HABITAT USE AND SEASONAL MOVEMENT PATTERNS OF FOUR-TOED SALAMANDERS (*HEMIDACTYLIUM SCUTATUM*) IN MASSACHUSETTS

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DEDICATION

To my husband and daughter,

for your enduring patience and encouragement.

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ABSTRACT

HABITAT USE AND SEASONAL MOVEMENT PATTERNS OF FOUR-TOED SALAMANDERS (*HEMIDACTYLIUM SCUTATUM*) IN MASSACHUSETTS

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Understanding the movement phenology of enigmatic species like the four-toed salamander (*Hemidactylium scutatum*) is essential to guide management practices for breeding habitat and the surrounding uplands. I examined the relationship between environmental variables and the directionality, timing, and magnitude of adult and juvenile four-toed salamander movements at two locations in eastern Massachusetts. Movements to and from breeding wetlands were monitored using drift fences with pitfall traps. Four-toed salamanders move from upland habitats to wetland areas in early spring and move away from wetlands in late spring. Nights during which four-toed salamander adults moved were related to the amount of precipitation occurring 24 hours earlier, and the phase of the moon at the time of movement. Adult movements increased with more precipitation and less moon light. Juvenile movements were similarly affected, and in addition they were more likely to move when temperatures were warm and days long. The number of adults moving could not be predicted by day length, mean temperature, precipitation, or lunar phase. As for many other amphibian species, management plans for four-toed salamanders must include the maintenance of suitable upland habitat near breeding wetlands. My results can be used to implement management strategies aimed at reducing human-related impacts on migrating four-toed salamanders (e.g., road closures to reduce road mortality).

I developed and evaluated the accuracy of classification and regression tree (CART) models at multiple spatial scales to predict suitable habitat and potential species occurrences of the four-toed salamander (*Hemidactylium scutatum*) in Massachusetts. I analyzed four-toed salamander Element Occurrence (EO) observations reported to the Massachusetts Natural Heritage and Endangered Species Program (NHESP) during 1990-2009 in response to fifteen environmental predictor variables at six different local and landscape-scales. The CART models were evaluated using a subset of data withheld from model development. The landscape-scale model measured at 2000 m was most successful at predicting four-toed salamander habitat. The 2000 m model correctly classified 92.4% of the training data and 87.7% of the verification data. When the 2000 m model was applied statewide, 30,195 wetlands were determined to be potentially suitable habitat for the four-toed salamander. The results of this study confirm the potential and value of classification and regression tree models for identifying potential habitat for rare or cryptic species. Predictive models could prove very useful for focusing survey effort and formulating conservation strategies for these species.

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CHAPTER 1

UNDERSTANDING THE MOVEMENT PHENOLOGY AND HABITAT USE OF THE FOUR-TOED SALAMANDER (*HEMIDACTYLIUM SCUTATUM*) IN MASSACHUSETTS

1.1 Introduction

Phenology of annual pond-breeding amphibian movements has been an increasing area of interest in recent years due to potential changes in temperature or the frequency and duration of rainfall caused by climate change. These climatic changes have the potential for detrimental effects on the hydroperiod of breeding ponds or overland migration for some species. Models describing the timing of amphibian movements often incorporate environmental predictors such as temperature and precipitation (Gascon 1991, Blaustein et al. 2001, Todd and Winne 2006, Hocking et al. 2008, Scott et al. 2008, Carroll et al. 2009, Neveu 2009). Since amphibians are dependent on adequate environmental moisture for water balance and respiration (Jørgensen 1997, 2000, Hillyard 1999), it follows that several studies have found a positive association between amphibian movements and daily rainfall amounts (Gascon 1991, Todd and Winne 2006, Timm, McGarigal, and Gamble 2007). However, the degree to which amphibians depend on precipitation varies widely between species and age-class (Todd and Winne 2006, Timm, McGarigal, and Gamble 2007). Consequently, warm, wet weather has been found to be correlated with earlier breeding events in some amphibians (Gascon 1991, Scott et al. 2008, Carroll et al. 2009), but not in others (Blaustein et al. 2001).

Models that accurately predict breeding movements can play an important role in amphibian conservation by informing the timing of wetland drawdowns, timber harvests, and road closures. Amphibian reproductive success is dependent on breeding ponds being available at the appropriate time and for an appropriate duration (Semlitsch 2000, Paton and Crouch 2002), and thus the timing of drawdowns, and other wetland management practices, is critical to their success. In addition, the quality of upland habitat surrounding breeding ponds is equally important as shown by amphibian populations migrating away from clear-cut forests (Semlitsch and Conner 2008), displaying reduced population sizes in clear-cuts (Grialou et al. 2000), and showing fewer detrimental effects in selective timber harvests (Stronjny and Hunter 2010). Road traffic can also negatively impact amphibians through direct mortality and by acting as a barrier to movement (Eigenbrod et al. 2008, Veysey et al. 2011), though these effects might be mitigated by properly timed road closures.

Recent efforts by biologists to understand the timing of movements of pond-breeding amphibians have concentrated on the most conspicuous species such as the spotted salamander (*Ambystoma maculatum*), marbled salamander (*Ambystoma opacum*), red-spotted newt (*Notophthalmus viridescens*), and wood frog (*Rana sylvatica*) (Paton et al. 2000, Paton and Crouch 2002, Vasconcelos and Calhoun 2004, Timm, McGarigal, and Compton 2007, Timm, McGarigal, and Gamble 2007, Hocking et al. 2008, Roe and Grayson 2008, Todd et al. 2011, Gravel et al. 2012), with little work being done on cryptic species such as the four-toed salamander (*Hemidactylium scutatum*). This species is especially difficult to study due to its small body size (Blanchard and Blanchard 1931, Berger-Bishop and Harris 1996, O'Laughlin and Harris 2000, Bruce 2005), restricted period of breeding migration (Blanchard 1923, Breitenbach 1982), and cryptic nest sites (Chalmers and Loftin 2006, Wahl et al. 2008). Despite these challenges, it is important to understand the factors influencing breeding migrations of this species since it is highly vulnerable to habitat loss and degradation (Klemens 1993, Hamer and McDonnell 2008, Windmiller and Homan 2008, Scheffers and Paszkowski 2011).

The Massachusetts Natural Heritage and Endangered Species Program (NHESP) along with Hyla Ecological Services collected breeding movement data for four-toed salamanders in Massachusetts during 1999, 2000, 2001, and 2003, and I used classification and regression tree analysis (CART), and Poisson regression, to predict animal movements based on several environmental factors. Movement responses in my analyses included 1) direction, 2) timing, and 3) magnitude.

1.2 Methods

1.2.1 Study Species and Sites

Four-toed salamanders are the smallest Plethodontid (lungless) salamander found in New England. Adults average 7-9 cm in total length (Blanchard and Blanchard 1931, Chalmers 2004). Females migrate from upland habitats in spring to lay eggs in *Sphagnum sp.* hummocks and other organic material found near pools of lentic waters or low flow streams (Wahl et al. 2008). Males have not been found to migrate to the nesting sites and little is known about their habitat use and ecology (Harris 2008). Females generally stay with the eggs from laying until hatching six weeks later (Harris et al. 1995). Larvae metamorphose approximately six weeks after hatching, and then adults and juveniles move into upland habitat (Blanchard and Blanchard 1931, Bishop 1941, Harris et al. 1995). Prior to over-wintering, females are believed to mate with males in the uplands, and then hold spermatophores until the following spring, though this part of their natural history has received little attention (Dieckmann 1927, Chalmers and Loftin 2006). NHESP and Hyla Ecological Services conducted the data collection for this study at two locations in eastern Massachusetts. The study area in Sudbury, Massachusetts, consisted of a semi-permanent pond and surrounding forest habitat (Regosin et al. 2005). The forest community at the Sudbury site consisted of pine–oak forest, red maple swamp, and mixed deciduous forest/shrubland (Regosin et al. 2005). The study area in Northborough, Massachusetts, consisted of forest and two vernal pools adjacent to athletic fields of a regional high school. Forest vegetation at the Northborough site was similar to that of the Sudbury site. The area was comprised primarily of pine–oak forest and red maple–shrub swamp. The pine-oak forest was dominated by white pine (*Pinus strobus*), white oak (*Quercus alba*), black oak (*Q. velutina*) and red oak (*Q. rubra*). The red maple-shrub swamp was predominately composed of red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), black birch (*Betula lenta*), smooth alder (*A. serrulata*), multiflora rose (*Rosa multiflora*), and tussock sedge (*Carex stricta*). Tussock sedge hummocks were the habitat used for nesting by four-toed salamanders (Goddard and Windmiller 2003).

