THE NEED TO MOVE: EXPLORING LANDSCAPE CONNECTIVITY THROUGH THE EYES OF THE NORTHERN LEOPARD FROG

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

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ABSTRACT

The northern leopard frog (*Rana pipiens*) is a species that depends on landscape connectivity to complete its lifecycle. However, due to historic and present anthropogenic landscape changes, this species encounters a variety of agriculture fields during migratory and dispersal movements. These landscape changes have potential to affect habitat connectivity for these frogs and may interfere with the species' life-cycle needs. Differing land-cover types have varying effects on movement, desiccation and predation of the northern leopard frog, which in turn affect the frog's ability to survive. Through creation and use of an agent-based model that can simulate individual frog movement on a modeled landscape, I explored habitat connectivity in the prairie-pothole region. I used northern leopard frog movement and desiccation data collected from two summers of field work to inform my modeled scenarios. The model I developed allows for the exploration of habitat connectivity under various patterns of land-cover change.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

For most species, movement is essential for life. Movement of seeds helps plants disperse, while animals move to forage, reproduce, find alternate habitat types, repopulate areas where they have been extirpated, and maintain genetic diversity needed to adapt to change. If individuals cannot move across a landscape to mix with individuals of other populations, local extinctions can result. Additionally, the smaller a population is, the more vulnerable it becomes to extinction if that population is also isolated, i.e., lacks the ability to intermix with other populations (Fagan and Holmes 2006).

Long-distance movements of animals can take one of two forms; migration or dispersal. Migratory movements consist of daily, seasonal, or even generational bi-directional movements among habitat types to meet specific life-history needs. Dispersal movements, however, are uni-directional movements away from a normal range and provide for the mixing of genetic materials, the population of new habitats or repopulation of previously occupied but currently vacant habitats (Semlitsch 2008).

When animals migrate, it is because there is a need for individuals to reach different environmental, habitat, or resource conditions. These movements can be to a breeding site (Webster et al. 2002), a more favorable climate (Peñuelas and Filella 2001), an overwintering area (Wilcove and Wikelski 2008), or better forage (Olson et al. 2006). Often, these bi-directional migratory movements are seasonal, as when birds leave northern habitats and travel south for the winter, returning north the following spring. The movement from an overwintering habitat to a breeding pond in the spring and back to an overwintering habitat in the fall is a typical migratory movement for amphibians (Semlitsch 2008).

In contrast to migratory movements, dispersal occurs when individuals leave their current home range and branch off from their original group or population; this is often one of the first priorities of juveniles (Sinervo 2007), although juveniles also use migratory movements to reach new habitat types. These movements of juveniles are often especially important for maintaining genetic diversity in populations (Rothermel and Semlitsch 2002). Besides providing gene flow (Gilbert and Singer 1973), there are many other reasons why dispersal is fundamental in maintaining populations (Paradis et al. 1998) including the maintenance of a functional population size (Vance 1980, Holt 1985, McPeek and Holt 1992) and sustaining carrying capacity limits. It has also been speculated that dispersal is important to predator-prey dynamics (Taylor 1990). Dispersal also maintains elements of source-sink dynamics in metapopulaions (Brawn and Robinson 1996). Since habitats differ from one area to another (Crowder et al. 2000), whether naturally or due to anthropogenic disturbances, source and sink populations can occur. Source populations are characterized by birth rates that exceed death rates, and therefore, excess individuals often disperse from source populations to inhabit surrounding habitats. Sink populations are characterized by death rates that exceed birth rates, and therefore, depend on genetic inputs from other populations (i.e., source populations) to maintain a species genetic diversity (Crowder et al. 2000).

Amphibians live a biphasic life and therefore migratory and dispersal movements often involve both aquatic and terrestrial habitats (Semlitsch 2008). Amphibians may use aquatic habitat for breeding and overwintering, as well as terrestrial habitat for foraging and overwintering. Because amphibians depend on both aquatic and terrestrial habitats, if either one becomes diminished, it can affect the entire lifecycle of an amphibian (Semlitsch 1998). In amphibians, dispersal movements are most often made by juveniles after they have metamorphed and exited a natal pond (Dole 1971), in contrast to migratory movements that are typically made by adults. If amphibian dispersal is hindered, genetic diversity is decreased and extinction of subpopulations can occur (Semlitsch 2008).

Landscape Connectivity

In order for amphibians to complete migratory and dispersal movements, they need to be able to move across a landscape matrix that often includes multiple land-use and resultant land-cover types. Landscape connectivity refers to the extent to which individuals are able to traverse intervening areas to reach needed habitat components. Individuals can easily move among habitat types in highly connected landscapes. However, when connections are severed, individuals often cannot reach needed habitats, and populations decline or become extinct (Corn and Fogleman 1984, Hayes and Jennings 1986, Stuart et al. 2004). Loss of landscape connectivity due to changes in land use has been a major factor contributing to worldwide declines in amphibian populations (Clarkson and Rorabaugh 1989, Bradford et al. 2004, Whitfield et al. 2016, Semlitsch et el. 2017).

Habitats become disconnected when barriers that hinder an individual's movement appear or completely replace the habitat. Roads can inhibit animal movement and prevent individuals from reaching breeding ponds (Gibbs 1998) because roads increase mortality rates for passing amphibians (Van Gelder 1973, Cooke 1988). Amphibians may avoid crossing dry areas because of desiccation risks; crossing extensive xeric habitats can disrupt their water balance (Bentley and Yorio 1976, Quaranta et al. 2009). Also, some amphibians are known to avoid agriculture landscapes when given the option to move through natural land cover (Rothermel and Semiltsch 2002, Mazerolle and Vos 2006). It has been shown that amphibian abundance is positively correlated with natural habitat cover (Hecnar and M'Closkey 1998). This is likely due to the fact that frogs can have higher desiccation rates in more barren fields (Mazerolle and Desrochers 2005) and alteration of natural habitats often changes the hydric condition of the landscape (O'Connor et al. 2006).

In the prairie-pothole region (PPR) of North America (Figure 1), transformation of native-prairie grasslands to crop fields and pasture lands has been extensive (Sampson and Knopf 1994). These transformations of native prairie to facilitate corn (*Zea mays*), soy (*Glycine max*), livestock production, and other agricultural land uses have fragmented and degraded the natural landscape (Blann 2006, Reynolds et al. 2006). Approximately 55% of the total land and water surface in North Dakota was converted to cropland by 1997 (Dahl 2014). Between 1997 and 2009 in the western prairie states (Montana, North Dakota and South Dakota) there was an additional 805,000-acre decrease in grassland. Since settlement, a total of 95% of total grassland in the PPR has been converted to agriculture (Dahl 2014). Overall, approximately 60 to 65% of the wetlands historically present in the PPR have been drained for agricultural production (Dahl 2014). These changes have disrupted the natural landscape and now both migrating and dispersing amphibians must move across novel landscapes to connect needed habitat types. Additionally, the loss of wetland habitats increases the distances between wetlands that amphibians must traverse to meet their diverse habitat needs (Swift and Hannon 2010).

In addition to decreased habitat connectivity, increased agriculture and other barriers that potentially affect an animal's movement, predation adds to the stressors of habitat loss (Evans 2004). Switching from natural habitat to agriculture can create a more optimal environment in which predators can more readily prey on birds and other prey sources (Evans 2004). Additionally, human control of apex predators on the landscape can result in smaller predators becoming more abundant, which can increase predation rates on the animals upon which these smaller predators prey (Evans 2004). Livestock can also increase predator abundance, as they can act as another food source for predatory animals that also feed on carrion (Fuller and Gough 1999). Many of the small predatory animals that potentially benefit from increases in agricultural lands and predator-control efforts such as weasels, minks, and multiple bird species (Evans 2004) are animals that also prey on amphibians.

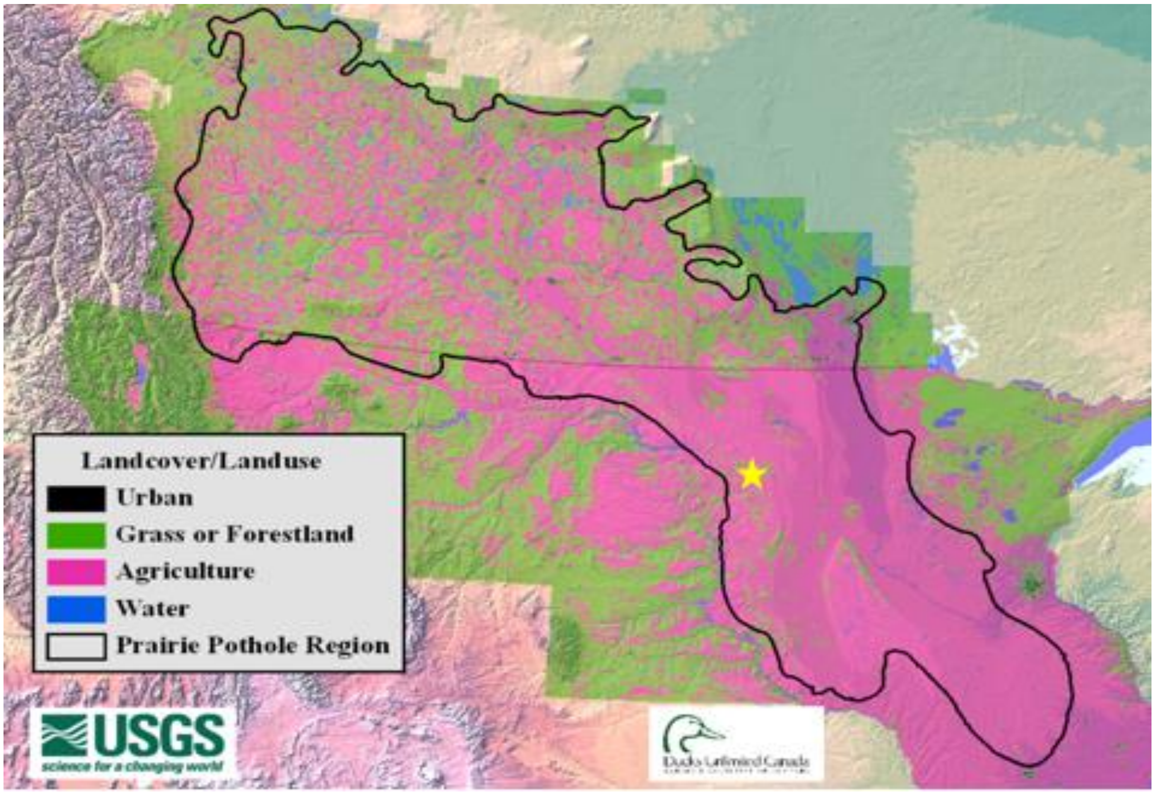


Figure 1. Study area location (yellow star) in the agriculturally dominated landscape of the northern Great Plains prairie-pothole region (PPR) (provided by USGS, unpublished figure).

Movement Rates

Movement rates vary by both species and habitat type. Studies have shown that land-use change effects amphibian desiccation rates (Rothermel and Luhring 2005) and survival rates (Karraker and Welsh 2006, Todd and Rothermel 2006), both of which influence amphibian movement rates. Distances amphibians travel can vary by species and location, and movement patterns can change from month to month (Matthews and Pope 1999), which can be correlated with foraging activities, dispersal, and migration. American toads (*Anaxyrus americanus*), for example, move from 400 to 1000 m from breeding locations to upland forested habitat (Forester et al. 2006). Frogs tend to move when they would be least likely to desiccate. Northern leopard frogs and American toads have been observed moving during rainfall events (Dole 1965, Forester et al. 2006). Some amphibian species are known to choose routes for migration and dispersal that are easier to travel. Birchfield and Deters (2005) noted that green frogs (*Rana clamitans*), when given a choice, will travel through short grass, which offers less resistance than traveling through forests. Although these frogs moved along the short grass, they still choose to stay close to tall-grass areas while moving, likely due to predation pressures; when approached, the frogs would jump into the long grass (Birchfield and Deters 2005). This strategy makes movement quicker for the frogs, but also allows them to have a path to safety if needed.

Desiccation

During movements, amphibians may expend higher or lower amounts of water depending on environmental factors and the habitat they are in. It is very important that amphibians maintain a sufficient water balance while traveling across terrestrial landscapes to connect the next piece of their lifecycle. If amphibians start to desiccate, its physiology can be affected.

It is essential for amphibians to maintain hydration during terrestrial migratory and dispersal movements as they travel to each needed habitat type (Spotilia and Berman 1976). As amphibians lose water, their oxygen consumption and metabolic rate start to become negatively impacted (Pough et al. 1983). As with movement rates, water-loss rates are species specific. As an example, the northern leopard frog has a higher water-loss rate than the marine toad (*Rhinella marina*) due to the northern leopard frog’s higher diffusion rate of water through their permeable skin (Bentley and Yorio 1976). Also, toads typically live a more terrestrial life than frogs and therefore have developed mechanisms to reduce water loss. Land-cover type and associated micro-environments play a role in the water loss as amphibians move through terrestrial landscapes. Vegetation can influence soil moisture, humidity, shading, wind speeds, litter cover, and other factors that influence water-loss rates at the micro-environment scale.

Amphibians have developed both behavioral and physiological means of reducing water loss in terrestrial environments. When adult anurans need moisture, they will go into a water conserving position where they crouch down to the ground so their stomach and feet are in contact with a moist area (Pough et al 1983). Another common method for anurans to conserve water and stay out of the hot sun is to burrow under leaf litter (Dole 1965). Burrowing under layers of vegetation helps avoid exposure to direct sun, heat, and wind. However, litter is often absent or greatly reduced in agricultural fields.

Other physiological factors (e.g., energy, thermoregulation, foraging, digestion rate, metabolic rate, etc.), in addition to maintaining a water balance, are important for amphibians to survive movements across terrestrial landscapes (O'Connor et al. 2006). If any of these factors are weakened due to environmental or anthropogenic conditions, injury, fatigue, and fatality can occur. Also, the effects of any can be magnified if an individual becomes dehydrated.

The Northern Leopard Frog: A Species on the Move

Although the conversion of natural habitats to agriculture has been studied in many species, the reaction of amphibians to anthropogenic change can depend on multiple factors (Stephens et al. 2013, Becker et al. 2016, Burraco and Gomez-Mestre 2016). Because these conversions may affect one species differently than another species, habitat connectivity studies are often performed at a species-specific level (Cushman 2006). Knowledge about how a species uses reproductive ponds, overwintering habitats, as well as other forms of necessary habitat, is important for understating what habitats need to be connected for a given species. Different species of amphibians may react differently to agriculture fields. Some species may hesitate entry into, or avoid altogether, a certain cover or crop type, whereas others may not (Henein and Merriam 1990). Natural landscapes vary in their characteristics and resources so each habitat type may require a different management strategy based on the specific species of concern (Pulliam 1992). More knowledge is needed on species-specific movements through terrestrial cover types (Rothermel and Semlitsch 2002). The northern leopard frog is abundant amphibian species in the PPR, and it's use for multiple habitats makes it an interesting species to study for habitat connectivity.

The vagility, or ability of an organism to move freely and migrate, and habitat requirements of the northern leopard frog make it an ideal species for exploring amphibian movements across the PPR landscape. It is important to study habitat connectivity in the PPR because of the anthropogenic changes this region has succumbed to. The northern leopard frog uses multiple habitats throughout its lifecycle in a process known as landscape complementation (Hazell 2003). If suitable connections are unavailable, the northern leopard frog may not be able to complete its lifecycle and probability of population persistence is low. To effectively manage each habitat utilized by the northern leopard frog, conservation strategies that cover all ranges of frog movements, from breeding wetlands, to upland foraging sites, to overwintering wetlands (and all habitats in-between) need to be considered.

Northern Leopard Frog Habitat Use

Adult northern leopard frogs move into reproductive wetlands during the spring (Dole 1967). Mating occurs at these sites, eggs are laid in the wetland ponds and the completely aquatic tadpoles mature here (Dole 1967, Mushet et al. 2012). Northern leopard frog reproductive wetlands are generally small (< 8 ha), palustrine, low salinity, and shallow (< 2 m; Smith and Keinath 2007). Reproductive wetlands without predatory fish are preferred, so ponds that seasonally dry around mid-summer are ideal. After breeding, adults often stay near the water for several weeks to escape cold air temperatures and find food or cover that might be limited in upland areas during spring (Dole 1967).

Following breeding and egg laying, northern leopard frog adults move to upland foraging sites (Dole 1965), which can be as far as three km from reproductive wetlands (Smith and Keinath 2007). While in uplands, northern leopard frogs often remain motionless in small areas they have cleared of vegetation (known as forms). Being in contact with the soil helps to prevent desiccation (Dole 1965). After metamorphosis, juvenile northern leopard frogs emerge from reproductive wetlands, forage near the wetland edge and gradually move to upland foraging areas. Both juveniles and adults will move from foraging areas to overwintering sites in late summer to early fall.

To facilitate frog survival, northern leopard frog overwintering sites consist of deep ponds in wetlands and lakes, or flowing streams with high oxygen levels (Smith and Keinath 2007). Once the frogs have reached their overwintering site in the fall, they enter torpor and remain relatively motionless until the following spring (Cunjak 1986, Emery 1972).

