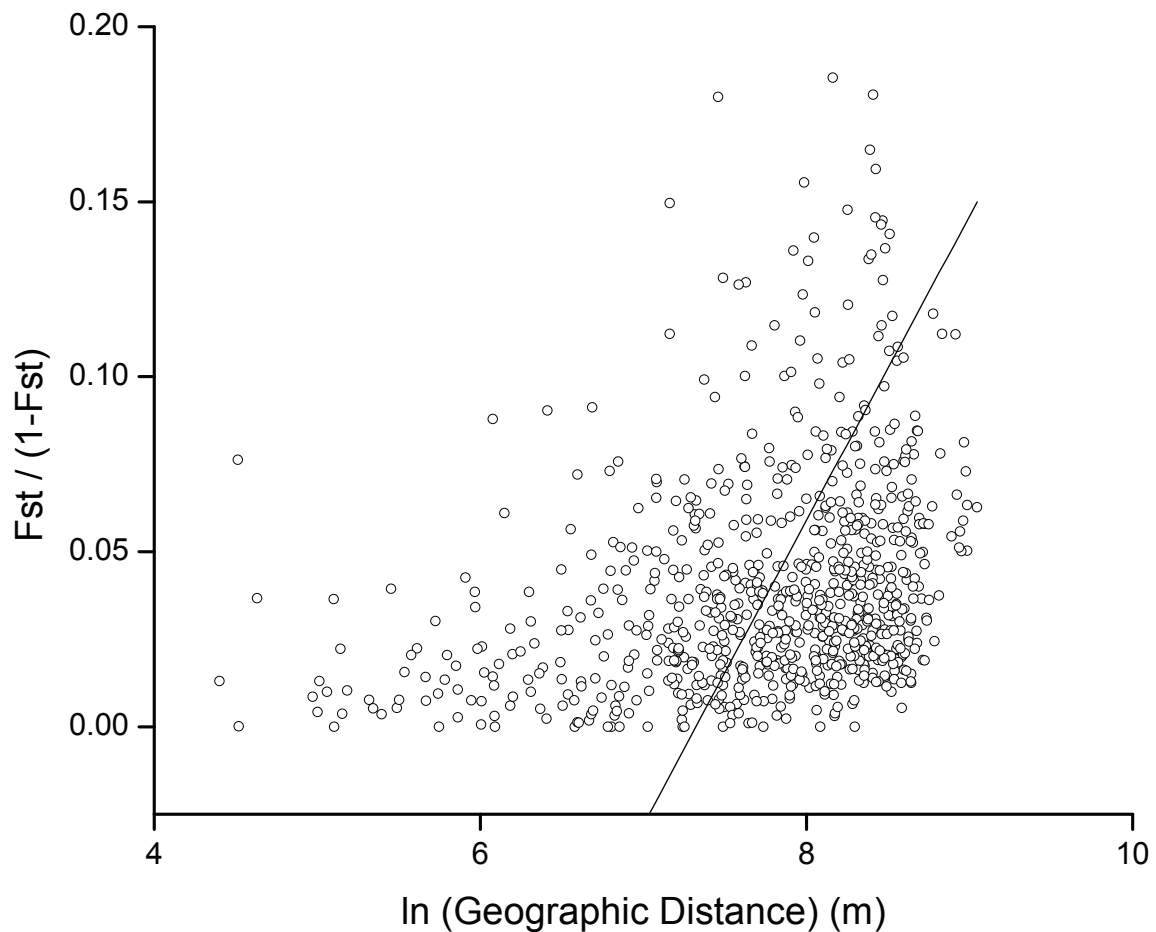