1.2.2 Salamander Sampling

Drift fences and pitfall traps were installed primarily for monitoring vernal pool obligate amphibians (Goddard and Windmiller 2003, Regosin et al. 2005), but this sampling method was also effective at capturing four-toed salamanders. At the Northborough site, sampling was conducted during the 2003 spring amphibian breeding season, from 25 March to 23 June. At the Sudbury site, sampling occurred from March 1999 to December 2001, however, the full fencing array was not completed until March 2000, just prior to the spring breeding migration.

Drift fences placed at each site formed a grid of uneven cells in a pattern radiating from seasonal pools (Figure 1.1). Drift fencing consisted of 90 cm high silt fence embedded 25 cm in the ground. A pair of 19-liter buckets (one on either side of the silt fence), placed every 15 m along the fence, served as pitfall traps and were sunken into the soil so that their tops were flush with the ground surface. In cases where the groundwater level was too high to allow operation of pitfall traps, a funnel-shaped minnow trap was placed against, and parallel to, the silt fence. A total of 201 pairs of traps were placed at the Northborough site, and 156 pairs of traps were placed at the Sudbury site. Each trap had a unique identification number and was mapped using a Global Positioning System (GPS) receiver. A moistened foam sponge and a specially designed small mammal escape device was placed in each bucket to reduce the chance of mortality for captured animals (Regosin et al. 2005).

Pitfall traps at the Sudbury site were checked after each rain event and at least every 2-3 days. Pitfall traps were checked daily at the Northborough site due to high population densities. All captured reptiles, amphibians, and mammals were identified, counted, and released on the opposite side of the drift fence from which they were captured. Four-toed salamanders were sexed, weighed, measured, and individually marked with either visual implant elastomer or toe clips before release.

Areas of potential nest sites were searched four times during the nesting season. Nests consisted of a cluster of eggs within a *Sphagnum sp*. or *Carex sp.* hummock, usually accompanied by an adult female. When a nest was found, it was given a unique identification number and flagged for later location. Additionally, nesting females were checked for identification codes, indicating they had been previously captured in a pitfall trap.

1.2.3 Environmental Variables

Based on common factors that affect the movement of pond-breeding amphibians (Semlitsch 1985, Timm, McGarigal, and Gamble 2007), I identified five environmental predictors that were evaluated in all models, and are detailed below:

Day length (DAYLENGTH) was defined as the number of hours from sunrise to sunset on the day of capture and was correlated with light intensity and date. Day length was calculated from the US Naval Observatory Sun Rise/Set Table for Worcester, Massachusetts. I believed that day length would be a critical factor determining the timing and directionality of movements, and the number of four-toed salamanders moving on a movement day. Adults overwinter in forested upland habitat and I expected that their movements would occur before those of juveniles and be directed toward the nesting wetland. Juveniles also overwinter in forested uplands but because they do not need to locate nesting sites, I assumed they would move toward wetlands later in the spring.

Mean temperature (MEANTEMP) was calculated in degrees Celsius from NOAA National Climatic Data Center Daily Surface Data collected at the Worcester, Massachusetts, weather station. I believed that mean temperature would be an important predictor variable because, like all pond-breeding amphibians in New England, four-toed salamanders are ectothermic and thus their body temperature is highly influenced by ambient temperature (Sexton et al. 1990). Mean temperature is unavoidably confounded with day length, and therefore the presence of one of these in a model may obscure the importance of the other.

Amount of precipitation the previous day (RAINAMOUNT24) was estimated in mm from midnight to midnight using NOAA National Climatic Data Center Daily Surface Data collected at the Worcester, Massachusetts, weather station. I assumed that precipitation would be a good predictor of the timing of movement, and number of four-toed salamanders moving, but not the directionality of movements. Since both juvenile and adult four-toed salamanders perform gas exchange via moistened skin, I expected that precipitation would affect by age classes equally.

Drought length (DROUGHTDAYS) was calculated from NOAA National Climatic Data Center Daily Surface Data as the number of days without rainfall preceding the day of interest. As with the preceding predictor, amount of precipitation the previous day, I believed that drought length would be a good predictor of the timing of movement, and number of four-toed salamanders moving, but not the directionality of movements. Due to the need for maintenance of a moist skin, I assumed that rainfall following an extended drought would induce migrations of four-toed salamanders.

Lunar phase (LUNARPHASE), the fraction of the moon surface illuminated, was based on US Naval Observatory estimates for the eastern United States. Based on other pond-breeding amphibians that demonstrate lunar-synchronized breeding cycles (Grant et al. 2009, 2013), I hypothesized that lunar phase might be a predictor of timing and directionality of movements, and the number of four-toed salamanders moving on a movement day. I expected that adults would be more likely to move, and in larger numbers, toward the nesting wetlands during new and full moons due to the increase in gravitational pull which may cue reproductive synchronization. I did not expect to see an effect of lunar phase on juvenile salamanders.

1.2.4 Models

I used CART models to predict the timing and direction of four-toed salamander movements, and Poisson regression to identify environmental variables associated with breeding migrations of salamanders. CART models consist of a decision tree with binary splits determined by continuous or categorical predictor variables. I used classification trees because the response variables for both the timing (movement nights vs. non-movement nights) and the direction (toward wetland vs. away from wetland) of movements were categorical. Classification trees are built by finding a rule based on a single variable that is most important in reducing variation in the dataset. The dataset continues to be split by rules until only terminal nodes exist. A terminal node is a point at which the dataset can no longer be split because all remaining cases belong to the same class, or the number of cases left is less than a specified criterion. I fully grew the classification trees and then pruned the trees to minimize the misclassification error without overfitting the data. Final classification trees were chosen after pruning, based on a 10-fold cross-validation and the 1 S.E. Rule (De'ath and Fabricius 2000). Statistical significance of each tree was based on a Monte Carlo permutation test using 500 permutations.

Poisson regression is a generalized linear model used to model count data. Count data usually have a Poisson distribution where the mean equals the variance and therefore linear regression based on a normal distribution is inappropriate. I used Poisson regression to model the magnitude of four-toed salamander movements because the response was a count of the number of salamanders captured each trap night. Model selection for Poisson regression was conducted using AIC forward and backward selection. Adjusted-r^2 values were calculated as a measure of model fit. I used the statistical package R version 2.10.1 to create CART and regression models using the "rpart" package (Therneau et al. 2009, R Core Team 2013). Descriptive analyses showed that the capture data were highly skewed, and therefore I square-root transformed these data prior to development of the models. Models were created for both adults and juveniles at the Northborough site. However, very few juvenile four-toed salamanders were captured at the Sudbury site, so models were created only for adults at that location. Age was based on snout-vent length (SVL), with individuals measuring less than 30 mm considered to be juveniles (Blanchard and Blanchard 1931). Individuals with unknown SVL were omitted. Due to the uncertainties associated with accurately sexing four-toed salamanders in the field, I did not attempt to consider gender in my analyses.

1.3 Results

Total captures at the Sudbury site was 66 and at the Northborough site was 487. At the Sudbury site, identification of juveniles using SVL was ambiguous, so all analyses were based on 32 known adults captured from 1999-2001. At Northborough, NHESP researchers were able to reliably determine the age of individuals and captures consisted of 250 juveniles and 104 adults.

1.3.1 Movement Days

Regression tree models for the Northborough site were significant in predicting the day salamanders would move for both adults ($p = 0.048$) and juveniles ($p = 0.045$). The most important discriminating variables for adults at Northborough were LUNARPHASE and RAINAMOUNT24 (Figure 1.2). Adults tended to move either when the moon was illuminated very little, or when the moon was well-illuminated but it had rained more than 52.07 mm the previous day (Figure 1.3). Juvenile movements were predicted by DAYLENGTH, LUNARPHASE, and RAINAMOUNT24. Juveniles typically moved late in the breeding season and when the moon was illuminated very little, but they would also move when the moon was illuminated, if it had rained more than 52.07 mm during the day (Figure 1.3). At the Sudbury site, no significant model was produced for adults ($p = 0.196$).

1.3.2 Movement Direction

At Northborough, models describing movement directionality were significant for both adults ($p = 0.02$) and juveniles ($p = 0.002$). Movement direction was only dependent on DAYLENGTH. In early spring, adults, and a small number of juveniles, moved toward the nesting wetlands, and by early summer, both adults and juveniles moved away from the wetlands (Figure 1.4). For Sudbury, I was unable to develop a significant model predicting movement direction in adults.

1.3.3 Number Moving

At Northborough, the Poisson regression model was not significant in predicting the number of adult salamanders moving on a given night ($r^2 = 0.02$, $p = 0.09$), though it was for juveniles ($r^2 = 0.20$, $p < 0.001$). For juveniles, MEANTEMP, DAYLENGTH, and their interaction were significant predictors. Large numbers of juveniles were likely to move when temperatures were warm and days long. At Sudbury, a significant statistical model was developed using all predictor variables except DROUGHTDAYS, but it explained very little of the variation in the number of adults moving ($r^2 = 0.03$, $p < 0.001$).

