BEHAVIORAL CHOICE AND DEMOGRAPHIC CONSEQUENCES OF WOOD FROG HABITAT SELECTION IN RESPONSE TO LAND USE

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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

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a candidate for the degree of Doctor of Philosophy

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BEHAVIORAL CHOICE AND DEMOGRAPHIC CONSEQUENCES OF WOOD FROG HABITAT SELECTION IN RESPONSE TO LAND USE

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ABSTRACT

Land use is a pervasive form of disturbance affecting natural systems on Earth. My dissertation research is set within the context of a large scale project referred to as Land-use Effects on Amphibian Populations (LEAP), where researchers in Maine, Missouri, and South Carolina are determining the effects of timber harvest on the persistence of amphibian populations.

The purpose of my dissertation research was to define adult wood frog non-breeding habitat in continuous oak-hickory forest and in response to timber harvest. I asked research questions that address the two components of habitat selection: 1) the behavioral choice, and 2) the demographic consequences of that choice.

To document behavioral choice, I allowed adults to move freely throughout the circular experimental timber harvest arrays (164 m radius) by using standard radio-telemetry techniques. Prior to timber harvest, I found that wood frogs were not distributed equally throughout oak-hickory forest. Adults used drainages as non-breeding habitat. In addition, the number of frogs that migrated to a specific drainage correlated with the distance between the pond and the drainage.

Following timber harvest wood frogs avoided clearcuts and increased movement rates in response to timber harvest. Further, I confirmed the consistency of this behavioral response by conducting experimental displacements and found that adults exhibit site fidelity to non-breeding habitat. Frogs displaced to the center of clearcuts evacuated the clearcuts in one night of rain and 20 of 22 frogs displaced back to the pond returned to the same drainage.

To determine demographic consequences, I estimated survival of frogs constrained within microhabitats. Desiccation risks for frogs located on forested ridgetops or in exposed areas within clearcuts were severe. Brushpiles within clearcuts provided microhabitats with similar desiccation risks as microhabitats within forested drainages.

I also determined survival of transmittered frogs that moved freely among microhabitats by radio-tracking 117 frogs over 3 years. I documented 29 predation events, 13 desiccation events, and 8 mortalities of unknown cause. Using Cox-proportional hazard models, I found that survival within the timber harvest array was 1.7 times lower than survival within continuous forest. Survival was lowest during the drought year of 2005 when all desiccation events occurred. My results indicated that predation and desiccation risks near the breeding ponds are ecological pressures that explain why adult amphibians migrate away from breeding habitat during the non-breeding season.

CHAPTER 1

THE INTRODUCTION

Tracy A. G. Rittenhouse

Why do I study wildlife habitat?

All ecological research today, regardless of the theoretical or applied nature of the research questions, is set within the context of mass species extinctions, a rapidly changing global climate, and the domestication of all wild places. Humans transform land to obtain resources including food, shelter, and commodities; however, this transformation is becoming a full fledged domestication, a monoculture of human habitat. We are now faced with the questions…Is a planet altered by human activities a place where wildlife can persist? Can humans persist? In addition to developing a greater understanding of the natural world, I believe that addressing these questions requires recognizing that the economy is a subsystem that exists within the constraints of biological realities (Daly & Farley 2004).

Our current economic system with the supporting governmental policies is deficient in the face of a world full of people (L. Krall, personal communication). We currently function as if economic growth is unlimited and yet two well established theories indicate that the assumptions of our economic models are not correct: the laws of thermodynamics and population dynamics of populations constrained by carrying capacity (Daly 1996). These theories indicate that the growth of our economy, defined as an increase in the human population and per capita consumption, occurs at the competitive exclusion of other species (Trauger et al. 2003).

Wildlife habitat contains the resources and environmental conditions that allow animals to occupy, survive, and reproduce within an area (Morrison et al. 1992). In my pursuit to understand the habitat requirements of amphibians, I strive to gain an understanding of factors required for local population persistence at a particular place. As scientists we strive for global relevance, but as ecologists we study places; those locations that contain a unique set of organisms and abiotic conditions that constrain ecological processes (Dale et al. 2000). In September 2007, John Wiens emphasize this point as part of a climate change symposium at The Wildlife Society meeting in Tucson, Arizona. The message from his talk was that conservation is about places. I believe that understanding the habitat requirements of local populations is one step towards the conservation of these places. Further, I believe that conserving places is needed for the persistence of wildlife as well as humans.

Land-use effects on natural systems

Disturbances, events that disrupt ecological systems, induce responses from individuals, populations, and/or communities. Although ecological communities are adapted to the rate and intensity of natural disturbances such as fire and hurricanes, the most pervasive form of disturbance affecting natural systems around the globe is land use or the purpose to which land is put by humans (Dale et al. 2000; Turner II & Meyer 1994). Most of the habitable surface of the earth was allocated to human use by the end of the 20th century. For example, the worldwide area of forested lands declined by 19%

between 1700 and 1980 (Richards 1990); in addition, the area currently used for human food production (i.e., cropland and pasture) covers approximately 40% of the land surface (Foley et al. 2005). This level of land cover change along with resulting changes to ecological processes and ecosystem function has led scientists to the consensus that land use impacts the ability of the Earth to provide the goods and services upon which humans depend, and thus ecological principles should be used to manage land use decisions (Dale et al. 2000). My dissertation research is set within the context of a collaborative NSF project referred to as Land-use Effects on Amphibian Populations (LEAP). The project contains four experimental manipulations that represent different intensities of land use to the terrestrial habitat surrounding amphibian breeding sites.

Overview of my dissertation research on amphibian habitat

My research stems from previous work initiated by my advisor that defined local amphibian populations based on the migration distances of individuals (Semlitsch 1998; Semlitsch & Bodie 2003). In essence he defined the amount of terrestrial habitat surrounding wetlands that is occupied by amphibians. I furthered this research by quantifying how individuals distribute themselves within this area (Rittenhouse & Semlitsch 2007). A new application of univariate density estimation allowed me to determine the intensity of use by different amphibian species at distances from 0 – 1000 m from wetland edges and revealed several over-arching patterns: 1) anurans use non-breeding habitat at much greater distances from wetlands than salamanders, 2) peak use of habitat for species in the eastern United States occurs near the wetland whereas peak use for species in the western United States may be skewed away from the wetlands, and

3) adult use of habitat immediately adjacent to wetlands (i.e., within 30 m) is low during the non-breeding season. Therefore, although habitat used by a local amphibian population extends hundreds of meters from wetlands, the intensity of use is not uniform within this area.

The fact that intensity of use differs throughout the extent of available habitat suggests that the area consists of a gradient of habitat quality (Franklin et al. 2000). High-quality habitat is identified as places where individuals survive and achieve high reproduction success (Van Horne 1983). Therefore, Wiens (1989) referred to the fitness potential of habitat, because these habitats produce individuals that contribute differentially to future generations. In addition, this gradient of habitat quality is likely altered in response to land use practices. Research questions related to land use often can be reduced to identifying the amount or intensity of land use that can be undertaken while allowing for the persistence of other species.

Amphibian research has begun to identify breeding habitat requirements, the extent of terrestrial habitat used by amphibians (Rittenhouse & Semlitsch 2007), and population responses to situations where land use truncates the extent of amphibian habitat (Harper et al. In Review). However, potential species-specific differences in non-breeding habitat use are unknown. The purpose of my dissertation research is to define adult wood frog non-breeding habitat in continuous oak-hickory forest and in response to land use. Timber harvest is the land use of interest in this case.

I approach this task by studying habitat selection of wood frogs. Habitat selection is defined as a hierarchical process of behavioral responses influenced by differential fitness of individuals which results in differential use of habitat (Jones 2001). The research questions I ask throughout my dissertation address the two components of habitat selection: 1) the behavioral choice, and 2) the demographic consequences of that choice.

In chapter 2, I describe adult wood frog habitat use prior to timber harvest. Habitat use is a quantification of where frogs occur after behavioral choices and the corresponding demographic consequences have occurred, and thus habitat use represents the result of habitat selection. In this chapter, I ask the question: Are adult wood frogs distributed evenly throughout continuous oak-hickory forest or clumped at a particular resource?

In chapter 3, my primary objective is to describe the behavioral response of wood frogs to LEAP timber harvest treatments applied to the forest surrounding the breeding ponds in Missouri. To document the behavioral choice, I allow adults to move freely throughout the experimental arrays by using standard radio-telemetry techniques. The behavioral response I observed was complete avoidance of clearcuts. This behavioral response was more extreme than the response observed in the LEAP arrays in Maine where wood frogs continued using clearcuts (S. Blomquist, personal communication).

Chapters 4 & 5 concern the demographic consequences and thus provide the physiological and ecological explanations for the extreme behavioral responses observed following timber harvest. The fourth chapter is cast within the context of migration. I argue that reduced survival may be an important cost of amphibian migration and thus provide survival estimates for a 64-day period following the breeding season. I demonstrate that survival consequences for adults moving freely throughout the timber harvest array consist of both predation and desiccation risks. Finally, in the fifth chapter

I control for predation and then investigate the physiological consequences (i.e., desiccation risks) of habitat choice by constraining juveniles to four microhabitats.

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CHAPTER 2

POST-BREEDING HABITAT USE OF WOOD FROGS IN A MISSOURI OAK-HICKORY FOREST

Tracy A. G. Rittenhouse and Raymond D. Semlitsch

Abstract

Fitness benefits to individuals from using a particular habitat during the non-breeding season are likely species- and habitat-specific. Our goal was to define the post-breeding habitat use of adult Wood Frogs (*Rana sylvatica*) within continuous oak-hickory forest in Missouri. We used radio-telemetry to determine if adult Wood Frogs are evenly spaced throughout this forest type or clumped at a particular resource. In addition, we determined microhabitat selection using conditional logistic regression that compares the microhabitat at frog locations to paired points located 2 m from the frog. Adult frogs migrated from breeding sites located on ridgetops into ephemeral, rocky ravines. Use of drainages by Wood Frogs depended on the distance between the breeding site and drainage, and the orientation of drainages relative to the pond edge influenced whether or not migratory paths of frogs are funneled or spaced apart. The most supported model of microhabitat selection indicated that frogs selected locations with increased leaf litter depth and air temperature, and with decreased humidity and light compared to paired points. Persistence of Wood Frog populations along the southwestern edge of their range requires successful annual migrations between breeding sites and forested drainages,

which are important non-breeding habitat for Wood Frogs in a Missouri oak-hickory forest.

Introduction

Pond-breeding amphibians use aquatic habitat for breeding and extensive amounts of terrestrial habitat during the non-breeding season to complete their complex life cycle (Semlitsch & Bodie 2003). Recent work has begun to highlight important habitat requirements of amphibians during the non-breeding season (e.g., Baldwin et al. 2006; Faccio 2003; Pilliod et al. 2002; Regosin et al. 2005; Sztatecsny & Schabetsberger 2005). Fitness potential of habitat, defined as the effect of habitat quality on individual survival and reproduction (Franklin et al. 2000), is essential for predicting the effects of habitat modification on population persistence. However, fitness benefits are likely species- and habitat- specific and behavioral plasticity may occur in wide-ranging species. Detailed studies of microhabitats used by amphibians within a particular vegetation community as well as mechanistic studies that link habitat use to population dynamics are needed to fully understand amphibian habitat requirements (Armstrong 2005).

The geographic range of Wood Frogs (*Rana sylvatica*) covers the eastern United States and Canada, with relic populations in the US Rocky Mountains and the Ozark region. Wood Frog populations occur within a wide variety of plant communities including deciduous oak-hickory forests, coniferous boreal forests, grassy meadows, aspen groves, and prairies, but they are largely absent from southeast coastal areas (Muths et al. 2005). The wide range indicates that Wood Frogs can live in vegetation communities consisting of either forests or grasslands depending on local weather conditions. As ectotherms amphibians are inherently linked to the microclimate conditions of their habitat (Feder & Burggren 1992). Vegetation structure can be as important as vegetation type or species, and habitat selection based on vegetative structure has been confirmed in other species (Griffin & Case 2001). In addition, habitat selection can change with environmental conditions; for example, Wood Frogs move from humus to leaves as substrate moisture decreases (Heatwole 1961; Patrick et al. 2006). The availability of refuge sites with moderate temperature and moisture levels is likely an important component of amphibian habitat selection during the non-breeding season (Bartelt 2000; Seebacher & Alford 2002). Identifying the structural features of the habitat that create preferred microclimates may facilitate comparison to other regions and thus improve our understanding of Wood Frog habitat use across its broad geographic range.

Our goal was to define the post-breeding habitat use of adult Wood Frogs within continuous oak-hickory forest in Missouri. The first objective was to determine if adult Wood Frogs are evenly spaced throughout this forest type or clumped at a particular resource. We used movement paths of radio-tagged frogs migrating from breeding sites to identify non-breeding habitat within the forest. The second objective was to determine if frogs select microhabitat during migration. We compared microhabitat variables at frog locations while the frog was present to microhabitat variables at paired points located 2 m from the frog. We develop a set of *a priori* models that test hypotheses regarding the relative importance of microclimate variation (e.g., soil temperature, relative humidity) and structural features of habitat (e.g., litter depth, percent canopy cover) and the relative importance of temperature and moisture in microhabitats used by Wood Frogs.

Methods

Study Site

The study was conducted at the Daniel Boone Conservation Area (DBCA), Warren County, Missouri, USA. DBCA is centered within a continuous tract of forest bordered by corn and soybean agriculture about 9 km to the north and by the Missouri River about 6 km to the south. The area contains mature, second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with sugar maple (*Acer saccharum*) beginning to establish in the understory (i.e., Outer Ozark Border Subsection as described by (Nigh & Schroeder 2002). Local relief (i.e., elevation change within 2.59 km^2) ranges from 46 – 76 m. Small, intermittent streams begin in DBCA and flow south towards the Missouri River, cutting through loess ridge tops and exposing limestone rock. Amphibian breeding sites are ponds that were constructed greater than 30 years ago on ridge tops as wildlife watering holes and were naturally colonized by a variety of amphibian species. We tracked Wood Frogs (*Rana sylvatica*) as they emigrated from three ponds located 375 – 1370 m apart (i.e., Pond 2 a.k.a. LEAP Pond 2, Pond 27 a.k.a. Teacup Pond, and Pond 5 a.k.a. LEAP Pond 5).

Radio-telemetry

We captured 6 female and 36 male Wood Frogs at three ponds during the two-day breeding period using hand captures and minnow traps. If transmitters could not be immediately attached upon capture, frogs were placed in enclosures (1 m X 2 m X 1 m) at the pond edge and held for less than 2 days. We attached 1.0 g transmitters (model BD-2 with whip antennae and 1 mm diameter tube; Holohil Systems Inc., Canada) using a belt constructed from 1 mm stretch bead cord (Mainstays Crafts, Sulyn Industries Inc.) (as in (Baldwin et al. 2006). Transmitter mass was on average 6.9 % of frog body mass. All frogs were fitted with transmitters on 6 or 7 March 2004 and released within 5 m of the pond edge. We relocated frogs during daylight hours for 50 consecutive days using a R2000 ATS receiver and yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). Upon homing to the frog, we obtained a visual sighting, carefully pulled out the whip antenna from beneath leaf litter, and placed a wire flag next to the frog. If the antenna was visible next to the flag upon subsequent relocations, we did not disturb the frog by obtaining a visual sighting. All movements greater than 10 cm were marked with a flag. Flags were later mapped with a compass and tape measure or GPS unit with submeter accuracy (Trimble Pathfinder Pro XL) and imported into Arcview (version 3.2; Environmental Systems Research Institute, Redlands, California, USA). For each frog, we calculated total distance traveled, net distance (i.e., straight line distance between first and last relocation), and maximum straight line distance traveled between daily relocations.

We analyzed the spatial distribution of frog locations at each pond using Ripley's *K* function (Ripley 1981; Venables & Ripley 2002) within the 'Spatial' library of program R (Ihaka & Gentleman 1996). Ripley's *K* quantifies spatial dependence between points at a range of spatial scales and is presented as a cumulative distribution function, $K(t)$, of the expected number of points within a given distance of a single point. The $K(t)$ function operates within a region D, the spatial extent of all points. We used $L(t)$, a square root transformation that linearized $K(t)$ and stabilized variance (Venables & Ripley 2002). We defined points as all frog locations at each pond. We calculated 95%

confidence envelopes by simulating 100 random point distributions where the number of points in each simulation was equivalent to the total number of frog locations at each pond. The domain for the simulated points was equivalent to the smallest dimension of D and was unique for each pond. We tested for non-random Wood Frog spatial distributions at each pond by comparing $L(t)$ to the 95% confidence envelopes. We classified the distribution as clumped if $L(t)$ fell above the simulated 95% confidence envelopes, uniform if it fell below the envelopes, and random if it fell within the envelopes.

Microhabitat

We collected microhabitat data at frog locations while the frog was present by placing probes within refugium as close to the frog as possible without actually touching the frog (i.e., within 8 cm). We also collected microhabitat data at three points paired to each frog location that were located 2 m from the frog. We placed the probes within the leaf litter as if a frog was present within the leaf litter. We chose the spacing of these points to determine if frogs select microhabitat within the last one to two jumps of migratory movements. One paired point was located 2 m from the frog in the direction from which the frog was previously located and two additional points were located 2 m from the frog at 90 degrees from the first direction (Cooper & Millspaugh 1999). We only collected microhabitat data at relocations spaced at least 5 m apart and we did not collect data at release points even if the frog remained there for several days. In addition, we only collected microhabitat data when frogs settled at a location for several days (i.e., periods without rain when the top layer of leaf litter was dry).

We collected 8 microhabitat variables, including soil temperature at 5 cm depth (Taylor Digital Pocket Thermometer), light at the surface of the leaf litter (silicone photovoltaic detector), air temperature and humidity within the refugium or leaf litter (Extech Hygro-Thermometer RH101), litter depth (ruler), canopy cover (spherical crown densiometer), diameter of coarse woody debris within 2 m, and percent ground cover (1 m^2 daubenmire frame). We classified coarse woody debris as no CWD, small CWD (i.e., presence of CWD 10 – 24 cm in diameter), and large CWD (i.e., presence of CWD greater than 25 cm in diameter). Approximately 85% of all ground cover was deciduous leaf litter with the remaining 15% being split between 6 other cover types (i.e., forbs/mosses, grass, fine woody debris, coarse woody debris, rock, bare soil); therefore, we used percent leaf litter as the ground cover variable.

We used conditional logistic regression to compare the microhabitat conditions at the frog location to the three paired points (i.e., unused locations), thus each strata (N = 100) was composed of 4 points. This logistic model uses data collected with a case-control sampling design; and thus we assume that used locations are rare within the habitat and paired locations were unused by frogs because we would have found frogs at these locations while collecting microhabitat data (Keating & Cherry 2004). We used an information-theoretic approach to determine support for models representing alternative hypotheses concerning Wood Frog microhabitat use (Burnham & Anderson 2002). We developed 4 *a priori* sub-global models to test whether frog locations were based on structural habitat features, microclimate variables, moisture conditions, or temperature conditions (Table 1). We further split the sub-global models into 8 *a priori* candidate models. In addition, we proposed a candidate model that contained variables suggested as being important within the physiological literature (Feder 1983; Jorgensen 1997; Seebacher & Alford 2002; Thorson 1955) and included a global model. We ranked the 14 *a priori* models and selected the best approximating model using the change in Akaike Information Criterion (ΔAIC) and Akaike weights (ω). We calculated odds ratios and 95% confidence limits for parameters in the most supported model to facilitate interpretation (Keating & Cherry 2004).

Results

Movements

We tracked 42 Wood Frogs for 42.6 ± 9.76 days. The belt attachment technique was both effective and efficient. None of the transmitters slipped, all frogs were fitted with belts within 2 days, and at the end of the study all transmitters were removed within 2 days. Abrasions were minimal but did gradually worsen over the 50 days, preventing us from replacing the first transmitter on each frog with a second transmitter.

We relocated frogs daily for a total of 1791 relocations (Appendix 1). Most of our relocations (i.e., 76.4%) verified that frogs did not move between locations (i.e., antenna in the exact same location as previous day). Frogs regularly spent 6 – 11 days at the same location and the maximum number of days at the same location was 24 days. When movements did occur, 56.5% of movements were less than 5 m and 17.9% of movements were greater than 20 m. Movements greater than 20 m occurred only 3.8% of the time and all corresponded with rain events. Frogs made migratory movements away from ponds on 24 and 25 March 2004 (mean total distance = 76.2 ± 62.3 m; max total distance = 248.9 m) during the first rain event post-breeding (total two-day rainfall =

5.1 cm; mean daily temperature = 16.1 C); therefore, as soon as an evening rainfall occurred frogs emigrated from breeding sites. We did not document any movement between ponds during the study period.