Habitat Connectivity and the Northern Leopard Frog

In their movements, northern leopard frogs encounter native-grass prairie as well as crop fields that potentially act as barriers to movements. Since native-prairie and wetland habitats in the PPR have been greatly reduced, the wetlands that the northern leopard frog highly depends on to complete its lifecycle have become separated by greater distances. Depending on the cover type through which it must move, a frog can become exposed to the sun, wind, and other environmental factors for longer periods of time that, in turn, could cause it to lose water faster than if moving through a more naturally vegetated area. In addition, frogs may become more visible to predators.

Because the northern leopard frog requires multiple habitats (breeding, foraging, overwintering) during its lifecycle, each habitat type and connections among them are necessary to sustain populations, and populations can be negatively affected if a needed habitat type or connection is lost. Since the northern leopard frog utilizes multiple habitat types, Management strategies are needed to consider each resource type and the connections to and from resource patches. It would not be beneficial to the species if only a single habitat type were to be protected, rather all required habitat types need to be protected in conjunction for the species to persist.

I used the northern leopard frog as my model species through which to explore landscape connectivity in the PPR of North America. My primary objectives were to 1) create an individual-based (i.e., agent-based) simulation model that would allow for the exploration of northern leopard frog movements across a modeled landscape in which key factors such as cover type, movement rates, desiccation, and predation could be varied; 2) obtain an increased knowledge of northern leopard frog movement rates in a variety of cover types; 3) estimate northern leopard frog desiccation rates in differing cover types; and 4) perform a series of model runs using information gained in objective 2 and 3 as a demonstration of the management and educational utility of the model developed under objective 1. It is my hope that the results of this research will facilitate wetland- and upland-management efforts of the U.S. Fish and Wildlife Service, U.S. Environmental Protection Agency, and others tasked with managing or regulating aquatic and terrestrial habitats in the context of large landscape settings. Additionally, the model I developed may prove useful as an educational tool, facilitating the exploration of generalized concepts related to animal movements and habitat fragmentation.

STUDY AREA

The 715,000 km^2 PPR covers a large portion of North Dakota, South Dakota, Minnesota and Iowa (Dahl 2014) in the United States, in addition to portions of Canada (Figure 1). The region's landscape is characterized by millions of small, shallow wetlands (i.e., prairie-pothole wetlands) left from retreating glaciers (Fenneman 1931). Ponded-water permanency of these wetlands can be ephemeral, temporal, seasonal, semi-permanent or permanent (Sloan 1972). Prairie-pothole wetlands receive water from precipitation (i.e., rain and snow), surface-water flows, and groundwater (Todhunter and Rundquist 2004). Prairie-pothole wetlands provide habitat for a variety of wildlife and the wetland systems improve water quality, retain floodwater, and charge groundwater (Whigham and Jordan 2003, Brauman et al. 2007). This region of North Dakota experiences variations in weather patterns which can contribute to ponded-water permanency of the wetlands (Sloan 1972). These patterns can consist of drought and wet cycles that often persist for 10 to 20 years (Karl and Riebsame 1984). Due to the small size of most prairie-pothole wetlands and high evapotranspiration rates that often exceed precipitation inputs, these wetlands are easily influenced by natural and anthropogenic-induced changes in the climate (Todhunter and Rundquist 2004). The PPR is dominated by grazed and ungrazed prairie grasslands, wetlands, and crop fields. Wetlands are vulnerable to tillage practices (Kantrud and Stewart 1984), which can reduce breeding areas for many species including the northern leopard frog.

To explore potential effects of wetland loss and land-cover conversions on landscape connectivity as related to the northern leopard frog, I developed an individual-based movement model and performed a series of movement-rate and water-loss-rate experiments. I conducted my model development work at North Dakota State University using NetLogo (an agent-based model development tool; Wilensky 1999). To parameterize my model, movement and desiccation rates were collected for the northern leopard frog.

Movement and desiccation studies were carried out in several fields located near the headquarters of the U.S. Fish and Wildlife Service (USFWS) Chase Lake National Wildlife Refuge (hereafter referred to as the Woodworth Station) and within 16.09 kilometers of Woodworth, North Dakota (Figure 2). Fields sampled varied by year. During the summer of 2015, ungrazed-grass and soy fields used in my experiments were located in the USFWS Roosevelt Waterfowl Production Area (hereafter referred to as the Roosevelt WPA). The corn field was a privately-owned field located 11.75 km northwest of the Roosevelt WPA. The grazed-grass field was 5.15 km southwest of the Roosevelt WPA at the Woodworth Station. In 2016, the ungrazed-grass field used was located immediately north of, and the grazed-grass field was immediately south of, the Woodworth Station. The corn field was located approximately 9.5 km southwest of the Woodworth Station on private land and the soy field was located immediately northwest of the Woodworth Station, also on private land.

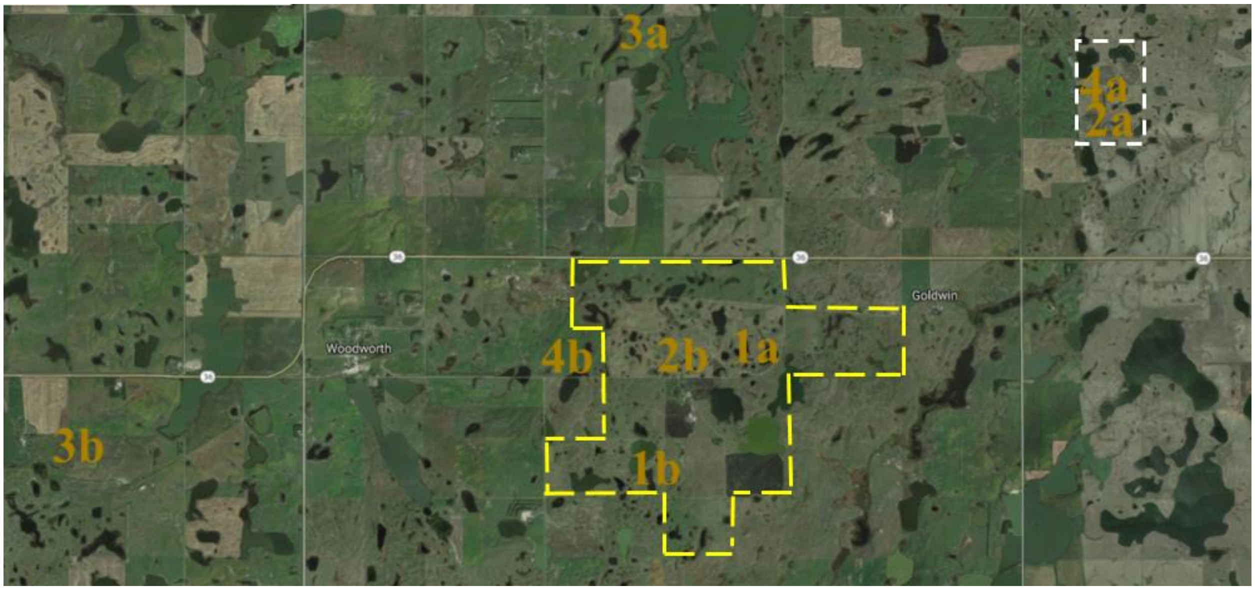


Figure 2. Location of fields used to study northern leopard frog (Rana pipiens) movement and desiccation rates during the summers of 2015 and 2016. The U.S. Fish and Wildlife Service's Roosevelt Waterfowl Production Area (outlined with white dashed line) and the boundaries of the Woodworth Station (outlined with yellow dashed line) are identified. 1, 2, 3, and 4 = grazed grass, ungrazed grass, corn, and soy, respectively. a and b = 2015 and 2016 sampling sites, respectively.

METHODS

Agent-based simulation models are useful tools to examine how landscape changes can affect a species by simulating different features (e.g., habitat change and fragmentation) that influence movements. Although simplifications of real systems, these models can be useful because they permit the examination of scenarios that may not be possible to explore on a real landscape. I constructed an agent-based simulation model to explore amphibian movements in altered landscapes of the PPR. The model I created incorporated movement rates and desiccations rates of the northern leopard frog.

I collected northern leopard frog movement and desiccation-rate data to inform my model and gain a better understanding of how different land-cover types impact movements and desiccation of this species. I explored movement rates during the summers of 2015 and 2016 by releasing juvenile northern leopard frogs in an enclosed area and allowing them to move freely through the cover type targeted by that enclosure while recording time taken to reach pitfall traps located around the enclosure's perimeter. Desiccation rates were estimated by weighing frogs before and after movements through various cover types, as well as by quantifying water loss from artificial (i.e., agar) frogs placed in each cover type. I also measured soil moisture within cover types to explore microscale environmental conditions relevant to northern leopard frog survival.

I used information gained from these movement and desiccation rate experiments to inform parameterization of the agent-based simulation model for a series of model runs demonstrating the usefulness of the model as a potential management and educational tool. The model I developed will contribute to furthering our understanding of northern leopard frog movements and factors that facilitate or impede connectivity among aquatic and terrestrial habitat features of the PPR.

Model Development

NetLogo is an agent-based model development program. NetLogo allows for users to build simulation models to examine movement patterns of individuals (i.e., agents) across various theoretical landscapes (Tissue and Wilensky 2004). Models developed with NetLogo have been used to simulate movements of various organisms, including beetles (Young et al. 2013), butterflies (Radchuk et al. 2013), desert baboons (King et al. 2011), and black-throated blue warblers (*Setophaga caerulescens*) (Railsback and Johnson 2011). I developed an individual-based movement model in NetLogo to simulate the migratory movements of juvenile northern leopard frogs as they travel from natal wetlands to wetlands that serve as their winter refuges.

I developed a baseline landscape in the model that consisted of a 5 X 5 arrangement of 25 square patches, with each patch representing a quarter-section of land (64.75 ha, 160 acres). The quarter-section is the most commonly used management unit in the region. The 5 X 5 arrangement of quarter-sections in the baseline landscape (Figure 3) represents a total area of 1,618.74 ha. (4,000 acres). Land-cover type can be independently varied within each of the 64.75 ha patches. Each ha within the model landscape is made up of approximately 619 individual pixels across which modeled agents can move. The total number of pixels making up the base landscape was 1,002,001. In the center of model landscape, I placed a 15.90 ha circular patch to represent an overwintering wetland. I created a 31.1 m buffer around the overwintering wetland. Individual frogs move randomly across adjacent pixels. However, when an individual frog is within 31.1 m of the overwintering wetland (i.e., reaches the buffer), movement is no longer random but directed towards the overwintering wetland. The directed movement when a frog nears an overwintering wetland is designed to account for the possibility that frogs can use chemical keys absorbed from the soil and topographical patterns of the landscape to assist with movement (Dole 1968). I also randomly placed 122 reproductive wetlands, each 2.07 ha in size, scattered across the landscape. The baseline landscape, and in particular the number and size of reproductive wetlands, is based on the land-cover types and wetland density per km^2 in the Roosevelt Waterfowl Production Area in Stutsman County, North Dakota. The terrestrial landscape made up by four landcover types form the upland (or foraging) habitat used by the northern leopard frog.

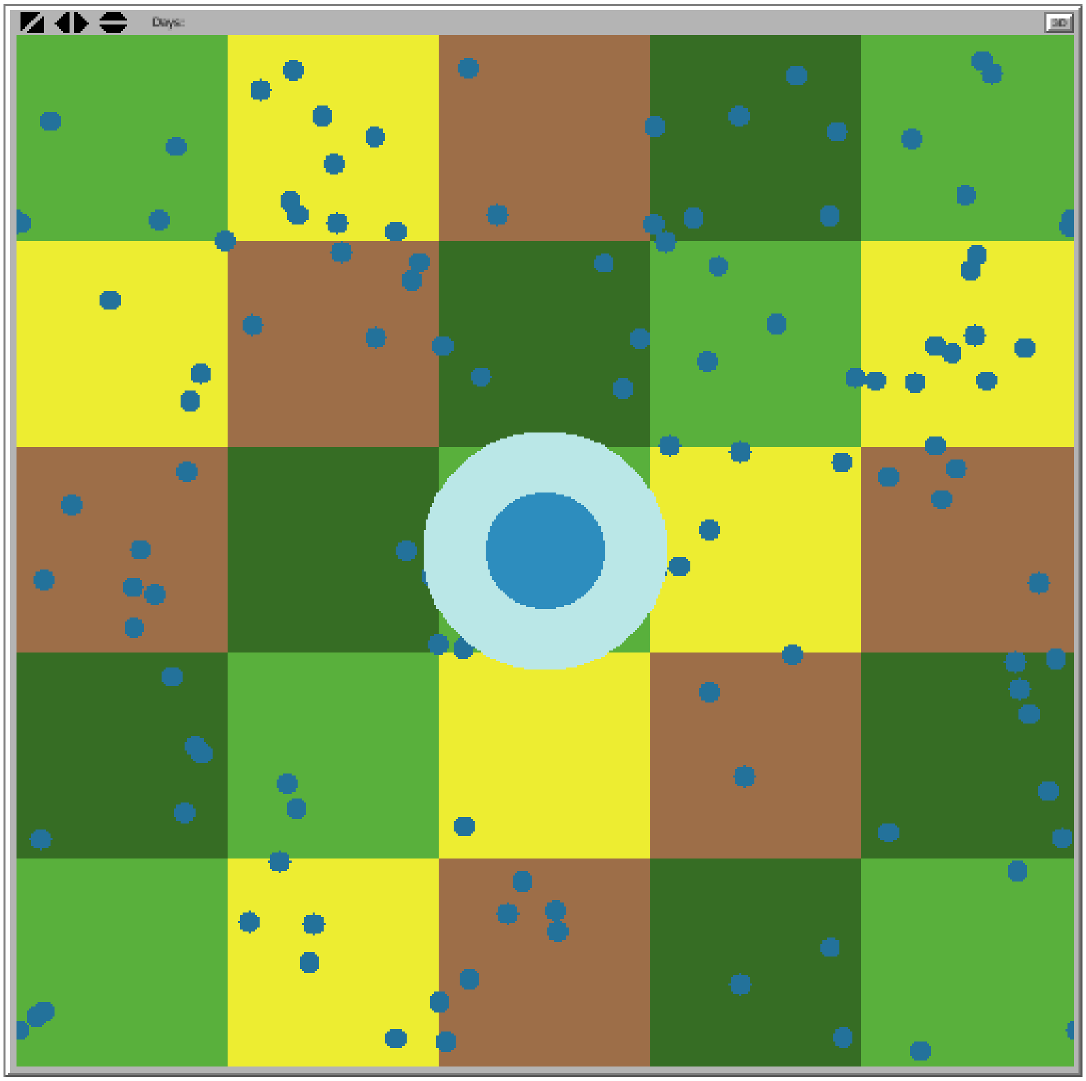
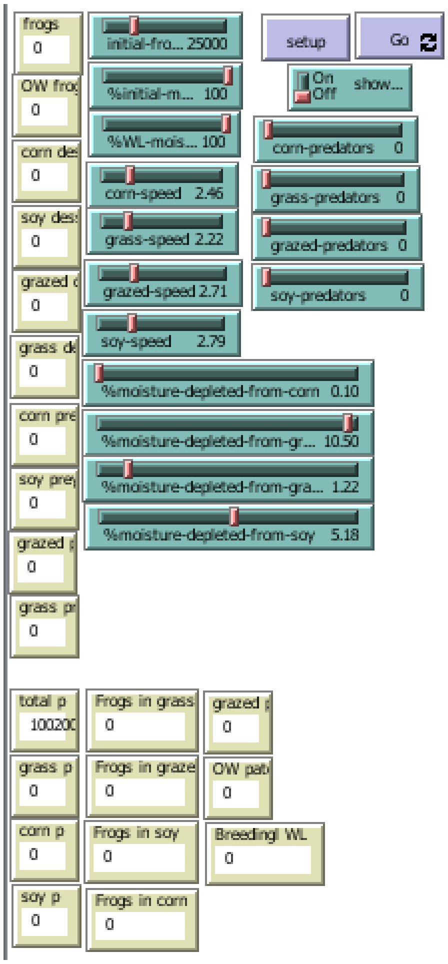


Figure 3. Baseline modeled landscape of the four cover types (grazed grass [dark green], ungrazed grass [medium green], corn [yellow], and soy [light green]), breeding wetlands (small blue circles), one overwintering wetland (blue circle in the center), and a 31.1 m buffer (light blue) surrounding the overwintering wetland.