1.4 Discussion

In order to effectively manage wetland habitats for viable breeding populations of amphibians, managers need a detailed understanding of the species requirements at each life-history stage and season of the year (Semlitsch and Bodie 2003). Studies seeking to understand the movement phenology of secretive species like the four-toed salamander are rare, but essential for maintaining biodiversity in wetlands and surrounding terrestrial habitats (Semlitsch and Bodie 2003, Trenham and Shaffer 2005, Harper et al. 2008).

Most field observations of four-toed salamanders are of females guarding nests, thus we have limited knowledge of the natural history of adult males and juveniles. No previous study has attempted to relate environmental variables to the movement patterns of four-toed salamanders, but Paton et al. (2000) found that most adults moved from early March to late May in New England. Past research has documented that migrating amphibians tend to move on rainy nights (e.g. Sexton et al. 1990, Timm, McGarigal, and Gamble 2007, Roe and Grayson 2008), and in this study, I also found this to be true, but in addition I found that lunar phase was also important. Individuals were more likely to move on non-illuminated nights, possibly to avoid detection by predators, but alternatively, there may be other lunar cues like gravitational pull that trigger synchronous movements (Grant et al. 2009). Breeding migrations triggered by favorable climatic variables maximizes offspring survival in ponds with brief and often uncertain hydroperiods, while minimizing adult mortality (Semlitsch et al. 1993).

Placement of drift fences at the Northborough site had greater success at capturing four-toed salamanders compared to the arrays at Sudbury. My results are in contrast to the few studies that have documented four-toed salamander captures using drift-fence arrays. At the Sudbury site, drift-fence trapping success was typically low for four-toed salamanders, but at Northborough the trapping success was unusually high (Table 1.1). I suspect that the focus on capturing vernal pool-breeding amphibians at Sudbury probably resulted in us not detecting significant movements of four-toed salamanders nesting in the adjacent wetland area. This is reflected in the Poisson regression model for the number of four-toed salamanders moving at Sudbury. A significant model was found for adults at Sudbury ($r^2 = 0.03$, $p < 0.001$), however, the model includes every variable except DROUGHTDAYS. This suggests that the sample size is just too small to make inferences at the Sudbury site. Many days where no captures were recorded are classified as days expecting large movements. It is likely that the large movements were missed by the study due to fence placement.

In order to effectively monitor four-toed salamander populations with drift fence arrays, it is necessary that the study design focus on the specific requirements of four-toed salamander nesting habitat. Since four-toed salamanders display a high degree of philopatry for nesting sites (Harris and Ludwig 2004), drift-fence arrays would be most effective when placed between known nest sites and upland habitat. In addition, it is likely that four-toed salamanders are able to climb out of pitfall traps and over drift fences, especially if the trap array is not rigorously maintained (Chalmers 2004). Since the drift-fence trap arrays may not have been impermeable to movement, they are likely unsuitable for studies seeking to determine absolute population estimates. However, despite the labor, costs and potential drawbacks involved in installing drift fence trap arrays (Enge 2001), the method does provide insight into the movement patterns and relative population distribution of adult male and juvenile four-toed salamanders that are seldom encountered during visual encounter surveys.

Conservation strategies for amphibian species, including four-toed salamanders, should include maintenance of suitable upland habitat near breeding wetlands (Trenham and Shaffer 2005), and a consideration of their movement phenology (Hocking et al. 2008). An understanding of when four-toed salamanders utilize upland habitats, and how they move through the landscape, is the necessary basis for reducing the population impact of road mortality, forest management practices, and habitat isolation, degradation, and loss. Effective road closures are dependent on predicting breeding migrations of four-toed salamanders, and my predictive models are a first step in providing this information. Future research should examine the role of upland habitat in supporting viable populations of four-toed salamanders, a topic that this study was unable to address.

The future of the four-toed salamander is uncertain regarding habitat development. Within the six-year period of 1999-2005, 11,412 ha of forest habitat in Massachusetts had been developed (DeNormandie and Corcoran 2009). In addition, 182 ha of wetlands were lost between 2001-2005 (MassDEP Wetlands Change Datalayer 2011). The continuing encroachment of human development on forested and wetland habitat over the next 30 years may mean that increased habitat isolation reduces connectivity and affects metapopulation dynamics that allow the four-toed salamander to persist in the landscape.

Table 1.1. Number of Four-Toed Salamander captures recorded in 6 studies using drift fence pitfall trap arrays.

Captures	Trap Nights	Site	Study
0	208	Woodstock, Vermont, USA	Faccio 2001
0	1,323	Acadia National Park, Maine, USA	Brotherton et al. 2004
12	10,560	Charlestown, Rhode Island, USA	Paton et al. 2000
22	30,540	Chesapeake Farms, Maryland, USA	McLeod and Gates 1998
487	36,582	Northborough, Massachusetts, USA	this study
42	209,040	Sudbury, Massachusetts, USA	this study
2	251,054	Penobscot Experimental Forest, Maine, USA	Stronjny and Hunter 2010

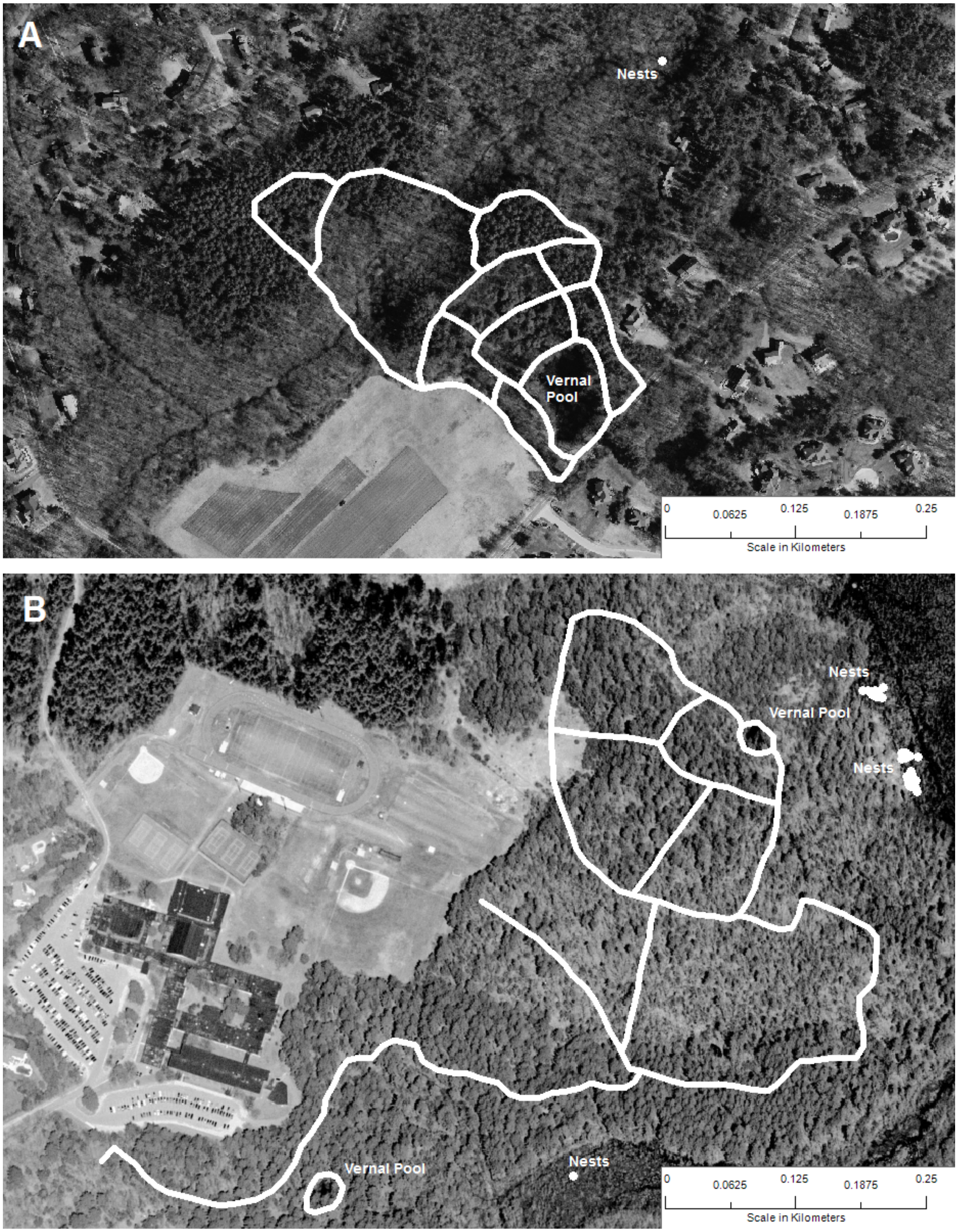

Figure 1.1. Drift fence arrays (in white) at A) Sudbury, MA and B) Northborough, MA study sites.