Macrohabitat

Wood Frogs made linear, directed movements from breeding sites located on ridge tops into ephemeral, rocky ravines (hereafter referred to as drainages) (Fig. 1). The $L(t)$ function for each pond fell above the 95% confidence envelopes, indicating that Wood Frogs had a clumped distribution at each pond. Wood Frogs were therefore not randomly or evenly spaced throughout the oak-hickory forest but clumped within drainages. Once frogs entered drainages, they did not return to a ridge top or move into different drainages during the 50 day study period. Frogs at Pond 5 directed movements towards the top of drainages (Fig. 1A). Movement paths for frogs at Pond 2 and Pond 27 were also directed towards drainages, but each frog directed its movement towards a slightly different part of the drainage (Fig. 1B and 1C). Notably, 17 frogs at Pond 5 migrated into the drainage to the southeast that begins approximately 30 m from the pond, 4 frogs migrated into the drainage to the west that begins approximately 70 m from the pond, and only 1 frog migrated into the drainage to the north that begins approximately 200 m from the pond (Fig. 1A).

Microhabitat

Prior to collecting microhabitat data, 93% of frogs were completely covered with leaf litter and we could see an eye or part of the body without moving any leaves for the remaining 7%. When we moved leaves after collecting microhabitat data to verify the location of the pelvic patch, 60% of frogs had their pelvic patch pressed against the soil and 40% of frogs were located within the leaf layer (i.e., pelvic patch on a leaf).

Clear separation occurred between the global model ($\omega = 0.9993$) and the other candidate models (Table 2), indicating support for the structural, microclimate, moisture, and temperature hypotheses. Frogs used locations with increased leaf litter depth and air temperature, and with decreased humidity and light compared to paired points located 2 m from frogs (Tables 3, 4). For example, odds ratios of coefficients indicate a 26% increase in the odds of a location being used by frogs for every 1 cm increase in litter depth and every 1 degree increase in air temperature (Table 3). In addition, frog locations were positively associated with small coarse woody debris but negatively associated with large coarse woody debris.

Discussion

All areas within oak-hickory forest were not used equally by adult Wood Frogs. Adult frogs migrated from breeding sites located on ridgetops into ephemeral, rocky ravines, indicating that these drainages are important non-breeding habitat for Wood Frogs in oak-hickory forests. Wood Frogs have previously been shown to use red maple forested wetlands or other wet forests during the summer (Baldwin et al. 2006; Regosin et al. 2005), but this habitat type and the associated sphagnum moss ground cover does not occur at our study site. Wood Frogs in Missouri used deciduous leaf litter. Leaf litter has a complex structure that prevents evaporative water loss (O'Connor et al. 2006) and has previously been shown to prevent water loss better than rock crevices, hollows under trees, or dense ground vegetation (Seebacher & Alford 2002).

Drainages may have been used by frogs during the spring and summer for a variety of reasons including the presence of refuge sites with appropriate microclimate conditions and abundant prey. Hydroregulation by frogs in terrestrial habitats involves absorbing water through the pelvic patch while sitting on moist substrates, because frogs constantly lose water across the skin into the air via evaporation (Heatwole & Lim 1961; Thorson 1955). Drainages likely facilitate the ability of frogs to regulate water by providing moist soil and cool temperatures. In a related experiment where water loss was measured simultaneously with both soil moisture and temperature, we found that survival of juvenile Wood Frogs held on ridge tops ranged from 7.5 – 11.8%, whereas survival within drainages ranged from 53.6 – 59.3%, indicating that mortality due to desiccation is reduced in drainages (Rittenhouse et al. In Review). In addition, drainages shade frogs from direct sunlight, shelter them from wind, and steep topography creates breaks in the leaf litter. We observed frogs completely covered with leaf litter but sitting in foraging postures when steep slopes created a gap out the side of the leaf litter. Finally, drainages with moist soil conditions may allow for increased invertebrate activity, thus increasing the probability of invertebrates approaching the sit and wait predator. Competition for food underlies habitat selection theories for birds and mammals (Fretwell & Lucas 1969; Jones 2001). Anurans seem to be less tied to food resources (Bartelt et al. 2004) because they are generalists that feed on invertebrates in proportion to their availability (Forstner et al. 1998). However, invertebrate mass within a habitat has been linked to anuran mass, indicating that prey availability can affect habitat quality (Sztatecsny & Schabetsberger

2005). The importance of prey availability in Wood Frog habitat selection warrants further investigation.

Our data suggest that use of drainages by Wood Frogs depends on the distance between the breeding site and drainage. Migrating between two spatially separated habitats presents a trade-off between the potential costs of migration and the potential fitness benefits of reaching non-breeding habitat of high quality. Migration costs include a large expenditure of energy for locomotion and exposure to visual predators. We did not investigate whether some drainages are higher quality habitat for Wood Frogs than other drainages; however, the three drainages at Pond 5 clearly differ in the number of frogs using the drainage. Intraspecific competition may be higher in drainages located near breeding sites compared to those located at greater distances due to the density of frogs within the drainage. Therefore, frogs that migrate to drainages far from breeding sites may experience high migration costs, but benefit from reduced intraspecific competition during the non-breeding season.

Our data also suggest that the orientation of drainages relative to the pond edge may influence how much terrestrial habitat is traversed by migrating frogs. When drainages were located at a perpendicular angle to the pond edge, as occurred at Pond 5, the movements of all frogs were directed towards the top of the drainage. In other words, frogs funneled through a small corridor of terrestrial habitat. When drainages were parallel to the pond edge, as occurred at Pond 2 and Pond 27, frogs radiated away from the pond in multiple directions and paths did not overlap as frequently. This pattern has been consistent among years (Rittenhouse, unpubl. data). Landscape configuration may therefore influence the degree to which habitat modification affects a local population.

Small scale timber harvest or development (e.g., one house) that occurs near a Wood Frog breeding site will likely affect adult breeding migrations. When drainages are perpendicular to the breeding site, the placement of the disturbance outside of movement corridors may minimize effects; whereas, habitat modification near breeding sites with parallel drainages may affect some proportion of the population regardless of placement.

Much to our surprise Wood Frogs remained in the exact same location for multiple days and did not make any daily foraging movements. We confirmed this result using thread-trailing tracking devices in following years (Rittenhouse, unpubl. data). However, daily telemetry relocations allowed us to observe hydrotactic movements within the leaf litter. Frogs sat high within the layers of leaves following rain events when litter was wet and moved lower within the leaves as the litter dried. By 3 to 4 days post rain when the top of the leaf litter was completely dry, approximately 60% of frogs would be sitting with their pelvic patch pressed against the soil. We observed on 13 occasions a frog sitting completely exposed on top of the leaf litter. All of these observations were on humid mornings immediately following rain. When we relocated these frogs either later the same day or the following day, frogs had moved less than 1 m and were under the litter, thus they were not migrating during daylight hours even when litter was wet.

Wood Frogs used deciduous leaf litter as microhabitat. Wood Frog microhabitat use in a Missouri oak-hickory forest therefore differs greatly compared to microhabitat use in more northern forests that contain sphagnum moss and humus (Baldwin et al. 2006). In addition, we found no indication that frogs choose to sit near shelter objects, such as coarse woody debris, rock outcrops, or any live vegetation. Although frogs did not use coarse woody debris greater than 25 cm in diameter, frog locations were positively associated with small pieces of coarse woody debris (i.e., 10 – 25 cm diameter). We did not quantify fine woody debris (i.e., < 10 cm diameter), but small sticks may provide important structure within the leaf litter layer.

Our most supported microhabitat model indicated that frogs used locations with increased leaf litter depth; however, we did not observe frogs seeking out the deepest litter in the forest, such as a leaf pile next to a rock or other object. We believe that the relationship between use and litter depth may not be linear, with frogs using moderate litter depths of approximately 6 cm. Frogs used humid locations (mean humidity = 76.3%) but humidity at frog locations was lower than paired locations. Explanations that incorporate the association with increased litter depth and decreased humidity include frogs using locations where leaves are less tightly packed or frogs pushing leaves apart when entering the litter. Space between the leaves may allow for air movement (i.e., reduced humidity levels) and may also increase access to invertebrates moving through the litter. Microhabitat use may therefore reflect the need to maintain hydration levels while also obtaining foraging opportunities. Increased digestion rates at warmer temperatures along with high evaporation and radiation rates when in direct sunlight likely explain the positive association of frogs using locations with low light levels and yet warm soil temperatures (Feder & Burggren 1992).

Conservation of pond-breeding amphibian populations requires the maintenance of both breeding and non-breeding habitat and the successful migration of individuals between these spatially separated habitats (Baldwin et al. 2006; Semlitsch 2000). Drainages within oak-hickory forest are a landscape feature of the habitat that allows for microclimate conditions within the leaf litter that serve as non-breeding habitat for Wood Frogs during the spring and summer. The persistence of Wood Frog populations along the southwestern edge of their range therefore requires successful annual migrations between breeding sites and drainages. Our data suggest that any attempts to enhance or create Wood Frog breeding sites within this portion of the range should consider the proximity and landscape configuration of breeding sites and forested drainages.

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Table 1. Fourteen *a priori* models of Wood Frog microhabitat selection at DBCA in Warren County, Missouri. Models were developed based on eight variables, including litter depth (litter), 3 categories of course woody debris (CWD), percent canopy cover (canopy), % leaf cover (leaves), % relative humidity (humidity), air temperature (airtemp), soil temperature (soiltemp), light (light). The global model contained all 8 variables.

Model Name	Variables
1. Structure	litter, CWD, canopy, leaves
2. StructureA	litter, CWD, leaves
3. StructureB	canopy
4. Microclimate	humidity, airtemp, soiltemp, light
5. ClimateA	humidity
6. ClimateB	light, airtemp, soiltemp
7. Moisture	litter, leaves, CWD, humidity
8. MoistA	litter, humidity
9. MoistB	leaves, CWD
10. Temperature	canopy, CWD, airtemp, soiltemp, light
11. TempA	canopy, soiltemp, light
12. TempB	CWD, airtemp
13. Literature	litter, humidity, soiltemp, light
14. Global	litter, CWD, canopy, leaves, humidity, airtemp, soiltemp, light

Table 2. Conditional logistic regression models ranked by AICc to test alternative models of Wood Frog microhabitat use in a Missouri oak-hickory forest. Models with low AICc and high Akaike weight (ω) have more substaintial support.

Model	k	AICc	ΔAICc	ω
Global	9	191.649	0.000	0.9993
Literature	4	207.039	15.390	0.0005
Microclimate	4	208.366	16.717	0.0002
MoistA	2	211.647	19.998	0.0000
Moisture	5	215.475	23.827	0.0000
ClimateB	3	216.300	24.651	0.0000
Temperature	6	219.113	27.464	0.0000
TempB	3	227.478	35.829	0.0000
ClimateA	1	229.855	38.207	0.0000
Structure	5	242.888	51.239	0.0000
StructureA	4	244.167	52.519	0.0000
TempA	3	247.109	55.460	0.0000
StructureB	1	253.983	62.335	0.0000
MoistB	3	258.256	66.607	0.0000

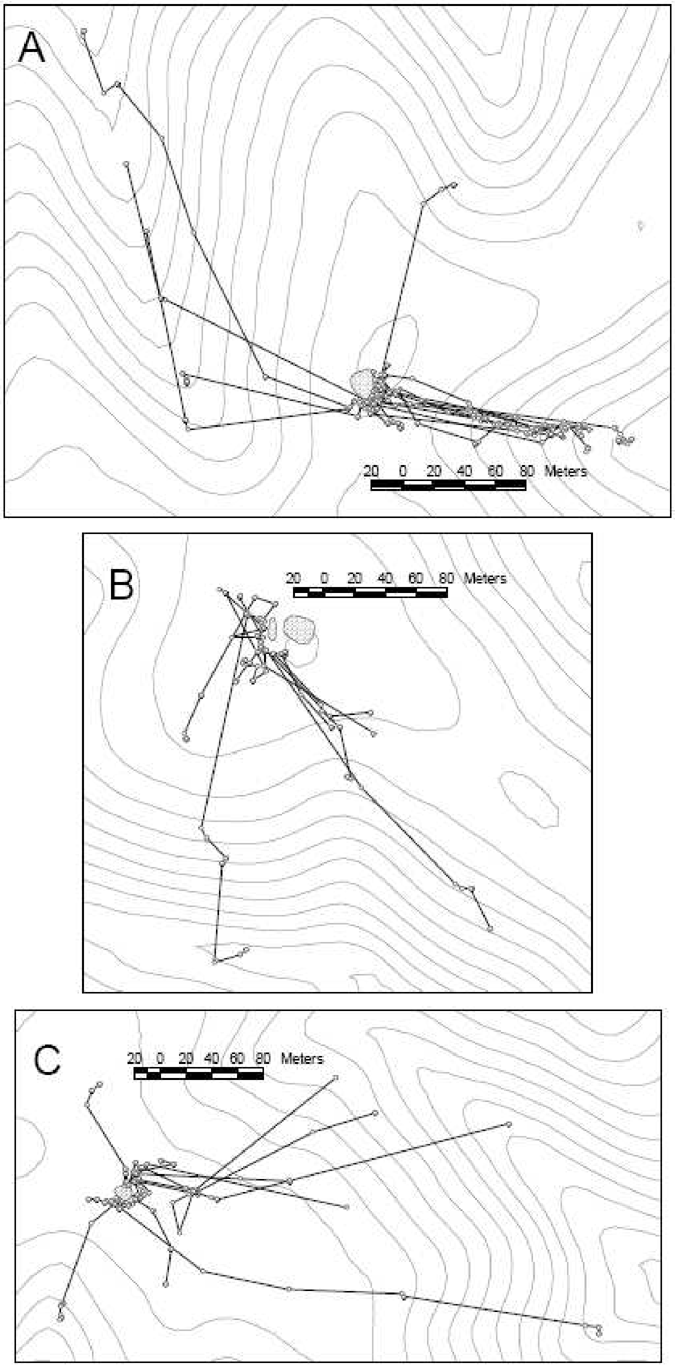
Table 3. Parameter estimates (coefficients and standard error), odds ratios, and 95% confidence limits from the most supported model explaining microhabitat conditions at frog locations in a Missouri oak-hickory forest.

						95% Confidence Limit	
Variable	Estimate	SE	Wald χ^2	P value	Odds Ratio	Lower	Upper
litter	0.234	0.081	8.428	0.004	1.264	1.079	1.480
humidity	-0.081	0.025	10.938	0.001	0.922	0.879	0.968
airtemp	0.237	0.077	9.523	0.002	1.267	1.090	1.473
light	-27.297	11.789	5.362	0.021	<0.001	<0.001	0.015
soiltemp	0.227	0.212	1.149	0.284	1.255	0.829	1.900
cwd small	0.405	0.340	1.415	0.234	1.668	0.624	4.455
cwd large	-0.298	0.528	0.318	0.573	0.826	0.153	4.468
pctcanopy	0.040	0.029	1.844	0.175	1.040	0.983	1.102
leaves	0.008	0.009	0.825	0.364	1.008	0.990	1.027

Table 4. Microhabitat characteristics of locations used by Wood Frogs and paired unused locations.

	Used by Frogs				Unused Locations			
Variable	Mean	Std Dev	Min	Max	Mean	Std Dev	Min	Max
litter (cm)	5.94	1.725	1.000	11.000	5.18	2.035	0.000	11.000
humidity (%)	76.31	14.375	34.200	95.100	80.48	12.366	33.600	96.600
airtemp (C)	53.09	11.881	30.800	97.100	51.45	10.661	30.500	85.600
light	0.32	0.037	0.225	0.388	0.33	0.033	0.244	0.410
soiltemp (C)	48.76	4.554	40.500	57.400	48.73	4.602	39.400	59.000
pctcanopy (%)	88.81	8.305	62.500	100.000	87.62	7.746	62.500	100.000
leaves (%)	85.90	16.227	20.000	100.000	83.60	20.695	0.000	100.000

Figure 1. Movement paths for 17 Wood Frogs at Pond 5 (A), 13 Wood Frogs at Pond 2 (B), and 12 Wood Frogs at Pond 27 (C). Frogs migrated from breeding sites located on ridge tops at the DBCA in Warren County, Missouri and into drainages that were used as non-breeding habitat. Each black line represents a movement path of one frog and was created by drawing a straight line between daily relocation points (i.e., open circles). Note that frogs did not migrate out ridge tops and that frogs at Pond 5 entered the top of the drainage with 1 frog migrating into the drainage to the north of the breeding site, 4 frogs migrating into the drainage to the west, and 12 frogs migrating to the closest drainage to the east.


A
20 0 20 40 60 80 Meters
B
20 0 20 40 60 80 Meters
C
20 0 20 40 60 80 Meters

Appendix 1. Summary of Wood Frog movements. We report the number of radio relocations (relocations), number of spatial locations where a frog was relocated (frog locations), total distance traveled (TotDis), straightline distance between first and last frog location (NetDis) and maximum straightline distance traveled in one day (MaxSMov).

ID	Sex	Pond	Mass (g)	SVL (mm)	relocations	frog locations	TotDis (m)	NetDis (m)	MaxSMov (m)
1.467	x	2	14.50	61	13	2	0.82	0.82	0.82
1.008	y	2	17.50	59	46	14	275.91	216.01	144.01
1.030	y	2	17.00	61	48	13	134.41	92.24	61.25
1.060	y	2	14.00	53	8	3	0.21	0.21	0.21
1.080	y	2	17.75	57	46	9	253.92	245.12	120.57
1.119	y	2	15.50	59	41	8	74.32	24.44	29.47
1.267	y	2	13.50	55	48	7	181.55	99.63	83.95
1.301	y	2	16.75	56	48	11	53.14	15.66	13.49
1.32	y	2	15.75	55	48	9	28.75	27.83	14.97
1.34	y	2	12.00	51	47	4	87.7	79.74	59.96
1.388	y	2	14.00	55	47	8	103.79	94.41	34.45
1.427	y	2	14.25	54	34	6	60.27	58.63	29.67
1.483a	y	2	11.00	51	27	2	0.24	0.24	0.24
1.100	y	2.5	16.00	57	48	9	320.12	289.29	237.67
1.149	y	2.5	17.00	58	48	9	218.96	194.39	101.62
1.170	y	2.5	13.25	53	47	5	81.29	67.77	33.59
1.189	y	2.5	18.00	60	48	9	118.8	85.71	58.06
1.209	y	2.5	15.50	58	48	8	33.93	31.38	17.77
1.229	y	2.5	15.75	58	48	9	86.98	21.93	32.66
1.483	y	2.5	13.75	55	18	4	171.96	167.24	159.18
1.518	y	2.5	14.50	58	47	12	408.03	393.34	143.11
1.538	y	2.5	18.50	60	38	10	147.84	132.26	79.96
1.559	y	2.5	12.50	51	44	12	130.39	47.50	38.19
1.571	y	2.5	13.25	54	47	14	110.54	103.87	66.14
1.467a	y	2.5	12.75	52	33	8	29.56	10.78	8.06
1.220	x	5	13.25	60	46	12	159.98	107.22	117.76
1.261	x	5	17.50	66	47	16	182.33	165.66	124.15
1.289	x	5	15.00	62	46	16	146.27	135.05	34.37
1.309	x	5	20.50	66	45	13	111.25	97.46	38.81
1.448	x	5	14.00	61	46	14	121.2	90.32	40.79
1.020	y	5	12.50	51	48	17	94.54	1.02	15.29
1.049	y	5	14.50	53	33	12	187.19	120.37	68.01
1.069	y	5	16.75	57	46	13	138.09	120.80	61.78
1.088	y	5	11.75	57	47	11	331.38	297.35	103.82
1.110	y	5	12.00	52	46	6	242.82	173.12	125.03
1.140	y	5	12.75	53	47	14	62.98	13.86	20.24
1.160	y	5	15.25	57	47	6	250.62	223.10	150.28
1.181	y	5	14.00	55	47	13	160.85	131.66	110.2
1.198	y	5	15.50	57	47	7	147.19	140.80	122.04
1.328	y	5	10.50	51	46	19	99.94	79.92	37.96
1.379	y	5	10.50	53	46	14	133.77	113.60	116.18
1.400	y	5	11.75	51	46	14	172.62	149.85	115.15

CHAPTER 3

BEHAVIORAL RESPONSE OF MIGRATING WOOD FROGS TO EXPERIMENTAL TIMBER HARVEST SURROUNDING WETLANDS

Tracy A. G. Rittenhouse and Raymond D. Semlitsch

Abstract

The behavioral responses of amphibians to timber harvest may be species-specific and may vary based on other factors in addition to canopy cover removal. To determine the behavioral response of adult wood frogs to timber harvest, we conducted experimental timber harvest within 164 m of replicate breeding sites, followed freely moving frogs throughout the timber harvest arrays using radio-telemetry, and tested the repeatability of the response by conducting two displacements. We found no evidence that wood frogs in Missouri use clearcuts as habitat. Although we were unable to verify if frogs traveled through or around clearcuts, timber harvest did not alter the location frogs migrated to for non-breeding habitat, as frogs reached drainages and traversed similar distances (i.e., total distance and net distance from pond) before and after timber harvest. The rate of travel (i.e., maximum distance traversed in one day) increased following timber harvest. Frogs released near the pond and those displaced to the center of clearcuts exited the entire timber harvest array in a single rainy night. Finally, wood frogs exhibited site fidelity to non-breeding habitat. When we displaced frogs back to the breeding ponds, 20 of 22 frogs returned to the same drainage that they had previously

migrated towards. We suggest that negative effects of timber harvest on amphibians may be minimized through the use of small timber harvests placed in locations that do not separate breeding and non-breeding habitat.