The interface to my model (Figure 4) has 15 sliders that allow for the setting of initial number of frogs in a simulation, the starting moisture content (%) of frogs, moisture (%) gained when frogs move thorough a wetland, moisture lost by frogs when moving through upland patches of various cover types (i.e., grazed grass, ungrazed grass, corn and soy), speed of movements within upland patches, and predation rates (set as number of predators by cover type). I included 21 monitors that track current frog numbers, number of frogs reaching the overwintering wetland, number of frogs by cover type that died due to desiccation, and number of frogs by cover type that died due to predation at the current time step in a simulation. A switch allows the user to view the current hydration status of individual frogs at any time-step during a simulation. If the switch is set to "on," a number displaying the current hydration status, as a percentage with 100% being fully hydrated, is attached to each frog. The switch can be set to "off" if the user does not desire to see these data. There are two buttons included in my model interface. When the "setup" button is clicked, the entire modeled landscape is shown on the interface and the initial number of frogs are randomly placed in reproductive wetlands facing in a random direction. When the "go" button is clicked, the frogs start to move in a straight line on the landscape with the goal of reaching the overwintering wetland in the center. If the frogs come within 60 pixels of the overwintering wetland (i.e., contacts the buffered area surrounding the overwintering wetland), they turn toward the center and continue in a straight line until they hit the edge of the overwintering wetland. Once reaching the overwintering wetland, they stop and are considered to have survived the simulation.

Each model simulation consists of 60 time steps with each step equaling a single day. At the end of each time step (i.e., day), the moisture level of each frog is determined based on the moisture level from the previous day, the number of pixels crossed, and the desiccation rate associated with the cover type for each crossed pixel. To determine if a frog died due to desiccation, I assumed a lower moisture percentage from Hall (1922), who reported that northern leopard frogs could lose up to 41% of their body weight before death. Therefore, in a simulation, if a frog's moisture level reaches 41%, it dies. If a frog crosses a reproductive wetland during its movements, that frog's moisture content is restored to 100%. Once frogs reach the overwintering wetland, they stop moving and are considered to have survived the run. After 60 time steps (i.e., 60 days) any frogs not in the overwintering wetland are assumed to be dead.

The model's aim is to simulate the movement of the northern leopard frog and provide insights into how landscape fragmentation and arrangement of different cover-types impact the likelihood that frogs reach a winter refuge.



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OW frog 0
corn des 0
soy des 0
grazed d 0
grass de 0
corn pre 0
soy prey 0
grazed p 0
grass pr 0
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%initial-m... 100
%WL-mois... 100
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grass-speed 2.22
grazed-speed 2.71
soy-speed 2.79
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grass-predators 0
grazed-predators 0
soy-predators 0
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grass p 0
corn p 0
soy p 0
Frogs in grass 0
Frogs in graze 0
Frogs in soy 0
Frogs in corn 0
grazed p 0
OW pat 0
Breeding WL 0

Figure 4. NetLogo interface with monitors, sliders, switches and buttons.

Principal Component Analysis

To evaluate effects of environmental factors in the general linear models, I quantified 96 daily meteorological measurements (one reading every 15 minutes) using Principal Components

Analysis (PCA). I obtained hourly recordings (from 0800 to 1600) of barometric pressure (kPa), temperature (C), relative humidity (%), precipitation (cm) and sustained wind speed (m/s) from a single weather station maintained by the U.S. Geological Survey at the Roosevelt WPA for all dates on which movement experiments were conducted. I computed a mean daily value for each of the meteorological measurements from the hourly recordings. I then performed a PCA (based on covariance's) on the z-scores of the mean daily values to reduce dimensionality of the meteorological data. Based on the results of the PCA, I used the first two principal component axes to quantify meteorological condition on a particular date.

Movement-rate Experiments

To better understand northern leopard frog movement rates through grassland and various crop types, I conducted a series of field-based experiments. I constructed circular fences with pitfall traps (hereafter referred to as arenas) within fields of differing cover types, i.e., grazed grass, ungrazed grass, corn, and soy. Each arena fence was 28.8 m in circumference and constructed from 71.1-cm-tall aluminum flashing and fiberglass support poles. Eight 18.93-liter (5-gallon) bucket-type pitfall traps were placed evenly around the inside edge of each arena fence. All pitfall traps abutted the encircling fence to ensure frogs could not pass between the fence and trap (figure 5).

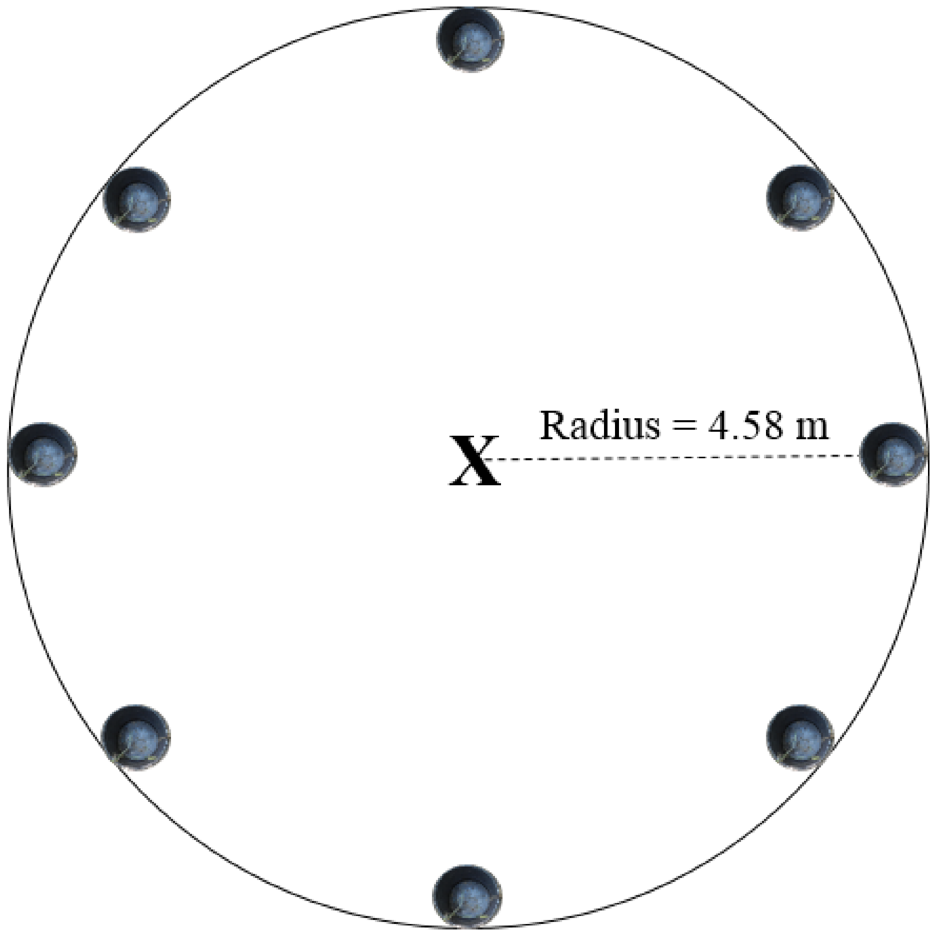

Figure 5. Layout of arenas used in northern leopard frog (Rana pipiens) movement- and desiccation-rate experiments. Black outer circle = 71.1-cm-tall metal-flashing fence. Smaller circles abutting fence = pitfall traps. X = release point for frogs. Time from release at X to capture in a trap was used to estimate movement rates. Mass loss was used to estimate desiccation rates.

Twenty young-of-the-year northern leopard frogs were released at the center of each arena on three occasions in 2015 and on six separate occasions in 2016 (Table 1). Thus, across the two years I conducted a total of nine trials in each of the four cover types. In 2015, frogs used in experiments were collected from a nearby wetland on the morning of each experiment. In 2016, frogs were collected the day before experiments due to a lower abundance of frogs at nearby wetlands, which necessitated additional time to capture sufficient numbers for the experiments. Frogs held overnight before being used in experiments were housed in five-gallon buckets covered with plastic wrap. Wetland water and sponges were placed in the bottom of each bucket to minimize water loss before being used in experiments and holes were made in the Saran™ wrap to maintain air flow.

At 0800 Central Daylight-savings Time (all time references henceforth are for Central Daylight-savings Time) on the day of an experiment, 20 frogs were released in the center of each arena. Following release of frogs in an arena, pitfall traps were checked every hour for captures. If a pitfall trap contained any frogs, the captured frogs were removed from the trap and placed in a Sterilite® 68.14-liter tote box. The tote box had wetland water and sponges covering the bottom. At 1600, traps were checked for the last time and arenas were exhaustively searched for any remaining uncaptured frogs. All frogs used in the experiment were then returned to the wetland where they were originally obtained.

Table 1

Dates of movement rate and desiccation rate experiments conducted in 2015 and 2016.

Year	Grazed grass	Ungrazed grass	Corn	Soy
2015	8/7/2015^{m}	8/5/2015^{m}	8/7/2015^{m}	8/5/2015^{m}
	8/11/2015^{m}	8/10/2015^{m}	8/11/2015^{m}	8/10/2015^{m}
	8/14/2015^{m}	8/13/2015^{m}	8/14/2015^{m}	8/13/2015^{m}
2016	8/2/2016^{m,d}	8/2/2016^{m,d}	8/2/2016^{m,d}	8/2/2016^{m,d}
	8/4/2016^{m,d}	8/4/2016^{m,d}	8/4/2016^{m,d}	8/4/2016^{m,d}
	8/9/2016^{m,d}	8/9/2016^{m,d}	8/9/2016^{m,d}	8/9/2016^{m,d}
	8/11/2016^{m,d}	8/11/2016^{m,d}	8/11/2016^{m,d}	8/11/2016^{m,d}
	6/16/2016^{m,d}	6/16/2016^{m,d}	6/16/2016^{m,d}	6/16/2016^{m,d}
	8/17/2016^{m,d}	8/17/2016^{m,d}	8/17/2016^{m,d}	8/17/2016^{m,d}

m = movement-rate experiment d = desiccation rate experiment

To estimate movement rates (m/hr) from the capture data, I first calculated the movement rate of a captured frog by dividing the distance from the arena center to the pitfall traps (4.572 m) by the time to capture (t_c, in hrs) (Rothermel and Semlitsch 2002).

$$\text{Speed of frog captured (m/hr)} = \text{Distance} / \text{time}$$

$$= 4.572 / t_c$$

I then computed the average speed for captured frogs (Avg. speed, in m/hr) in each cover type. Using the average meters per hour for captured frogs in each cover type, I computed the average speed for all frogs using the following formula:

Average meters per hour = (# frogs captured per arena * Avg. speed of frogs captured) + (# frogs not captured * speed of frogs not captured) / (# frogs captured + # frogs not captured)

The speed of frogs not captured was assumed to be 0 m/hr. Thus, this formula was simplified to:

Average meters per hour = (# frogs captured per arena * Avg. speed)

/ (# frogs captured + # frogs not captured)

I then converted average meters per hour into pixels per hour. Each pixel in my NetLogo landscape represented 4.019 meters. Thus:

Pixels/hr = Average meters per hour / 4.019

Lastly, I multiplied pixels/hr by 24 hrs to obtain a daily movement rate estimate for each cover type. This value gave me a starting point for each cover type around which to vary daily movement rates in my modeled scenarios (see section on model simulations).

Movement-rate Analysis

To further explore northern leopard frog movement within cover types, I evaluated the effects of land cover, Julian day, year, meteorological condition and soil moisture on frog capture rates using general linear models. I separated the analysis of captures (per eight hours) into two groups of linear models in which 1) temporal factors (Julian day and year) and land cover were included as independent variables, and 2) environmental factors (meteorological condition and soil moisture) and land cover were included as independent variables. In the first group, I modeled captures as a linear function of land-cover category, Julian day, year (as a categorical variable) and all interactions. Based on results from this full model, I constructed several *post hoc* models to simplify the evaluation of temporal and land-cover effects. These included modeling captures as a function of i) land cover, Julian day and the interaction of land cover and Julian day, ii) land cover alone, iii) Julian day alone and iv) restricted land-cover categories (grass versus non-grass), Julian day and their interaction. In the second group, I modeled captures as a linear function of land-cover category, meteorological condition (quantified by the first two principal components of a PCA of meteorological data), soil moisture and all interactions. Based on results from this model, I constructed several *post hoc* models to further evaluate environmental and land-cover effects. These included modeling captures as a function of i) land cover, meteorological condition (PCA axis 1) and their interaction, ii) land cover, meteorological condition (PCA axis 2) and their interaction, iii) meteorological condition alone (PCA axis 2), iv) mean daily wind speed alone and v) mean relative humidity. Finally, I constructed three *post hoc* linear models of captures, the first being a function of Julian day and meteorological condition (PCA axis 2), the second being a function of Julian day and mean daily wind speed and the third a function of Julian day and relative humidity to evaluate the combined effects of the leading temporal and environmental factors on frog capture rates.

Desiccation-rate Experiments

Desiccation affects a frog’s ability to survive while traveling through various cover types. Thus, desiccation rate is a key variable in amphibian movement models. In order to gain a better understanding of northern leopard frog desiccation rates in various cover types, I measured mass change of individual frogs during my movement-rate experiments, conducted experiments with frog replicas made from agar, and collected soil-moisture readings in each of the fields that were used for the movement-rate experiments. Use of frogs from my movement experiments provided information on water loss from actual frogs. Use of agar frogs allowed me to gain detailed information on desiccation rates in various microenvironments within differing cover types. Information on soil moisture allowed further exploration of factors that affect desiccation rates.

In 2016, I estimated change in mass (i.e. water loss) from 80 northern leopard frogs used in my movement-rate experiments (20 in each of four cover types). The day before being used in an experiment, frogs were divided into groups and placed in 18.93-liter plastic buckets (20 frogs each) that were labeled with one of the cover types (grazed grass, ungrazed grass, corn, soy). The frogs within each bucket were individually marked with a unique letter on their chins using a 2% solution of gentian violet dye and a fine-tip paint brush. This method was observed to be a reliable alternative to marking techniques (e.g., toe clipping) that cause physical changes to an individual (Martin and Murray 2011). Once each frog was labeled with their identifying letter, they were placed in a Saran™ wrapped 18.93-liter plastic bucket containing wetland water and sponges, and held overnight as described for the movement experiments. On the morning of the experiment, I measured the mass to the nearest hundredth gram of each frog approximately 45 minutes prior to release in arenas. As part of the movement-rate experiments, frogs were released into the center of their respective arena at approximately 0800, and pitfall traps in each arena were checked for captures every hour between 0800 and 1600 as previously described. If a frog was caught in a pitfall trap, it was identified by letter and immediately weighed. Once captured frogs were identified and weighed they were placed in a Sterilite® 68.14-liter tote box. After conclusion of an experiment, i.e., after 1600, the arena was searched for any remaining frogs, which were captured, identified, weighed and added to the container with the other captured frogs. All frogs were then returned to the wetland where they were originally obtained.

In the summer of 2016, I also deployed 240 replica agar frog in fields used in the movement-rate experiments because agar frogs lose water as a free water surface with the same shape and size when exposed to the same environmental conditions (Bentley 1976, Spotila and Berman 1976, Wygoda 1984, Buttemer and Thomas 2003, Wygoda et al. 2011, Wardziziak et al. 2014) and there are no behavioral factors to consider (e.g., eating, sheltering). Agar frogs provide a reliable estimate of the baseline evaporation rates expected in various land-cover types and have comparable properties such as temperature and skin permeability (Navas and Araujo 2000).

Agar replicas of reptiles and amphibians have been used in research to compare live individuals to artificial specimens, and generally show consistent patterns with live specimens (Navas and Araujo 2000, Schwarzkoph and Alford 1996, Spotila and Berman 1976). I made the agar frogs by mixing dehydrated agar powder (Agar-Agar) culture media and water, then pouring the mixture into CybrTrayd® frog-shaped soap molds (product number: A126) to cure overnight. Each agar frog was approximately 71 mm long, 46 mm wide, and 20 mm tall and weighed approximately 19.23 grams (range = 11.36 g to 23.89 g). Agar frogs were stored overnight in a refrigerator. Ten agar frogs were placed at randomly selected locations in each field on days when a movement experiment occurred. Prior to placing agar frogs in a field at 0800, I measured the mass (±0.01 g) of each. After placement in a field, agar frogs were reweighed every two hours until 1600.

I quantified instantaneous rate of mass change (g/g/d) for each individual from my 2016 movement rate experiments as the difference of the natural log of mass at release and natural log of mass at capture divided by the elapsed time. A small number of frogs gained over two grams (44 individuals out of 477 captures) and were omitted from computations determining mean desiccation rates for the model because these individuals were assumed to have recently ingested prey items. These frogs did not spend any time sitting, and likely desiccating, in pitfall buckets, and therefore may represent a more realistic desiccation rate.

I estimated the instantaneous rate of change in mass (g/g/d) for each individual agar frog from the slope of a linear regression fit to the natural log of mass and time observations for that replica. Data was excluded from my analyses in cases where the replica frog may have been partially eaten by an animal in the field. I then calculated the mean instantaneous rate of change in mass (g/g/d) for both real and agar frogs in each field on each date. To see if soil moisture played a role in desiccation rates of frogs, I recorded soil moisture in each field using a ML3 – ThetaProbe Moisture Sensor from Delta-T Device. During the summer of the 2015 field season, soil moisture measurements were made at four randomly selected locations in each field on three occasions (morning, noon, and afternoon) during the second and third sampling sessions. During the 2016 field season, four measurements (from randomly selected locations) were made in each field, also on three occasions (morning, noon, and afternoon) but during the second to sixth sampling sessions. I calculated the mean daily soil moisture for each field on each sampling session from the 12 measurements taken throughout the day.