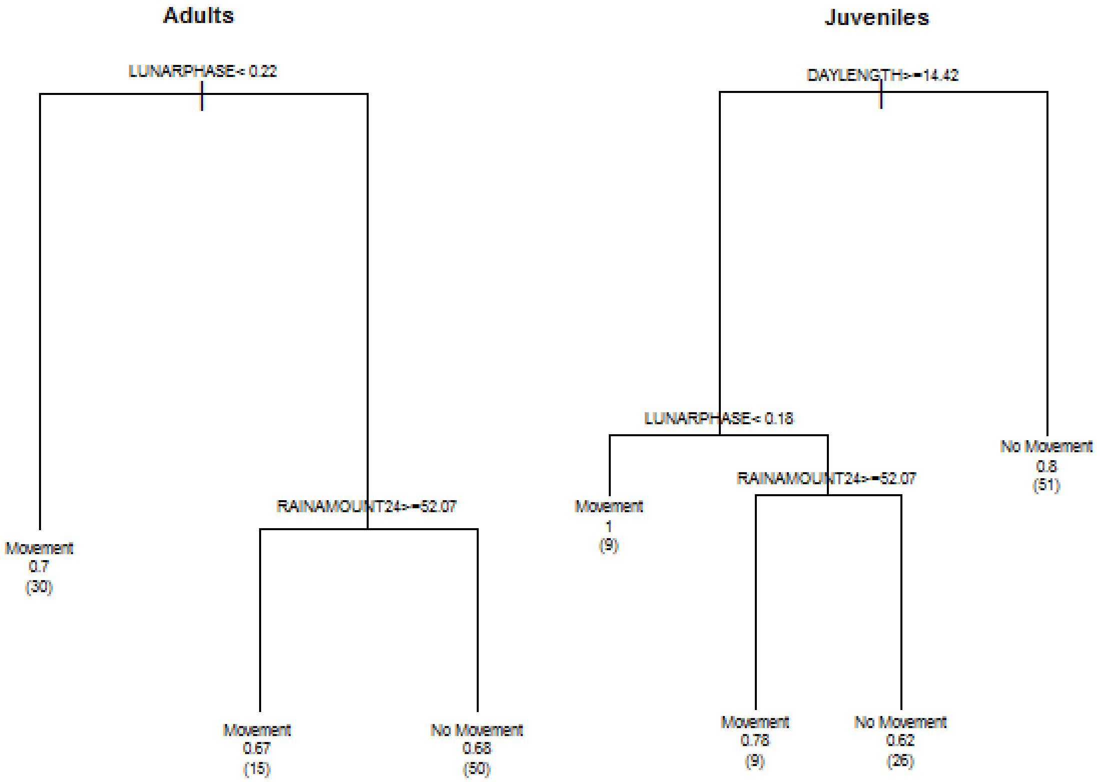

Figure 1.2. Classification trees describing the timing of adult and juvenile four-toed salamander movements at Northborough, MA, 2003. Observations (days the pitfall traps were open) were classified by a set of environmental variables. If an observation was "true" for an expression it was moved to the left branch, otherwise it was placed on the right branch. The final leaves are the response categories of "Movement" or "No Movement". The value at the top of each final leaf is the percentage of observations that match the leaf category, with the number of observations in parentheses.

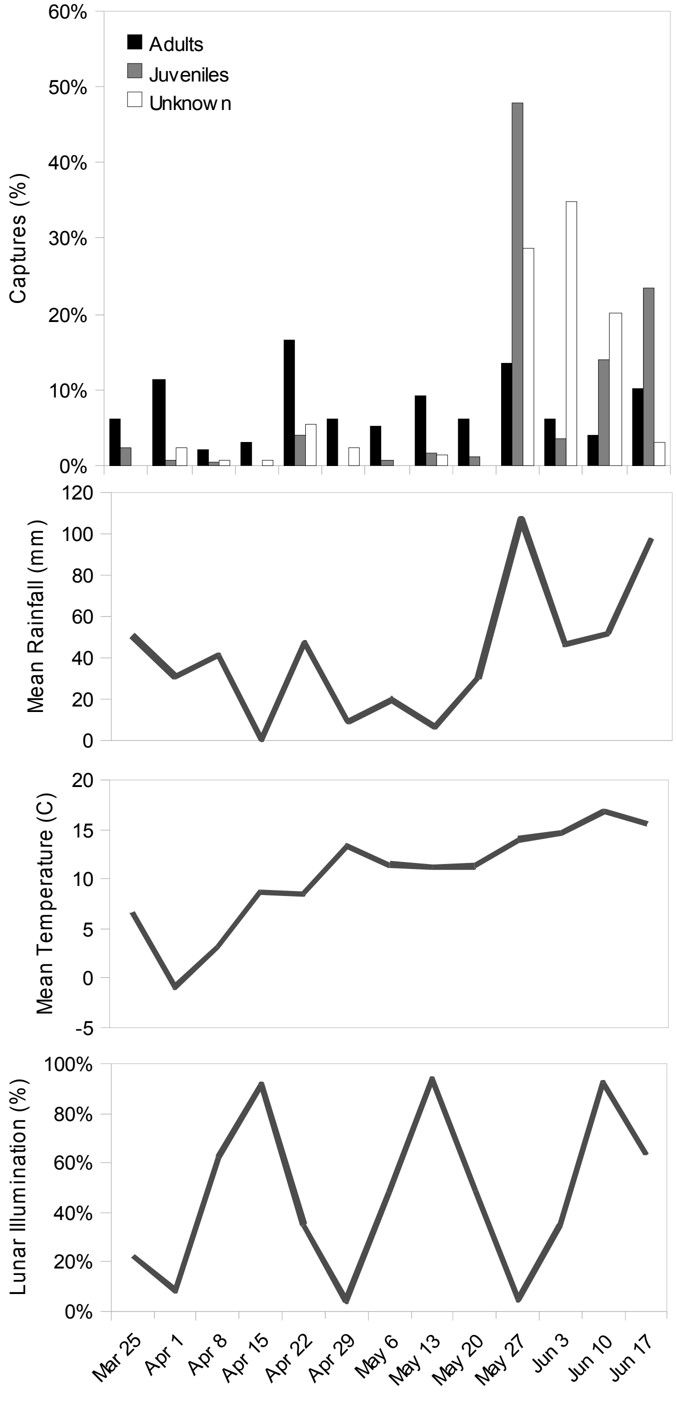

Figure 1.3. Four-toed salamander captures in relation to mean rainfall, mean temperature and lunar illumination during the 2003 nesting period in Northborough, Massachusetts.