Introduction

Habitat selection is defined as a hierarchical process of behavioral responses influenced by disproportionate survival and fitness of individuals which results in differential use of habitat (Block & Brennann 1993; Hutto 1985; Jones 2001). The two components of this process, the behavioral choice and the demographic consequences of that choice, can be used to understand how species respond to changes in land use and management. For example, three hypotheses were recently posed for explaining why amphibian abundance often declines following timber harvest, which includes one demographic mechanism (i.e., direct mortality) and two behavioral mechanisms (i.e., retreating underground or evacuating off site; Semlitsch et al. 2008). Amphibians experimentally constrained within harvested stands have reduce survival relative to control stands (Harper & Semlitsch In Review; Todd & Rothermel 2006), with sources of mortality including fire ants (Todd et al. 2007) and desiccation (Rittenhouse et al. In Review; Rothermel & Luhring 2005). Although reduced survival can be a consequence of staying within recently harvested stands, behavioral research is required to determine when and how individuals may be exposed to these consequences.

The behavioral responses of amphibians to timber harvest may vary from complete avoidance of open canopy areas to extensive use of these areas. For example, spotted salamanders halted migration on approach to a forest-grassland edge and did not find the forested habitat on the other side of the breeding site (Rittenhouse & Semlitsch 2006). Further, both frogs and salamander evacuated recent clearcuts in Missouri, with an estimated 8.7 – 30 % of the breeding population of salamanders exiting the clearcuts (Semlitsch et al. 2008). In contrast, captures of amphibians at drift fences placed within harvested stands verify that avoidance of open canopy areas is not complete (Patrick et al. 2006; Todd & Rothermel 2006). Further, western toads monitored with radio-transmitters used slash piles along the edges of clearcuts (Bartelt et al. 2004) and gray treefrogs preferentially oviposited in artificial pools placed on the clearcut side as opposed to the forested side of edges (Hocking & Semlitsch 2007). The range of behavioral responses documented based on these studies suggests that the behavioral response may be species-specific and may vary based on other factors in addition to canopy cover removal.

We previously demonstrated that wood frogs in Missouri breed in ponds located on ridge tops and summer in rocky ravines with flowing water following large rain events (Rittenhouse & Semlitsch 2007). To determine the behavioral response of wood frogs to timber harvest, we conducted experimental timber harvest surrounding replicate breeding sites and followed freely moving frogs throughout the timber harvest array using radio-telemetry. Our objectives were to determine if adult wood frogs respond to timber harvest by 1) selecting alternative summer habitat other than the ravines used prior to harvest, 2) increasing distances traveled due to movements around as opposed to through harvested stands, or 3) changing the rate of travel while migrating away from breeding sites. In addition, we experimentally tested the repeatability of this behavioral response by displacing frogs back to the breeding site following an initial migration away from breeding sites and displacing frogs to the center of the timber harvest treatments.

Methods

Description of Study Site and Timber Harvest Treatments

We conducted this study at the Daniel Boone Conservation Area (DBCA; 1,424 ha), Warren County, Missouri, USA. DBCA contains mature, second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with sugar maple (*Acer saccharum*) beginning to establish in the understory (i.e., Outer Ozark Border Subsection as described by (Nigh & Schroeder 2002). Amphibian breeding sites are ponds constructed 27 – 47 years ago on ridge tops as wildlife watering holes that were naturally colonized by a variety of amphibian species (Hocking et al. In Review).

We conducted experimental timber harvest in summer and fall of 2004 surrounding four replicate amphibian breeding ponds as part of the NSF Collaborative Project "Land-use Effects on Amphibian Populations" (LEAP). Timber harvest arrays consisted of four forestry treatments: clearcut with high levels of coarse woody debris (High-CWD), clearcut with less CWD (Low-CWD), partial canopy removal, and control forest. Each array was circular with a 164 m radius, centered on a pond, divided into four equal quadrants (~2.11 ha each), and a forestry treatment was randomly applied to each quadrant with the condition that the control and partial were opposite of each other. All marketable timber greater than 25 cm in diameter at breast height was removed for sale in the two clearcut treatments. High-CWD treatments had the remaining trees (< 25 cm DBH) felled and left on the ground. Low-CWD treatments had the remaining trees girdled and left standing to reduce the CWD on the ground available to amphibians. Partial harvest treatments were thinned to a basal area of 5.6 m^2 per hectare or approximately 60% stocking level by girdling or felling poor quality trees and undesirable species (primarily *Acer saccharum*). Control treatments were not experimentally manipulated and more information can be found in (Semlitsch et al. 2008). Data reported here was collected within 2 of the 4 replicate arrays (i.e., Pond 2 and Pond 5), which are located 1200 m apart.

Data Collection

We radio-tracked adult wood frogs in 2004 (n = 42), 2005 (n = 46), and 2006 (n = 26) as they migrated away from Pond 2 or Pond 5 following the breeding season. Additional information from the pre-harvest year of 2004 not provided in this manuscript can be found in Rittenhouse and Semlitsch (2007). We captured frogs at the ponds by hand and using minnow traps in 2004 and drift fences with pitfall traps in 2005 and 2006. We attached transmitters (model BD-2 with whip antennae and 1 mm diameter tube; Holohil Systems Inc., Canada) weighting 1.0 g or approximately 7% of average frog body mass by using a belt constructed from 1 mm stretch bead cord (Mainstays Crafts, Sulyn Industries Inc.) (as in Baldwin et al. 2006; Rittenhouse & Semlitsch 2007). Within a given year most frogs were fitted with transmitters within a 3 – 4 day period. If transmitters could not be immediately attached upon capture, we placed frogs in enclosures (1 m X 2 m X 1 m) at the pond edge for less than 2 days.

Frogs were released within 5 m of the pond edge in 2004 and 2005. Frogs were experimentally displaced to the center of the timber harvest treatments in 2006 and thus frogs were released approximately 80 m from the pond edge in this year only. On 4 April 2005, we conducted an experimental displacement just prior to a forecasted evening rain event. We displaced frogs from their current location back to the original release location near the pond.

We located frogs daily during daylight hours for the life of the transmitters (approximately 50 days) using a R2000 ATS receiver and yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). Upon homing to the frog, we obtained a visual sighting, carefully pulled out the whip antenna from beneath leaf litter, and placed a wire flag next to the frog. If the antenna was visible next to the flag upon subsequent relocations, we did not disturb the frog by obtaining a visual sighting. All movements greater than 10 cm were marked with a flag. Flags were later mapped with a compass and tape measure or GPS unit with submeter accuracy (Trimble Pathfinder Pro XL or Trimble Geo XT) and imported into Arcview (version 3.2; Environmental Systems Research Institute, Redlands, California, USA).

Analysis

We calculated several movement parameters for each frog, including total distance traveled (TotDis: sum of distances between successive relocations, net distance (NetDis: straightline distance between first and last relocation), and maximum straight-line distance traveled in one day (MaxSMov). We chose 20 m from the pond as the criteria for determining if frogs had begun migration away from the pond (Madison 1997), and thus we only included frogs that migrated greater than 20 m in all analyses. Mortality due to predation or desiccation was the primary reason frogs did not reach 20 m within the tracking period (Rittenhouse et al. In Prep). We used analysis of variance to test for effects of sex, year, and sex interacting with year on these three movement parameters. We used log-likelihood ratios to test if the number of relocations within quadrants and the number of frogs evacuating quadrants differed among quadrants. We used linear regression to correlate the bearing between the first and last location prior to displacement with the first and last location following displacement in 2005.

Results

In 2005 and 2006, the number of frog relocations in each treatment were not equal (n = 427 in control, n = 412 in partial, n = 230 in CWD-high, and n = 185 in CWD-low ($\chi^2_{0.05, 3}$ = 32.87, P < 0.001) and 310 relocations were outside of the timber harvest array. In 383 of the 415 relocations in the two clearcut treatments, frogs were within a few meters of the release point (Figure 1); therefore, relocations of frogs in clearcuts were a result of us placing frogs in clearcuts. In only two occasions, frogs remained in a clearcut following a large movement. One frog (ID 2379) spent 17 days in a clearcut after moving 60 m into the center of High-CWD and one frog (ID 2228) entered 15 m into Low-CWD (Figure 1a). We believe that the lack of relocations in the two clearcuts is because frogs avoided clearcuts.

Following displacement back to the ponds in 2005, 20 out of 22 frogs moved towards the same drainage for a second time (Figure 2). The two frogs (ID 2538, 2261) that switched drainages were at pond 5 (Figure 2b). Several frogs returned to within meters of their location prior to displacement during the one night of rain (e.g., ID 2809, 2759, 2427, 2289). The bearing between first and last location prior to displacement was strongly correlated with the bearing between first and last location following displacement (df = 1, F = 27.47, $P < 0.001$, $R^2 = 0.5787$; Figure 3).

The displacement to the center of the treatments in 2006 did not prevent frogs from reaching the drainages (Figure 1b and 1d). Aside from small movements (< 5m) near the release point, surviving frogs displaced into the two clearcut treatments exited the quadrants during one night of rain; whereas, frogs displaced to the partial or control treatments did not exit the quadrants during one night of rain ($\chi^2_{0.05, 2} = 6.744$, $P < 0.025$). Further, six frogs released in the clearcuts moved into the control or partial; whereas, zero frogs moved from control or partial into the clearcuts. The release point in the center of the clearcut was approximately 80 m from closed canopy in three directions; however, movements were directed towards drainages rather than the closest forest (Figure 1b and 1d) and frogs did not move towards drainages by simply traveling downhill. For example, a frog (ID 3960) displaced to the center of Low-CWD went to the southeast drainage where the majority of the breeding population spends the summer (Rittenhouse & Semlitsch 2007) as opposed to downhill drainage located to the north (Figure 1d). Further, the bearing for the movement paths of three frogs displaced to the High-CWD was approximately 164° (Figure 1b). These frogs initially traveled uphill as opposed to downhill into the drainage located 262° from the release point.

We found no effects of sex and year on total distance ($F_{5, 77} = 0.42$, $P = 0.8362$) or net distance ($F_{5, 77} = 0.78$, $P = 0.5641$) (Table 2). However, maximum single movement in a one day period differed based on both sex ($F_{1, 77} = 3.91$, $P = 0.0514$) and year ($F_{2, 77} = 2.90$, $P = 0.0609$), with Tukey pair-wise comparisons indicating a significant difference between 2004 and 2005, with 2006 being intermediate (Figure 4). Although only statistically significant for MaxSMov, males tended to move greater distances than females during the 50 day tracking period immediately following the breeding season (Figure 5).

Discussion

Habitat selection consists of a behavioral choice and a demographic outcome of that choice (Jones 2001). Our results reveal the behavioral response of radio-transmittered wood frogs within experimental timber harvest surrounding ponds in Missouri. Timber harvest within 164 m of ponds did not prevent frogs from reaching ravines that serve as non-breeding habitat, nor did timber harvest alter which ravines were used as non-breeding habitat. Total distance and net distance traveled during the 50 day tracking period were also similar before and after timber harvest. However, we found no evidence of frogs actively using clearcuts as habitat. Further, the increased mean maximum single movement in one day indicates that the rate of travel increased following timber harvest as frogs evacuated the entire harvest array during one night of rain. Although we were unable to verify if frogs traveled through or around clearcuts, we conclude that timber harvest surrounding the breeding sites did not alter the non-breeding habitat frogs migrated to for non-breeding habitat, but timber harvest increased the rate of travel.

Wood frog use of clearcuts as habitat varies regionally. Our movements paths based on daily relocations demonstrate that adults do not use clearcuts in Missouri. In contrast, results from both drift fences (Patrick et al. 2006) and radio-telemetry (S. Blomquist, personal comm.) demonstrate that wood frogs in Maine travel through clearcuts and use moist areas within clearcuts as habitat during the spring. This range of behavior displayed by wood frogs suggests that the demographic consequences of using recently harvested stands vary regionally. We estimated that survival in Missouri was 1.7 times lower while transmittered frogs were within the circular timber harvest array compared to survival prior to timber harvest (Rittenhouse et al. In Prep). Although western toads have been shown to use brush piles within clearcuts (Bartelt et al. 2004) and these microhabitats reduce desiccation risks when wood frogs are constrained within these microhabitats (Rittenhouse et al. In Review), we found no evidence in our study that wood frogs seek out brush piles within clearcuts. Even when we displaced frogs to the center of clearcuts frogs did not utilize brush piles for conserving moisture. Avoiding recently harvested stands may be an adaptive behavior for frogs in Missouri due to increased mortality risks in clearcuts. We suggest that the degree of behavioral response to land use may be more extreme on the edge of the species range (e.g., in Missouri where conditions are relatively dry) relative to other parts of the species range (e.g., in Maine where clearcuts have more standing water than control forest (Patrick et al. 2006)).

Our results support the evacuation hypothesis for explaining reduced amphibian abundance on clearcut plots following timber harvest, which was recently revealed for a several pond-breeding species (Semlitsch et al. 2008). We found that wood frogs did not use the clearcuts when size and placement of the timber harvest allowed frogs to avoid clearcuts. However, the randomization of the harvest treatments resulted in a configuration where most frogs could travel in fairly straight lines from the ponds to the drainages without entering either of the clearcut treatments. When we displaced frogs to the center of the treatments to ensure frogs encountered the clearcuts during migration, frogs exited the clearcuts during the first rain event, further supporting the evacuation hypothesis. In addition to evacuating quickly, the displacement verified that frogs orient movements towards summer habitat as opposed to the closest location with closed canopy and that a displacement of 80 m did not hinder the ability of adults to return to non-breeding habitat.

Many pond-breeding amphibians are known to be philopatric to breeding sites (Gamble et al. 2007; Marsh et al. 2000; Watters & Kats 2006). Approximately 80% of wood frog metamorphs returned to natal wetlands as breeding adults and nearly all adults that breed multiple times are faithful to breeding sites (Berven & Grudzien 1990; Vasconcelos & Calhoun 2004). However, in some situations where wetlands are in close proximity adults may switch ponds based on the presence of predator or competitors (Petranka & Holbrook 2006). Our displacement results indicate that amphibians also exhibit site fidelity to non-breeding habitat. Ninety percent of the wood frogs we displaced back to ponds moved towards the drainage to which they migrated prior to displacement. Compass orientation is well known in amphibians (Sinsch 1990) and was likely the homing method used to return to a known target. Our results suggest frogs were able to adjust their compass to account for the 80 m displacement but this short distance displacement does not confirm true navigation abilities. Previous indications of site fidelity to non-breeding habitat included adult newts migrating in the same direction following displacement back to the breeding site (Jehle 2000), mark-recapture studies of wood frogs in a peat bog during the summer (Bellis 1965) and gray treefrogs in foraging habitat (Johnson et al. 2007), and emigration towards favorable non-breeding habitat (Jenkins et al. 2006; Marty et al. 2005; Rittenhouse & Semlitsch 2006). Site fidelity can indicate that resources are limiting and that search behavior to locate additional resources is risky. Density-dependence in terrestrial habitat that affects growth and survival for juvenile wood frogs (Harper & Semlitsch 2007) is an additional indication that non-breeding habitat can be an essential but limiting resource.

Our results also indicate that the migratory movements of frogs were not limited by energy stores. The short breeding season of wood frogs has been explained based on energy reserves because male frogs begin the breeding season with enough stored energy (i.e., glycogen) to call for 5 hours per night for 5 nights (Wells & Bevier 1997). After breeding, wood frogs in Missouri migrate away from breeding sites during the first rain event. When we displaced frogs back to the pond, we hypothesized that the remaining energy reserves may prevent frogs from evacuating the clearcuts in a single night and thus determine if frogs could travel through or around the clearcuts. However, most frogs traveled the 164 m distance a second time and were relocated on the opposite side of the clearcuts the following morning. Frogs that migrated less than 164 m were relocated in control or partial forested quadrants the following morning. These results indicate that frogs were unwilling to stop while within clearcuts and were motivated to find forested ravine habitat. The ability to make these migratory movements a second time after displacement may have resulted from wood frogs leaving the breeding site prior to expending all energy reserves or successfully obtaining prey during the migratory period.

We conclude that wood frogs in Missouri behaviorally avoided clearcuts in their migrations from breeding to non-breeding habitat and our two experimental displacements confirmed the consistency of this behavioral response. Wood frogs successfully migrated from breeding to non-breeding habitat through the timber harvest array, but these findings depict short-term behavioral responses. Long term effects of sustaining high movement rates for multiple breeding seasons are unknown and amphibians require long, slow rain events as opposed to short downpours to accomplish these single long-distance movements. In addition, our results suggest that the size and placement of clearcuts may influence the behavioral response, with larger stands leading to further increases in distances traversed and risk of mortality. However, the maximum distance frogs are able to traverse in a single night is also unknown: we observed a maximium daily distance of 332 m. Finally, although clearcuts in our study did not prevent adults from migrating away from breeding sites, our results may not be applicable to migrating juveniles, which are vulnerable to desiccation due to small size and also an important life stage for population regulation.

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Table 1. Net distance (m) and bearing (° with 1 as north, 90 as east, 180 as south, 270 as west) between the first and last relocations prior to displacement (1) and following displacent (2) back to the pond in 2005.

Pond	ID	Netdis1	Netdis2	Bearing1	Bearing2
2	2020	169.36	18.31	14.92	62.52
2	2100	191.62	124.34	36.26	46.37
2	2189	240.00	72.11	1.48	35.34
2	2198	375.59	43.98	341.92	42.70
2	2228	281.93	130.27	293.07	295.76
2	2289	214.21	203.34	235.80	243.59
2	2320	156.66	102.05	234.35	274.06
2	2379	65.22	11.44	231.07	214.37
2	2427	239.57	233.28	214.12	215.43
2	2621	69.41	10.39	66.96	89.65
5	2070	122.20	85.64	338.30	331.58
5	2109	139.44	0.00	158.73	0.00
5	2149	136.98	99.10	338.12	333.60
5	2160	120.93	8.14	347.75	240.59
5	2261	224.30	160.89	75.71	137.63
5	2301	348.69	135.87	110.79	152.65
5	2328	113.78	20.93	174.61	183.07
5	2538	203.74	185.89	136.22	73.24
5	2720	282.74	56.15	126.75	180.87
5	2759	45.49	29.91	341.88	348.72
5	2809	213.55	199.85	62.09	62.30
5	2910	180.05	98.08	352.48	351.71

Table 2. Analysis of variance results testing the effects of year (2004, 2005, 2006), sex and the interaction of year and sex.