Desiccation-rate Analysis

I examined correlations between captures and desiccation rates to provide insight on potential physiological characteristics of moving frogs, and further modeled desiccation rates using a group general linear model with effects of land cover and environmental conditions. I tested pairwise correlations of total captures, the daily mean desiccation rate of frogs at a site, and the daily mean desiccation rate of agar frogs at a site using the Pearson product moment (ρ) and a t-test. I used a general linear model with effects of land cover and: 1) Julian day and interaction with land cover, 2) soil moisture and interaction with land cover, 3) PCA axis 2 and interaction with land cover, 4) relative humidity and interaction with land cover and 5) wind speed and interaction with land cover to model desiccation rate. I also constructed *post hoc* models in which desiccation rate was linearly modeled with each of the following factors alone: soil moisture, PCA axis 2, relative humidity and wind speed. Finally, I repeated the general linear models described above in which land cover was paired with soil moisture, PCA axis 2, relative humidity or wind speed to model desiccation rates of the agar frogs. For All statistical analyses, I assumed statistical significance at the 0.05 level using JMP software (SAS Institute 2012).

Model Simulations

I ran a series of simulations to compare frog survival using the baseline desiccation rate estimated using water-loss data from real frogs versus that estimated from agar-frog data (Table 2, Group 1). For these simulations, I used the a landscape (Figure 3) in which four of the dominant land-cover types of the PPR (grazed grass, ungrazed grass, corn, and soy) were equally present (hereafter referred to as the baseline landscape),. Movement rate was set to 2.46 pixels per day in corn, 2.22 pixels per day in ungrazed grass, 2.71 pixels per day in grazed grass and 2.79 pixels per day in soy and number of predators was set to zero. Initial number of frogs was set at 25,000. I first ran simulation real frog desiccation rates and compared it to agar frog desiccation rates to determine which set of parameters I would use for the rest of my simulations. I ran 10 simulations with the real frog desiccation rate and 10 with the agar frog desiccation rate. From this set of runs, I determined that desiccation rates estimated from real frogs provided the most realistic result because real frogs can absorb moisture from the soil and vegetation whereas agar frogs do not, so I used the value calculated from real frogs as my baseline desiccation rate in all subsequent runs.

I then performed a model run in which the movement and desiccation rates were set based on the results of my movement and desiccation rate experiments (hereafter referred to as the baseline movement and desiccation rates, respectively). For this simulation, I used the baseline landscape. I then performed a series of model simulations in which I individually varied the number of frogs, or their rates of movement, desiccation, or predation, each set using the model’s sliders (Table 2). These simulations were modeled to determine if the changes in movement and desiccation met the assumptions for changes in survival in the model. I also explored various combinations and patterns of land-use and habitat fragmentation by varying land-cover types in the baseline landscape. The five landscape patterns of habitat fragmentation I tested are shown in Figure 6.

Table 2

Parameters that were adjusted to run each of the simulations in groups one through seven.

Parameter Tested	Setting Adjusted	Setting Used
Group 1: Desiccation rate estimated from real frogs vs. agar frogs	Dessication Rate	Corn 0.1, ungrazed grass 10.50, grazed grass 1.22, soy 5.18
	Dessication Rate	Corn 14.63, ungrazed grass 28.02, grazed grass 38.47, soy 23.77
Group 2: Initial number of frogs	Number of Frogs	1,000
	Number of Frogs	2,500
	Number of Frogs	5,000
	Number of Frogs	10,000
	Number of Frogs	20,000
Group 3: Movement Rate	0.25 of the Baseline speed	Corn 0.62, ungrazed grass 0.56, grazed grass 0.68, soy 0.70
	0.5 of the Baseline speed	Corn 1.23, ungrazed grass 1.11, grazed grass 1.36, soy 1.40
	Baseline speed	Corn 2.46, ungrazed grass 2.22, grazed grass 2.71, soy 2.79
	1.5 X Baseline speed	Corn 3.69, ungrazed grass 3.33, grazed grass 4.07, soy 4.19
	2 X Baseline speed	Corn 4.92, ungrazed grass 4.44, grazed grass 5.42, soy 5.58

Table 2

Parameters that were adjusted to run each of the simulations in groups one through seven (continued).

Parameter Tested	Setting Adjusted	Setting Used
Group 4: Desiccation rate	0.25 of the Desiccation rate	Corn 0.025, ungrazed grass 2.625, grazed grass 0.305, soy 1.295
	0.5 of the Desiccation rate	Corn 0.05, ungrazed grass 5.25, grazed grass 0.61, soy 2.59
	Baseline Desiccation rate	Corn 0.1, ungrazed grass 10.50, grazed grass 1.22, soy 5.18
	1.5 X Desiccation rate	Corn 0.15, ungrazed grass 15.75, grazed grass 1.83, soy 1.77
	2 X Desiccation rate	Corn 0.2, ungrazed grass 21, grazed grass 2.44, soy 10.36
Group 5: Predation rate	0 predators to 1 frog	0
	1 predator to 50 frogs	100
	1 predator to 10 frogs	500
	1 predator to 5 frogs	1000
	1 predator to 2.5 frogs	2000
Group 6: Land-use	Landscape (grazed grass)	100%
	Landscape (ungrazed grass)	100%
	Landscape (corn)	100%
	Landscape (soy)	100%
Group 7: Fragmentation	Landscape A	A single 1618.75 ha ungrazed grass patch
	Landscape B	Ungrazed grass patch size = 841.57 ha
	Landscape C	Ungrazed grass patch size = 323.75 ha
	Landscape D	Ungrazed grass patch size = 129.50 ha
	Landscape E	Ungrazed grass patch size = 64.75 ha

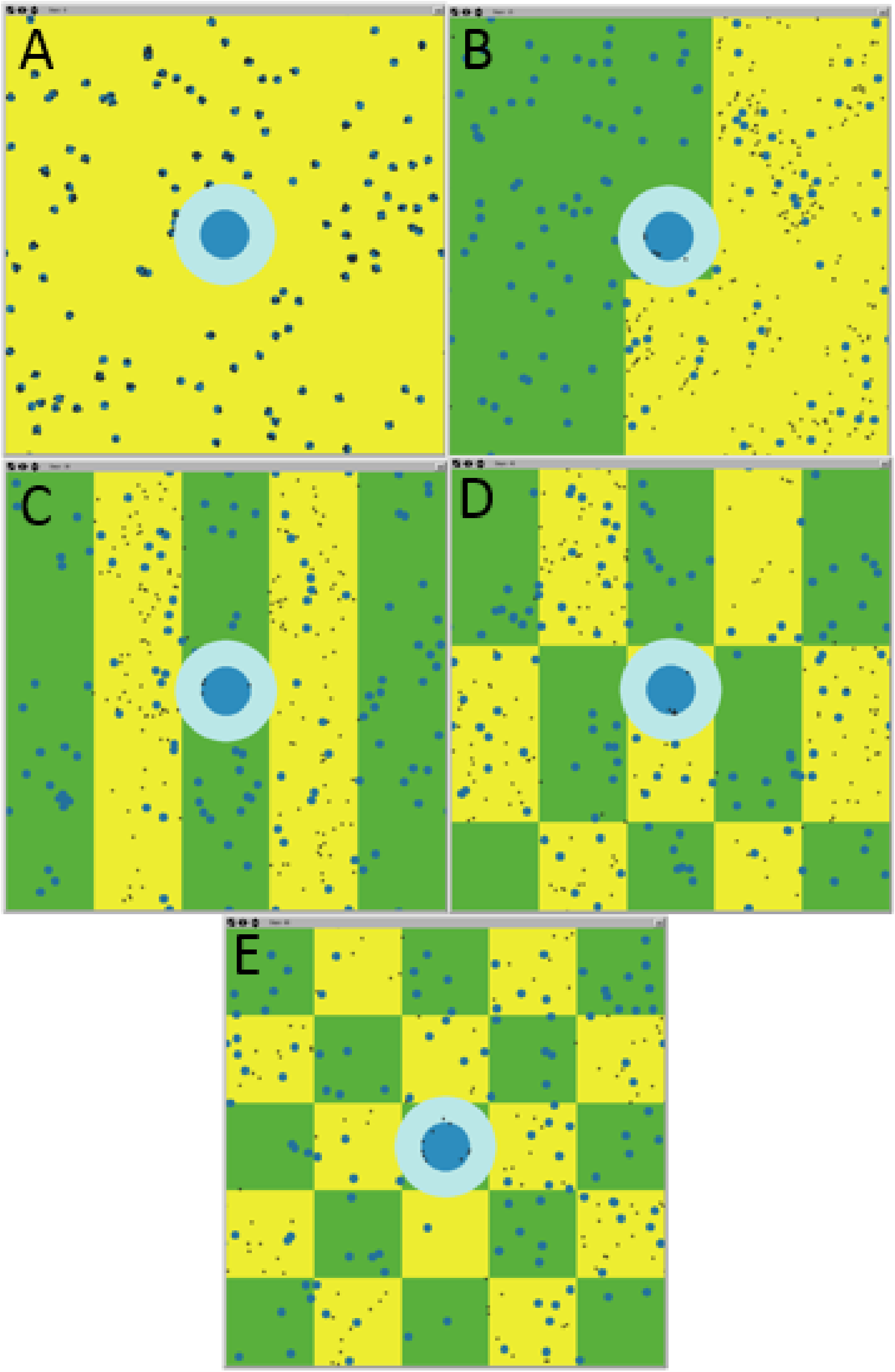

Figure 6. Modeled landscapes (labeled A, B, C, D, and E) with increasing levels of habitat fragmentation. Green = ungrazed grass. Yellow = corn. Circles in the center represent an overwintering wetland and its buffer. Smaller circles represent reproductive wetlands.

Following the baseline simulation, I performed a series of simulations in which I varied the initial number of frogs from 1,000 to 20,000 to test the influence of this parameter on model results. I wanted to identify a starting number that minimized the time of each model run (i.e., greater numbers of agents on the landscape result in increased processing times) while still providing a realistic number of frogs reaching the overwintering wetland. All runs were performed using the baseline landscape. Based on results from my field experiments, movement rate was set at 2.46 pixels per day for corn, 2.22 pixels per day for ungrazed grass, 2.71 pixels per day for grazed grass and 2.79 pixels per day for soy. Desiccation rate was set at a daily loss of 0.1% for corn, 10.5% for ungrazed grass, 1.22% for grazed grass and 5.18% for soy, also based on field experiment results. The number of predators was set to zero. I did not find a significant difference in survival rates (%) with an increase in frogs, and thus opted to use 5,000 as the initial number of frogs in all subsequent model runs as model runtime using 5,000 agents was very manageable.

I next performed a series of model runs simulating distinct changes in movement rates, desiccation rates and number of predators. I first performed 10 simulations of each of the following movement rate adjustments in the baseline landscape using the baseline desiccation rate with 0 predators but adjusting the movement rate to 25%, 50%, 150%, and 200% of the baseline movement rates estimated from my 2015 and 2016 movement-rate experiments (Table 2, Group 3). I then performed 10 simulations of each of the following desiccation rate adjustments in the baseline landscape using the baseline movement rate with 0 predators, but adjusting the desiccation rates to 25%, 50%, 150%, and 200% of the real frog desiccation rate data from the 2016 field season (Table 2, Group 4). For the last set of parameter adjustment simulations, I performed 10 simulations at each of the following predator adjustments in the baseline landscape using the baseline movement rate and the baseline desiccation rate but adjusting the number of predators from zero to 2000 (Table 2, Group 5).

To explore the influences of land-use and fragmentation, I performed several runs where the modeled landscape was 100% grazed grass, 100% ungrazed grass, 100% corn, or 100% soy; or one of five landscape patterns of increasing landscape fragmentation. All landscapes were built from my original landscape where each of the 25 patches represented a 64.75 ha patch. I first took my baseline model and changed all of the patches to grazed grass and ran 10 simulations in that land cover type. I then did the same for ungrazed grass, corn, and soy (Table 2, Group 6). I then performed a series of fragmentation simulations using five landscape patterns of increasing habitat fragmentation (Table 2, Group 7). For these simulations, I started off with a landscape that was 100% ungrazed grass (landscape A). I then added increasing amounts of corn in various sized patches to increase fragmentation (landscapes B, C, D, and E; Figure 6)

RESULTS

Results are presented in the order of: 1) PCA on the meteorological data during the 2015 and 2016 field seasons, 2) analysis of the northern leopard frog movement data collected during 2015 and 2016, 3) analysis of the northern leopard frog water-loss data collected in 2016, and 4) outcomes of the NetLogo model simulations based on the model parameters developed from the field experiments. Appendix I provides a description of the agent based northern leopard frog migration model, and explanation of the visual interface and how it is used to model adjust parameters and monitor output of a simulation. A final section of Appendix I includes instruction on extending the model to incorporate other data, species, or landscapes for simulation.

Principal Components Results

The PCA of the five meteorological variables indicated 76% of the variation in the meteorological data was explained by the first two components. PCA axis 1 explained approximately 53% of the variation, and was positively related to relative humidity (eigenvector coefficient of 0.49; Table 3) and negatively related to temperature (eigenvector coefficient of -0.55; Table 3) and barometric pressure (eigenvector coefficient of -0.42; Table 3). PCA axis 2 explained approximately 26% of the variation, and was positively related to relative humidity (eigenvector coefficient of 0.47; Table 3) and total precipitation (eigenvector coefficient of 0.48; Table 3), but negatively related to wind speed (eigenvector coefficient of -0.62; Table 3). I used PCA axis 1 or PCA axis 2 to quantify meteorological conditions as a single factor in models of captures. All eigenvalues and eigenvectors are shown in Table 3.

Table 3

Results of Principal Component Analysis (PCA) of meteorological factors used to reduce environmental variables in models of capture rates of northern leopard frogs. Eigenvalues (ƛ) are indicated in the first row, with coefficients for the respective meteorological factors indicated in the columns for each eigenvector (e.g., PCA axis 1, PCA axis 2, etc.).

	Eigenvector				
ƛ	2.65	1.15	0.72	0.41	0.06
Meteorological Factor	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Barometric Pressure	-0.42	0.40	0.50	-0.64	0.11
Relative Humidity	0.49	0.47	-0.27	-0.13	0.66
Temperature (F)	-0.55	0.08	0.14	0.62	0.53
Total precipitation	0.40	0.48	0.57	0.43	-0.32
Wind speed	0.34	-0.62	0.57	-0.09	0.41

Movement Rate Experiments

Effects of Land Cover and Temporal Factors on Movement

I did not detect a significant difference in captures between years or land-cover types, but movement rates were significantly related to Julian day. Total captures correspond to movement rates of frogs because movement rates were calculated from number of capture and uncaptured frogs. The model in which total captures were modeled as a function of land cover, Julian day, year, and all interactions did not explain a significant amount of variation ($F_{15,20} = 1.20$, $P = 0.34$, $R^2 = 0.47$). Again, only Julian day had a significant effect ($F_{1,20} = 7.05$, $P = 0.02$, $R^2 = 0.19$). The *post hoc* model in which total captures were modeled as a function of land cover, Julian day, and the interaction between land cover and Julian day did not explain a significant amount of variation ($F_{7,28} = 2.11$, $P = 0.08$, $R^2 = 0.35$; Figure 7a), with only Julian day having a significant effect ($F_{1,28} = 11.17$, $P < 0.01$, $R^2 = 0.26$). Land cover alone did not explain a significant amount of the variation in total captures ($F_{3,32} = 0.52$, $P = 0.67$, $R^2 = 0.05$; Figure 7b), with average meters per hour for grazed grass, ungrazed grass, corn, and soy of 0.37, 0.45, 0.41, and 0.47, respectively. For the Netlogo simulation model these averages result in the number of pixels a frog will travel each day in grazed grass, ungrazed grass, corn, and soy (i.e., the baseline movement rate) of 2.79, 2.46, 2.71, and 2.22, respectively. While land cover alone did not explain variation in captures, Julian day alone explained over 25% of the variation in total captures ($F_{1,34} = 11.52$, $P < 0.01$, $R^2 = 0.25$; Figure 7c).