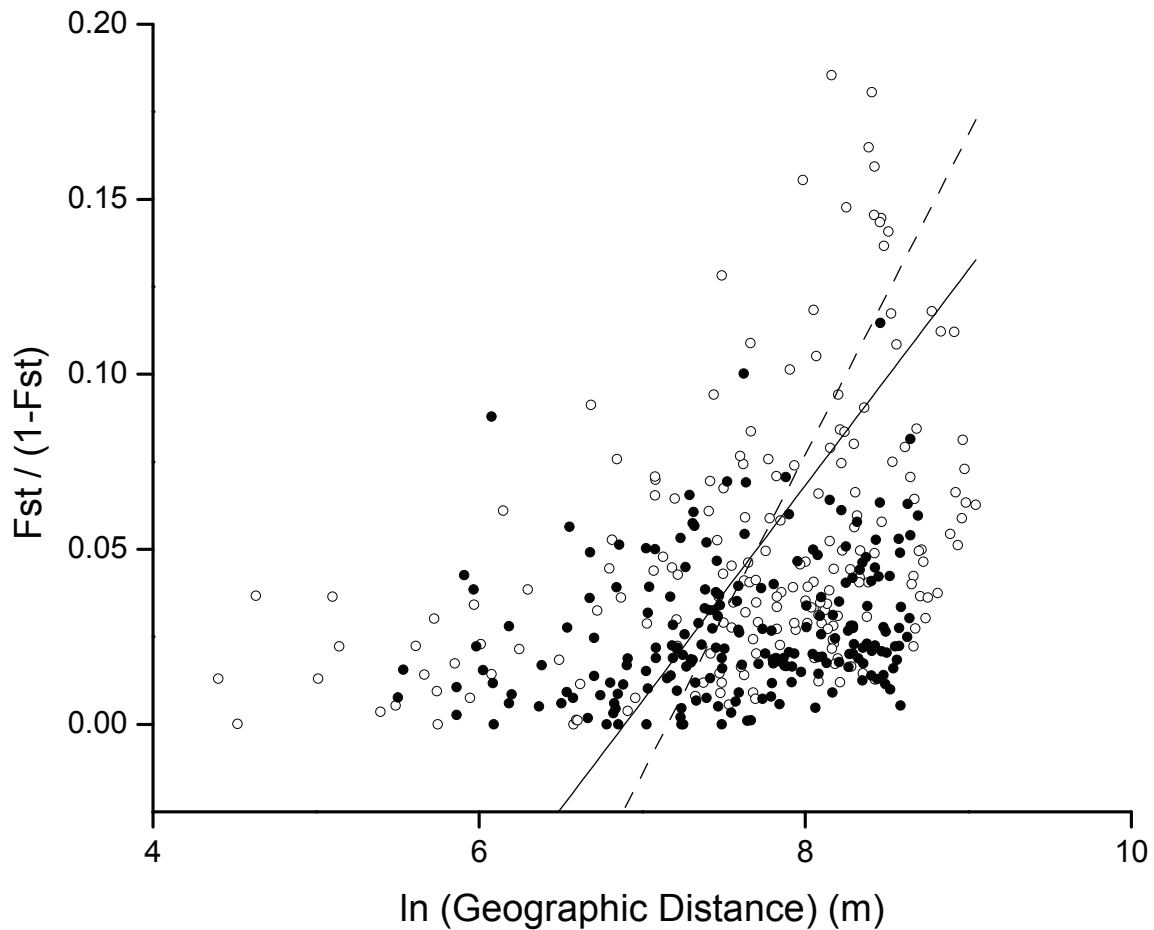