Response Variable	Source of Variation	DF	MS	F-value	P-value
	year	2	3746.51	0.46	0.631
NetDis	sex	1	6397.94	0.79	0.376
	year*sex	2	4659.24	0.58	0.564
	error	77	622274.84	8081.49	
	year	2	2525.37	0.28	0.759
TotDis	sex	1	5912.22	0.65	0.423
	year*sex	2	1820.51	0.20	0.819
	error	77	701467.87	9109.97	
	year	2	13133.09	2.90	0.061
MaxSMov	sex	1	17712.98	3.91	0.051
	year*sex	2	2925.09	0.65	0.527
	error	77	348396.5065	4524.63	

Figure 1. Movement paths for all wood frogs that traveled greater than 20 m at Pond 2 in 2005 (A), Pond 2 in 2006 (B), Pond 5 in 2005 (C), and Pond 5 in 2006 (D). Movement paths begin near the ponds in 2005 and only represent movements prior to displacement. Movement paths begin in the center of the treatments in 2006 due to displacement to these locations. Each line represents the movement path of an individual created by drawing a straight-line between successive relocation points depicted as circles. Gray lines (B and D) represent frogs displaced to the center of clearcuts.

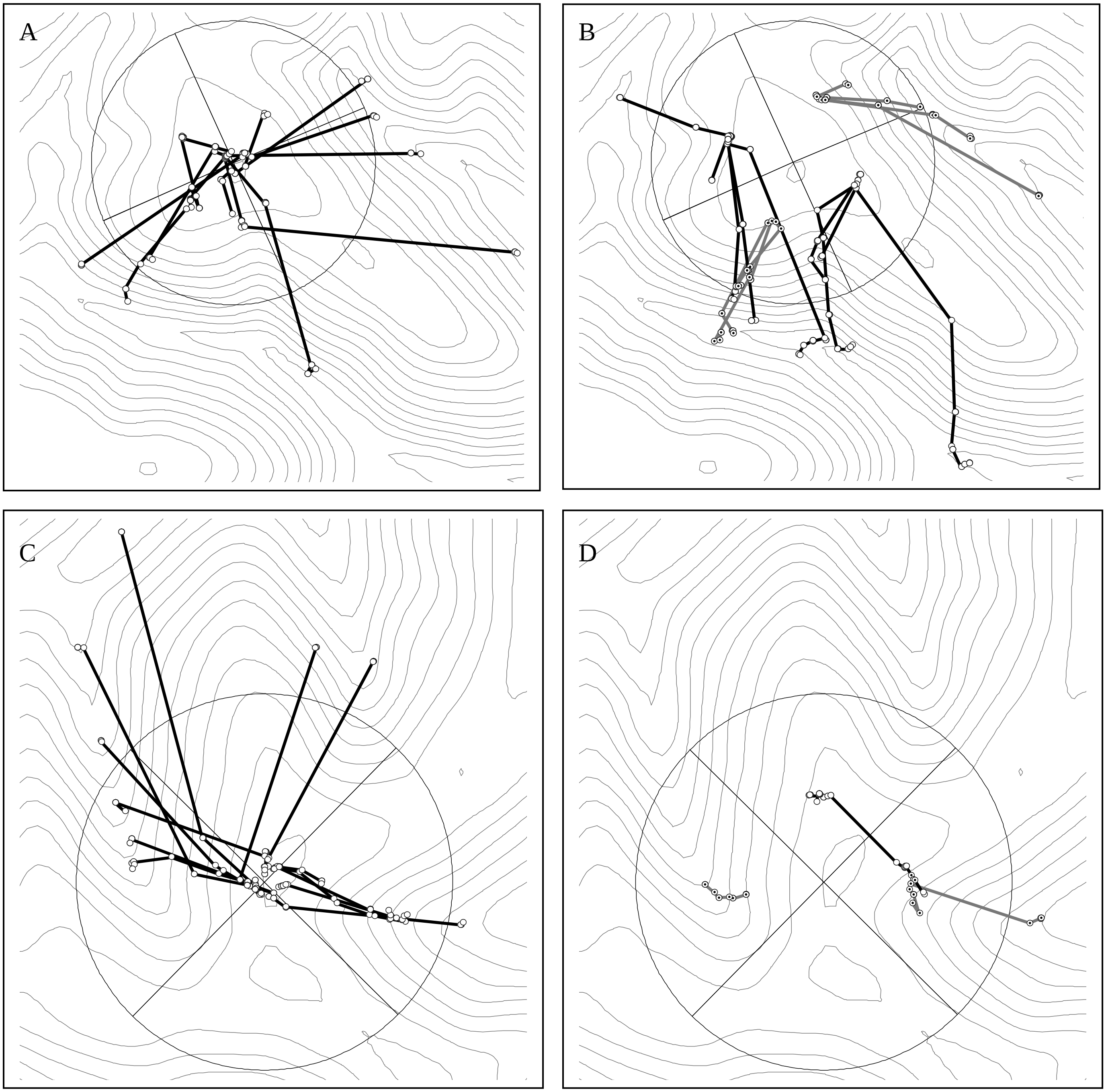
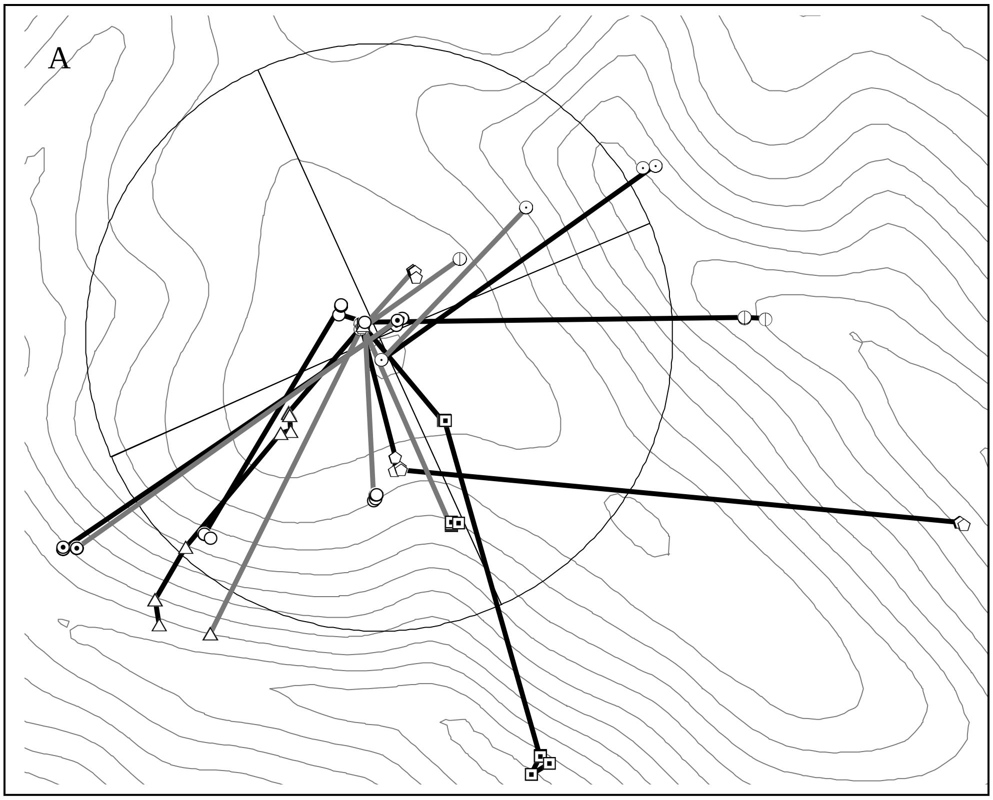

A
B
C
D

Figure 2. Movement paths for all wood frogs in 2005 that traveled greater than 20 m both before and after displacement back to the Pond 2 (A) and Pond 5 (B). Black lines represent movement paths prior to displacement and gray lines represent movement paths following displacement. Individuals are depicted with unique symbols. Note that the black and gray lines overlap for some individuals, such as the frog at Pond 2 depicted by a black spot within a circle or the frog at Pond 5 depicted by an open circle within a circle. The frogs depicted with an open square and an open circle were the two frogs at Pond 5 that did not return to the same drainage.


A

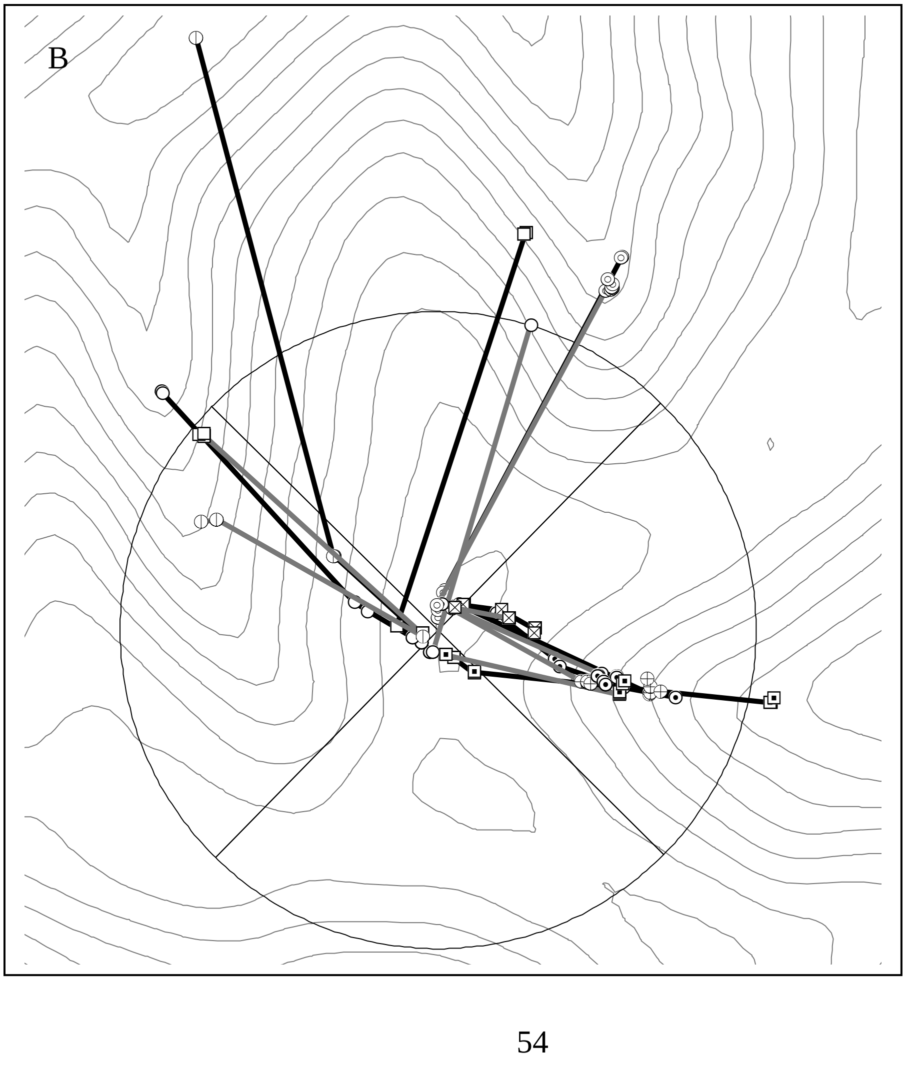

B

Figure 3. Linear regression showing the correlation between the bearing from the first to the last relocation prior to displacement to the bearing from the first to the last relocation following displacement back to the pond in 2005.

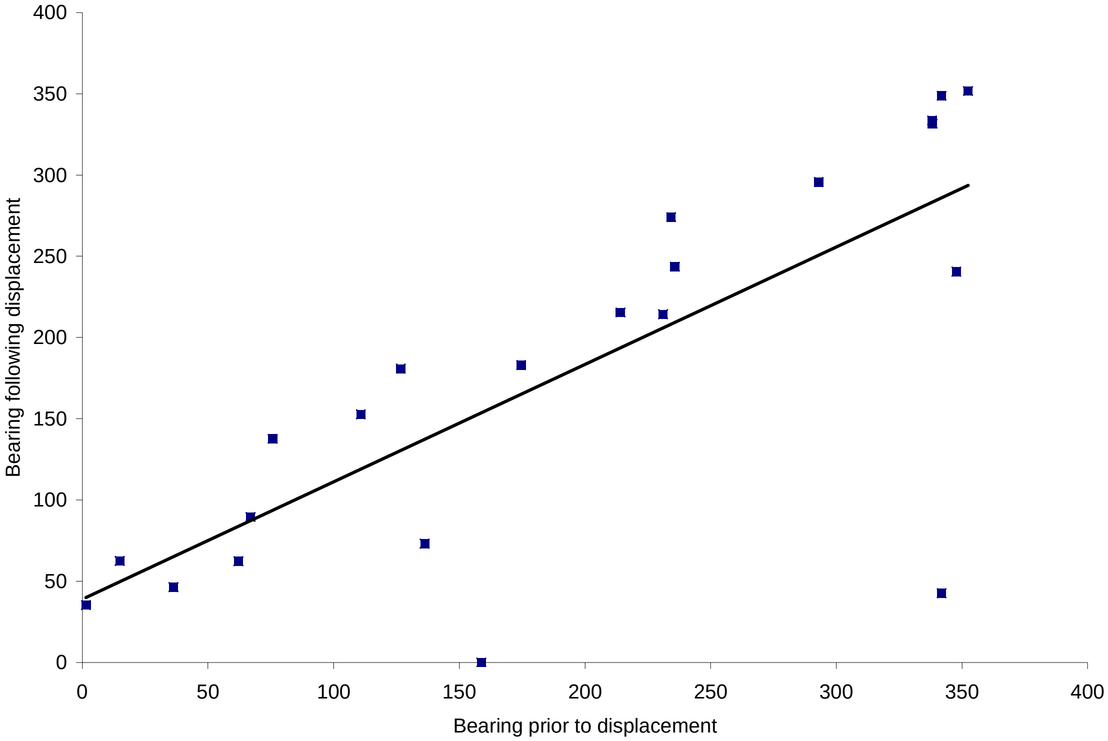
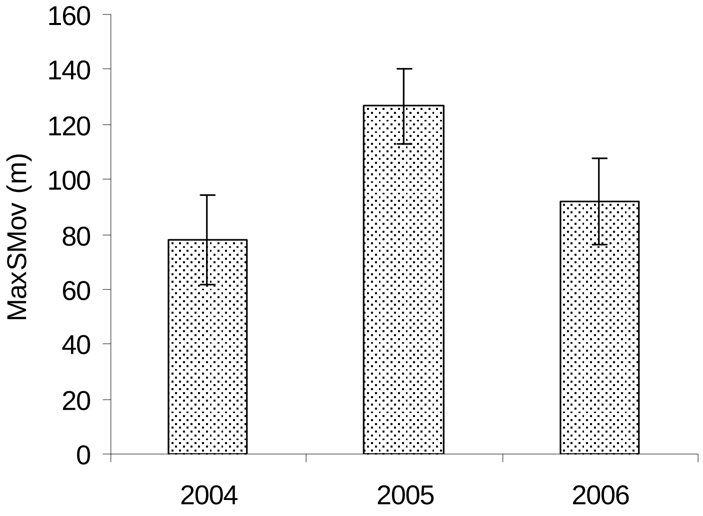
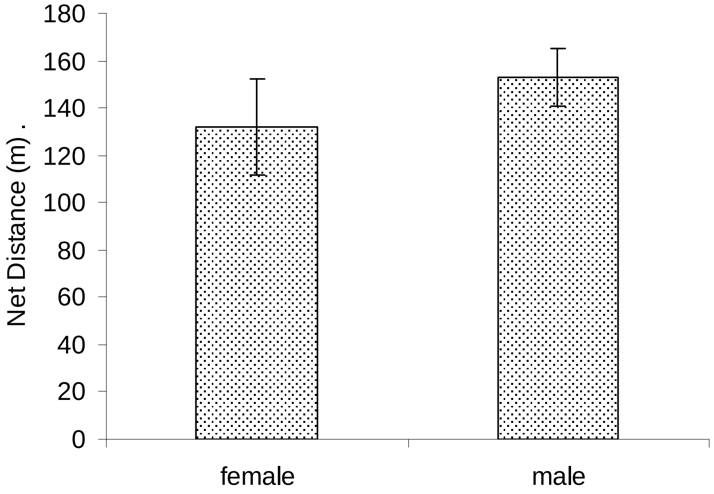

400
350
300
250
200
150
100
50
0
0
50
100
150
200
250
300
350
400
Bearing following displacement
Bearing prior to displacement

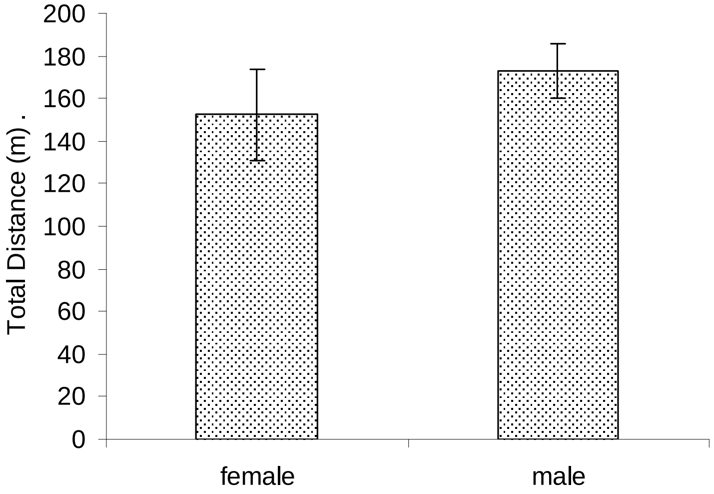
Figure 4. Least square means of maximum single movement distance between daily relocations (i.e., maximum distance traversed in a single day). This distance differed by year, with pair-wise comparisons indicating that the distance was lower in 2004 prior to timber harvest than in 2005.

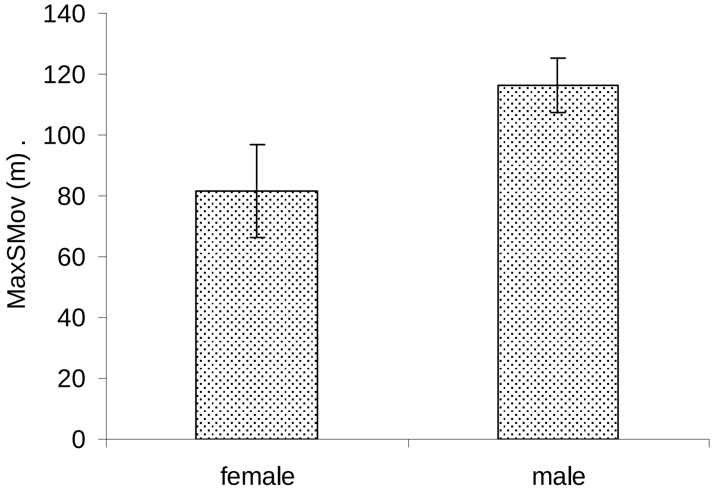


MaxSMov (m)
0
20
40
60
80
100
120
140
160
2004
2005
2006

Figure 5. Least square means for net distance (A), total distance (B), and maximum single movement distance (C) in a single day. Although males tended to move greater distances than females in all three variables, MaxSMov is the only statistically significant difference between males and females.


Net Distance (m) .
180
160
140
120
100
80
60
40
20
0
female
male


Total Distance (m) .
200
180
160
140
120
100
80
60
40
20
0
female
male


MaxSMov (m) .
140
120
100
80
60
40
20
0
female
male

CHAPTER 4

COSTS ASSOCIATED WITH BREEDING MIGRATIONS: KNOWN-FATE SURVIVAL ESTIMATES FOR WOOD FROGS

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Abstract

Migration presents a trade-off for individuals between the potential fitness benefits of reaching high quality breeding and non-breeding habitat versus the potential costs of migration. Within an information theoretic framework, we examined the costs of migration for adult wood frogs in response to timber harvest and annual weather conditions using Cox proportional hazard estimates of survival. In 2004 prior to timber harvest, survival did not differ between the inside (0.75, SE = 0.078) and outside (0.73, SE = 0.235) of the 164 m radius circular timber harvest arrays. Following timber harvest, survival inside that array in both 2005 and 2006 (0.22, SE = 0.065; 0.42, SE = 0.139) was lower than survival outside of the array and prior to harvest. Sources of mortality included predation in all years and desiccation in the drought year of 2005. The most supported models for explaining both predation and desiccation risks reflected behaviors as opposed to timber harvest or weather conditions. Both predation and desiccation risks increased when frogs made frequent movements or were located near breeding ponds. These optimal behaviors for survival were the same before and after timber harvest; however, the survival consequences for not adopting these behaviors were more severe

following harvest. Our results provide empirical evidence for 1) the ecological pressures that influence migratory behavior and 2) differential survival in relation to migratory behavior which reveals why frogs move relatively long distances away from breeding sites.