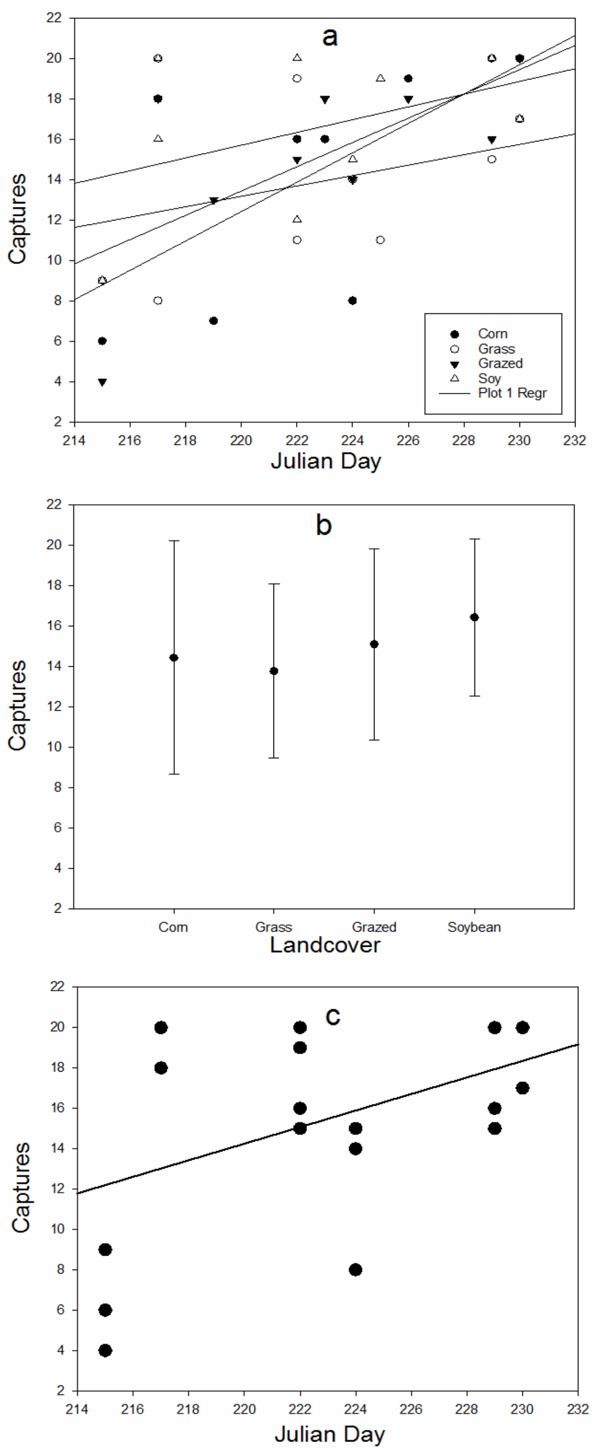

Figure 7. Variation in northern leopard frog (Rana pipiens) captures (i.e., movement rate) was not explained by (a) Land cover, Julian day and their interaction nor by (b) land cover alone, but (c) total captures increased significantly with Julian day.

Effects of Land Cover and Environmental Factors on Movement

Movement rates were significantly related to wind speed and relative humidity. The model in which total captures were modeled as a function of land cover and meteorological data as quantified by PCA axis 1 did not explain a significant amount of variation in total captures ($F_{7,28} = 0.62$, $P = 0.74$, $R^2 = 0.13$) (Figure 8a), nor did the model with land cover, meteorological data as quantified by PCA axis 1, soil moisture, and all interactions ($F_{15,16} = 0.59$, $P < 0.84$, $R^2 = 0.36$). However, over 47% of the variation in total captures was explained by land cover, meteorological data as quantified by PCA axis 2, and their interaction ($F_{7,28} = 3.60$, $P = 0.07$, $R^2 = 0.47$) (figure 8b) but only PCA axis 2 had a significant effect ($F_{1,28} = 0.48$, $P < 0.001$, $R^2 = 0.42$). The model in which total captures were modeled as a function of land cover, meteorological data as quantified by PCA axis 2, soil moisture, and all interactions did not explain a significant amount of variation in total captures ($F_{15,16} = 1.46$, $P = 0.23$, $R^2 = 0.58$), but again PCA axis 2 had a significant effect ($F_{1,16} = 4.99$, $P = 0.040$, $R^2 = 0.13$). PCA axis 2 explained over 40% of the variation in total captures ($F_{1,34} = 23.89$, $P < 0.001$, $R^2 = 0.41$). Modeling captures as a function of relative humidity (the second most dominant component of PCA axis 2) (figure 8c) explained over 26% of the variation ($F_{1,34} = 12.24$, $P = 0.001$, $R^2 = 0.26$), while modeling captures as a function of wind speed (the first most dominant component of PCA 2) explained approximately 19% of the variation ($F_{1,34} = 8.22$, $P = 0.007$, $R^2 = 0.19$) (figure 8d).

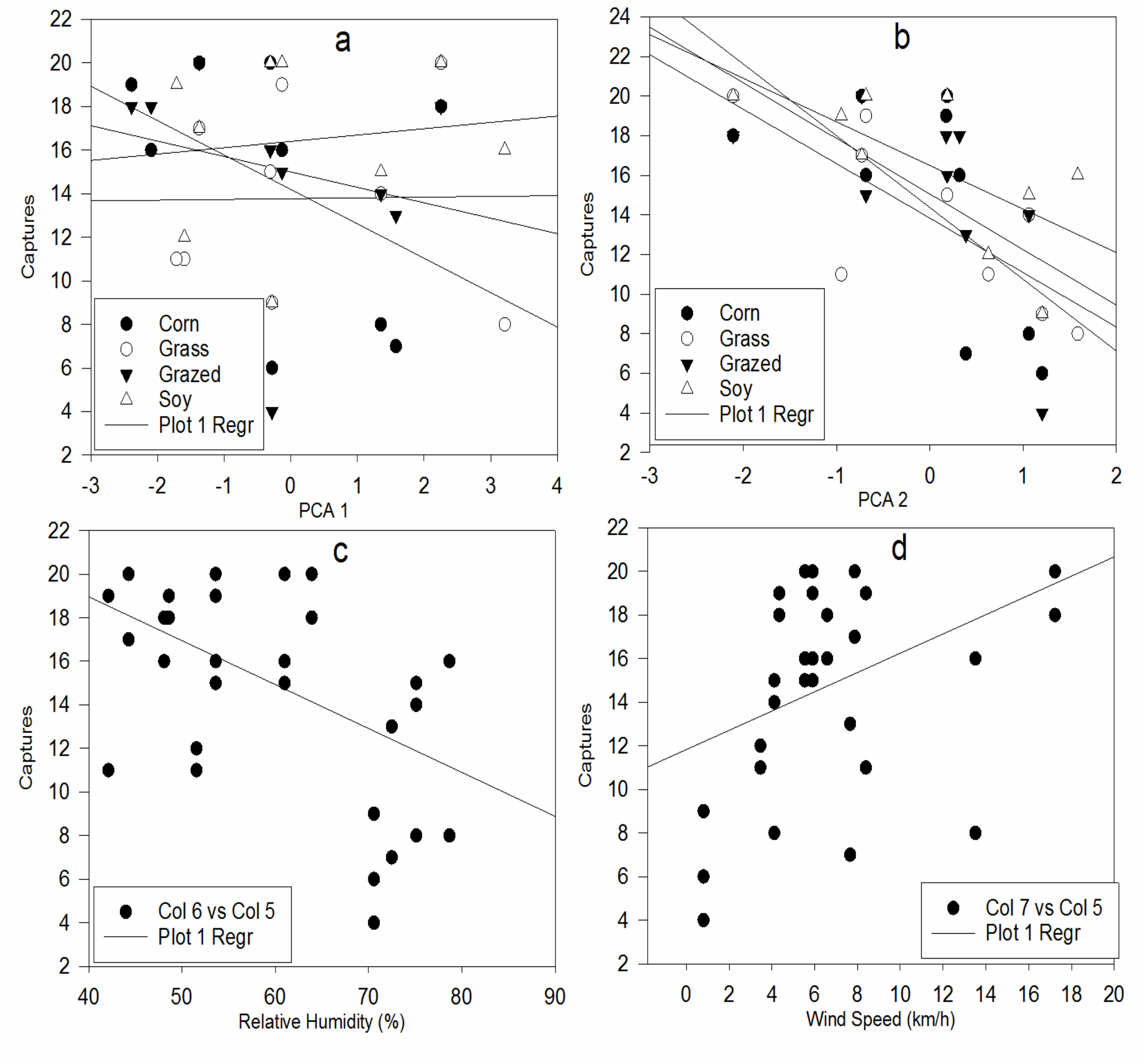

Figure 8. Northern leopard frog (Rana pipiens) total captures were not significantly explained by PCA axis 1 (a), but were significantly explained by PCA axis 2 (b). Relative humidity (c) and wind speed (d) were significant environmental factors influencing captures of northern leopard frogs.

Effects of Julian Day and Environmental Factors on Movement

Both Julian day and environmental factors significantly affected movement rates. The model in which total captures were modeled as a function of Julian day and meteorological conditions (as quantified by PCA 2) explained a significant amount of variation in total captures

($F_{2,33} = 24.28$, $P < 0.001$, $R^2 = 0.59$), with both Julian day ($F_{1,33} = 14.90$, $P = 0.001$, $R^2 = 0.18$) and PCA 2 ($F_{1,33} = 27.92$, $P < 0.001$, $R^2 = 0.34$) having significant effects. The model in which total captures were modeled as a function of Julian day and wind speed also explained a significant amount of variation ($F_{2,33} = 20.15$, $P < 0.001$, $R^2 = 0.55$), with both Julian day ($F_{1,33} = 26.03$, $P < 0.001$, $R^2 = 0.36$) and wind speed ($F_{1,33} = 21.75$, $P < 0.001$, $R^2 = 0.30$) having significant effects. Finally, the model in which total captures were modeled as a function of Julian day and relative humidity also explained a significant amount of variation in total captures ($F_{2,33} = 8.01$, $P = 0.002$, $R^2 = 0.33$), but neither Julian day ($F_{1,33} = 3.05$, $P =0.090$, $R^2 = 0.06$) nor relative humidity ($F_{1,33} = 3.62$, $P = 0.066$, $R^2 = 0.07$) alone was significant.

Desiccation Rates

Total captures were negatively correlated with mean desiccation rates of frogs, but were not related to mean desiccation rates of agar frogs. Captures were significantly correlated with the mean instantaneous rate of change in mass of frogs ($\rho = -0.65$, $n = 24$, $P < 0.001$; Figure 9a). However, captures were not related to the instantaneous rate of change in agar frogs ($\rho = -0.31$, $n = 24$, $P = 0.147$; Figure 9b), and the instantaneous rates of change for frogs and agar frogs were not correlated ($\rho = 0.33$, $n = 24$, $P = 0.115$; Figure 9c). Desiccation rates for real and agar frogs were used to determine desiccation rates in the model. Real frog desiccation rates in the modeled environment for corn, ungrazed grass, grazed grass, and soy were 0.10, 10.50, 1.22, and 5.18, respectively. Agar frog desiccation rates in the modeled environment for corn, ungrazed grass, grazed grass, and soy were 14.63, 28.02, 38.47, and 23.77, respectively.

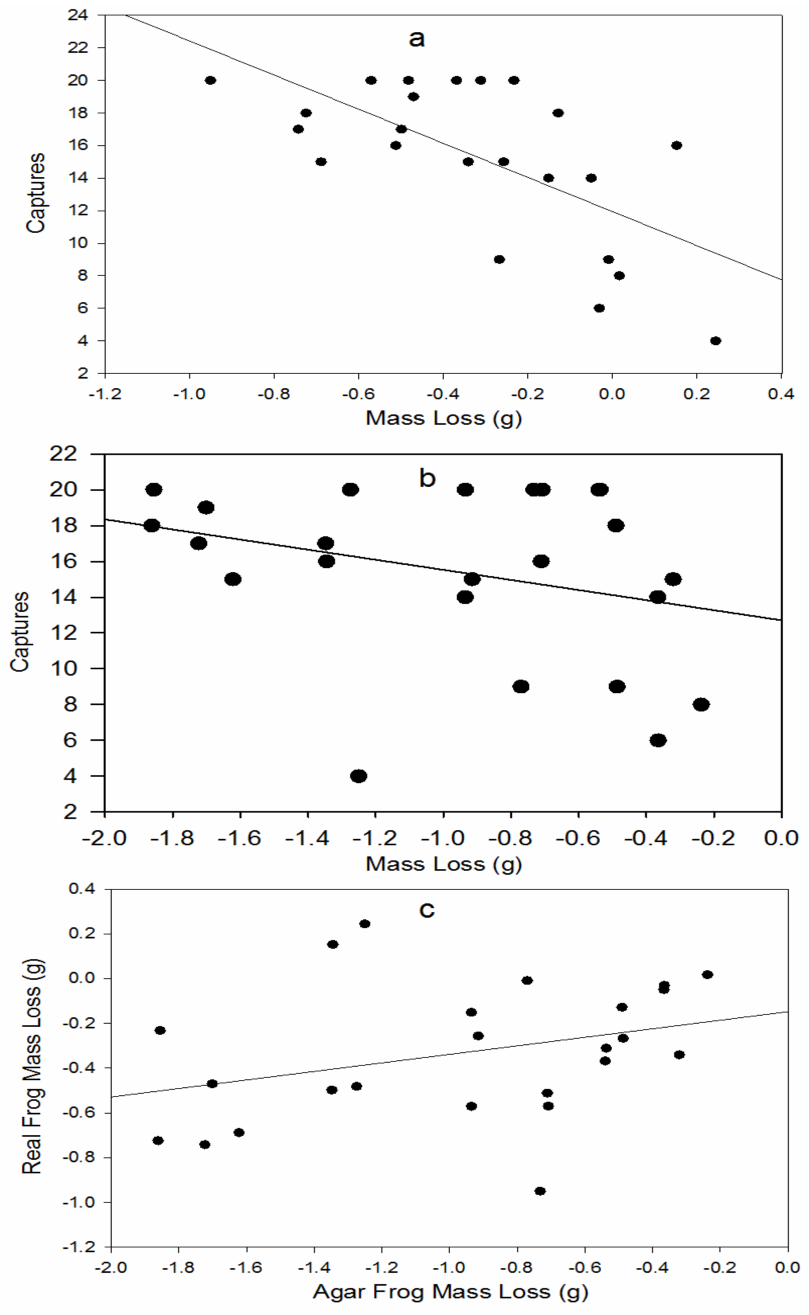

Figure 9. Total northern leopard frog (Rana pipiens) captures were negatively related to mass loss (i.e., desiccation) of real frogs (a) but not related to mass loss of agar frogs (b). Desiccation of real frogs and agar frogs were not significantly correlated (c).

Effects of Environmental Factors on Desiccation

General linear models also indicated that observed desiccation rates of frogs were related to soil moisture, relative humidity, and wind speed. Land cover, soil moisture, and the interaction between the two did not explain a significant amount of the variation in desiccation rates ($F_{7,12}$ = 1.19, P = 0.379, R^2 = 0.41), but in this model soil moisture had a significant effect ($F_{1,12}$ = 4.82, P = 0.049, R^2 = 0.24). While land cover and environmental conditions quantified by PCA axis 2 explained 75% of the variation in desiccation rates ($F_{7,16}$ = 6.89, $P < 0.001$, R^2 = 0.75), only PCA axis 2 had a significant effect in the model ($F_{1,16}$ = 30.26, $P < 0.001$, R^2 = 0.47). Land cover and relative humidity did not explain a significant amount of variation in desiccation rates ($F_{7,16}$ = 1.46, P = 0.250, R^2 = 0.39), but relative humidity did have a significant effect in the model ($F_{1,16}$ = 6.06, P = 0.026, R^2 = 0.23. Land cover and wind speed explained over 60% of the variation in desiccation rates ($F_{7,16}$ = 3.88, P = 0.012, R^2 = 0.63), but only wind speed had a significant effect in the model ($F_{1,16}$ = 14.37, P = 0.002, R^2 = 0.33). Finally, land cover and Julian day did not explain variation in desiccation rates ($F_{7,16}$ = 0.46, P = 0.848, R^2 = 0.17), and none of the individual factors were significant. Soil moisture alone explained over 20% of the variation in desiccation rates ($F_{1,18}$ = 5.23, P = 0.035, R^2 = 0.23; figure 10a). However, the second principal component of the meteorological data (i.e., PCA 2) explained over 45% of the variation in desiccation rates ($F_{1,22}$ = 19.60, $P < 0.001$, R^2 = 0.47). Relative humidity explained approximately 23% of the variation in desiccation rates ($F_{1,22}$ = 6.61, P = 0.017, R^2 = 0.23; Figure 10b), while wind speed accounted for approximately 33% of the variation in desiccation rates ($F_{1,22}$ = 10.99, P = 0.003, R^2 = 0.33; Figure 10c).