Figure H.2 Relationship of pairwise genetic distances to pairwise geographic distances between newly colonized populations (open circles, dashed regression line) and between established populations (closed circles, solid regression line) in an *Ambystoma tigrinum* metapopulation. The slope of the regression line was significantly greater than zero for both newly colonized ($F_{ST} / (1 - F_{ST}) = -0.25 + 0.091 [\ln (\text{Geographic Distance})]$; $r = 0.41$, $P < 0.0026$) and established populations ($F_{ST} / (1 - F_{ST}) = -0.18 + 0.062 [\ln (\text{Geographic Distance})]$; $r = 0.24$, $P = 0.017$). The 95% confidence intervals of slope for newly colonized and established populations did not overlap when bootstrapping over all population pairs (newly colonized = 0.076 – 0.11, established = 0.052 – 0.072), indicating that IBD was significantly greater for newly colonized than established populations. However, 95% confidence intervals did overlap when bootstrapping over independent population pairs (newly colonized = 0.047 – 0.19, established = 0.087 – 0.11), which is a more conservative approach (Bohanak 2002).



CURRICULUM VITAE

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EDUCATION

Ph.D., Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign (UIUC), May 2011 (expected)

B.A., Biology, Augustana College (IL), *Summa cum laude*, 2004

PROFESSIONAL EXPERIENCE

TEACHING (* indicates Teacher Ranked as Excellent by students, UIUC)

2010 Lecturer & Coordinator, IB105 Environmental Biology, UIUC, Fall*
2009 Teaching Assistant, IB372 Honors Ecology and Evolution, UIUC, Fall
2009 Teaching Assistant, IB451 Conservation Biology (Graduate), UIUC, Spring*
2008 Teaching Assistant, IB204 Genetics, UIUC, Fall*
2008 Teaching Assistant, IB199 Genetics Merit, UIUC, Fall*
2008 Teaching Assistant, IB302 Evolution, UIUC, Spring*
2007 Teaching Assistant, IB203 Ecology, UIUC, Fall*
2007 Teaching Assistant, IB150 Organismal and Evolutionary Biology, UIUC, Spring*
2007 Teaching Assistant, IB199 Organismal and Evolutionary Biology Merit, UIUC, Spring
2006 Teaching Assistant, IB203 Ecology, UIUC, Fall*
2005 K7-12 Substitute Teacher, MSD of Wayne Township, Indianapolis, IN

UNDERGRADUATE ADVISING

2009 IB390 Introductory Research, Fall, 2 students
2009 IB390 Introductory Research, Spring, 1 student
2008 IB390 Introductory Research, Fall, 1 student
2008 IB390 Introductory Research, Summer, 1 student
2007 IB390 Introductory Research, Spring, 4 students

RESEARCH

2005 Research Technician, Institute of Ecosystem Studies, NY, Summer
2004 Research Technician, University of Missouri at Columbia, Summer
2003 National Science Foundation (NSF) Research Experiences for Undergraduates, Institute of Ecosystem Studies, NY, Summer

HONORS AND AWARDS

- 2010 NASA-Michigan State University Professional Enhancement Award, US Regional Association of the International Association for Landscape Ecology (US-IALE)
- 2010 University of Illinois Fellowship, Spring
- 2009 John G. and Evelyn Hartman Heiligenstein Outstanding Teaching Assistant Award, School of Integrative Biology, UIUC
- 2009 Best talk by a Ph.D. candidate, 11th Annual Graduate Student Symposium in Ecology and Evolutionary Biology, UIUC
- 2009 Student Travel Award, US-IALE
- 2008 Best talk by a graduate student, 100th Annual Meeting of the Illinois State Academy of Science, Champaign, IL
- 2008 Best talk by a Ph.D. candidate, 11th Annual Graduate Student Symposium in Ecology and Evolutionary Biology, UIUC
- 2007 NSF Graduate Research Fellowship Program – *Honorable Mention*
- 2006 NSF Graduate Research Fellowship Program – *Honorable Mention*
- 2005-08 University of Illinois Distinguished Fellowship, UIUC

GRANTS

- 2010 Program in Ecology, Evolution, and Conservation Biology (PEEC) Travel Grant, UIUC, \$250
- 2009 PEEC Summer Research Grant, UIUC, \$850
- 2009 PEEC Travel Grant, UIUC, \$400
- 2008 Theodore Roosevelt Memorial Grant, American Museum of Natural History, \$1500
- 2008 PEEC Summer Research Grant, UIUC, \$500
- 2007 Graduate College Conference Travel Grant, UIUC, \$300
- 2007 Illinois Wildlife Preservation Fund, Large Fund, Illinois Department of Natural Resources. Co-PI's: Christopher A. Phillips Robert L. Schooley, \$5000
- 2007 Philip W. Smith Memorial Fund, Illinois Natural History Survey, \$1200
- 2006 Research Grant, Illinois State Academy of Science, \$350
- 2006 Graduate Student Research Grant, Chicago Herpetological Society, \$300

PUBLICATIONS

Peer-Reviewed Articles:

- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2011. Connectivity of agroecosystems: dispersal costs can vary among crops. *Landscape Ecology* 26:371–379.
- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2010. Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*. *Landscape Ecology* 25:1589–1600.
- Cosentino, B. J.**, W. H. Lowe, and G. E. Likens. 2009. Demography and movement of the northern spring salamander in four New Hampshire headwater streams. *Verh. Internat. Verein. Limnol.* 30:677–680.