Introduction

Migration presents a trade-off for individuals between the potential fitness benefits of reaching high quality breeding and non-breeding habitat versus the potential costs of migration. The response of individuals to this trade-off can be observed through alterations in migratory behavior, such as the route traveled, timing, duration, and distances migrated. Migratory behavior is central to individual-based definitions of migration and provides insight into mechanisms of the migration process (Dingle & Drake 2007). Further, natural selection acts on migration through changes in migratory behavior of individuals in response to current conditions and differential survival or reproduction (Gauthreaux 1980). However, the full scope of species migration includes not only the migratory behavior of individuals but the ecology of populations (Dingle & Drake 2007).

Migration arises in populations where replacement rates (R_o), a function of survivorship (l_x) and birth rate (m_x), are greater for migrants than for non-migrants (Gauthreaux 1980). Increased reproductive success is the ultimate benefit of migrations. For example, young of neotropical migrating birds are born into habitat with seasonally abundant food resources and adults over-winter where foraging habitat allows them to acquire adequate energy for reproduction the following year (Gauthreaux 1980; Sillett & Holmes 2002). In comparison, costs of migration are most extreme when survival is reduced because mortality excludes future reproductive success. Robust estimates of reproductive success and adult survival in natural populations under varying conditions enhance our understanding of migration. Further, population measures reveal the function of migration between spatial separate habitats (Dingle & Drake 2007).

Amphibians that retain aquatic egg and larval life stages benefit from the abundant food resources and minimal predators found in ephemeral wetlands used as breeding habitat. Costs of migration are likely not trivial for pond-breeding amphibians because many species are known to forego breeding migrations in a given year to increase reproductive success in subsequent years (Church et al. 2007). First, migration includes an expenditure of energy. Amphibians that are early spring breeders rely on fat reserves obtained during the previous fall for over-wintering, movements to the breeding site, and breeding activities (i.e., calling and mating). For example, the short breeding season of wood frogs may be limited by energy reserves, because male frogs begin the breeding season with enough stored energy in the form of glycogen to call for 5 hours per night for 5 nights (Wells & Bevier 1997). Movements away from the breeding site then require energy for locomotion and thus the migration distances frogs may be limited by energy reserves. Second, movement activity may attract predators (Skelly 1994; Yoder et al. 2004). Longer migration distances may increase exposure to predators, resulting in increased predation risks. In addition to energy expenditure and predation risk, water balance is a critical process for amphibians in terrestrial habitats (Jorgensen 1997; Seebacher & Alford 2002). Leaving non-breeding habitat that contains adequate moisture levels and migrating on the surface of the leaf litter may expose frogs to desiccation risks. Local weather conditions may modify desiccation risks on both daily (e.g., weather fronts that bring rainfall) and yearly (e.g., drought versus wet years) time scales.

Terrestrial adult pond-breeding amphibians undergo round-trip breeding migrations that include movements to aquatic breeding habitats and return movements to non-breeding habitat (Semlitsch et al. 2008). For example, adult wood frogs (*Rana sylvatica*) use of non-breeding habitat declines as the distance between breeding sites and non-breeding habitat increases (Rittenhouse & Semlitsch 2007b). This result suggests that adults returning to non-breeding habitat must balance the potential fitness benefits of reaching high quality non-breeding habitat with the costs of migration. Further, we suggest that land use in the habitat surrounding wetlands may alter this trade-off, and thus influence the distances amphibians migrate from breeding sites. The habitat requirements of local amphibian populations have been defined based on migration distances (Rittenhouse & Semlitsch 2007a; Semlitsch & Bodie 2003). Therefore, quantifying the costs of migration will enhance our understanding of the habitat requirements of local amphibian populations.

We examined the cost of migration of adult wood frogs during movements from breeding ponds to non-breeding habitat by identifying sources of mortality and estimating survival rates. Our first objective was to test whether survival rates varied in response to varying environmental conditions resulting from experimental timber harvest and annual weather conditions. Our second objective was to determine which factors contribute to increased predation risks and desiccation risks of migrating frogs. We used known fate telemetry data to identify sources of mortality and Cox proportional hazard models that allow for both time-dependent and -independent covariates to assess the effects of covariates at the time of each mortality event.

Methods

Study Site

We conducted our study at the Daniel Boone Conservation Area (DBCA; 1,424 ha) in Warren County, Missouri, USA. The area contains mature, second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with sugar maple (*Acer saccharum*) beginning to establish in the understory (i.e., Outer Ozark Border Subsection as described by (Nigh & Schroeder 2002). Local relief (i.e., elevation change within 2.59 km^2) ranges from 46 – 76 m. Small, intermittent streams (referred to as drainages) begin in DBCA and flow south towards the Missouri River, cutting through loess ridge tops and exposing limestone rock. Amphibian breeding sites are ponds that were constructed 27 – 47 years ago on ridge tops as wildlife watering holes and were naturally colonized by a variety of amphibian species (Hocking et al. In Review).

The first year of data collection (2004) occurred prior to timber harvest under typical to slightly cool and moist spring weather conditions. The average daily spring temperature was 20.02 ± 9.27 C and total rainfall was 49.91 cm. For the purpose of summarizing weather conditions, we defined spring as 1 February through 30 June. Central Missouri experienced a severe spring drought in 2005 which ranked as the 3rd driest spring on record (NOAA weather station in St. Louis) and spring rainfall in 2006 was also below average. Average daily spring temperature was 21.45 ± 9.32 C in 2005 and 21.82 ± 10.08 C in 2006 and total spring rainfall was 34.87 cm in 2005 and 38.56 cm in 2006.

Timber harvest treatments were applied in summer and fall of 2004 as part of a collaborative project referred to as Land-use Effects on Amphibian Populations (LEAP). Each timber harvest array applied to replicate amphibian breeding sites (i.e., Pond 2 and 5) consisted of four forestry treatments: clearcut with high levels of coarse woody debris (high-CWD), clearcut with less CWD (low-CWD), partial canopy removal, and control forest (Semlitsch et al. 2008). Each array was circular with a 164 m radius, centered on a pond, divided into four equal quadrants (~2.11 ha each), and a forestry treatment was randomly applied to each quadrant with the condition that the control and partial were opposite of each other. In clearcuts, all marketable timber greater than 25 cm in diameter at breast height was removed for sale. High-CWD treatments had the remaining trees (< 25 cm DBH) felled and left on the ground. Low-CWD treatments had the remaining trees girdled and left standing to reduce the CWD on the ground. Partial harvest treatments were thinned to a basal area of 5.6 m^2 per hectare or approximately 60% stocking level by girdling or felling poor quality trees and undesirable species (primarily *Acer saccharum*). Control treatments were not experimentally manipulated.

Data Collection

We radio-tracked adult frogs at three ponds in 2004 (i.e., Pond 2, Pond 27 or Teacup Pond, and Pond 5) and at two ponds in both 2005 and 2006 (i.e., Pond 2 and Pond 5). We captured frogs at the ponds by hand and using minnow traps in 2004 and drift fences with pitfall traps in 2005 and 2006. We attached transmitters (model BD-2 with whip antennae and 1 mm diameter tube; Holohil Systems Inc., Canada) weighting 1.0 g or approximately 7% of average frog body mass by using a belt constructed from 1 mm stretch bead cord (Mainstays Crafts, Sulyn Industries Inc.) (as in(Baldwin et al. 2006; Rittenhouse & Semlitsch 2007b). Within a given year most frogs were fitted with transmitters within a 3 – 4 day period. If transmitters could not be immediately attached upon capture, we placed frogs in enclosures (1 m X 2 m X 1 m) at the pond edge for less than 2 days. We released frogs within 5 m of the pond edge in 2004 and 2005, and approximately 80 m from the pond edge within the center of the timber harvest treatments in 2006. Release date was 6 March 2004, 23 March 2005, 10 March 2006 and varied based on when the breeding season ended. We assumed that transmitters do not increase predation risk, because radio-transmitters have limited effects on wood frog anti-predator behavior (Blomquist & Hunter Jr 2007).

We relocated frogs during daylight hours for 50 consecutive days using a R2000 ATS receiver and yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). Upon homing to the frog, we obtained a visual sighting, carefully pulled out the whip antenna from beneath leaf litter, and placed a wire flag next to the frog. If the antenna was visible next to the flag upon subsequent relocations, we did not disturb the frog by obtaining a visual sighting. All movements greater than 10 cm were marked with a flag. Flags were later mapped with a compass and tape measure or GPS unit with submeter accuracy (Trimble Pathfinder Pro XL or Trimble Geo XT) and imported into Arcview (version 3.2; Environmental Systems Research Institute, Redlands, California, USA).

We obtained the fate of all individuals and categorized mortality as predation, desiccation, or unknown. Predation was assigned when the transmitter was recovered with tooth marks and/or body parts from the frog. Desiccation was defined as events where frogs were found at the same location as the previous day, depleted of body water with no signs of predation. Unknown was assigned to events where frogs were found with no signs of predation or desiccation.

Analysis

We used an information-theoretic approach to investigate support for three sets of models representing hypotheses regarding: 1) survival, 2) predation, 2) desiccation. First, we assessed competing models that represent the effects of timber harvest and yearly weather conditions on wood frog survival (response = alive or dead) while migrating away from breeding ponds. The most supported model for explaining the effects of timber harvest and drought was used as a candidate model in the other two investigations. We then assessed models that represent alternative hypotheses for wood frog predation risk (response variable = depredated or not depredated) and desiccation risk (response variable = desiccated or not desiccated).

We identified both time -independent and -dependant covariates hypothesized to affect predation or desiccation risks (Table 2). These covariates were based on individual characteristics (e.g., sex, body condition, movement frequency), location within the landscape (e.g., net distance from pond), and daily weather conditions (e.g., high temperature, total rainfall, number of days since a rainfall greater than 10mm) obtained from a weather station in Hermann, Missouri, about 8 km from DBCA. We found multicollinearity among weather variables using the variance inflation factor from a multiple regression model (Allison 2002). Therefore, we limited the number of weather variables in a candidate model, often only including the number of days since a large rainfall. Large rainfall was defined as 10 mm of rain or the amount of rain needed to recharge the moisture within the leaf litter layer (O'Connor et al. 2006).

Each candidate model was expressed as a Cox proportional hazard regression model (Cox 1972). Cox proportional hazard models use a partial likelihood function to estimate a hazard function based on a “risk set” of all the individuals alive on a given day, and thus the hazard for an individual is a proportion of the hazard for any other individual (Allison 1995). The relative effects of covariates on the hazard function can be estimated without the researcher specifying a baseline hazard function (i.e., the baseline hazard function is estimated by setting all covariates equal to zero (Allison 1995). A valuable characteristic of this model is its ability to handle both time-independent and -dependent covariates, because we can assess the affect of a time-dependent covariate at the time of the mortality event (Yoder et al. 2004). For example, we assessed the effect of net distance from the pond at the time and distance of the mortality event. We used the counting process syntax in SAS to incorporate time-dependent covariates (Allison 2002) (PROC PHREG; SAS Institute year) with time measured as Julian date. Although the value for time-dependent covariates changes over time, the model estimates a single coefficient for the time-dependent covariate and inferences can be drawn at any time point. Our data spans a 64 day period from Julian day 66 – 130 (i.e., 6 March – 9 May) and we report inferences drawn at Julian day 130.

We ranked the candidate models within each of the three model sets and selected the best approximating model using the change in Akaike Information Criterion (ΔAIC) and Akaike weights (ω). We model averaged the top ranking models that were within 2

AIC units of each other for both the predation and desiccation analyses and inferences are drawn from the model-averaged coefficients. We calculated hazard ratios and 95% confidence limits for parameters in the final model to facilitate interpretation (Keating & Cherry 2004). The hazard ratio describes the relative risk between values of an individual covariate, by representing the magnitude of change resulting from an incremental change in covariate. Hazard ratios greater > 1 indicate increasing risk and ratios < 1 indicate decreasing risk.

Hypotheses for Survival Models

To fully encapsulate data collected before and after the experimental timber harvest, we included *a priori* models that represent the effects of timber harvest treatment interacting with year and a model based solely on year. Timber harvest treatment was expressed in two ways, by classifying frog locations as within control, partial, high-CWD, low-CWD, or outside of the timber harvest array (covariate referred to as 'treatment') or by classifying frog locations as inside or outside of the 164m circular timber harvest array (covariate referred to as 'array').

Hypotheses for Predation Models

We developed a set of 13 *a priori* candidate models based on hypotheses that predation risk would increase when close to breeding ponds due to the high density of frogs attracting predators and if frogs made frequent daily movements that may attract predators. We hypothesized that predation risk would increase after many days without rain due to scent accumulating at a location, or on windy days due to disturbance of the boundary layer of air near the ground that may disperse scent. The most supported model from the survival analysis was included as a candidate model to explore the effects of timber harvest and drought on predation. We hypothesized additive effects when these conditions occurred in combination. We hypothesized that movement frequency and days since rainfall greater than 10 mm would interact, because remaining in the same location may limit exposure to predators but after several days without rain scent of frogs may accumulate at that location. We hypothesized that movement frequency and net distance from pond would interact. Frogs that move frequently may be depredated more than frogs that remain still, when frogs are located close to the pond due to predators searching areas with high density of frogs. Frogs may have similar predation risks regardless of movement frequency when far from ponds because predators may not search for frogs when frog densities are low.

Hypotheses for Desiccation Models

We developed a set of 15 *a priori* candidate models based on hypotheses that desiccation risk would increase when close to breeding ponds because of their location on ridgetops or if a frog made frequent daily movements suggesting the microhabitat at the location is poor quality. We also hypothesized additive effects when these conditions occurred in combination. We hypothesized that movement frequency and net distance from pond would interact, because when close to ponds frogs that moved frequently may be exposed to desiccation risks more than frogs that did not move. When far from ponds moisture in drainages is more readily available and thus frogs may have similar desiccation risks regardless of movement frequency. The most supported model from the survival analysis was included as a candidate model to explore the effects of timber harvest and drought on predation. We also hypothesized that daily weather conditions would greatly influence desiccation risk. Desiccation risk was hypothesized to increase with increased daily maximum and minimum air temperatures, low daily relative humidity, average daily dew point and sustained wind, and with decreased daily rainfall and number of days since 10mm rain. We restricted the number of covariates in each candidate model due to limited number of desiccation events and multicollinearity between weather variables. Therefore, most candidate models contain only one weather covariate or combinations with the least amount of multicollinearity.

Results

We tracked a total of 117 adult wood frogs in three years (table 1). One frog was not included because the transmitter was shed during the first movement. Several classifications of mortality events warrant explanation. First, six mortality events were assigned as predation based on transmitters recovered 5 – 20 m from the previous relocation with the belt still tied and without teeth marks. We do not believe transmitters were shed because frogs had previously made large movements. In 4 of these 6 events, the PIT tag inserted between the skin and muscle of the frog for identification was found within a meter of the transmitter. Second, one transmittered frog was lost in 2005 on the 52nd day of tracking. We believe the battery failed (40 day manufacturer's warrantee) and censored this frog at last visual location. Third, on the 39th day of tracking in 2006 following a rain event, we found 7 transmitters with broken belts and antennas through the litter in the exact same location as the previous day. We attributed this event to belts becoming brittle and breaking as opposed to predation, because on the previous day we had noticed a frog sitting within a broken belt and had replaced the belt. Further, transmitters in all suspected predation events were found > 1 m from the previous location. Two transmitters were also found in a similar manner near the completion of the study in 2005. These nine events were censored and not included as mortality events.

Causes of Mortality

We classified 29 mortality events as predation, 13 as desiccation, and 8 as unknown (Table 1). We confirmed predation by eastern garter snakes (*Thamnophis sirtalis*) (n = 6) using forced regurgitation to retrieve the frog and transmitter from the snakes' stomachs. We suspect a wide range of other predators: raccoon or other medium sized mammal based on frogs found missing large body parts (e.g., leg or head) (n = 8) and when a PIT tag was found with no body parts (n = 6); raptors or owls (n = 5) based on transmitters found in avian scat or greater than 300 m from the location the previous day; turkey (n = 1) based on scratches in the leaf litter; small mammal (n = 3) based on frogs lying on their back with small bites on the stomach or hind legs or a transmitter found in a burrow. Mortality events classified as unknown are suspected to result from handling stress (n = 3), exposure to below freezing temperatures when in a clearcut at a location with very leaf litter (n = 1), and old-age (n = 4). We suspect old-age based on individuals located at the edge of standing water with no sign of physical injury. In no other instances were frogs located in standing water.

Survival Models

The most supported survival model for explaining effects of the experimental timber harvest and drought on survival contained the interaction between year and frog locations classified as inside or outside the 164 m timber harvest array ($\omega = 0.89$; table 3). Therefore, the effects of timber harvest on survival were most apparent when data within the four harvest treatments was combined. Inferences from the most supported model indicate that survival inside the array (0.75, SE = 0.078) did not differ from outside the array (0.73, SE = 0.235) in 2004 prior to timber harvest. Survival inside the array was 0.22 (SE = 0.065) and 0.42 (SE = 0.139) in 2005 and 2006, and thus survival was lower inside the array than outside following timber harvest and was the lowest during the drought year (Figure 1). The candidate models with harvest treatment were not well supported when ranked against models with timber harvest expressed as inside or outside the array. A limited number of mortality events occurred in each of the four timber harvest treatments and the estimated coefficients within the models were not significant (all $P > 0.07$ for Wald χ^2). However, survival decreased in the expected order (i.e., control > partial > CWD retained > CWD removed) for models that contained the four timber harvest treatments.

Predation Models

Survival from predation while frogs migrated from breeding ponds to non-breeding habitat for a 90 day period was 0.67 (SE = 0.089) (figure 2). Predation risk was best described by two competing models that both contained the variables net distance from pond and movement frequency (table 3). Based on model averaged estimates, survival from predation increased when frogs are located at greater distances from the pond and decreases for frogs that frequently make daily movements (table 5). For example, cumulative survival for frogs located within 250 m of the breeding pond was less than 0.90, indicating that predation risks are greatest near the pond (figure 3). Wood frogs often remained in the exact same location for multiple days as indicated by a mean movement frequency of 0.33 ± 0.172 movements per total days tracked. Survival from predation was highest for frogs that remained in the exact same location for multiple days and lowest for frogs that shifted within the leaf litter on a daily basis (figure 3). We found no evidence that predation risks were high on rainy days when frogs made large migratory movements.

Desiccation Models

Survival from desiccation while frogs migrated from breeding ponds to non-breeding habitat for a 90 day period was 0.997 (SE = 0.00452) (figure 2). All 13 desiccation events occurred between 30 March and 11 April 2005, with 8 of these mortality events between 5 April and 8 April 2005. In contrast to our a priori expectation, candidate models describing dry, hot weather conditions were not the most supported models (table 3). Desiccation risk was best described based on two competing models that both contained the variable net distance from pond. Survival from desiccation increases when frogs are located farther from ponds (table 5), with cumulative survival less than 0.90 for frogs within 50 m of the pond (figure 4). Although single factor weather models were not well supported, the confidence intervals for the estimated coefficients suggest that desiccation was related to several weather variables, including number of days since rain greater than 10 mm (β = 0.1656, CI = 0.1262 – 0.3246), daily low humidity (β = 0.0499, CI = 0.0034 – 0.0966), and daily average dew point (β = 0.1246, CI = 0.0139 – 0.2352).

Discussion

Migrations between breeding and non-breeding habitat entail costs such as reduced survival or reduced reproduction (i.e., time or energy allocated to movement prevents foraging to acquire additional energy for future reproduction). Our results indicate that reduced survival is a cost of migration for adult wood frogs migrating from breeding ponds to non-breeding habitat. To the best of our knowledge these results are the first known-fate survival estimates produced for an amphibian. Mortality resulted from two sources: predation by a variety of predators and desiccation. In addition, survival declined in response to timber harvest and a severe drought year; however, these environmental conditions were not the best factors for explaining predation risk and desiccation risk. Notably, two covariates that reflect behavioral choices made by individuals explained both predation and desiccation risk: the location of a frog in the landscape relative to the breeding site and the movement frequency of that frog. Therefore, our results provide empirical evidence for 1) the ecological pressures that influence migratory behavior and 2) differential survival in relation to migratory behavior which reveals why frogs move relatively long distances away from breeding sites.