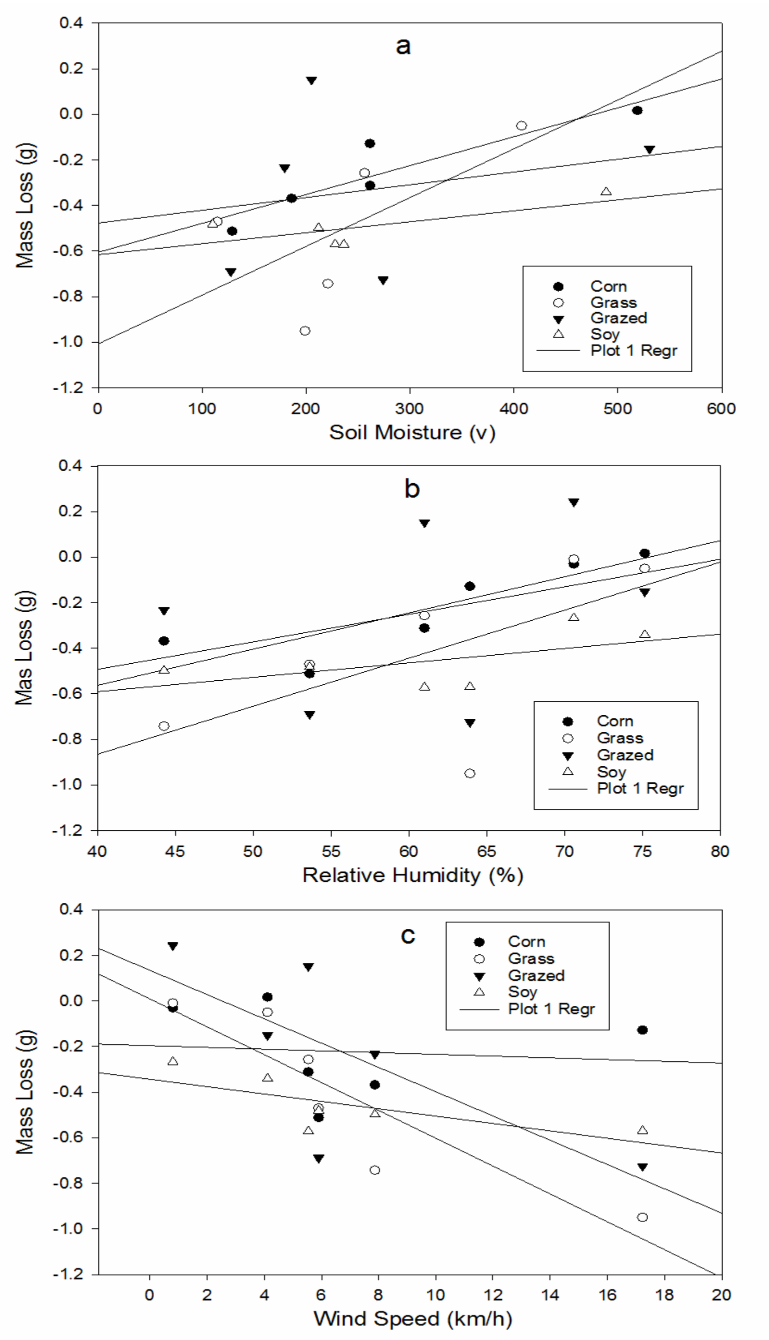

Figure 10. Change in Northern leopard frog (Rana pipiens) mass was negatively correlated with soil moisture (a) and relative humidity (b) and positively correlated with wind speed.

Effects of Land cover and Environmental Factors on Desiccation

Both land cover and environmental factors (e.g., soil moisture, relative humidity, wind speed) affected desiccation rates of agar frogs. Land cover, soil moisture, and the interaction between the two explained over 80% of the variation in desiccation rates of agar frogs ($F_{7,12}$ = 7.24, $P = 0.002$, $R^2 = 0.81$; Figure 11a,), and in this model both land cover ($F_{3,12}$ = 9.80, P = 0.002, $R^2 = 0.47$) and soil moisture ($F_{1,12}$ = 19.59, $P = 0.001$, $R^2 = 0.31$) had significant effects (but the interaction term was not significant). Land cover and environmental conditions quantified by PCA axis 2 explained 66% of the variation in desiccation rates of agar frogs ($F_{7,16}$ = 4.40, $P = 0.007$, $R^2 = 0.66$), and again both land cover ($F_{3,16}$ = 7.67, $P = 0.002$, $R^2 = 0.49$) and PCA 2 ($F_{1,16}$ = 6.81, $P = 0.019$, $R^2 = 0.15$) had significant effects. Land cover, relative humidity, and the interaction between the two explained over 90% of the variation in desiccation rates of agar frogs ($F_{7,16}$ = 24.22, $P < 0.001$, $R^2 = 0.91$; Figure 11b), and in this model land cover ($F_{3,16}$ = 30.39, $P < 0.001$, $R^2 = 0.49$), relative humidity ($F_{1,16}$ = 65.92, $P < 0.001$, $R^2 = 0.36$) and their interaction ($F_{1,16}$ = 4.14, $P = 0.024$, $R^2 = 0.07$) all had significant effects. Land cover, wind speed, and the interaction between the two explained over 50% of the variation in desiccation rates of agar frogs ($F_{7,16}$ = 2.81, $P = 0.041$, $R^2 = 0.55$; Figure 11c), but only land cover had a significant effect ($F_{3,16}$ = 5.85, $P = 0.007$, $R^2 = 0.49$). In all of these models, rates of mass loss of agar frogs were highest in grazed grass fields, second highest in ungrazed grass fields, second lowest in soy fields and lowest in corn fields.

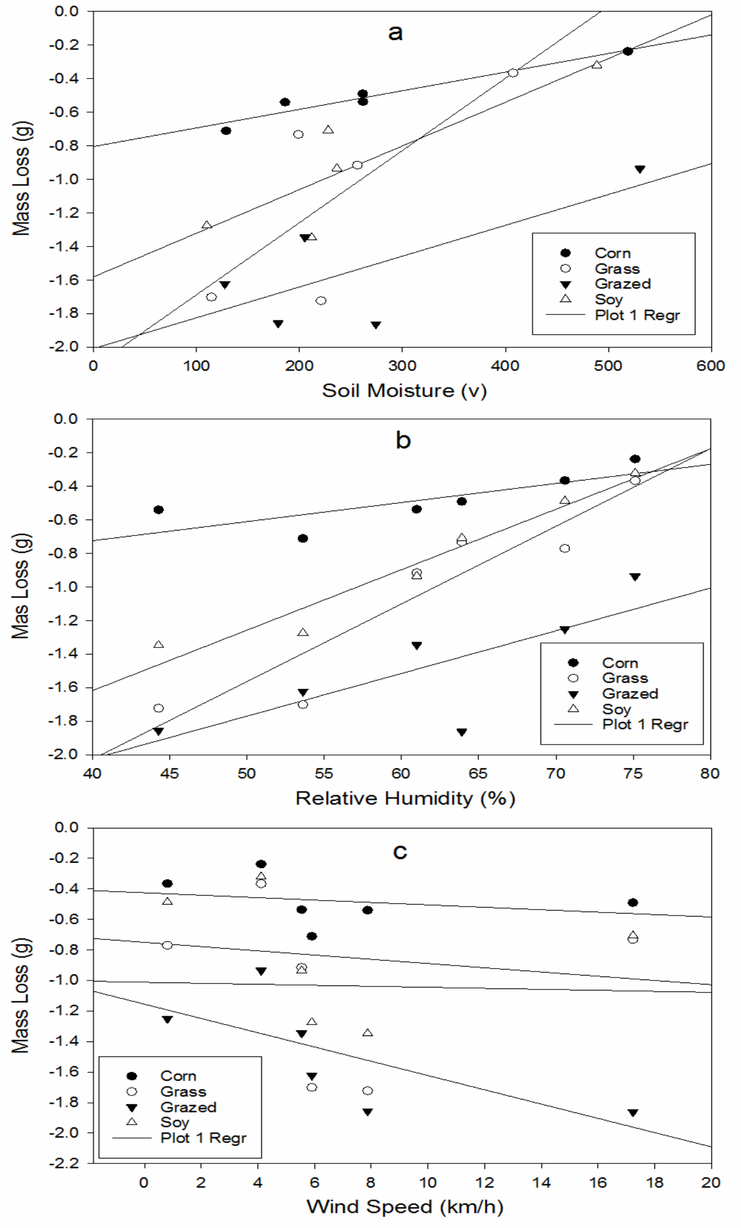

Figure 11. Change in agar-frog mass was negatively correlated with soil moisture (a) and relative humidity (b) and positively correlated with wind speed.

Model Simulations

In my first set of model runs used to test the performance of desiccation rates based on estimates from real frogs versus agar frog mass loss, significantly more frogs made it to the overwintering wetland when desiccation rates were based on data collected from the real frogs ($F_{1,18} = 32.728$, df = 1, $P < 0.001$) (Figure 12c). Additionally, when using estimates from real frogs, death counts varied significantly among cover types ($F_{3,36} = 296.519$, df = 3, $P < 0.001$), with more frogs dying in ungrazed grass than in corn, grazed grass, or soy ($P < 0.001$), more frogs dying in soy than corn and grazed grass ($P < 0.001$) and more frogs dying in grazed grass than corn ($P < 0.001$) (Figure 12a). However, when using desiccation rates derived from agar frog data, the number of frogs dying did not significantly differ among cover types ($F_{3,36} = 0.765$, df = 3, $P < 0.521$) (Figure 12b). Given the differences revealed by using cover-type specific desiccation estimates derived from real-frog data, I opted to use these desiccation rate estimates as my baseline rates in all subsequent analyses. I choose real frog desiccation rates over agar frog desiccation rates because unlike agar frogs, real frogs urinate and have the potential absorb moisture from their surroundings.

In my model with the baseline parameters and the baseline landscape there was an average of 872 frogs that desiccated in grazed grass, 1635 frogs that desiccated in ungrazed grass, 29.9 frogs that desiccated in corn and 1462.4 frogs that desiccated in soy (Table 4). The average number of frogs that successfully made it to the overwintering wetland was 94, or 1.9% (Table 4) which is lower than the sustainable survival rate of 18% for the California tiger salamander (*Ambysotma californiense*) (Trenham et al. 2005).

Table 4

Average number of frogs that desiccated in each land-cover type, average number of frogs that made it to the overwintering wetland and the percentage of frogs that survived (made it to the overwintering wetland) in the baseline NetLogo modeled environment.

Average number of Desiccated Frogs - Grazed Grass	Average number of Desiccated Frogs - Ungrazed Grass	Average number of Desiccated Frogs – Corn	Average number of Desiccated Frogs - Soy	Average number of frogs that made it to OW	Percentage of Frogs that Survived
872	1635.5	29.9	1462.4	94	1.9 %

Table 5

The percent of frogs that died due to predation and the percent that survived (made it to the overwintering wetland) as predators increased in the modeled environment.

# predators	**0**	**100**	**500**	**1000**	**2000**
% survival of frogs	1.9	1.9	2	2	1.7
% eaten in grazed grass	0.0	0.0	0.1	0.2	0.3
% eaten in ungrazed grass	0.0	0.1	0.5	0.9	1.9
% eaten in corn	0.0	0.1	0.7	1.3	2.2
% eaten in soy	0.0	0.0	0.1	0.2	0.5
Total % eaten	0.0	0.2	1.4	2.6	4.9

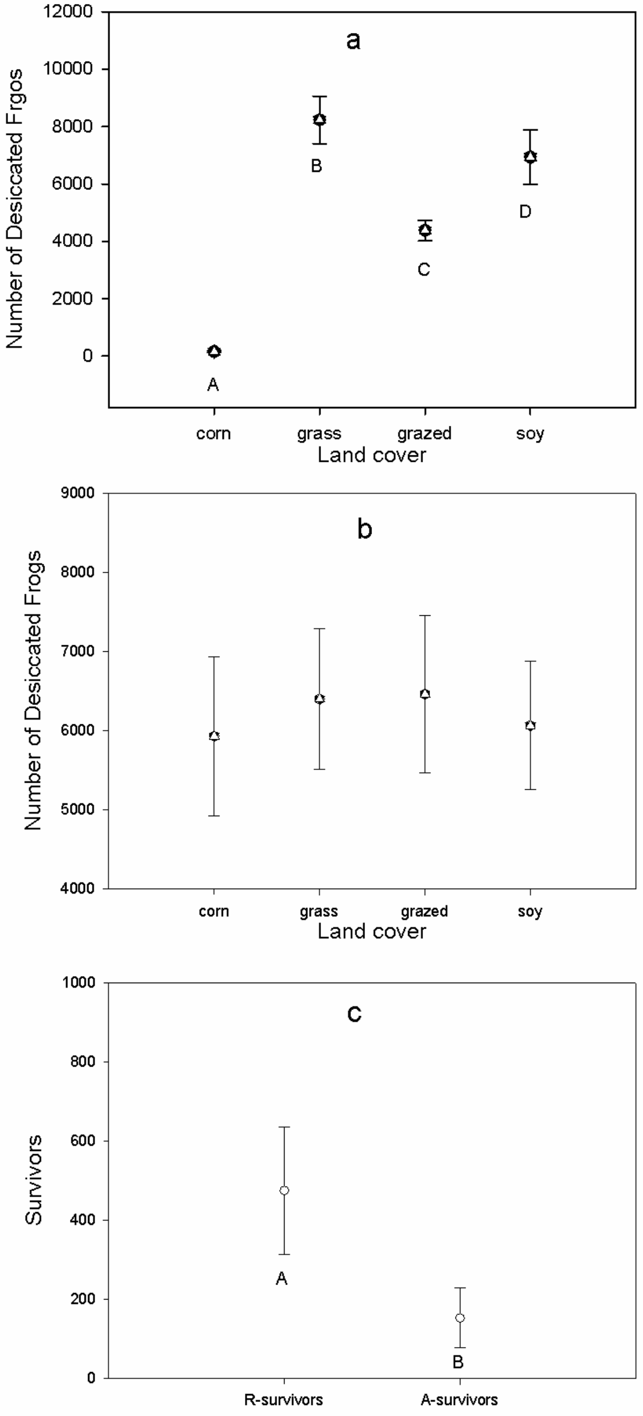

Figure 12. The number of simulated frogs that died in each land-cover type when real-frog desiccation rates were used (a) and when agar frog desiccation rates were used (b). The lower graph (c) shows the number of frogs reaching the overwintering wetland (survivors) in the baseline landscape when desiccation rates derived from real-frog data were used (R-survivors) versus rates derived from agar-frog data (A-survivors).

Survival rate did not significantly change when I varied the initial number of frogs in the simulation. However, survival did significantly increase as movement rate increased, and decreased as desiccation rate increased. In the group of simulations in which only the number of frogs present in the simulations varied, there was no difference in the fraction of frogs that made it to an overwintering wetland ($F_{1,48}$ = 0.479, P =0.491) suggesting that survival rate in the model does not change with increasing frogs (Figure 13a). In simulations in which the movement rate was varied from 25% to 200% of the baseline movement rate, the number of frogs that survived increased significantly with increasing rates of movement ($F_{1,48}$ = 90.481, P < 0.001) (Figure 13b). In simulations in which desiccation rate were similarly varied, the number of frogs reaching the overwintering wetland decreased significantly ($F_{1,48}$ = 12.622, P < 0.001) (Figure 13c). However, increasing the number of predators did not have a significant effect on the number of frogs surviving ($F_{4,45}$ = 0.680, P = 0.609) (Figure 13d, Table 5). Although the number of frogs that survived did not seem to be affected by an increase in predators, the number of frogs being eaten by predators did increase in each field as the number of predators was increased ($F_{4,195}$ = 48.288, P < 0.001) (Figure 16).

Survival differed among land-cover types in the simulations in which desiccation rate or movement rate varied. The number of frogs that died in grazed grass ($F_{1,48}$ = 167.960, P < 0.001) and corn ($F_{1,48}$ = 56.884, P < 0.001) significantly increased with an increasing desiccation rate (Figure 14a). However, the number of frogs that died in ungrazed grass ($F_{1,48}$ = 0.636, P = 0.429) and soy ($F_{1,48}$ = 2.435, P = 0.124) did not change significantly as desiccation rates increased (Figure 14a). The number of frogs that died in ungrazed grass ($F_{1,48}$ = 57.125, P < 0.001), grazed grass ($F_{1,48}$ = 69.345, P < 0.001), corn ($F_{1,48}$ = 30.180, P < 0.001) and soy ($F_{1,48}$ = 15.765, P < 0.001) all changed significantly as movement rate varied (Figure 14b).

In the simulations in which the land-use was changed to 100% for each cover, there were significant differences in the number of frogs that made it to the overwintering wetland ($F_{3,36}$ = 57.834, P < 0.001) (Figure 15a). More frogs made it to the overwintering wetland in the 100% corn landscape compared to the 100% ungrazed grass landscape (P < 0.001), and the 100% soy landscape (P < 0.001). More frogs made it to the overwintering wetland in 100% grazed grass landscape when compared to the 100% ungrazed grass landscape (P < 0.001) and 100% soy landscape (P < 0.001). However, there was no significant difference in the number of frogs making it to an overwintering wetland between the 100% corn and 100% grazed grass landscapes (P = 0.080) and the 100% soy and 100% ungrazed grass landscapes (P = 0.700).

Under various scenarios of habitat fragmentation, there were significant differences in the number of frogs that made it to an overwintering wetland ($F_{4, 55}$ = 15.865, P < 0.001) (Figure 15b). More frogs made it to an overwintering wetland in the most fragmented landscape (landscape E, average patch size = 64.75 ha) versus the unfragmented landscape (landscape A, a single 1618.75 ha patch of ungrazed grass) (P < 0.001). The trend of increasing survival with increasing fragmentation held true for other landscape patterns as well. There was a significant difference in survival between landscape E, and fragmented landscapes D (129.5 ha patch size) (P = 0.005) and fragmented landscape B (841.57 ha patch size) (P = 0.008). There was also a greater number of frogs that made it to an overwintering wetland in fragmented landscape C (323.75 ha patch size) compared to the unfragmented landscape (landscape A) (P < 0.001). Survival in fragmented landscape B was also significantly different than survival in unfragmented landscape A (P = 0.006), and in landscape D versus A (P = 0.009). There was not a significant difference in the number of frogs that survived when landscape E was compared to landscape C (P = 0.567), when landscape C was compared to landscape B (P = 0.339), when landscape C was compared to landscape B (P = 0.425) or when landscape B was compared to landscape D (P = 1.000).