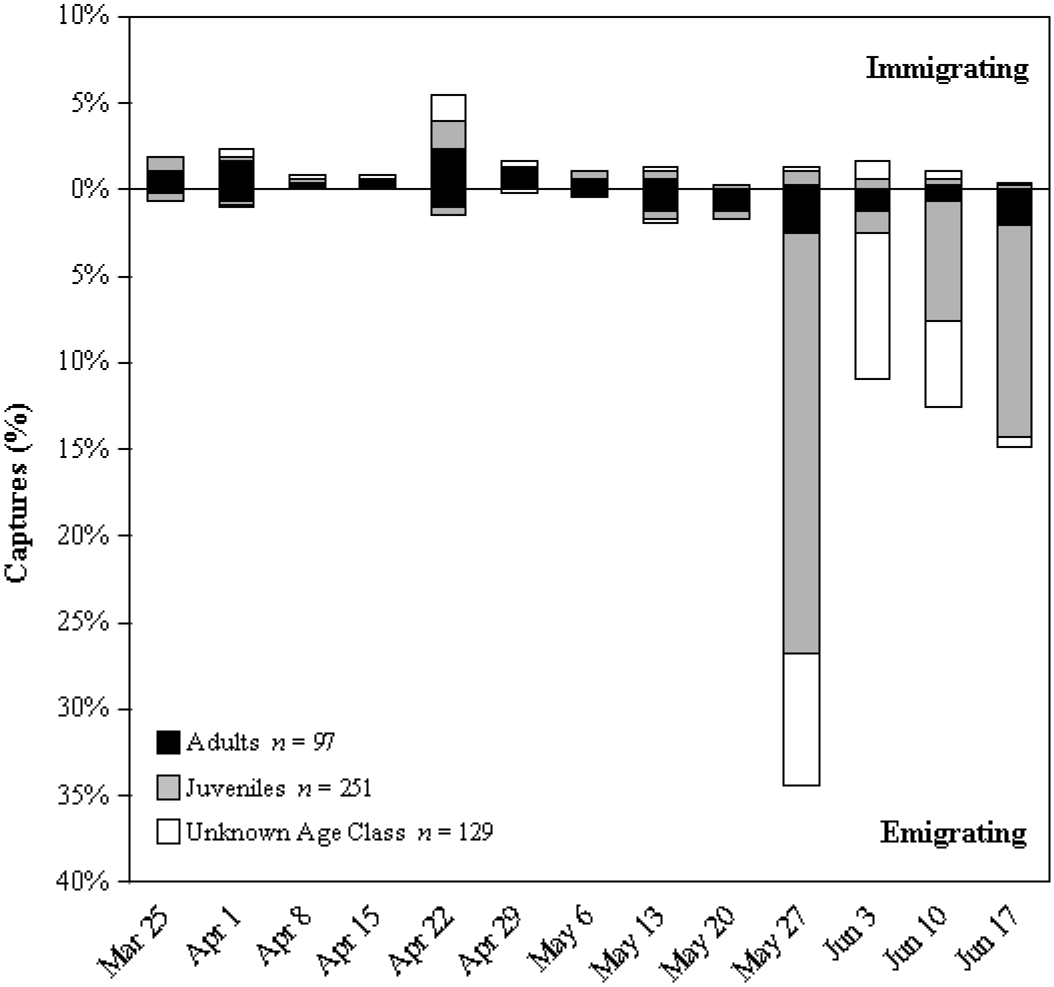

Figure 1.4. Timing of immigration to, and emigration from, nesting wetlands for four-toed salamanders at Northborough, Massachusetts.

CHAPTER 2

MODELING POTENTIAL HABITAT FOR THE FOUR-TOED SALAMANDER (*HEMIDACTYLIUM SCUTATUM*) IN MASSACHUSETTS

2.1 Introduction

Although many factors have contributed to amphibian population declines in recent history, habitat loss and degradation are considered to be major causes (Houlahan and Findlay 2003, Cushman 2006). Tools for identifying and prioritizing viable breeding habitat for amphibian populations are needed to mitigate the effects of habitat deterioration (Baldwin and DeMaynadier 2009). Using remotely sensed data to build predictive habitat models applied across entire landscapes, potentially suitable habitat can be identified without the need for exhaustive and cost-prohibitive large scale field surveys.

Conservation of amphibian diversity increasingly requires modeling habitat relationships at large spatial scales (Stuart et al. 2004). Historically, amphibian habitat relationship studies have focused on characterizing habitats at small, site-level scales where site-specific habitat factors are assumed to have a dominant influence because of the characteristically limited dispersal and relatively small home ranges of most amphibians (Semlitsch and Bodie 2003). However, there is mounting evidence that landscape-scale habitat characteristics are important predictors of amphibian occurrence and abundance (Stoddard and Hayes 2005, Suzuki et al. 2008, Veysey et al. 2011, Scherer et al. 2012). Fine spatial scales appear to reflect constraints on individuals whereas those at broader scales may reflect biological constraints manifested at the population level (Stoddard and Hayes 2005). Habitat models developed at fine scales are are typically not useful in guiding conservation of species at broad landscape scales. Field surveys used to gather data for fine-scale habitat relationship models are too labor intensive and costly to be conducted over a broad landscape. Remote sensing and GIS technologies make it possible to examine habitat relationships across broad landscapes and can be used by managers to develop conservation assessments.

Landscape-level research on the spatial distribution and habitat selection of four-toed salamanders (*Hemidactylium scutatum*) is rare. Four-toed salamanders are a secretive species found in small isolated populations across their range in eastern North America, which covers 31 U.S. states and 4 Canadian provinces (Petranka 1998). The species is listed as imperiled or critically imperiled in 8 states and 2 provinces and vulnerable to extirpation in 11 states and 1 province (NatureServe 2013). In Massachusetts, the four-toed salamander was placed on the protected species list in 1994 as a result of limited observations of the species across the state. In 2008, state biologists determined that populations were stable enough in the central and eastern portions of the state to warrant removal from the Massachusetts protected species list, but the distribution of populations across the state, particularly west of the Connecticut River was not well documented. Most habitat relationship studies of four-toed salamanders have been conducted at a fine scale (Chalmers and Loftin 2006, Wahl et al. 2008) or have evaluated behaviors of individuals or groups in laboratory settings (Harris and Gill 1980, Breitenbach 1982, Harris et al. 1995, 2003, Carreño et al. 1996, Carreño and Harris 1998, Harris and Ludwig 2004). The degree to which four-toed salamanders are dependent on local versus landscape factors, and their interactions, is unknown. Studies conducted on pool-breeding amphibians suggest that scale-dependent effects vary with species (Porej et al. 2004, Herrmann et al. 2005, Veysey et al. 2011). I propose that GIS layers of habitat features across Massachusetts can be effectively used to develop habitat suitability models for the four-toed salamander that can be readily used for statewide conservation planning.

To better understand the distribution of four-toed salamanders in Massachusetts, I developed a landscape model of suitable habitat for the species. I used classification and regression tree analysis (CART) to identify important variables influencing the distribution of four-toed salamanders in Massachusetts. My study's explicit goals were to: 1) Develop and evaluate the accuracy of a model predicting presence/absence of four-toed salamanders in Massachusetts wetland habitat, 2) identify an effective spatial scale for managing four-toed salamander conservation, and 3) describe the frequency of occurrence of four-toed salamanders in Massachusetts wetlands.

2.2 Methods

2.2.1 Study Area

The study area included the entire land area within the state of Massachusetts (27,337 km^2). Massachusetts falls within two of the U.S. Environmental Protection Agency's ecoregions: the Northeastern Highlands to the west and the Northeastern Coastal Zone to the east. The Northeastern Highlands are mostly mountainous and generally forested with northern hardwoods and some spruce-fir at higher elevations (Swain and Kearsley 2001). Forest cover is typically lower in the Northeastern Coastal Zone with agricultural, urban and suburban development where the topography is gentler (Swain and Kearsley 2001). Elevation ranges from 0 m along the shores of the Atlantic Ocean to 1,062 m at Mount Greylock in the Berkshire Highlands. Mean January temperatures range from -12.0 ºC to 4.4 ºC and mean July temperatures range from 13.3

ºC to 29.0 ºC (NOAA 2011). Annual precipitation ranges from about 110.0 cm along the coastal lowlands to greater than 142 cm in the Berkshire Highlands (NOAA 2011). Eleven salamander species are known to occur in Massachusetts (Cardoza and Mirick 2009).

2.2.2 Study Species

Four-toed salamanders are the smallest Plethodontid (lungless) salamander found in Massachusetts. Adults average 7-9 cm in total length (Blanchard and Blanchard 1931, Chalmers 2004). Females migrate from upland habitats in spring to lay eggs in *Sphagnum sp.* hummocks and other organic material found near pools of stagnant water or low flow streams (Wahl et al. 2008). Males have not been found to migrate to the nesting sites and little is known about their habitat use and ecology (Harris 2008). Females generally stay with the eggs from laying until hatching six weeks later (Harris et al. 1995). Larvae metamorphose approximately six weeks after hatching, and then adults and juveniles move into upland habitat (Blanchard and Blanchard 1931, Bishop 1941, Harris et al. 1995). Prior to over-wintering, females are believed to mate with males in the uplands, and then hold spermatophores until the following spring, though this part of their natural history has received little attention (Dieckmann 1927, Chalmers and Loftin 2006).

2.2.3 Spatial Scale Definitions

A goal of this research was to identify local and landscape-scale variables that predict the occurrence of four-toed salamanders in potentially suitable wetland habitats in Massachusetts. I assessed three models of the influence of land use at the local scale (30 m, 350 m, and 500 m) and three models at the landscape scale (1000 m, 2000 m, 3000 m). Each scale represents a nested straight-line buffer distance around a wetland within which land use was evaluated. Four-toed salamanders have been found to largely remain within 350 m of a nesting wetland (Goddard and Windmiller 2003). However, traditional drift fences used to estimate travel distances disrupt salamanders from their normal movement patterns and may underestimate typical movement distances. Therefore, I evaluated local-scale land use at 350 m and 500 m buffer distances as well as the current Massachusetts buffer zone of 30 m designated to protect wetland habitat.