The location of frogs relative to breeding ponds affected desiccation risk, with the highest risk near breeding ponds and decreasing risk at greater distances from the pond. Wood frog breeding sites at our study site are ponds primarily located on ridgetops, whereas the non-breeding habitat is moist drainages with intermittent flow following rain events (Rittenhouse & Semlitsch 2007b). Desiccation risk varied with distance from the pond, because frogs at greater distances from ponds were located within moist and cool drainages and we never observed desiccation events in drainages. Further, in a related experiment where we removed predation risks and constrained frogs to microhabitats to determine the consequences of remaining on ridgetops, survival within drainages was 2.3 times higher than on ridgetops (Rittenhouse et al. In Review). Our results demonstrate that variation in habitat quality may provide the ecological pressures for amphibian migration.

Predation risks were also highest for wood frogs located near breeding ponds and we suggest that high predation risks near breeding sites may also influence migration in other species of pond-breeding amphibians. High predation risks have been noted near amphibian breeding sites (Toledo 2005; Wassersug & Sperry 1977). Further, the density of adults immediately adjacent to wetlands (i.e., within 30 m) is low outside of the breeding season (Patrick et al. 2006; Rittenhouse & Semlitsch 2007a). Congregation reduces the effectiveness of being a cryptic prey item, because predators decrease movement rates to increase searching activities when cryptic prey are clumped or at high densities (Gendron & Staddon 1983). In addition, a recent mark-recapture study found that survival for male tiger salamanders can be up to 54% lower during the breeding season than for males that skipped breeding and remained in non-breeding habitat (Church et al. 2007). Although the authors showed how energy demands may explain the mortality during the breeding season, increased predation in or near breeding habitat is an additional source of mortality that may also contribute to reduced survival near breeding sites. Amphibians with annual migrations make tradeoffs between the benefit of converging on areas with abundant resources for their young and their own survival cost of using habitat with high predation risks.

The diversity of predators we documented expands the known list of wood frog predators (Baldwin et al. 2007) and indicates that wood frog behavior is constrained by the need to simultaneously avoid predators that use olfactory, auditory, and visual cues to locate prey. Avoiding visual predators is clearly important because wood frog coloration closely matches the oak-hickory leaf litter used as microhabitat in Missouri (Rittenhouse & Semlitsch 2007b). Leaf litter microhabitats used by frogs may limit olfactory predators. For species above the litter such as rabbits or birds, scent trails do not form on windy days because the wind disperses the odorant and the concentration becomes too low to detect within a short distance of the prey; however, breezy days create a linear odor plume that predators use as a scent trail. For example, breezy days (3–10 km/hr) provide the optimal wind speeds for bird dogs use of odor trails (Conover 2007). Our results indicate that predation risks for wood frogs increased once conditions became windy. On still or breezy days, the structure of leaf litter may prevent the spread of odorants by maintaining wind velocities within the litter near zero (Geiger 1965), but strong wind may break into the leaf litter layer and disperse odorants.

Further, we found predation risks increased as movement frequency increased, indicating that *small* movement within leaf litter may attract visual and potentially auditory predators. Although availability of water has been used to explain why amphibians migrate during rainy nights (Madison 1997; Timm et al. 2007), migrating at night may also limit visual predators and wet leaf litter may mask the noise created by saltatory movements. Notably, we found no evidence of predation while frogs were making *large* movements at night during rain. This result conflicts with research on birds and mammals that indicates that predation risks increase with longer movement distances (Alerstam et al. 2003; Johnson & Gaines 1990; Yoder et al. 2004).

Drought conditions in 2005 resulted in thirteen desiccation events and this source of mortality was not observed in the other two years. Water balance has been hypothesized as a driving process for amphibians in terrestrial habitats (Jorgensen 1997; Thorson 1955) and mark-recapture studies have found reduced adult survival in years with low rainfall (Berven 1990), but the direct observation of desiccation events on free-ranging animals was only possible through the use of radio-telemetry. Movements can be a reflection of the severity of the habitat. For example, wood frogs in New Brunswick restricted movement to rainfall events when in forest fragments more than pristine bogs (Mazerolle 2001). We found that wood frogs were not willing to attempt large movements without rain even when the soil moisture conditions at their present location were causing them to desiccate. Further, we showed that desiccation risk increased for frogs that made daily movements within the leaf litter. These small movements could be the response of frogs to the poor quality of the microhabitat, thus indicating that frogs were attempting to find a location with moister substrate. Alternatively, frogs that remained perfectly still in water conserving postures may have maintained body water better than frogs that made movements. The low movement frequency and the unwillingness to move without rain indicate that oak-hickory forest in Missouri may be a harsh environment for wood frogs. We suggest that the availability of water may be a limiting factor for wood frogs along the southwestern edge of the species range. Drought conditions, such as an increase in the number of days between rain events or a decrease in soil moisture levels, could limit long term population persistence.

We found that survival following timber harvest was 1.7 times lower than during the pre-harvest year. Survival was reduced even though frogs were allowed to move freely throughout the timber harvest arrays and thus our results support previous findings using enclosures studies. For example, although southern toads (*Bufo terrestris*) were captured in both clearcut and forested stands, survival and growth was lower for toads contained within clearcuts than in forested stands (Todd & Rothermel 2006). In our study, timber harvest reduced survival, but the model that reflected timber harvest was not the best predictor of either predation or desiccation risks when ranked against other *a priori* hypotheses. Models that reflected behavioral choices made by individual frogs (i.e., low movement frequency and moving away from the breeding site) were the best predictors of risk and these behaviors that produced the optimal survival strategies for avoiding risk were the same both before and after timber harvest. The notable difference following harvest was that the survival consequences for not adopting these behaviors were more severe.

In some situations, variation in adaptive behaviors in response to high mortality risks may regulate population dynamics in response to habitat change faster than demographic processes. For example, tadpoles generally maximize time and size at metamorphosis by increasing foraging in habitats with abundant food resources. When predation risk is high, tadpoles balance the trade-off between foraging and hiding from predators by reducing activity in habitats with abundant food resources (Anholt & Werner 1995). However, variation in adaptive behaviors may not allow adult wood frogs to persist in Missouri under intense timber harvest or prolong drought conditions. Predation and desiccation risks were both reduced when frogs remained still and moved far from the breeding site. Further, optimal behaviors within continuous forest or during average weather conditions did not change relative to optimal behaviors following timber harvest and during drought. Therefore, adopting an alternative behavior following timber harvest or during drought will not increase the likelihood of survival for adults faced with these conditions.

The tradeoff between the costs and benefits of migration influences the net distance amphibians migrate from wetlands. These distances have been used to define the habitat requirements of pond-breeding amphibians (Rittenhouse & Semlitsch 2007a; Semlitsch & Bodie 2003), and thus an understanding this trade-off will enhance our ability to predict the extent of local populations. Our results demonstrate the survival cost to migrating adult wood frogs. We found that both predation and desiccation risks decreased at greater distances from wetlands. These ecological pressures explain why adult amphibians migrate away from breeding habitat during the non-breeding season. Although increased exposure to predators due to movement activities can be a migration risk for many birds and mammals, amphibians seem to minimize this risk by migrating on rainy nights. In addition, the distances amphibians migrate based on balancing this trade-off will likely change in response to both natural and anthropogenic alterations of the habitat. We found reduced survival in response to timber harvest and drought weather conditions, which suggests amphibians that evacuate recently harvested stands may be responding to the low survival probabilities (Semlitsch et al. 2008). When timber harvest occurs between breeding and non-breeding habitat this evacuation behavior may result in amphibians migrating greater distances from wetlands and thus may extend the amount of habitat required for the persistence of a local population.

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Table 1. Summary of number of wood frogs tracked and the causes of mortality

	No. with transmitters	Number	Cause of Mortality		
Year	(males, females)	Deaths	Predation	Dessication	Unknown
2004	42 (36, 6)	9	9	0	0
2005	49 (29, 20)	31	13	13	5[2a,3b]
2006	26 (17, 9)	10	7	0	3[2a1c]

a Suspected senescence death.
b Suspected handling stress death. Died the day after being held.
c Suspected exposure death, in clearcut w/ minimal litter and air temp below freezing.

Table 2. Description of covariates used in Cox proportional hazard models.

Variable Name	Description
year	year of study (2004, 2005, or 2006)
treatment	frog location classified as control, partial, clearcut high CWD, clearcut low CWD, or outside the timber harvest array
array	frog location classified as inside or outside of circular timber harvest array
sex	male or female
body condition	snout vent length divided by body mass
movfreq	number of movements (> 10 cm) divided by the number of daily relocations
netdispond (m)	net distance from pond to frog location
netdisstream (m)	net distance from drainage to frog location
tenmm (mm)	number of days since rainfall greater than 10 mm
precip (mm)	total daily rainfall
temphigh	daily high air temperature
templow	daily low air temperature
humdlow	daily low air humidy
dewavg	daily average dew point
wind	daily high sustained wind speed

Table 3: Cox proportional hazard models ranked by the change in AICc for wood frog survival, survival from predation, and survival from dessication in a Missouri oak-hickory forest, USA, 2004 - 2006.

Model	loglike	k	AIC	AICc	Δ AICc	ω
SURVIVAL						
array*year	-201.992	5	413.984	414.003	0	0.899
year	-207.222	2	418.443	418.447	4.444	0.097
treatment*year	-198.571	14	425.142	425.268	11.266	0.003
null	-215.926	0	431.851	431.851	17.849	0
PREDATION						
netdispond movfreq tenmm windhigh	-112.115	4	232.231	232.243	0	0.551
netdispond movfreq	-114.815	2	233.629	233.633	1.39	0.275
main effects model	-111.096	7	236.192	236.226	3.983	0.075
array*year netdispond movfreq tenmm windhigh	-109.791	9	237.582	237.637	5.394	0.037
array*year netdispond movfreq	-111.931	7	237.862	237.896	5.653	0.033
netdispond	-118.609	1	239.218	239.22	6.977	0.017
movfreq tenmm mov*ten	-117.988	3	241.977	241.984	9.741	0.004
movfreq	-120.059	1	242.117	242.118	9.875	0.004
movfreq*netdispond	-121.046	1	244.092	244.094	11.851	0.001
array*year mov*net tenmm windhigg	-114.529	8	245.057	245.101	12.858	0.001
null	-123.202	0	246.403	246.403	14.16	0
arry*year mov*net	-117.253	6	246.506	246.531	14.289	0
array*year	-118.711	5	247.422	247.44	15.198	0
DESSICATION						
netdispond	-44.613	1	91.226	91.228	0	0.64
netdispond movfreq	-44.217	2	92.435	92.438	1.211	0.349
array*year	-45.123	5	100.246	100.264	9.036	0.007
movfreq*netdispond	-50.14	1	102.281	102.282	11.054	0.003
tenmm dewavg windhigh	-49.006	3	104.011	104.018	12.791	0.001
main effects model	-42.06	12	108.119	108.213	16.986	0
dewavg	-53.347	1	108.693	108.695	17.467	0
tenmm	-54.627	1	111.253	111.254	20.027	0
humdlow	-54.679	1	111.357	111.359	20.131	0
templow	-55.213	1	112.426	112.428	21.2	0
movfreq	-56.034	1	114.067	114.068	22.841	0
precip	-56.24	1	114.48	114.481	23.253	0
null	-57.572	0	115.145	115.145	23.917	0
temphigh	-57.48	1	116.961	116.962	25.734	0
windhigh	-57.541	1	117.082	117.083	25.855	0

Table 4: Parameter estimates, standard errors, Wald statistic, and hazard ratio from the most supported wood frog survival model.

Covariate	df	β	Std Error	Wald χ^2	P value	Hazard Ratio
		SURVIVAL				
inside array X pre-harvest	1	0.36512	0.79723	0.2098	0.647	1.441
outside array X pre-harvest	1	0.43089	1.23171	0.1224	0.7265	1.539
inside array X post-harvest	1	1.8593	0.73756	6.3549	0.0117	6.419
outside array X post-harvest	0					

Table 5. Parameter estimates, standard errors, 95% confidence intervals, and harzard ratio based on model-averaged estimates for predation and desiccation analyses.

Covariate	df	β	Std Error	lower 95% CI	upper 95% CI	Hazard Ratio
PREDATION						
netdispond	1	-0.0097	0.00377	-0.01724	-0.00217	0.9903
movfreq	1	3.63368	1.29086	1.05196	6.21541	37.8519
tenmm	1	0.00558	0.03097	-0.05635	0.06751	1.0056
windhigh	1	0.06479	0.05909	-0.05339	0.18297	1.0669
DESICCATION						
netdispond	1	-0.06752	0.02649	-0.12051	-0.01454	0.9347
movfreq	1	0.49405	0.93567	-1.37729	2.36539	1.6389

Figure 1. Cox proportional hazard survival estimates with 95% confidence intervals from the most supported survival model. Survival outside of the array (open circles) was greater than 70 % in all three years; whereas, survival inside of the array (filled circles) was reduced following timber harvest. Survival was lowest inside the array during the drought year of 2005.

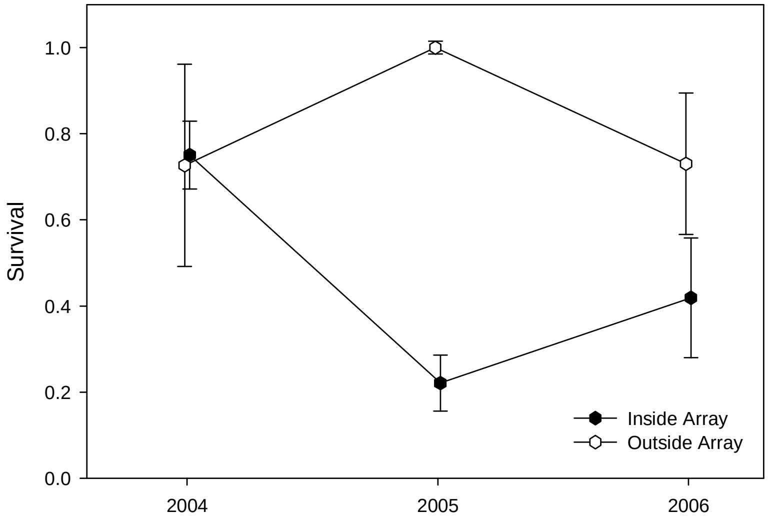

Survival
1.0
0.8
0.6
0.4
0.2
0.0
2004
2005
2006
Inside Array
Outside Array

Figure 2. Baseline survival functions for the survival analysis (A), the predation analysis (B), and the desiccation analysis (C). The gray lines represent 95% confidence intervals around the predation and desiccation functions.

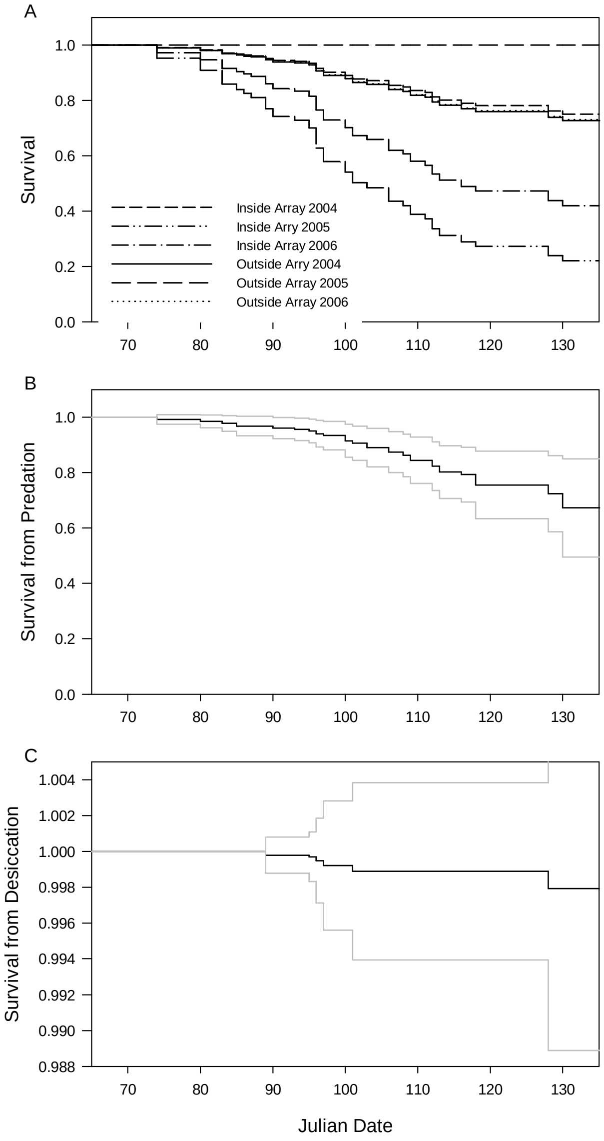

A
Survival
1.0
0.8
0.6
0.4
0.2
0.0
70
80
90
100
110
120
130
Inside Array 2004
Inside Arry 2005
Inside Array 2006
Outside Arry 2004
Outside Array 2005
Outside Array 2006
B
Survival from Predation
1.0
0.8
0.6
0.4
0.2
0.0
70
80
90
100
110
120
130
C
Survival from Desiccation
1.004
1.002
1.000
0.998
0.996
0.994
0.992
0.990
0.988
70
80
90
100
110
120
130
Julian Date

Figure 3. Survival estimates with 95% confidence intervals inferred following model averaging of the most supported predation models. We estimated survival for the range of values for each variable while holding the other variables at their mean value.

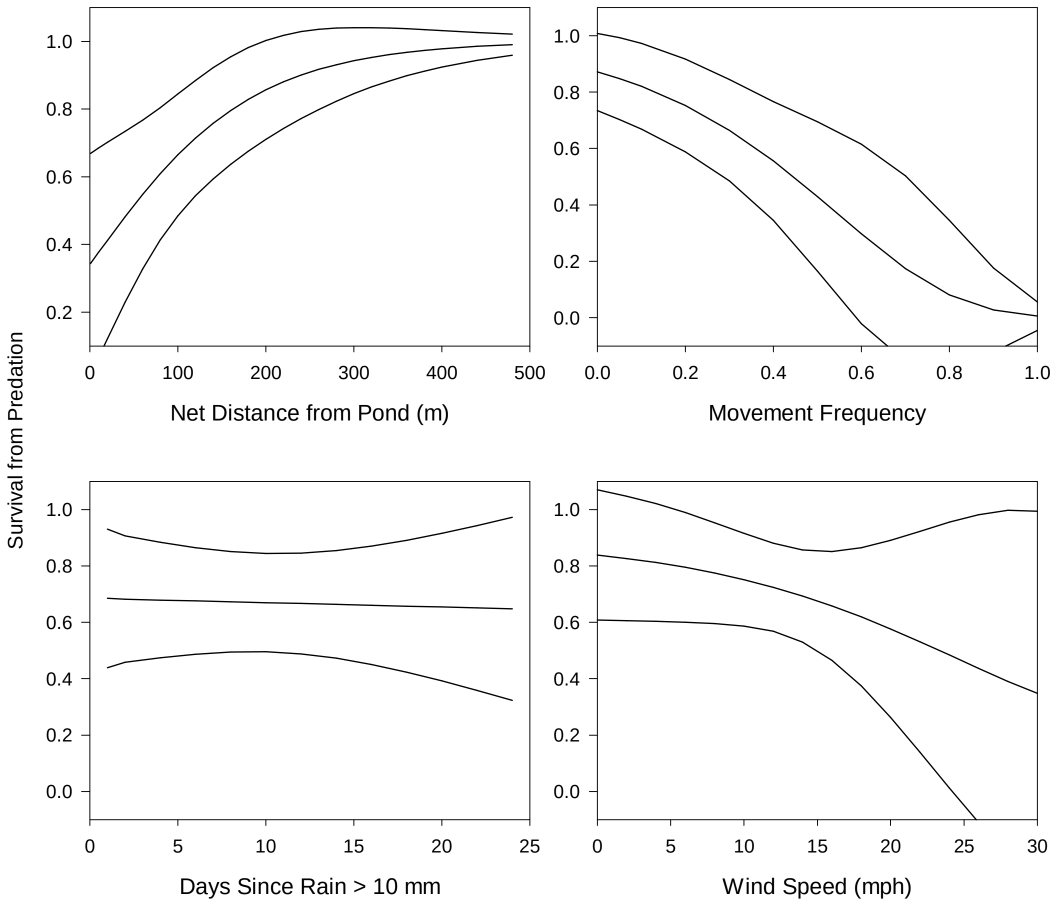
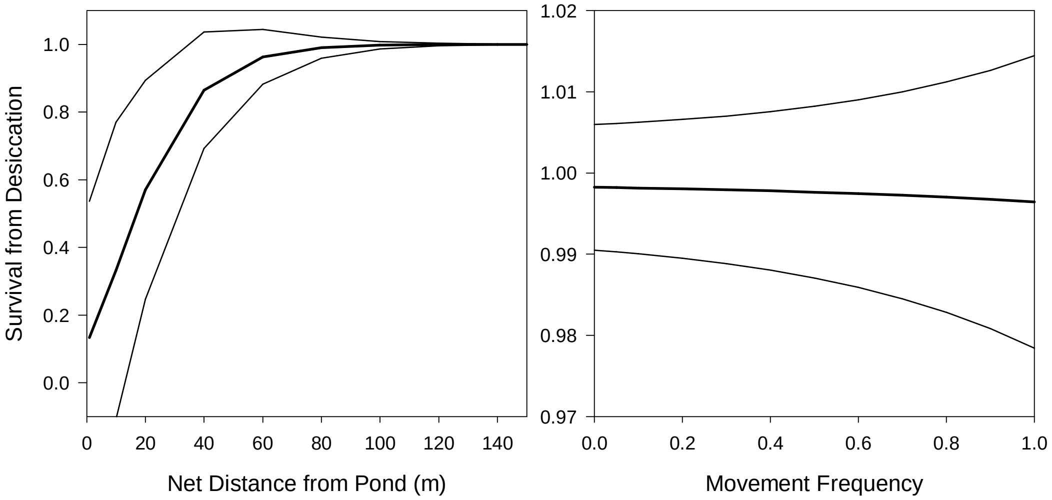

Survival from Predation
1.0
0.8
0.6
0.4
0.2
0
100
200
300
400
500
Net Distance from Pond (m)
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Movement Frequency
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
Days Since Rain > 10 mm
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Wind Speed (mph)

Figure 4. Survival estimates with 95% confidence intervals inferred following model averaging of the most supported desiccation models. We estimated survival for the range of values for each variable while holding the other variables at their mean value.