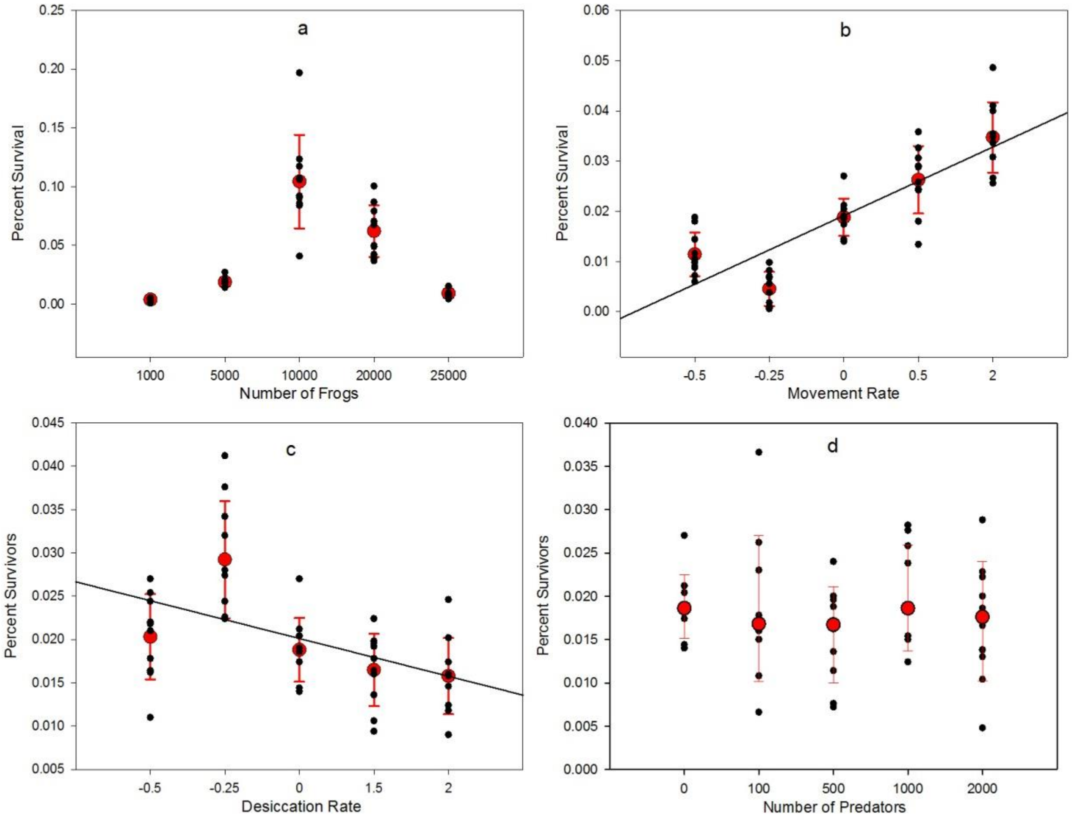

Figure 13. Percent of frogs surviving when number of initial frogs (a), movement rates (b), desiccation rates (c) and predation were varied.

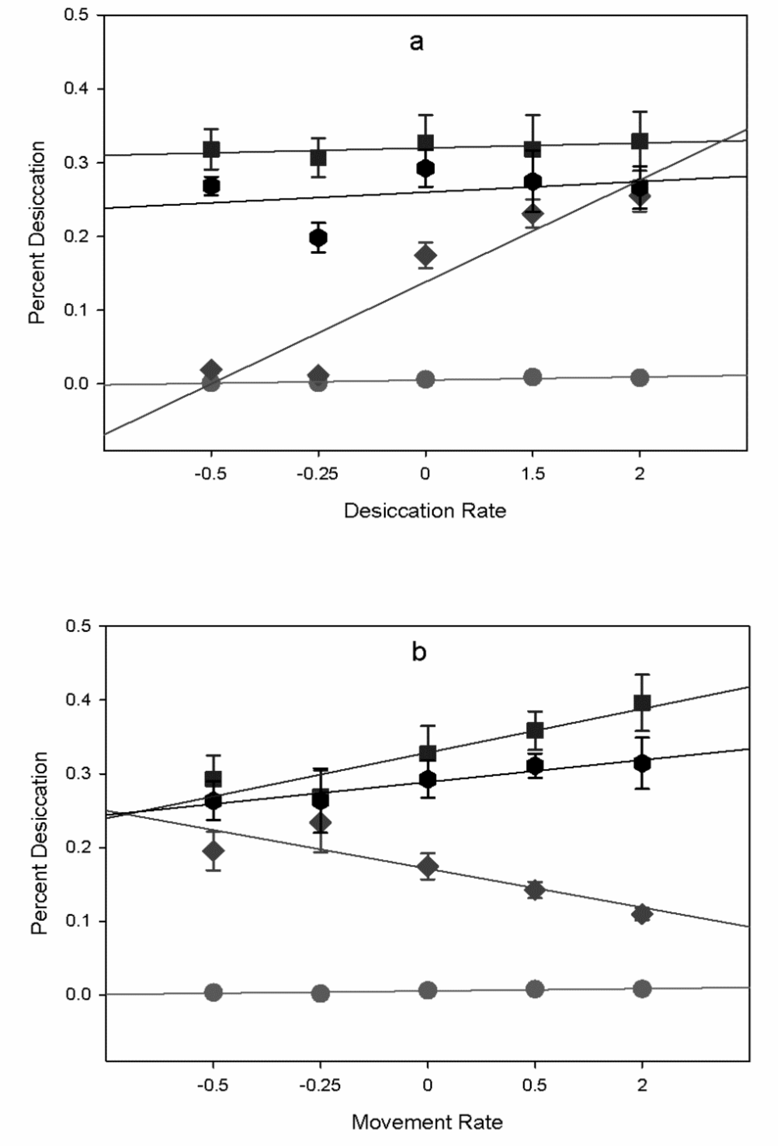

Figure 14. The percentage of frogs that died when desiccation rates were varied (a) and when the movement rates were varied (b). Diamonds = grazed grass, squares = ungrazed grass, circles = corn, hexagons = soy.

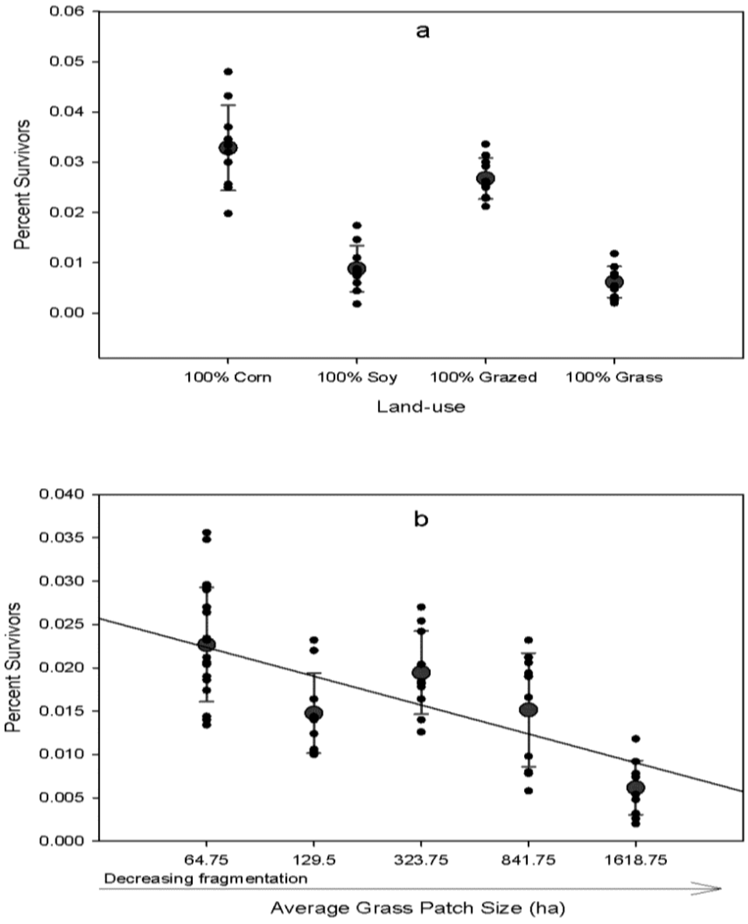

Figure 15. The percentage of frogs reaching the overwintering wetland (survivors) in homogeneous landscapes of four cover types (a) and under increasing conditions (lower average patch size) of habitat fragmentation.

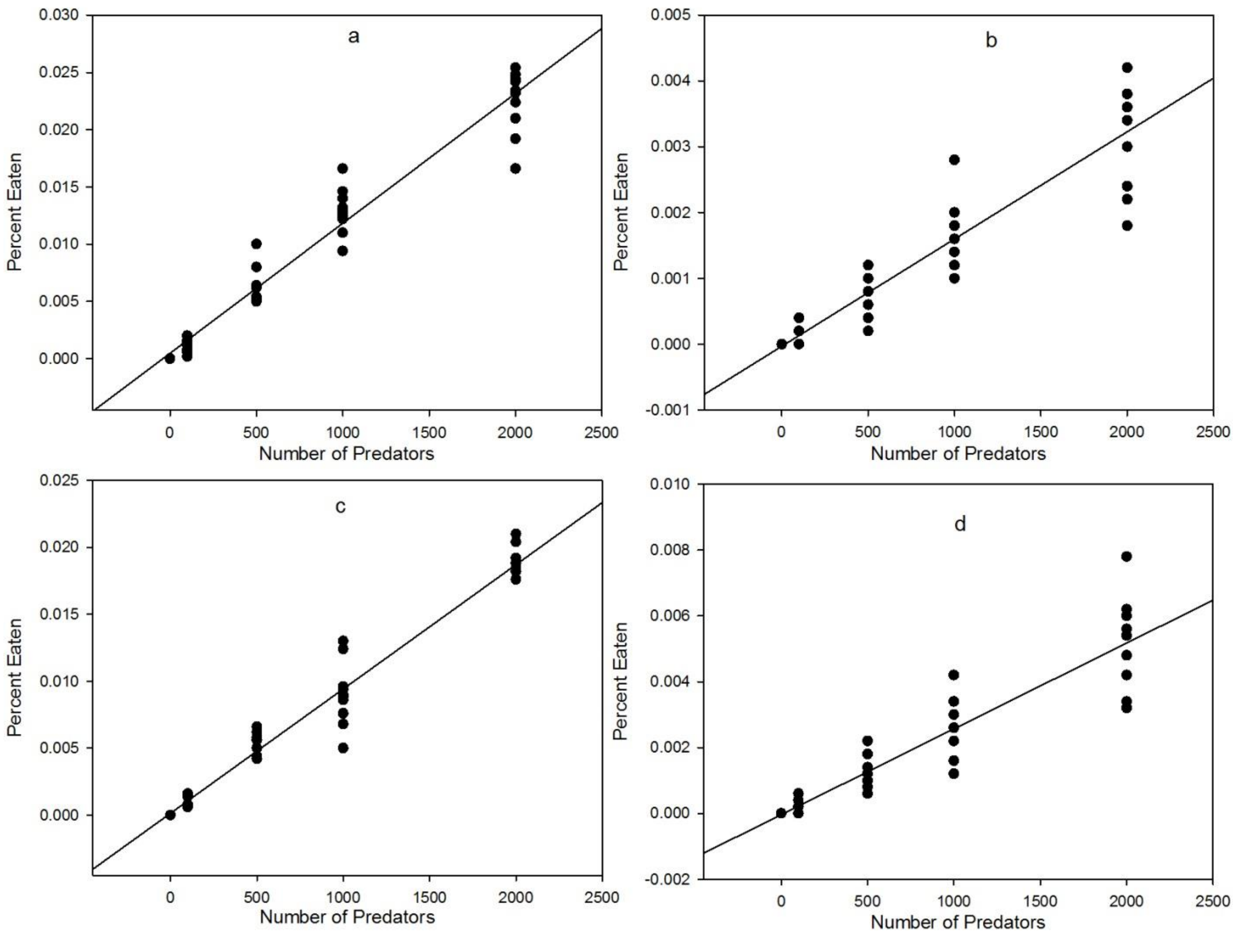

Figure 16. The percent of frogs that were eaten as predators increased in the modeled environment in a) corn, b) ungrazed grass, c) grazed grass and d) soy.

DISCUSSION

A Model for Exploring Movement

The agent-based model I developed in NetLogo facilitates exploration of amphibian movements across anthropocentrically altered landscapes. It is crucial that we take steps to understand better the potential impacts that land-use change has on species that rely on the affected habitat (Matthews et al. 2007). In the model I developed, the landscape can be altered to represent a desired change, and movement, desiccation and predation patterns for the northern leopard frog can be observed in the modeled landscape before real world changes are adopted. The model I developed can also help distinguish landscape patterns that help or hinder the survival of the northern leopard frog as it moves from a reproductive wetland to an overwintering site. In this model, the northern leopard frog moves about different landscapes at speeds that can be varied with land-cover type, while desiccating and at rates that can also be varied with land cover and potentially being eaten by a varied number of predators.

Information gained from field experiments was used to inform my adjustment of settings for various parameters in model runs. The ability to vary movement rates, desiccation rates, moisture gained in wetlands, initial moisture and predator abundance either separately or in combination is a key feature of the model. Thus, as our understanding of these factors increases, the modeled environment can easily be adapted to accommodate knowledge gained. Also, whereas my model uses the northern leopard frog as the species of interest, as more information on movement and desiccation rates of other amphibian species becomes available, this model can be easily altered to accommodate these additional species.

Movement Rates

In my movement-rate experiments, although statistical power limited my ability to detect a significant effect, there was a trend for frogs to move less in ungrazed grass compared to grazed grass, corn, and soy (Figure 7b). Grazed grass and crop fields could provide a faster route through which juvenile northern leopard frogs travel. They may also use grazed grass and crop fields if the route to overwintering or other wetland habitat is shorter through these fields than routes through ungrazed grass. In fact, Birchfield and Deters (2005) found that green frogs (*Lithobates clamitans)* will use the path of least resistance when given a choice. Another amphibian not seemingly affected by agriculture land cover is the spadefoot toad (*Spea multiplicata, S. bombifrons*). Agriculture did not seem to affect the spadefoot when the abundance of this species was compared in playas surrounded by cropland versus grassland (Gray et al. 2004). However, this could also be due to the agriculture landscape restraining spadefoots to the playas inside the cropland (Kolozsvary and Swihart 1999). Amphibians in the PPR may even be adapting to the agriculturally dominated landscape. Kolozsvary and Swihart (1999) concluded that the abundance of amphibians in agricultural lands is likely an adjustment to the conversion of grassland to crop fields and the massive reduction of natural wetlands.

I found that movement rates increased as summer progressed. This change was likely influenced by changes in wind and relative humidity. As Julian day increased during my study period (Figure 7c), days became windier (Figure 8d), relative humidity declined (Figure 8c) and movement rates increased. Many species have adapted biological clocks, which are linked to environmental factors to aide in migration (Hamer 2016) and help direct physiological and behavior changes to allow a species to adapt to its environment (Amaral et al 2014). Frogs likely increased their movement rates in my experiments in response to these two environmental factors (Figure 8c and 8d), which would possibly indicate that they are moving to seek refuge from the wind and low humidity. This would contradict a study by Bellis (1962) who showed that wood frogs (*Lithobates sylvaticus*) are more active when the humidity is higher and less active when low. However, Bellis also observed that northern leopard frogs can apparently handle stressful environmental conditions such as low humidity. It is possible that movement occurs when frogs seek refuge from unfavorable environmental conditions. Frogs in my experiment were removed from wetlands and placed in arenas with lower humidity conditions than the wetlands, and thus may have moved more quickly in their search for more favorable environmental conditions. Also, as frogs move, they expend moisture. Similar to my findings, others have shown that amphibians move more quickly on windier days (e.g., Phillips et al. 2007, Hurlbert 1969). Precipitation was infrequent during my experiments and therefore my ability to detect its effect on frog movement rates was limited. However, previous studies have observed amphibians having higher rates of movement during and immediately after rainfall events (Martof 1953a, Martof 1953b, Blanchard 1930, Bellis 1962). Although I detected a positive trend between movement and temperature, it was not significant. Increased movement or activity with increased temperature is not uncommon in amphibians. As temperature increases, amphibians are more likely to desiccate, so this may cause movement to seek shelter. For instance, salamanders attempted to escape enclosed spaces when temperature was increased (Hutchison 1958). Lastly, as summer advanced and winter approached, the urgency to find a winter refuge, and therefore movement rates, likely increased.