Although the literature suggests that landscape-scale factors are important when modeling amphibian habitat relationships, determining the appropriate scale at which to evaluate habitat characteristics is inconsistent among studies often due to a lack of detailed information about the habitat use of the study species. The most common approach is to create multiple equidistant buffers to determine the best scale for predicting species distributions (Herrmann et al. 2005, Baldwin et al. 2006, Rinehart et al. 2009, Jacobs and Houlahan 2011, Charney 2012). In some cases, this has been more effective than evaluating scales based on expert opinion (Charney 2012). The most successful landscape-scale models of pond-breeding amphibian habitat use have used buffer distances from 1000 m to 3000 m (Houlahan and Findlay 2003, Herrmann et al. 2005, Charney 2012). Because very little is known about four-toed salamander upland habitat use, I decided to evaluate land use at 1000 m, 2000 m, and 3000 m buffer distances.

2.2.4 Model Set Development & Variables

I used a classification and regression tree model (CART) to predict the occupancy of four-toed salamanders in Massachusetts wetland habitat at multiple spatial scales. In order to create a CART model useful for predicting four-toed salamander wetland habitat, wetlands were identified that had confirmed recent presence of the species using Element Occurrence (EO) records from the Massachusetts Natural Heritage and Endangered Species Program (NHESP). Only EO points recorded after 1990 were used for developing the model in order to focus on information relevant to the present habitat use of four-toed salamanders. Any location where an individual was collected or observed constituted an EO for a four-toed salamander. Due to the secretive nature of four-toed salamanders, EOs primarily indicated nesting locations and occasional observances along roadsides. A polygon layer was created in ArcMap 10.1 from the Massachusetts Department of Environmental Protection (MassDEP) Wetlands GIS layer representing the nearest wetlands to the EO points. An equal number of random wetlands was also selected from the MassDEP wetlands layer. This resulted in a dataset of 263 occupied wetlands, and 263 random wetlands.

Based on a review of relevant literature, I identified 15 variables that I suspected could be associated with four-toed salamander occurrence (Table 2.1). To minimize correlations of variables within the models during model development, I eliminated one of each pair of variables with a Kendall's rank correlation (τ) greater than 0.50 or less than -0.50.

The density of wetlands in the landscape and hydroperiod heterogeneity influences amphibian abundance, occupancy, and diversity (Brodman 2009). I included predictor variables representing various aspects of wetland morphology (TYPE,

PERIMETER, AREA, COMPLEXITY, ELEVATION) in the models. These variables did not vary across spatial scales. Wetland TYPE, PERIMETER, and AREA were obtained from the MassDEP Wetlands data layer. COMPLEXITY was calculated from the PERIMETER to AREA ratio of each wetland. ELEVATION was calculated from MassGIS Digital Elevation Model using Geospatial Modeling Environment (GME, Beyer 2012), which returns the mean raster elevation value contained within each wetland polygon.

Expanding agriculture and development is expected to cause further habitat loss, upland habitat degradation, wetland isolation, and reduced wetland heterogeneity (Houlahan and Findlay 2003, Brodman 2009). To evaluate potential land use predictor variables at multiple spatial scales, multiple buffers were created around each wetland in the dataset using GME. The 40 land use categories available in the MassGIS 2005 Land Use data layer were pooled into 7 variables: FOREST, SHRUBLAND, OPEN LAND, WETLAND, OPEN WATER, AGRICULTURE, and DEVELOPMENT (Table 2.1). The percentage of buffer area covered by each land use variable was calculated using GME and then arcsine transformed. The transformation eliminated the 0-100% limitation of a percentage and prevented the violation of one of the classification and regression tree assumptions. In addition to land use, the cumulative length of roads (ROADS) from the Massachusetts Department of Transportation (MassDOT) Roads data layer was calculated within each buffer using GME.

Seasonal wetlands are ecologically important for the conservation of salamanders because of their unique assemblages of species and roles in habitat connectivity (Brodman 2005). In addition, fishless ponds have been described as a potentially important feature for the survival of four-toed salamander larvae (Chalmers 2004). As such, the number of certified vernal pools (CVP) and potential vernal pools (PVP) within each buffer were calculated using GME and included as predictor variables in the model set (Table 2.1).

2.2.5 Model Selection & Validation

I chose to use CART models to predict the occupancy of four-toed salamanders in Massachusetts wetland habitat because the response variable (presence vs. random) was categorical and the results can be easily applied by managers to assess potential suitable habitat from statewide GIS wetland data. CART models consist of a decision tree with binary splits determined by continuous or categorical predictor variables. Classification trees are built by finding a rule based on a single variable that is most important in reducing variation in the dataset. The dataset continues to be split by rules until only terminal nodes exist. A terminal node is a point at which the dataset can no longer be split because all remaining cases belong to the same class, or the number of cases left is less than a specified criterion. I used the statistical package R version 2.10.1 to create CART models using the “rpart” package (Therneau et al. 2009, R Core Team 2013). I fully grew the classification trees and then pruned the trees to minimize the misclassification error without overfitting the data. Final classification trees were chosen after pruning, based on a 10-fold cross-validation and the 1 S.E. Rule (De’ath and Fabricius 2000). Statistical significance of each tree was based on a Monte Carlo permutation test using 500 permutations.

The model dataset was randomly partitioned *a priori* for model building (75%, n=394) and model evaluation (25%, n=130). Evaluations of model reliability were conducted with the reserved data and based on percent correct classification. The accuracy of the CART models was assessed as a measure of the usefulness in identifying potential habitat for four-toed salamanders at multiple spatial scales. The most accurate models were applied to the statewide MassDEP wetlands data layer to enumerate wetlands identified as potentially suitable habitat.

2.3 Results

2.3.1 Wetland Characteristics

Local and landscape variable measurements varied greatly between occupied and random wetlands (Tables 2.2, 2.3). Occupied wetlands were generally characterized by a larger perimeter to area ratio, were located in the vicinity of larger numbers of seasonal pools and were surrounded by higher percentages of forest and fewer roads than random wetlands. There was a negative correlation ($\tau < -0.50$) at buffer distances of 1000 m or greater between percent forest and percent development and a positive correlation ($\tau > 0.50$) at buffer distances of 1000 m or greater between percent development and cumulative road length. As buffer distances increased, the mean percent development increased from 4.0% to 20.2% in occupied wetlands and from 7.5% to 21.5% in random wetlands. Percent forest averaged 60.9% (range 0.1-99.5%) among the occupied wetlands and averaged 51.1% (range 0-100%) among the random wetlands within the six buffer distances. The widest range occurred within the 30 m buffer. At larger buffer distances, there were fewer wetlands lacking forests within the buffer. Similarly, the farther a buffer extended from the wetland, the greater the chance of encountering road segments.

2.3.2 Local Scale Models

The most accurate predictive model of four-toed salamander occurrence was the 350 m model (Table 2.4). The pruned 350 m classification tree contained 4 splits and had and an overall classification accuracy of 75.4% (Figure 2.1). The most important discriminating variables were TYPE, CVP, COMPLEXITY, and FOREST. Four-toed salamanders were detected at 199 of the 265 wetlands predicted by my model to contain this species. Probability of four-toed salamander occurrence was highest in geometrically complex bogs, deep and shallow marshes, shrub swamps, and wooded swamps surrounded by greater than 79.6% forest and at least one certified vernal pool within 350 m. When the 350 m model was applied statewide, 81,295 wetlands were determined to be potentially suitable habitat for the four-toed salamander.

2.3.3 Landscape Scale Models

Support for landscape-level influences on four-toed salamander occurrence was greater than support for local-scale influences (Table 2.4). The most accurate model of four-toed salamander occurrence was the 2000 m model. The pruned 2000 m classification tree contained 3 splits and had and an overall classification accuracy of 91.2% (Figure 2.2). The most important discriminating variables were CVP, PVP, and TYPE. Four-toed salamanders were detected at 248 of the 280 wetlands predicted by my model to contain this species. Probability of four-toed salamander occurrence was highest in bogs, deep and shallow marshes, shrub swamps, and wooded swamps with greater than 15 certified vernal pools or 6 potential vernal pools within 2000 m. When the 2000 m model was applied statewide, 30,195 wetlands were determined to be potentially suitable habitat for the four-toed salamander.

2.4 Discussion

To identify an effective scale of management for four-toed salamanders in Massachusetts, I compared local and landscape scale predictive models of four-toed salamander occurrence in wetlands across the state. My results suggest that management for this species would be more effective at the landscape scale than at the local scale. Four-toed salamander occurrence is best predicted by variables measured within a 2000 m wetland buffer. Specifically, I found that four-toed salamander occurrence was highest in bogs, marshes, shrub swamps, and wooded swamps with a large number of nearby seasonal pools and insensitive to elevation, roads, and land use other than forest. My research suggests that four-toed salamander occurrence is affected by environmental variables well outside the Massachusetts 30 m regulated wetland buffer designed to protect wetland habitat. Developing effective forest management rules that minimize habitat fragmentation and maximize seasonal pool conservation is essential for protecting four-toed salamander habitat.