- Lowe, W. H., M. A. McPeck, G. E. Likens, and **B. J. Cosentino**. 2008. Linking movement behavior to dispersal and divergence in plethodontid salamanders. *Molecular Ecology* 17:4459–4469.
- Hager, S. B., and **B. J. Cosentino**. 2006. An identification key to the rodent prey found in owl pellets: employing incisor size to distinguish among genera. *American Biology Teacher* 68:135–144.
- Lowe, W. H., G. E. Likens, and **B. J. Cosentino**. 2006. Self-organization in streams: the relationship between movement behavior and body condition in a headwater salamander. *Freshwater Biology* 51:2052–2062.

Articles in Review:

- Hager, S. B., **B. J. Cosentino**, and K. J. McKay. Scavenging rates on bird victims of window collisions in an urban landscape.

Technical Reports:

- Cosentino, B. J.**, C. A. Phillips, and R. L. Schooley. 2008. Wetland occupancy and landscape connectivity for Blanding's and Western Painted Turtles in the Green River Valley. INHS Technical Report 2008(55).

Book Reviews:

- Hager, S. B., and **B. J. Cosentino**. 2006. Book review of *The Naked Emperor: Darwinism Exposed*. *Reports of the National Center for Science Education* 26(6):27–28. Invited Paper.
- Mollan, T., **B. J. Cosentino**, and J. J. Williams. 2005. Review: Law, Darwinism, and Public Education: the Establishment Clause and the Challenge of Intelligent Design. *Reports of the National Center for Science Education* 25(3–4):27–28.
- Williams, J. J., S. B. Hager, and **B. J. Cosentino**. 2004. Invited Review: Darwin's Proof: The Triumph of Religion Over Science. *Reports of the National Center for Science Education* 23(3–4):43–44.
- Cosentino, B. J.**, J. J. Williams, L. B. Guderyahn, and S. B. Hager. 2003. Review: *Designer Universe: Intelligent Design and the Existence of God*. *Reports of the National Center for Science Education* 23(1):28.

CONTRIBUTED PRESENTATIONS

- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2010. Habitat quality and matrix heterogeneity influence metapopulation dynamics in a pond-breeding salamander. US-IALE, Athens, GA.
- Schooley, R. L., and **B. J. Cosentino**. 2010. Biofuels, connectivity, and wildlife: building on a shaky foundation. US-IALE, Athens, GA.
- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2009. Effects of upland habitats on desiccation risk and movement decisions in tiger salamanders. Midwest Fish and Wildlife Conference, Springfield, IL.

- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2009. From physiology to metapopulation dynamics: effects of desiccation risk on connectivity in tiger salamanders (*Ambystoma tigrinum*). US-IALE, Snowbird, UT.
- Cosentino, B. J.** 2009. From physiology to metapopulation dynamics: effects of desiccation risk on tiger salamanders (*Ambystoma tigrinum*). Graduate Student Symposium in Ecology and Evolutionary Biology, UIUC.
- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2008. Effects of habitat structure on tiger salamander metapopulation dynamics in northern Illinois. Midwest Fish and Wildlife Conference, Columbus, OH.
- Lowe, W. H., G. E. Likens, M. A. McPeck, and **B. J. Cosentino**. Linking movement behavior to dispersal and divergence in plethodontid salamanders. Annual Meeting of the Hubbard Brook Cooperators, West Thornton, NH.
- Lowe, W. H., M. A. McPeck, G. E. Likens, and **B. J. Cosentino**. Dispersal and divergence in plethodontid salamanders. Ecological Society of America, Milwaukee, IL.
- Cosentino, B. J.**, C. A. Phillips, and R. L. Schooley. 2008. Do local and landscape-level habitat characteristics influence pond occupancy by painted turtles (*Chrysemys picta*)? Annual Meeting of the Illinois State Academy of Science, Champaign, IL.
- Cosentino, B. J.** 2008. Wetland occupancy patterns for tiger salamanders (*Ambystoma tigrinum*) in northern Illinois. Graduate Student Symposium in Ecology and Evolutionary Biology, UIUC.
- Cosentino, B. J.**, R. L. Schooley, and C. A. Phillips. 2007. Site occupancy patterns for tiger salamanders and painted turtles in northern Illinois. Midwest Fish and Wildlife Conference, Madison, WI.
- Lowe, W. H., M. A. McPeck, G. E. Likens, and **B. J. Cosentino**. 2007. Dispersal and divergence in plethodontid salamanders. Conference on the Biology of Plethodontid Salamanders. San Cristóbal de las Casa, Chiapas, Mexico.
- Cosentino, B. J.**, W. H. Lowe, and G. E. Likens. 2007. Demography and movement of the northern spring salamander in four New Hampshire headwater streams. Congress of the International Association of Theoretical and Applied Limnology, Montreal, Canada.
- Lowe, W. H., G. E. Likens, M. A. McPeck, D. C. Buso, **B. J. Cosentino**, and B. T. Greene. 2006. Controls and consequences of dispersal in streams. American Society of Limnology and Oceanography, Victoria, Canada.
- Cosentino, B. J.**, and S. B. Hager. 2005. An identification key to the rodent prey found in owl pellets: employing incisor size to distinguish among genera. Annual Meeting of the Illinois State Academy of Science, Galesburg, IL.
- Cosentino, B. J.**, W. H. Lowe, and G. E. Likens. 2004. Population biology and movement behavior of the northern spring salamander, *Gyrinophilus porphyriticus*, in four New Hampshire headwater streams. Annual Meeting of the Illinois State Academy of Science, Charleston, IL.