Increased frog movement throughout the summer could also be caused by photoperiod. It has been observed that photoperiod is responsible for the downstream movement of Atlantic

Salmon (Zydlewski 2014) and is in fact, responsible for the transition of salmonid fish from fresh water to sea water (Ebbesson et al. 2011).

The type of movement (i.e., migration or dispersal) can also influence movement rates, with migration and dispersal taking place during different times of the year. My experiments started in midsummer when juvenile northern leopard frogs leave reproductive wetlands and migrate to upland foraging areas. During this time, certain fields may not be ideal to cross due to lack of food resources, low humidity, high temperatures, or other unfavorable environmental conditions. As the season progresses, and frogs prepare to make their journey to an overwintering wetland, fields that were not favorable to movement before may become favorable at this time. Furthermore, frogs face an entirely different set of environmental conditions in spring when young-of-the-year disperse from overwintering sites in search of unoccupied reproductive wetlands. Humidity, wind and temperature are all factors that change throughout the year, and my observations suggest frog movements would also change throughout the year in response to these factors. When the humidity is high or the wind speed is low, frogs may be hesitant to move but may move more quickly if movement becomes a necessity.

Microclimates also affect frogs as they move through various land-cover type. Besides soil moisture, all of the environmental measurements that I recorded were retrieved from a single weather station that was located at the Roosevelt WPA. This did not allow for the comparison of microclimate conditions on each land-cover type. Each field has different factors that could affect temperature, wind speed, humidity and soil moisture within the field. When migration from foraging areas to overwintering wetlands takes place, it is often synchronous with the harvest of corn and soy in some years but not in others. There could be differences in microclimate in these fields after harvest (when standing vegetation is removed), and this could also affect the movement rates of northern leopard frogs. They may be open at the time of year when adult northern leopard frogs migrate to breeding wetlands, and then be fully vegetated during summer dispersal of adults and juveniles to foraging areas and barren once again when frogs migrate to overwintering sites. Thus more detailed studies on how the amount of vegetation and other microclimatic factors affect northern leopard frog movement through agricultural fields could be used to refine model parameters for movement.

Desiccation Rates

Movement rates (as measured by captures within an eight-hour period) was negatively related to change in mass (i.e., desiccation) of real frogs (Figure 9a). I considered mass change in real frogs more representative of changes associated with desiccation than loss in agar frogs because my real-frog data reflects both water loss and gains associated with foraging and the ability to offset loss from environmental conditions through behavior. For instance, amphibians will seek refuge to avoid desiccation (Pough et al. 1983).

So, do frogs move because they are drying out or are they drying out because they are moving? The answer to this question is likely a combination of the two. Evidence in the literature suggests that drying out because they are moving may play the larger role. If the northern leopard frogs were experiencing high water loss, it would be likely that they would limit their activity which would correspond with behaviors in the Puerto Rican Frog (*Eleutherodactylus coqui*) which tend to cease activities when they are more prone to lose moisture at a quicker rate (i.e., non-rainy nights) (Pough et al. 1983). In my arena experiments, frog movement rates were slightly higher in agriculture fields, while being slightly slower in ungrazed grass. So, although frogs had the highest desiccation rates in the ungrazed grass, they were also in that field longer due to the slower movement rate. Frogs may have possible taken shelter in the longer grass to avoid complete desiccation, but still desiccating at a slower rate for a longer period. The lack of leaf litter may cause frogs to move quicker to avoid desiccation, hence, having a higher movement rate in the agriculture fields and potentially a higher desiccation rate. Shoemaker and Nagy (1977) found that osmoregulation affects digestion, metabolism and overall wellbeing of amphibians.

On the other hand, some evidence indicates frogs move more quickly to seek shelter from conditions causing high desiccation rates. Cane toads (*Rhinella marina*) were observed to travel on a straighter path when further away from a source of water (Tingley and Shine 2011). Not only does movement seem to be affected by desiccation, but shelter choices as well. Tingley and Shine (2011) used plaster toad models to determine that shelters used by cane toads had lower rates of evaporation when compared to random areas.

My agar-frog models did indicate that different land cover can significantly affect desiccation rates. Although the agar-frog desiccation rates were not related to the capture rate of frogs (Figure 9 b) or the rate at which real frogs lost mass (Figure 9 c), agar frogs lost the most mass in grazed grass, with un-grazed grass being second, and soy and corn being third and fourth, respectively. The grazed-grass field had the lowest vegetation height and therefore lacked potential shelter from the sun and wind, a factor affecting evaporation rates in frogs (Tingley and Shine 2011).

The greater the soil moisture, the less mass (i.e., water) was lost in both real and agar frogs. Dispersing and migrating frogs depend on soil moisture to maintain a water balance while moving. This is especially important for juveniles moving from breeding wetlands to upland terrestrial habitat (Rittenhouse et al. 2008) because this type of dispersal is affected by microclimate responses such as variation in soil moisture (Nowakowski et al. 2015). Amphibians are known to obtain water from the soil and surrounding vegetation by pressing their feet and stomachs to them to absorb moisture (Dole 1965). So again, the agar frogs provide an estimate for desiccation that may be offset by behavioral responses of real frogs.

Model Simulations

The development of the model allowed me to explore the effects of differing landscapes, movement rates and desiccation rates on frog survival. I was able to easily adjust different parameters in my model to see outcomes under different conditions. I was also able to examine frog survival in a landscape that has been completely changed to a new cover type or a landscape that has been fragmented to various degrees.

In simulations using the baseline landscape, land-cover effects were only evident with the lower desiccation rates. Based on real frog desiccation rates most frogs died in ungrazed grass, with soy being second, grazed grass being third and corn fourth. However, with the higher rates based on agar frogs, there was not a significant difference among land covers, indicating that sensitivity to land cover interacts with desiccation rate. Thus, sensitivity of frog mortality to land cover is context dependent.

Model results were also insensitive to changes in the initial number of frogs that started the simulation. This has practical implications for conducting analyses with the model. Increasing the number of individuals in an agent-based model increases computational time. Therefore, minimizing the number of individuals represented in a simulation to determine effects on a variable of interest (e.g., fraction surviving) enables the user to conduct more simulations in a particular time frame.

However, model results did vary when movement rate was varied. Unsurprisingly, more frogs made it to an overwintering wetland in simulations with higher movement rates. The fraction of frogs surviving did increase linearly as the movement rate was varied by 25% below up to 200% above the baseline rates established from the field studies (Figure 13b). However, the number of frogs desiccating in grazed grass, ungrazed grass and soy habitat was similar at lower movement rates but at higher movement rates the numbers desiccating in ungrazed grass and soy increased while the numbers in grazed grass decreased (Figure 14b).

Model results also varied as the desiccation rate varied. More frogs made it to the overwintering wetland when the desiccation was lowest. However, the fraction of frogs surviving did not change linearly as desiccation rate varied (Figure 13c). For instance, the fraction of frogs desiccating in ungrazed grass stayed at approximately 30% when the desiccation rate was increased as well as when it was decreased from the baseline level. However, the fraction desiccating in the other fields increased slightly to a plateau as the desiccation rate was increased (Figure 14a). Nonlinear response generally indicates that more simulation scenarios are required when a user is assessing the effects of a parameter with the model.

There was no detectable difference in frog survival rate when the number of predators in the simulation varied (Table 5). This suggests that relative to desiccation, mortality due to predation (as represented by a predator moving randomly in the landscape) is compensatory. However, it is important to note that the predators in my modeled landscape are not representative of predators on a real landscape. My modeled predators move at random and only "eat" a frog if they land on the same pixel as a frog. The probability of this occurring can be varied by changing the number of predators, but even with 2000 predators on the modeled landscape, the effect of predation was minimal when compared to the high rates of frogs dying due to desiccation or failing to reach the overwintering site by the end of the 60-day simulations.

Unexpectedly, fragmentation of ungrazed-grass increased survival. In the simulations, ungrazed-grass patches were associated with the highest baseline desiccation rates and the slowest movement rates. As the fragments of grass patches became smaller, more frogs reached the overwintering habitat and survived (Figure 13b). Frogs had a much lower chance of surviving in the one large ungrazed-grass patch at 1618.75 ha than they did when there was an equal mix of grass patches and corn patches that were 129.5 ha each (Figure 13b). Larger patches require longer times for an individual frog to traverse, and every step they took in the grass, the more drying they experience. Conversely when patches of corn (which had the lowest desiccation and highest movement rates) increased in size (i.e., fragmentation of corn decreased), frogs experience the least desiccation and greater survival (Figure 13b). Although, from my experiments, corn facilitated movements better than ungrazed grass due to the lower desiccation rates that frogs observed, research has shown that habitat change can impact a magnitude of species (Tilman et al. 2011, Gonthier et al. 2014, Almeida-Gomes and Rocha 2015). However, the model simulations demonstrated that as suboptimal habitat is fragmented, survival can be enhanced.

Ungrazed grassland should not be considered the natural, optimal habitat for species endemic to the PPR (such as the northern leopard frog). Large herds of American bison (*Bison bison*) and other ungulates historically grazed the prairie-pothole region landscape. Also, other factors not included in my model likely affected these results. For instance, ungrazed grass may provide better cover from predators or may facilitate movement better at other points in the annual cycle of the northern leopard frog. As well as edges of grazed grass or agriculture may be used to speed up movements. Bullfrogs (*Lithobates catesbeianus*) for example are a species that utilizes corn edges to travel at a quicker rate. Cricket frogs (Acris blanchardi) will use hay fields and grazed grass for dispersal. These species are edge specialists and may use agriculture to their advantage to disperse quickly (Youngquist 2014). Some species, such as the the *Norops* lizard use edges to their advantage during certain time of the year depending on the environmental conditions (Schlaepfer and Gavin 2001). The Cerro Utyum robber frog (*Eleutherodactylus podiciferus*) and the Chiriqui robber frog (*Eleutherodactylus cruentus*) are more sensitive to edges and are negatively impacted by edges (Schlaepfer and Gavin 2001). The message here is that larger patches of less-suitable habitat lower survival. This is compatible with research performed for the Biological Dynamics of Forest Fragments Project, which found that species richness is directly related to patch fragment sizes, meaning that suitable habitat patches should be reasonable extensive in size to properly support species richness (Laurance et al 2002). Moreover, this finding is robust across taxa, as many species are sensitive to habitat fragmentation (Lovejoy et al. 1986; Rylands and Keuroghlian 1988; Schwartzkopf and Rylands 1989; Stouffer and Bierregaard 1995; Stratford and Stouffer 1999; Powell and Powell 1987; Vasconcelos 1988; Klein 1989; de Souza and Brown 1994; Brown and Hutchings 1997).

Study Limitations and Future Implication

I suggest that future studies take place on the movement and desiccation rates of both juvenile and adult northern leopard frogs. With a better understanding of the desiccation and movement rates of the northern leopard frog throughout its lifecycle, the model presented here could be refined to provide a better tool for understanding the effects of land cover on this species over the entire year. Moreover, my field study methods provide a useful technique for measuring movement rates. However, if my study method was to be used for adult northern leopard frogs, much deeper pitfall traps would need to be used, as adults can easily jump out of a 5-gallon bucket. Adults are also harder to capture since they disperse after they have finished breeding. Whereas movement rates were accurately derived from my arena experiments, the desiccation rates I measured may be biased. The ability to stay moist is a vital factor in ensuring the survival of individuals, yet this factor did not vary with land cover for the northern leopard frog in this study. I suggest looking at other factors within land-cover types that may offset effects of cover on water loss or otherwise ensure the survival of the northern leopard frog. Some of these factors include predator abundance, exposure to predators in different land covers, microhabitat shelters and food availability. Survival rates would likely be significantly altered if these factors were included in revisions of the model.

In previous studies in which habitat was altered or lost, amphibians were negatively impacted (Corn and Fogleman 1984, Hayes and Jennings 1986, Stuart et al. 2004, Clarkson and Rorabaugh 1989, Bradford et al. 2004, Sjogren 1991, Gibbs 1998, Quaranta et al. 2009, Bentley and Yorio 1976, Hecnar and M’Closkey 1998, Mazerolle and Desrochers 2005). Movement of adults and juveniles through agriculture fields in the fall season as well as during spring migration needs to be determined to fully model effects of land cover. The general approach outlined here for juveniles could be modified for adults, and expanded in scope. For instance, I would suggest installing more arenas in each land-cover type, such as three different arenas in three different corn fields. This would require eight extra arenas (two more arenas for each of the three land covers), which would mean 180 additional frogs would have to be captured and marked. I think an experiment such as this would be realistic under circumstances where there were multiple researchers or technicians working on the project simultaneously. In addition, tracking individual adult northern leopard frogs through each of the land covers via radio telemetry during spring would provide additional information on movement rates that could perhaps serve as a “reality” check to model results. Finally obtaining data on variation in microclimate across land-cover types would provide better insight into the mechanisms responsible for movement and desiccation rate differences. Coupling these data with the model would then provide managers, and other decision makers, with a tool for exploring how alternative landscapes impact northern leopard frogs in the PPR.

Using an agent based simulation model can help researches make assumptions about reality. However, models do not always include every possible aspect of reality. My model for example has features in it that are not necessarily completely realistic. In reality, frogs can gain moisture from vegetation (Dole 1963) and tend to move quicker during rainfall events (Dole 1965).

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APPENDIX. MODEL DESCRIPTION

What is it

The purpose of this model is to use movements of the northern leopard frog (*Rana pipiens*) to explore habitat connectivity. If habitats are disconnected, northern leopard frogs are unable to move to the next habitat needed in their complex lifecycle. In this model, individuals start in a reproductive wetland and move around the landscape until they find the overwintering wetland located at the center of the simulated landscape. When they reach this point, they stop. If they do not reach the overwintering wetland within 60-days, they are declared dead.

How it works

The northern leopard frogs represented in this model are juveniles that have recently exited the breeding pond and now must move to an overwintering wetland in order to survive until the next season. When the frogs are moving about the landscape, they desiccate and may end up dying if they do not encounter a wetland. When they move through a wetland, they increase their moisture level. If they come into contact with a predator (e.g., snake, avian predator), they are declared eaten.

How to use it

Use sliders in the model to adjust initial number of frogs, moisture replenished if a wetland is encountered, movement speed by cover type, desiccation rate by cover type, and predator abundance by cover type. Use monitors to track of how many total frogs are in the mode, how many frogs have died in each cover type due to desiccation and predation, and how many frogs have made it to the overwintering wetland. In addition, use monitors to count the number of pixels in each cover type, and the number of pixels represented by the overwintering wetland and reproductive wetlands. Use the switch in this model to show the percentage of moisture frogs have left. Once the sliders have been adjusted, or just use the default, simple click the setup button and then the go button. The model will then perform a 60-day simulation.

Parameters

Initial-frogs: number of live frogs at the simulation start

Initial-moisture: How much moisture (%) frogs have at simulation start

WL-moisture: how much moisture (%) frogs recover if they move through a wetland

corn-speed: how fast frogs move through corn

grass-speed: how fast frogs move through un-grazed grass

grazed-speed: how fast frogs move through grazed grass

soy-speed: how fast frogs move through soy2

moisture-depleted-from-corn: how much moisture frogs lose while moving through corn

moisture-depleted-from-grass: how much moisture (%) frogs lose while moving through grass

moisture-depleted-from-grazed: how much moisture (%) frogs lose while moving through grazed

moisture-depleted-from-soy: how much moisture (%) frogs lose while moving through soy

corn-predators: number of predators in corn

grass-predators: number of predators in grass

grazed-predators: number of predators in grazed

soy-predators: number of predators in soy

show-moisture?: Switch that shows or hides current frog moisture (%) status

Monitors

frogs: counts the total number of frogs

OW frogs: counts frogs that have made it to the overwintering wetland

corn dess.: counts frogs that have died due to desiccation in corn

corn prey: counts frogs that have died due to predation in corn

soy dess.: counts frogs that have died due to desiccation in soy

soy prey: counts frogs that have died due to predation in soy

grazed dess.: counts frogs that have died due to desiccation in grazed

grazed prey: counts frogs that have died due to predation in grazed

grass dess.: counts frogs that have died due to desiccation in grass

grass prey: counts frogs that have died due to predation in grass

Things to notice

Observe the different monitors to see how many frogs have died in each land cover type and how many frogs have made it to the overwintering wetland. Notice how the number of frogs that die in each land cover change if the predator and desiccation rate sliders are adjusted. The higher the predator and desiccation rate in each cover type, the more likely a frog is to die by predation in that area.

Things to try

Leave all the predators rates set at the same number of predators in each cover type and try adjusting the desiccation rate sliders. Watch how many frogs die in each cover type. Now make the desiccation rates equal for each cover type and adjust the predator slider. You can try this with all of the sliders including wetland moisture. For example, if some wetlands dry during the season, maybe the moisture recovered should be less than 100%. You can this by lowering the %WL moisture so frogs gain less moisture when traveling through a wetland.

Extending the model

- Can add different land covers, or have current patches represent different land covers.
- The patches around the overwintering wetland should be changed to transparent or invisible.

- To change the crop type, you must go to code and change patch color. There could be an option to change how many patches of differing cover types.