Survival from Desiccation
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120
140
Net Distance from Pond (m)
1.02
1.01
1.00
0.99
0.98
0.97
0.0
0.2
0.4
0.6
0.8
1.0
Movement Frequency

CHAPTER 5

THE ROLE OF MICROHABITATS IN THE DESICCATION AND SURVIVAL OF ANURANS IN RECENTLY HARVESTED OAK-HICKORY FOREST

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Abstract

Understanding how critical life history stages respond to habitat change is essential for predicting how amphibian populations respond to anthropogenic land use. Juvenile survival is a sensitive vital rate in pond-breeding amphibians, suggesting that modest changes in juvenile survival could greatly affect population growth rate. Current survival estimates indicate that mortality is the fate of many juveniles, yet the sources of mortality for juveniles and potential survival differences among microhabitats are unknown. We compared water loss and survival rates of recent American toad, green frog, and wood frog metamorphs contained within four microhabitats, two of which occur in uncut control forest (i.e., Forest Ridgetop and Forest Drainage) and two within recently harvested forest (i.e., Clearcut Open, Clearcut Brushpile). Survival was higher in Forest Drainages than Forest Ridgetop, indicating that microhabitats within continuous forest are not equally suitable. Brushpiles of course woody debris reduced desiccation risks in clearcuts as indicated by survival difference between Clearcut Open and Clearcut Brushpiles and survival in Clearcut Open was very low for all species in both years. We found species differences in survival as well as a species by microhabitat interaction in water loss rates. These results are best explained by observed behavioral differences as opposed to physiological differences among species. We conclude that desiccation can be a major source of mortality for recent metamorphs entering terrestrial habitats, especially habitat altered by anthropogenic land-use. Desiccation risks are greatest in areas with low soil moisture conditions, which for our study included microhabitats within clearcuts without coarse woody debris, forested ridgetops, and years with below average rainfall.

Introduction

All vital rates do not contribute equally to the growth rate of a population. Therefore, understanding how sensitive life history stages respond to habitat change is essential for predicting how amphibian populations will respond to anthropogenic land use. Recent population modeling work on pond-breeding amphibians has demonstrated that juvenile survival in terrestrial habitats is an important vital rate in determining population growth (Biek et al. 2002; Vonesh & De la Cruz 2002). Consequently, a reduction in juvenile survival will likely reduce the population growth rate more than an equal reduction in other life stages such as the egg or larval stages. Juveniles are therefore a critical life stage for understanding the effects of anthropogenic land use, and yet this life stage is the least understood component of pond-breeding amphibians' complex lifecycle.

Although little is known about habitats used or the distances traveled by juveniles, mortality is clearly the fate of most juveniles. The number of adults entering a wetland to breed for the first time is often orders of magnitude lower than the number of recent metamorphs produced from that wetland, especially when recruitment from a wetland is exceptionally high (e.g., > 360,000 metamorphs; Gibbons et al. 2006). Further, the time period just following metamorphosis may be a period when mortality risks are exceptionally high. Metamorphs leaving a wetland are exposed to high rates of predation (Wassersug & Sperry 1977), and the high surface to volume ratio of emerging metamorphs makes them prone to desiccation (Schmid 1965). Further, recent enclosure experiments have documented high mortality in the first year following metamorphosis (Rothermel & Semlitsch 2006; Todd & Rothermel 2006), and within this first year much of the mortality may happen in the first few weeks (Harper 2007a).

Land-use practices such as timber harvest have the potential to increase rates of juvenile amphibian mortality. Negative local effects of timber harvest on amphibians has been widely accepted since a review of 18 studies found that total captures of amphibians on control sites was 3.5-fold greater than on clearcut stands (deMaynadier & Hunter 1995) and recent work confirms this conclusion (e.g., Karraker & Welsh Jr. 2006; Renken et al. 2004). Amphibians are capable of behaviorally avoiding areas without canopy cover when more suitable habitat is readily available (Patrick et al. 2006; Rittenhouse & Semlitsch 2006), but the direct consequences of being present within a large harvested area are largely unclear. Terrestrial enclosure studies of amphibians have been used to confine juveniles in harvested habitats (Harper 2007b; Rothermel & Semlitsch 2006; Todd & Rothermel 2006). These studies have used enclosures of a size that allows individuals to select from a range of microhabitats within the enclosure, and have assumed that mortality was the fate of individuals not recaptured. Although we believe this assumption is reasonable, confirming the source of mortality by comparisons with known fate studies is crucial for our understanding of the effects of land use on the juvenile life stage.

We hypothesize that finding microhabitats that allows juveniles to remain hydrated is key to survival during the first few weeks post metamorphsis. Further, adequate microhabitats may be limited in continuous forest and may become more limited when timber harvest removes the canopy cover. In terrestrial habitats, selecting microhabitats that minimize water loss is essential to remaining hydrated and thus to survival (Seebacher & Alford 2002). Amphibian skin in most species provides virtually no resistance to the movement of water and thus essentially acts like an open water surface (Adolph 1932; Jorgensen 1997). Water must be absorbed by sitting on moist substrate as water is constantly lost to the air via evaporation (Hillyard et al. 1998; Thorson 1955). Low amphibian abundance within harvested stands is often attributed to the greater range of daily and seasonal air and soil temperatures in open versus closed canopy areas (Chen et al. 1997). Some byproducts of timber harvest, such as coarse woody debris and slash piles, may serve as microclimate refuges minimizing the harsh microclimate conditions following canopy removal (Bartelt et al. 2004; Patrick et al. 2006).

Our primary objective was to determine if desiccation is a major source of mortality for juveniles in terrestrial habitats and the relative difference in the rate of desiccation among microhabitats. We designed an enclosure study where the fate of individuals is known and provide survival estimates that can be compared to other enclosure studies where the fate is unknown. Our second objective was to determine if increased desiccation risks in recent clearcuts relative to uncut stands could explain the previously observed low abundance levels of amphibians in harvested stands. In addition, we test whether coarse woody debris minimizes desiccation risks and whether desiccation risks differ among amphibian species constrained within the same microhabitats. Therefore, we estimate and compare rates of water loss and survival estimates of three anuran species held in enclosures within four microhabitats, two of which occur in control forest and two within recently harvested forest.

Methods

Study Area

We conducted this experiment in July of 2005 and 2006 at the Daniel Boone Conservation Area (DBCA) in Warren County, Missouri, USA. The forest at DBCA is typical of the Ozark Region with an overstory dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.) and an understory of sugar maples (*Acer saccharum*) (Kabrick et al. 2002; Nigh & Schroeder 2002). The area contains dissected hills with deep, narrow ravines that expose loess soils. Relief ranges from 60 – 100 m. Mean annual precipitation is 102 cm, mean daily minimum temperature in January is -8.3°C and the mean daily maximum temperature in July is 32.2°C. In 2005, Missouri experienced the driest spring in over 20 years (NOAA weather summaries for St. Louis, Missouri). Total spring rainfall from 1 March 2005 through the period of our experiment was 30 cm. Total spring rainfall in 2006 (40 cm) was similar to the 20 year average (43 cm) in the spring (Weather Underground: http://www.wunderground.com/).

To incorporate the spatial variability among ravines, ridgetops and clearcuts, we conducted this experiment at two sites located 1 km apart within DBCA. Each site contained a clearcut stand (Clearcut) and an uncut stand (Forest). We identified two microhabitats within each stand, and thus the four microhabitats studied were Forest Ridgetop, Forest Drainage, Clearcut Open, and Clearcut Brushpile. The two Forest microhabitats were within second growth, mature (75 – 100 yrs) oaks and hickories. We defined Forest Ridgetop as a flat area near the top of hills with continuous canopy cover and Forest Drainage as a 20 m wide area centered on a ravine where water flows intermittently after large rain events. The two Clearcut microhabitats were primarily on ridge tops and within stands harvested in 2004 as part of a multi-regional, collaborative study referred to as LEAP (NSF Collaborative Project: Land-use Effects on Amphibian Populations). Harvest involved removing all marketable tree trunks greater than 25 cm in diameter, leaving all crowns on the ground, and felling all non-marketable trees. We defined Clearcut Open as locations with grasses and forbs within the harvested stand, but lacking tree trunks or crowns and Clearcut Brushpile as locations where the crowns of oak trees were left.

Study Species

We collected American toad (*Bufo americanus*) and wood frog (*Rana sylvatica*) eggs from DBCA and raised them until metamorphosis in cattle tanks as part of a different study (Harper 2007b). We raised these metamorphs in a laboratory at University of Missouri for approximately one month, because a pilot study indicated that small size at metamorphosis of these species hindered our ability to accurately measure water loss in the field. Metamorphs were fed crickets *ad libitum*. We collected recently metamorphosed green frogs (*Rana clamitans*) from a pond in the study area one day prior to the experiment. Prior to initiating the experiment, we transferred all frogs to containers without food for approximately 24 hours and placed frogs in standing water for approximately 8 hours to ensure frogs were fully hydrated.

Study Design

We used three factors in a full-factorial design with four replicates: microhabitat (four factor levels: Forest Ridgetop, Forest Drainage, Clearcut Open, and Clearcut Brushpile), species (three factor levels: wood frog, green frog, and American toad), and year (two factor levels: 2005 and 2006). The statistical unit of replication was an enclosure that contained one frog ($N_{total} = 96$). We constructed enclosures out of hardware cloth rolled into a circular tube (0.635 cm^2 mesh size, 46 cm tall, 15 cm diameter). This enclosure size allowed individuals to be found following desiccation when both mass and volume are greatly reduced and was previously used by Rothermel & Luhring (2005) and Rothermel & Semlitsch (2002).

The two Clearcut microhabitats were interspersed within each site and the two Forest microhabitats were spatially segregated within each site. We selected the location of each enclosure by spacing enclosures within a stand an equal distance from each other and at least 15 m apart. Clearcut Brushpile enclosures were each placed within a unique oak tree top, thus enclosures contained large pieces of bark especially in year 2 but did not contain coarse woody debris. We installed 12 enclosures in each microhabitat (totaling 48 enclosures in each year) and we used 16 individuals of each species each year (totaling 48 individuals in each year). We installed the enclosures using a post-hole digger to separate the soil in a ring 7 – 10 cm deep and inserted one end of the tube into the ring, thus minimizing disturbance to the soil, litter, and vegetation. We then packed the soil around the edge of the tube and constructed a lid out of fiberglass window screening to prevent escape.

Starting at 18:00 on 14 July 2005 and 6 July 2006, we systematically weighed each frog with a scale (Acculab PP-2060D) and placed the frog in a randomly assigned enclosure. We collected three soil moisture (TH2O probe and HH2 data logger, Dynamax Inc.) and three soil temperature (Taylor 9841 digital thermometer) measurements at a depth of 7 cm and within 0.5 m of each enclosure. This procedure took approximately 3 – 4 hours due to the distance among enclosures. We repeated this procedure by returning to enclosures in the same order every 6 hours for 24 hrs (i.e. 18:00, 24:00, 6:00, 12:00, and 18:00 CST). Therefore, although we could not measure all frogs simultaneously, the mass for a given individual was measured at approximately 6 hour intervals. Frogs remained undisturbed within the enclosure except when removed to measure weight. We assumed all decreases in mass during the 30 hr experiment were due to water loss. When mortality occurred, we obtained a mass for that time period, noted the mortality, and removed the individual from the experiment without replacement (sample size decreased over time). Green frogs that appeared healthy at the completion of the experiment were released in the pond of capture and the remaining frogs were preserved.

Analysis

We examined two response variables, survival and proportion of water loss as measured by the change in mass over 30 hrs, and performed all analyses within SAS version 9.1. We used proportion of water loss as opposed to total amount of water loss to account for size differences among individuals. We tested for differences in proportion of water loss among species, microhabitats, and years using Analysis of Variance (ANOVA). We treated the proportion of water loss over the 4 time intervals as a repeated measure of each individual. We estimated survival rates and 95% confidence intervals using the binomial distribution survival method for discrete-time intervals (PROC GENMOD). We compared survival rates among species, among microhabitats, and between years using a likelihood ratio statistic. Finally, we used a repeated measure analysis of variance to compare soil moisture and soil temperature among microhabitats and between years.

Results

Water Loss

All three anuran species were unable to remain fully hydrated while constrained within the four microhabitat treatments. The proportion of water lost by each species, as measured by proportion of weight loss, differed among microhabitats and this pattern also differed between years (i.e., species × microhabitat × year interaction; d.f. = 6, 320, $F = 2.44$, $P = 0.0253$; Fig. 1). American toads lost more water in Clearcut Open during year 1 than year 2, while they lost similar proportions of water among the other microhabitats in both years. Green frogs in year 1 lost similar proportions of water in each microhabitat; whereas, green frogs in year 2 lost the most water in Clearcut Open and the least in Clearcut Brushpiles. Wood frogs lost a large proportion of water in Clearcut Open and Forest Ridge habitats, but remained hydrated in the Clearcut

Brushpile and Forest Drainage habitats. Wood frogs responded to all microhabitats similarly between years.

Water loss was generally low during the night and increased during daylight hours in all microhabitats; however, the proportion of water lost within each time interval differed among microhabitats (i.e., time × microhabitat interaction; d.f. = 12, 320, F = 3.16, P = 0.0003; Fig. 2). The 95% confidence intervals show that water loss increased in Clearcut Open [0.4816, 0.6897] during time interval 3 (i.e., 06:00 – 12:00) more than in either the Forest Ridgetop [0.1748, 0.4919], Forest Drainage [0.0190, 0.2112], or Clearcut Brushpile [-0.0220, 0.3535] microhabitats. Water loss during each time interval did not differ by species (d.f. = 8, 320, F = 1.46, P = 0.1716).

Survival

Survival in year 1 (0.480, SE = 0.580, N = 22) was lower than survival in year 2 (0.739, SE = 0.585, N = 32; $\chi^2 = 9.37$, P = 0.0022; Fig. 3). Survival differed among species ($\chi^2 = 41.78$, P < 0.0001; Fig. 3). American toads survival was highest (0.872, SE = 0.608, N = 23), followed by green frog survival (0.645, SE = 0.592, N = 19), and then wood frog survival (0.254, SE = 0.594, N = 12). Survival also differed greatly among microhabitats ($\chi^2 = 62.38$, P < 0.0001; Fig. 3). Survival was highest in Forest Drainage (0.873, SE = 0.619, N = 20), followed by Clearcut Brushpile (0.871, SE = 0.620, N = 18), next was Forest Ridgetop (0.378, SE = 0.596, N = 11), and lowest was in Clearcut Open (0.195, SE = 0.602, N = 5). All three species in both years had the lowest survival in Clearcut Open. Survival in Forest Drainage was the most consistent between years and was comparable to survival within Clearcut Brushpiles.

Soil Moisture and Soil Temperature

Percentage soil moisture differed among microhabitats and between years (i.e., microhabitat × year interaction; d.f. = 3, 399, F = 3.33, P = 0.0197; Fig. 4). Soil moisture was greater in year 2 for all microhabitats except for Clearcut Brushpile where soil moisture decreased in year 2. Soil moisture within a year did not change over the 4 time intervals. Soil temperature differed among microhabitats, over time, and between years (i.e., microhabitat × time × year interaction; d.f. = 12, 399, F = 2.12, P = 0.0152; Fig. 5). Daily fluctuation in soil temperatures was fairly moderate in three of the microhabitats, but soil temperature varied greatly over the 4 time intervals in the Clearcut Open. Soil temperatures in year 2 were approximately 4°C cooler than in year 1 at each time interval.

Discussion

Microhabitat conditions within both uncut and harvested forest affected the ability of frogs to remain hydrated. Desiccation can therefore be a major source of mortality for recent metamorphs entering terrestrial habitats and is likely the fate of individuals not recaptured in other enclosure studies. Similar desiccation risks have also been found for ambystomatid salamanders (Rothermel & Luhring 2005). In addition, we found that when soil moisture levels are low, desiccation occurs within hours (i.e., Clearcut Open) and within a day (i.e., Forest Ridge), emphasizing the importance of soil moisture to amphibians in terrestrial habitats. Finally, the rapid water loss in areas within Clearcut

Open suggests that reduced abundance levels in clearcuts with low levels of coarse woody debris compared to uncut forest is the result of desiccation mortality.

Our results demonstrate that the microhabitats within continuous forest are not equally suitable for amphibians (Patrick et al. in review; Rittenhouse & Semlitsch 2007). Although Forest Ridgetop and Forest Drainage microhabitats were located within 50 – 100 m of each other and leaf litter was present throughout both, low soil moisture in Forest Ridgetop caused frogs to experience higher desiccation mortality than frogs in Forest Drainage. This result was initially surprising, because amphibians at our study site use breeding sites primarily located on ridgetops. Further, leaf litter correlates with diversity and evenness (DeGraff & Rubis 1990) and is a habitat feature that blocks wind and reduces evaporative water loss (Seebacher & Alford 2002). However, high water loss rates on Forest Ridgetops suggest that leaf litter was not enough to shelter frogs from the wind on ridgetops. In addition, adult wood frogs at this study site were recently radio-tracked migrating from breeding sites on ridgetops to drainages (Rittenhouse & Semlitsch 2007). Ravines within oak-hickory forest are therefore an important feature of amphibian terrestrial habitat in Missouri, indicating that successful migration from natal ponds to drainages may be crucial for juvenile survival within oak-hickory forests.

Survival in Clearcut Open was 19.5%, demonstrating severe demographic consequences for amphibians in some microhabitats within clearcuts. Migrating amphibians may behaviorally avoid areas without canopy cover (Patrick et al. 2006; Rittenhouse & Semlitsch 2006; Semlitsch et al. In Review), but amphibians emerging from overwintering or aestivation sites may be caught within clearcuts when harvest occurs during inactivity periods and some individuals may choose to travel through harvested stands (Patrick et al. 2006; Todd & Rothermel 2006). Coarse woody debris within clearcuts may serve as important microhabitats in these situations (Bartelt et al. 2004; Chazal & Niewiarowski 1998; Pough et al. 1987). In our study, brushpiles mitigated the negative desiccation effects of timber harvest on amphibians by providing microhabitats with increased soil moisture and shade. Soil moisture in brushpiles even exceeded soil moisture levels on forested ridgetops, causing frogs to experience less water loss and higher survival within Clearcut Brushpiles compared to both Clearcut Open and Forested Ridgetop microhabitats. However, brushpiles may also provide habitat for many amphibian predators. Predation is an important source of mortality that was not included in our study, but we observed a garter snake coiled around a Clearcut Brushpile enclosure attempting to depredate a frog. In addition, radio-tagged adult wood frogs at this site were never relocated within brushpiles following timber harvest (Rittenhouse unpub. data), suggesting that frogs may not use brushpiles in an attempt to avoid predation.