PROFESSIONAL ACTIVITIES

Guest Lectures and Presentations:

- 2011 Guest Lecture, IB105 Environmental Biology, UIUC. Agriculture and ecology.
- 2011 Guest Lecture, NRES407 Wildlife Population Ecology, UIUC. Conservation genetics.
- 2010 Guest Lecture, NRES407 Wildlife Population Ecology, UIUC. Conservation genetics.
- 2009 Guest Lecture, IB372 Honors Ecology and Evolution, UIUC. Evolution and conservation biology.
- 2009 Guest Lecture, IB451 Conservation Biology, UIUC. Metapopulation dynamics and conservation.
- 2009 Guest Lecture, NRES407 Wildlife Population Ecology, UIUC. Conservation genetics.
- 2008 EcoLunch Speaker, UIUC. Model selection and multimodel inference in ecology.
- 2008 Guest Lecture, IB204 Genetics, UIUC. Epistasis.
- 2008 Guest Lecture, OTS Neotropical Herpetology Graduate Course, Costa Rica. Occupancy modeling for amphibians and reptiles.
- 2008 Guest Lecture, IB464 Herpetology, UIUC. Conservation genetics of amphibians.
- 2008 Guest Lecture, NRES407 Wildlife Population Ecology, UIUC. Conservation genetics.
- 2007 Guest Lecture, BI401 Research Experiences in Field Biology, Augustana College, IL. Modeling species occupancy and connectivity in fragmented landscapes.
- 2007 Guest Field Instructor, NRES285 Field Experience, UIUC. Amphibian monitoring research techniques.
- 2007 Invited Speaker, Illini Biological Society Research Symposium, UIUC. Tips for obtaining undergraduate research experiences.
- 2005 Guest Lecture, BI333 Vertebrate Zoology, Augustana College, IL. Plethodontid salamander ecology.

Local Organizing or Committee Service:

- 2010 Coordinator, 12th Annual Graduate Student Symposium in Ecology and Evolution, UIUC
- 2009 Moderator, 11th Annual Graduate Student Symposium in Ecology and Evolution, UIUC
- 2007-08 Fellowship Board Executive Committee, Student Member, Graduate College, UIUC
- 2007-08 Social Coordinator, Graduate Students in Ecology and Evolutionary Biology, UIUC
- 2007 Co-Organizer, Darwin Day screening of “Flock of Dodos: The Evolution-Intelligent Design Circus”, UIUC
- 2006 Co-Organizer, “Alternative Careers in Ecology, Evolution, and Environmental Science” Workshop, UIUC
- 2005 Co-Organizer, Darwin Day lecture by Dr. Robert Pennock (Michigan State), UIUC

External Reviewer:

Journal of Animal Ecology, Conservation Biology, Herpetological Review, Landscape Ecology