Wetland type and geometric complexity were factors that appeared repeatedly in my multiple scale occurrence models. Although landscape characteristics have been found to influence pond-breeding amphibian presence, wetland characteristics have been found to influence species density (Herrmann et al. 2005). The importance of wetland type and perimeter to area ratio for four-toed salamanders in this study suggests a similar relationship. Four-toed salamander occurrence has been shown to be dependent on plant species and vegetation community type, presence of flowing water, and presence of woody debris at the wetland scale (Chalmers and Loftin 2006). The plants found in occupied wetlands (e.g. *Sphagnum sp.*) are common in bogs, marshes, and wooded swamps (Chalmers and Loftin 2006). In addition, seasonal pools with higher geometric complexity enhance the effects of shoreline vegetation and tend to have shorter hydroperiods (Brooks and Hayashi 2002). Pond-breeding amphibians are typically constrained to wetlands with a sufficiently long hydroperiod for metamorphosis that also lack larval predators. Because the four-toed salamander has a very brief larval period relative to other pond-breeding amphibians, wetlands with shorter hydroperiods may provide less competition during development.

Seasonal pools had the strongest effect on four-toed salamander occupancy within the 2000 m scale model. Seasonal pools are known to be important habitats for many amphibians (Gibbons et al. 2006, Petranka 2007, Harper et al. 2008), and their persistence over time may help to maintain important connections within metapopulations (Semlitsch 2000, Trenham and Shaffer 2005, Karraker and Gibbs 2009). Although four-toed salamanders are not obligate seasonal pool breeders, the inclusion of seasonal pools in my model suggests that temporary ponds may serve a role in recruitment and thus the distribution of four-toed salamanders in Massachusetts.

Four-toed salamander wetland occupancy was weakly associated with forest cover. Percent forest appeared as a discriminating variable in only the 350 m model. A positive relationship between forest cover and wetland occupancy has been shown for several terrestrial salamander species (Gibbs 1998*a*, *b*, Guerry and Hunter 2002, Trenham et al. 2003, Herrmann et al. 2005). However, shoreline nesting habitat for four-toed salamanders has been found to be negatively correlated with forested habitats (Chalmers and Loftin 2006). It is unclear whether the low explanatory power of forest cover in this dataset may be attributed to the relatively high availability of forested habitat in the Massachusetts landscape, or other processes not measured in this study.

My results indicate that remotely sensed landscape features can be correlated with the range-wide occurrence of four-toed salamanders. The CART modeling approach provided us with easily interpretable results that can be used to identify previously undocumented breeding habitat for the four-toed salamander, or estimate the proportion of suitable habitat available for mitigation and management efforts. The ability to predict occupancy and reduce survey effort is a valuable tool for wildlife managers, along with being useful for focusing survey effort and formulating conservation strategies for uncommon species. However, my study only addressed the conditions that affect occurrence at breeding wetlands. Understanding the factors that affect the distribution of four-toed salamanders in non-breeding habitat is equally important for species management. I identified more than 30,000 wetlands in Massachusetts that have features signifying the likely potential for four-toed salamander nesting habitat, though many are geographically isolated from one another. As such, special effort should be made to protect wetland complexes and potential occupied wetlands that could act as metapopulations. In addition, wetlands in western Massachusetts should be surveyed for four-toed salamanders to determine the size of their populations and their connectedness. If these wetlands only support small, isolated populations of four-toed salamanders, it is critical to protect them and reestablish movement corridors through the surrounding upland habitats.

The future of the four-toed salamander is uncertain regarding climate change. Assessments of regional climate models over the northeastern United States suggest that over the next 25-50 years Massachusetts will experience a 2.6°C temperature rise and a 5.75% overall increase in precipitation (Rawlins et al. 2012). These changes could cause an overall loss of short hydroperiod wetlands, depending on whether small-scale depressions may become new short hydroperiod wetlands. Because four-toed salamanders are dependent on short hydroperiod wetlands to reproduce, the future of four-toed salamander management may include mitigating against the impacts of climate change via irrigation of breeding wetlands, removal of competitors and predators adapted to wetlands with longer hydroperiods, and by improving habitat connectivity and quality to allow for potential range-shifts.

Table 2.1. Predictor variables used in development of a CART model for predicting presence of four-toed salamanders.

Variable	Definition	Source
TYPE	Wetland type (e.g. bog, wooded deciduous swamp)	MassDEP Wetlands (2009)
PERIMETER	Perimeter length (m) of wetland	MassDEP Wetlands (2009)
AREA	Area (m^2) of wetland	MassDEP Wetlands (2009)
COMPLEXITY	Perimeter to area ratio	MassDEP Wetlands (2009)
ELEVATION	Mean elevation (m) of wetland	MassGIS Elevation Contours (2003)
CVP	Number of certified vernal pools within buffer	NHESP Certified Vernal Pools (2013)
PVP	Number of potential vernal pools within buffer	NHESP Potential Vernal Pools (2000)
ROAD	Total length (m) of roads within buffer	MassDOT Roads (2012)
FOREST	Proportion of buffer area where tree canopy covers at least 50% of the land	MassGIS Land Use (2005)
SHRUBLAND	Proportion of buffer area that is predominantly shrub cover, brushland, and successional habitat	MassGIS Land Use (2005)
OPEN LAND	Proportion of buffer area that is vacant land, idle agriculture, rock outcrops, and barren areas	MassGIS Land Use (2005)
WETLAND	Proportion of buffer area that is wetland including forested and non-forested wetlands, salt marshes and bogs	MassGIS Land Use (2005)
OPEN WATER	Proportion of buffer area that is open water	MassGIS Land Use (2005)
AGRICULTURE	Proportion of buffer area that is active cropland or pasture	MassGIS Land Use (2005)
DEVELOPMENT	Proportion of buffer area that is developed land including industrial, commercial, residential, recreational, transportation and waste facilities	MassGIS Land Use (2005)

Table 2.2. Habitat characteristics of wetlands used to develop local-scale classification and regression tree models.

Variable	Scale	Present sites mean	Present sites SD	Random sites mean	Random sites SD	*P*
PERIMETER	all	1,698	3,403	6,678	23,190	0.003
AREA	“	67,251	218,786	941,656	7,183,787	0.088
COMPLEXITY	“	0.07	0.04	0.04	0.03	< 0.001
ELEVATION	“	114	98	110	125	0.728
CVP	30 m	0.15	0.62	0.03	0.24	0.008
	350 m	1.22	2.04	0.56	1.64	< 0.001
	500 m	1.77	2.57	0.82	2.27	< 0.001
PVP	30 m	0.19	0.50	0.19	0.72	0.935
	350 m	1.84	2.11	3.39	8.36	0.012
	500 m	3.08	3.48	5.00	10.46	0.015
ROAD	30 m	85	200	711	4,149	0.035
	350 m	1,963	1,759	9,291	33,725	0.002
	500 m	3,435	2,670	13,529	45,958	0.002
FOREST	30 m	1.02	0.35	0.87	0.33	< 0.001
	350 m	0.91	0.24	0.79	0.25	< 0.001
	500 m	0.90	0.22	0.78	0.24	< 0.001
SHRUBLAND	30 m	0.02	0.10	0.01	0.04	0.639
	350 m	0.02	0.05	0.03	0.07	0.203
	500 m	0.02	0.05	0.03	0.07	0.112
OPEN LAND	30 m	0.02	0.07	0.03	0.09	0.095
	350 m	0.07	0.10	0.08	0.09	0.534
	500 m	0.08	0.09	0.09	0.08	0.234
WETLAND	30 m	0.37	0.29	0.41	0.31	0.284
	350 m	0.36	0.18	0.36	0.19	0.757
	500 m	0.36	0.16	0.36	0.18	0.927
OPEN WATER	30 m	0.02	0.08	0.11	0.17	< 0.001
	350 m	0.04	0.08	0.11	0.14	< 0.001
	500 m	0.06	0.09	0.12	0.14	< 0.001
AGRICULTURE	30 m	0.07	0.18	0.09	0.21	0.290
	350 m	0.14	0.17	0.18	0.19	0.016
	500 m	0.15	0.15	0.19	0.18	0.016
DEVELOPMENT	30 m	0.20	0.25	0.28	0.28	0.005
	350 m	0.39	0.23	0.45	0.26	0.012
	500 m	0.41	0.21	0.46	0.25	0.018

Table 2.3. Habitat characteristics of wetlands used to develop landscape-scale classification and regression tree models.