We found large differences among species in their ability to prevent water loss and mortality. We suggest that physiological differences alone can not explain the species differences. Skin is similar among most amphibian species including the three study species and it does not prevent evaporative water loss (Jorgensen 1997; Tracy 1976). Small species differences in evaporative water loss are attributed to differences in body shape (i.e., round species have smaller surface area / volume ratio than flat species) (Thorson 1955), characteristics of the blood (Burggren & Vitalis 2005), and initial water content (i.e. amount of water in a frog when fully hydrated) (Thorson 1955). For example, terrestrial amphibian species increase their initial water content by storing water in the bladder, and thus prolonging the amount of time until desiccation by having more water to loose(Jorgensen 1997). Physiological differences among species are detected in laboratory studies with accurate measurements techniques. We suggest that behavioral differences, such as sitting in a water conserving postures (Pough et al. 1983), account for the large species differences we found by measuring change in mass in the field. We observed all species active on top of the leaf litter or vegetation at night when microclimate conditions, such as low temperatures, high relative humidity, and dew on vegetation, were not limiting. Water loss increased significantly for all species at sunrise, but the behavioral response of each species differed. Water conserving behaviors by green frogs were not apparent, as they occurred on top of leaf litter most often and readily jumped as we searched enclosures. Wood frogs sat under the leaf litter with their bellies pressed against the soil to absorb moisture and would remain in this position until touched. Similar behavior has been observed in adult wood frogs (Rittenhouse & Semlitsch 2007). American toads absorbed soil moisture and prevented evaporative water loss by burrowing into the soil layer and this burrowing behavior made toads difficult to locate.

An intriguing result was that species differences in water loss were not consistent among microhabitat types (i.e., species × microhabitat interaction; Fig. 1). For example, both wood frogs and American toads in year 1 lost water in Clearcut Open microhabitat; however, in the Forest Ridgetop American toads remained fairly hydrated while wood frogs did not. Behavioral differences must be causing this interaction, because physiological differences among species would result in the same species having the lowest water loss in all microhabitats. Burrowing behavior in toads was more evident on

Forested Ridgetops than Clearcut Open, potentially due to reduced mulch layer and soil compaction following harvest. The burrowing behavior of toads reduces the amount of skin exposed to evaporative water loss. Preventing water loss from the skin is not necessary when moisture can be readily absorbed from the soil (Heatwole & Lim 1961); however, when soil moisture is extremely low as occurred on Forested Ridgetops, the burrowing behavior of toads allows them to persist longer than the other species. This species by microhabitat interaction (Fig. 1) also resulted from wood frogs remaining the most hydrated in the two moistest microhabitats (i.e., Clearcut Brushpiles and Forest Drainage). Although all three species can absorb moisture from the soil, wood frogs capitalized on this shared ability by flattening themselves against moist soil to increase the surface area contact. Amphibian behaviors in terrestrial habitats warrant further research, because understanding behavioral differences among species may improve our ability to explain abundance patterns within terrestrial habitats and to predict which species may be most threatened by habitat modification.

Desiccation risks in clearcut stands likely decreases with succession. American toads were the only species to show reduced water loss in Clearcut Open after one year of regeneration, suggesting toads may use dew or shade produced by ground vegetation. Successional changes in Clearcut Brushpiles may explain the increased survival of all species in year 2. One year of decomposition resulted in large pieces of bark on the ground in year 2 that may serve as a moisture conserving structure for amphibians within brushpiles. However, the effectiveness of brushpiles in reducing desiccation risk also varied based on the amount of vines and other vegetation covering the oak treetop with a tent-like structure. Only some of the oak treetops in year 1 were completely covered with vines, whereas all treetops were completely covered with vegetation in year 2. The dense covering may help frogs remain hydrated, but the vegetation may also prevent rainfall from reaching the soil, as suggested by soil moisture decreasing in year 2 within Clearcut Brushpiles but increasing in the other microhabitats.

Successional changes partially contributed to increased survival within clearcuts during year 2, but survival also increased in both forested microhabitats, suggesting that daily and seasonal weather differences also influenced survival rates between years. Increased spring rainfall in year 2 was reflected in our results as increased soil moisture in all microhabitats except the Clearcut Brushpiles. In addition, the daily high temperature was 4°C cooler in year 2 compared to year 1. The rate of evaporative water loss via skin increases as temperature increases (Jorgensen 1997), thus amphibians in hot temperatures must obtain more moisture from the soil to remain hydrated than amphibians in cool temperatures. Therefore, drier conditions and warmer temperatures likely contributed to lower survival rates in year 1 than year 2.

Experimental studies that elucidate the mechanisms driving observed abundance patterns inform potential management options for altering these abundance patterns. Low survival rates due to desiccation are one plausible explanation for low amphibian abundance levels in recently harvested forests. Therefore, reducing desiccation risks for amphibians will likely reduce the deleterious effects of forest harvest on local amphibian populations. One management option is the retention of down wood to maintain soil moisture within harvested stands. Our study examined the survival consequences of being constrained within particular microhabitats. Low survival over the 30 hrs indicates that harvested stands with low levels of coarse woody debris and distances from the center of harvested stands that greatly exceed maximum daily movement distances of amphibians may prevent successful dispersal through or out of a stand. Further research should address habitat choices made by individuals that are allowed to move freely through the landscape. For example, Bartelt (2004) found that radio-tagged boreal toads used slash piles on the edge of clearcuts. More behavioral research is required before we can provide management recommendations regarding the size and configuration of forest stands that may allow an amphibian to disperse successfully from harvested stands. Finally, species differences in our study highlight the need to consider species-specific responses to timber harvest as opposed to assuming that all amphibian species respond to forest management in a similar manner.

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Figure 1. Species-specific water loss by microhabitats. Water loss, measured by proportion of initial mass, differed among species and between year 1 (A) and year 2 (B). Water loss was measured as proportion of initial mass. Dead individuals were weighed during the time interval when initially found and then removed from the experiment. Error bars represent standard error.

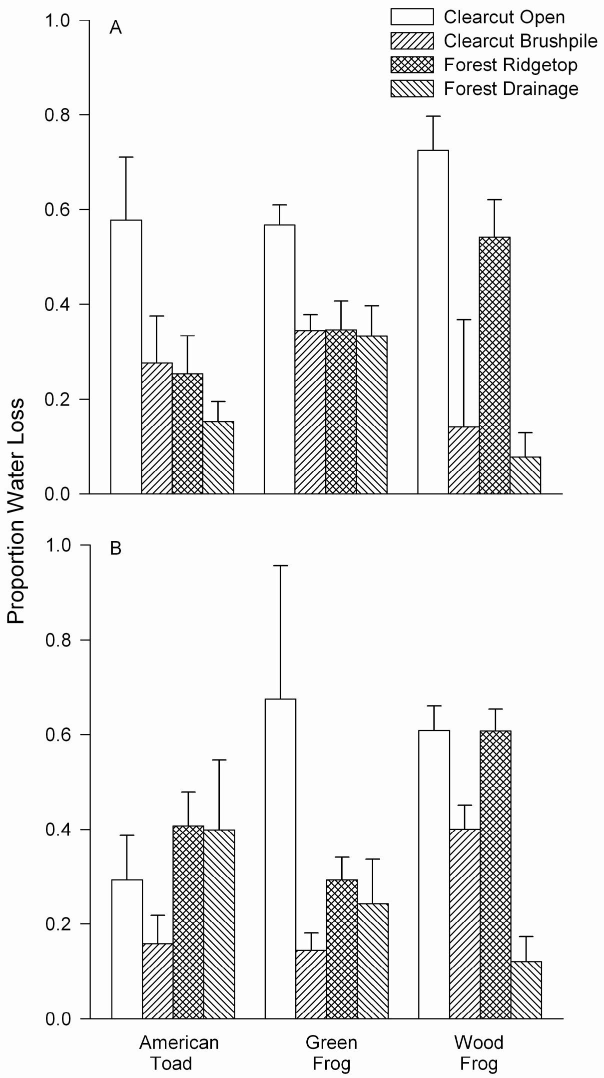

A
B
Clearcut Open
Clearcut Brushpile
Forest Ridgetop
Forest Drainage
Proportion Water Loss
1.0
0.8
0.6
0.4
0.2
0.0
American Toad
Green Frog
Wood Frog

Figure 2. Mean proportion water loss over by microhabitats. Water loss was measured as proportion of initial mass. Dead individuals were weighed during the time interval when initially found and then removed from the experiment, thus sample size decreases over time. Water loss increased at 06:00 for all species, but the increase was greatest in Clearcut Open where many individuals are dead. Clearcut microhabitats are indicated with dashed lines and open symbols. Forest microhabitats are indicated by solid lines and closed symbols. Error bars represent standard error.

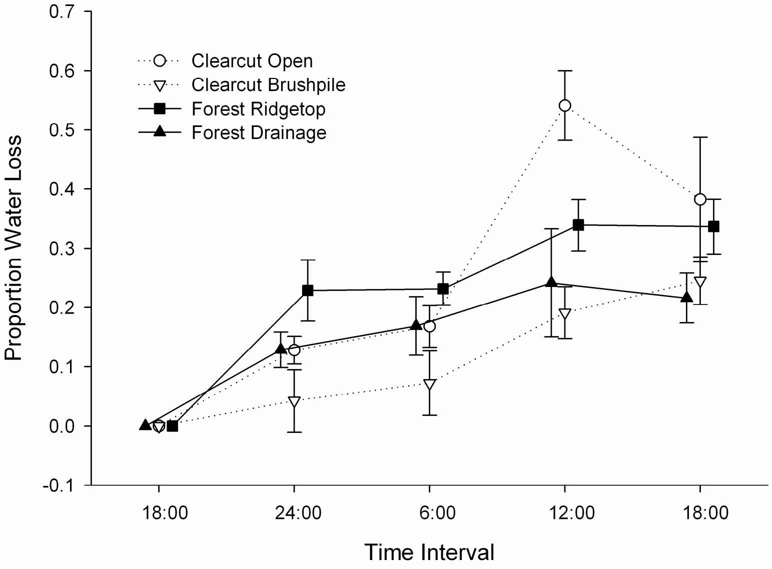

Clearcut Open
Clearcut Brushpile
Forest Ridgetop
Forest Drainage
Proportion Water Loss
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
18:00
24:00
6:00
12:00
18:00
Time Interval

Figure 3. Survival curves for American toads (A, B), green frogs (C, D) and wood frogs (E, F) held within enclosures in four microhabitats in year 1 (A, C, E) and year 2 (B, D, F). Clearcut microhabitats are indicated with dashed lines and open symbols. Forest microhabitats are indicated by solid lines and closed symbols. Error bars represent 95% confidence intervals.

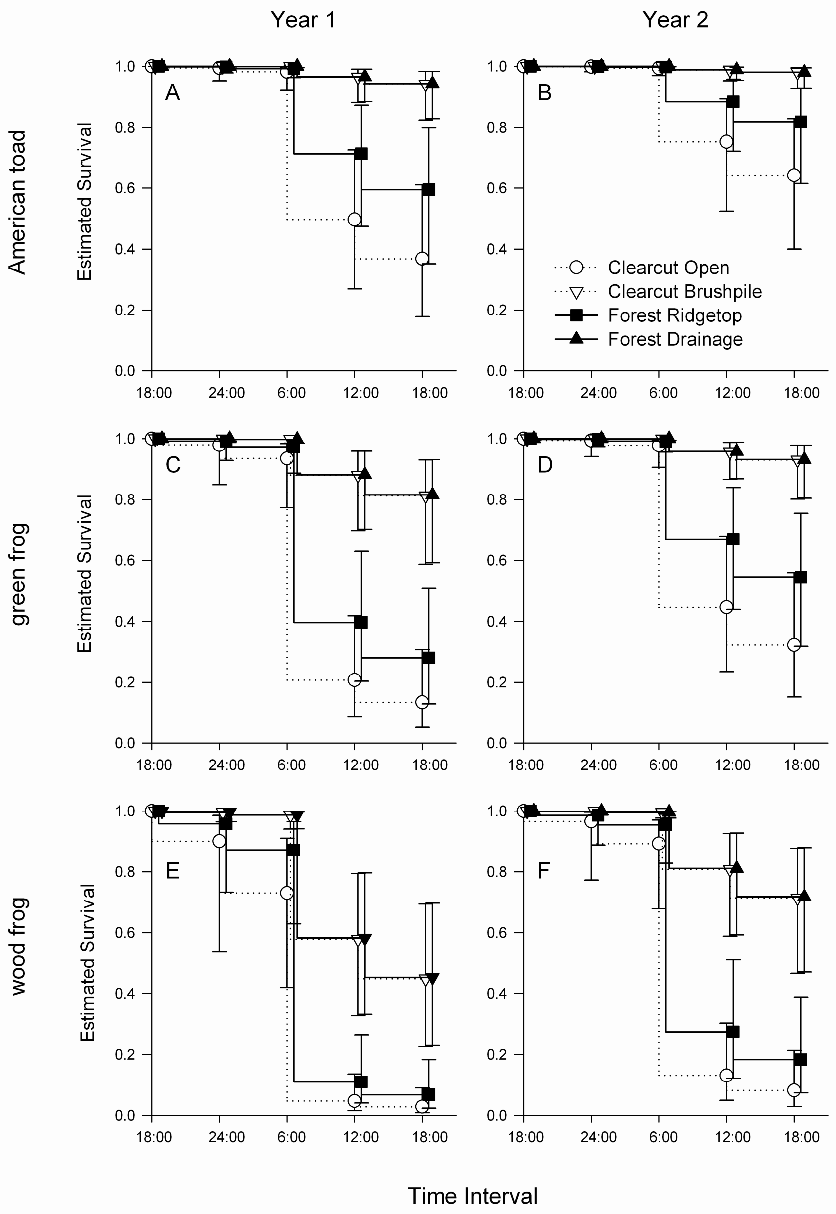

Year 1
Year 2
American toad
green frog
wood frog
Estimated Survival
A
B
C
D
E
F
1.0
0.8
0.6
0.4
0.2
0.0
18:00
24:00
6:00
12:00
18:00
Clearcut Open
Clearcut Brushpile
Forest Ridgetop
Forest Drainage
Time Interval

Figure 4. Percent soil moisture increased in year 2 in all microhabitats except Clearcut Brushpile. Error bars represent standard error.

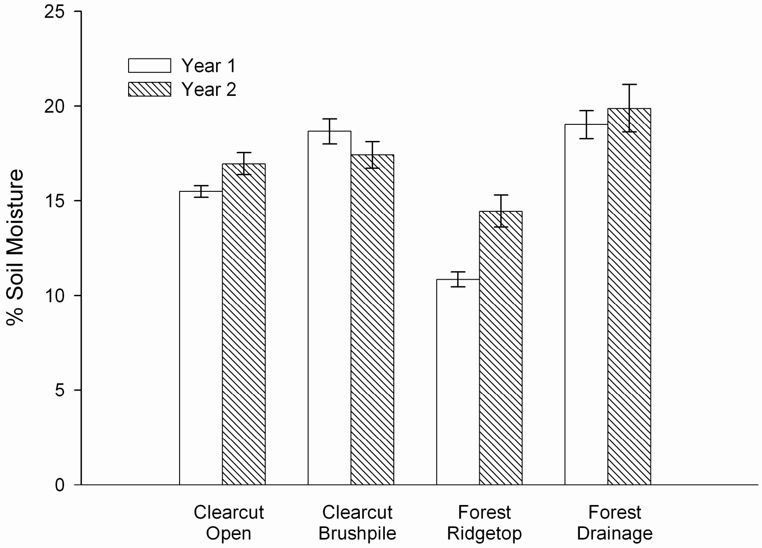
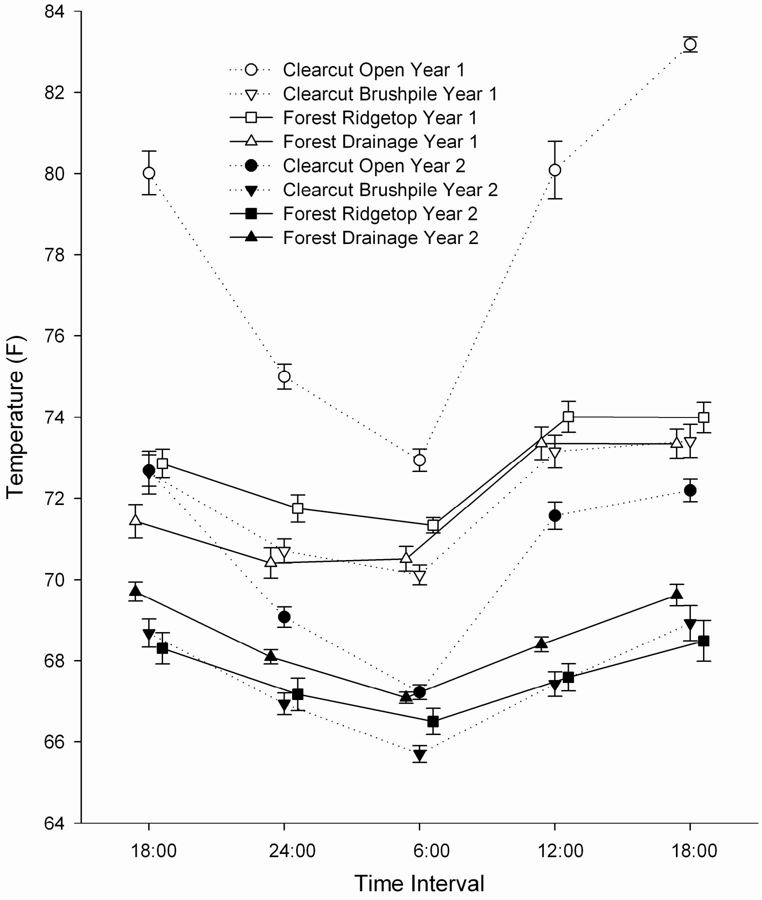

% Soil Moisture
0
5
10
15
20
25
Year 1
Year 2
Clearcut Open
Clearcut Brushpile
Forest Ridgetop
Forest Drainage

Figure 5. Soil temperature over time differed among microhabitats. Soil temperature decreased during the night and increased during the day in all microhabitats, but the magnitude of the change within a year was much greater in Clearcut Open compared to the other microhabitats. Soil temperature was hotter in year 1 (open symbols) compared to year 2 (closed symbols). Clearcut microhabitats are represented by dashed lines and forest microhabitats are represented by solid lines. Error bars represent standard error.


Clearcut Open Year 1
Clearcut Brushpile Year 1
Forest Ridgetop Year 1
Forest Drainage Year 1
Clearcut Open Year 2
Clearcut Brushpile Year 2
Forest Ridgetop Year 2
Forest Drainage Year 2
Temperature (F)
84
82
80
78
76
74
72
70
68
66
64
18:00
24:00
6:00
12:00
18:00
Time Interval

VITA

Tracy Ann Green Rittenhouse was born on 1 March 1978 in Robbinsdale, Minnesota and grew up in New Hope, Minnesota. Following her graduation from Robbinsdale Armstrong High School in 1996, she enrolled at the University of Wisconsin-Madison and earned a B.S. from the Department of Wildlife Ecology in May 2000. Tracy began her graduate tenure at the University of Missouri-Columbia under the guidance of Raymond D. Semlitsch in May 2000. She married Chadwick D. Rittenhouse on 5 October 2002 and she earned a M.A. from Division of Biological Sciences in December 2002. Tracy completed an internship with the Wisconsin Wetland Association in February 2007 in fulfillment of the MU Graduate Certificate in Conservation Biology and she earned a Ph.D. from the Division of Biological Sciences in December 2007. Tracy and her husband are moving to Madison, Wisconsin. She is pursuing funding opportunities for a post-doctoral position with Joy B. Zedler, a wetland restoration biologist, as well as, conservation activities with local NGOs.