		Present sites		Random sites		
Variable	Scale	mean	SD	mean	SD	*P*
PERIMETER	all	1,698	3,403	6,678	23,190	0.003
AREA	"	67,251	218,786	941,656	7,183,787	0.088
COMPLEXITY	"	0.07	0.04	0.04	0.03	< 0.001
ELEVATION	"	114	98	110	125	0.728
CVP	1000 m	3.84	4.91	2.32	4.79	0.002
	2000 m	18.26	21.83	7.49	12.04	< 0.001
	3000 m	28.26	21.16	15.17	19.20	0.130
PVP	1000 m	8.52	7.49	12.35	19.56	0.011
	2000 m	9.50	11.31	35.24	38.08	< 0.001
	3000 m	57.78	41.16	68.77	60.45	0.036
ROAD	1000 m	11,798	6,602	30,628	83,787	0.002
	2000 m	44,888	22,121	80,032	156,538	0.002
	3000 m	100,838	46,288	149,287	223,481	0.003
FOREST	1000 m	0.87	0.19	0.78	0.23	< 0.001
	2000 m	0.85	0.17	0.78	0.22	0.002
	3000 m	0.83	0.17	0.77	0.20	0.002
SHRUBLAND	1000 m	0.03	0.04	0.04	0.07	0.037
	2000 m	0.04	0.04	0.05	0.08	0.045
	3000 m	0.04	0.03	0.05	0.07	0.165
OPEN LAND	1000 m	0.10	0.06	0.10	0.06	0.864
	2000 m	0.10	0.05	0.10	0.04	0.751
	3000 m	0.11	0.04	0.10	0.04	0.872
WETLAND	1000 m	0.37	0.15	0.36	0.14	0.730
	2000 m	0.36	0.13	0.36	0.12	0.981
	3000 m	0.35	0.11	0.36	0.11	0.559
OPEN WATER	1000 m	0.10	0.10	0.15	0.13	< 0.001
	2000 m	0.13	0.09	0.17	0.10	< 0.001
	3000 m	0.15	0.08	0.18	0.09	< 0.001
AGRICULTURE	1000 m	0.18	0.13	0.21	0.14	0.024
	2000 m	0.20	0.10	0.21	0.12	0.219
	3000 m	0.20	0.09	0.22	0.11	0.092
DEVELOPMENT	1000 m	0.43	0.18	0.48	0.23	0.033
	2000 m	0.46	0.17	0.48	0.20	0.167
	3000 m	0.47	0.17	0.48	0.19	0.391

Table 2.4. Model results for the occurrence of four-toed salamanders in wetlands in Massachusetts Covariate abbreviations are listed in Table 2.1.

		Correct Classification Rate	
Model	Variables	Train	Verify
30 m	COMPLEXITY + OPEN WATER	0.741	0.685
350 m	TYPE + CVP + COMPLEXITY + FOREST	0.774	0.692
500 m	TYPE + CVP + COMPLEXITY + OPEN WATER	0.764	0.677
1000 m	TYPE + CVP + COMPLEXITY	0.734	0.646
2000 m	TYPE + CVP + PVP	0.924	0.877
3000 m	TYPE + COMPLEXITY	0.708	0.677

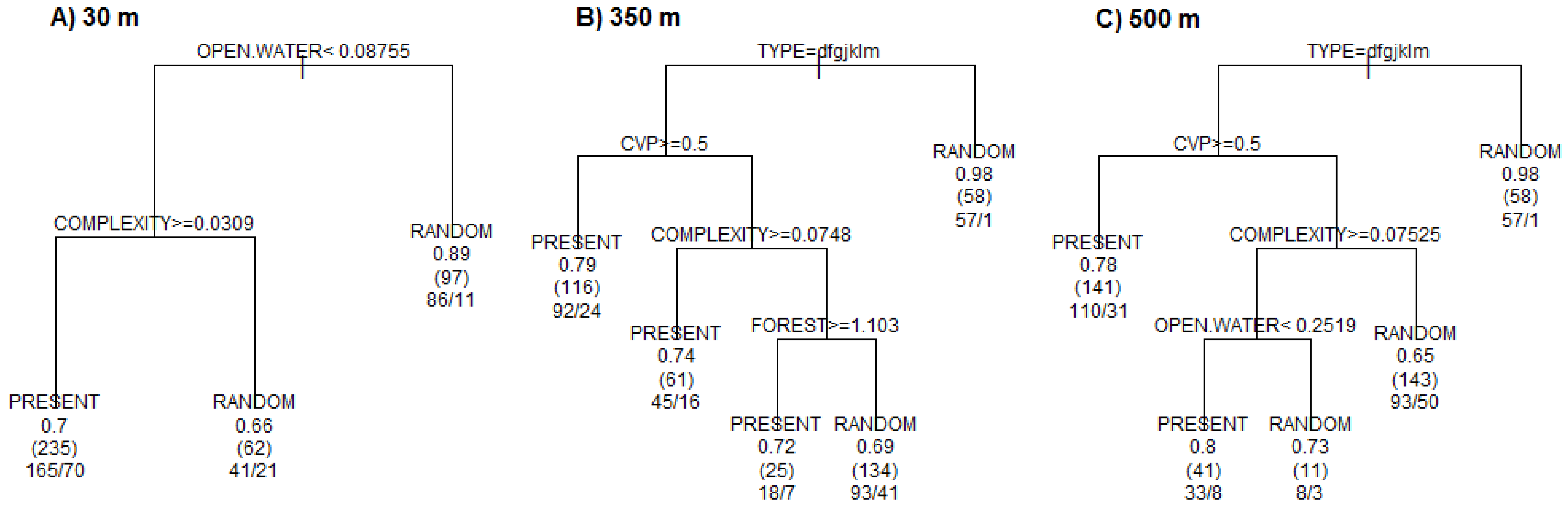

Figure 2.1. Local-scale classification and regression tree models describing the occurrence of four-toed salamanders in Massachusetts wetlands. Wetlands are classified by a set of environmental variables. Observations that are "true" for the expression go to the left branch, otherwise they go to the right branch. The value at the top of each final leaf is the percentage of observations that match the leaf category. The value in parenthesis indicates the number of wetlands in the leaf. The values at the bottom of each leaf are the number of correctly/incorrectly classified observations. Wetland type d=bog, f=deep marsh, g=shallow marsh, j=shrub swamp, k=deciduous forested wetland, l=coniferous forested wetland, m=mixed forested wetland.

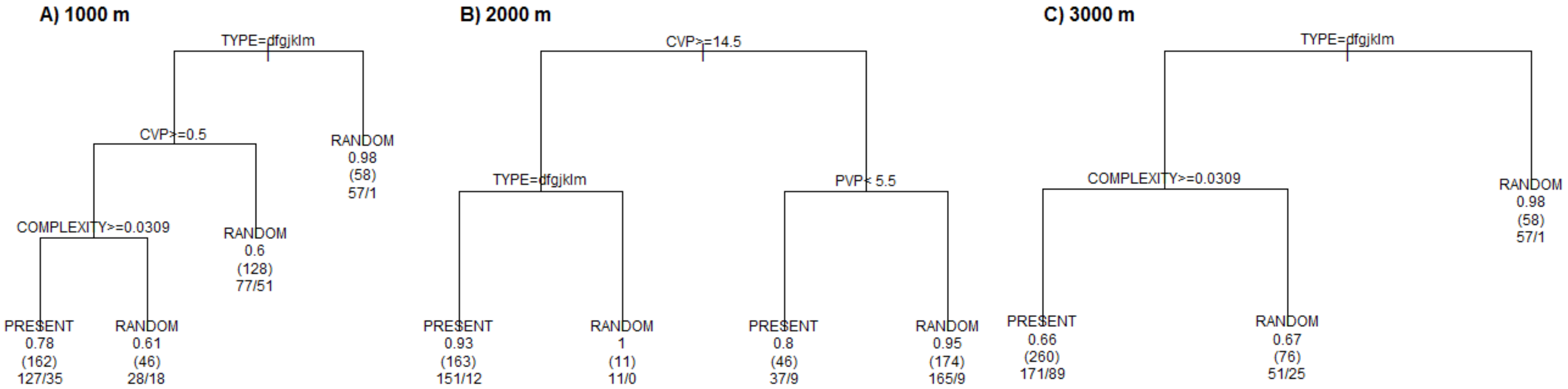

Figure 2.2. Landscape-scale classification and regression tree models describing the occurrence of four-toed salamanders in Massachusetts wetlands. Wetlands are classified by a set of environmental variables. Observations that are "true" for the expression go to the left branch, otherwise they go to the right branch. The value at the top of each final leaf is the percentage of observations that match the leaf category. The value in parenthesis indicates the number of wetlands in the leaf. The values at the bottom of each leaf are the number of correctly/incorrectly classified observations. Wetland type d=bog, f=deep marsh, g=shallow marsh, j=shrub swamp, k=deciduous forested wetland, l=coniferous forested wetland, m=mixed forested wetland.

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