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Annual variation in timing, orientation and effects of weather on Jefferson (*Ambystoma jeffersonianum*) and spotted (*A. maculatum*) salamander movements in central Kentucky

By

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Chair, Advisory Committee

Member, Advisory Committee

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Annual variation in timing, orientation and effects of weather on Jefferson salamander (*Ambystoma jeffersonianum*) and spotted salamander (*A*mbystoma *maculatum*) movements in central Kentucky

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Master of Science
Eastern Kentucky University
Richmond, Kentucky
2012

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
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DEDICATION

This thesis is dedicated to
my family and friends for
their continuing support and
encouragement throughout my academic career.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Stephen Richter, for his guidance and support through my graduate career. I would also like to thank my other committee members, Dr. David Brown and Dr. Charles Elliott, for their comments and assistance over the past three years. This project would not have been possible without assistance in the field from Michelle Guidugli and David Cravens. I would like to express thanks to my parents for their continued moral support and love throughout this journey.

ABSTRACT

Annual variation in temporal and spatial patterns of amphibian migration and dispersal are poorly understood. To address this issue, a circular drift fence was installed around an ephemeral pond at the Central Kentucky Wildlife Management Area, Madison County, Kentucky. The pond was checked daily for salamander movements from 17 January 2010 to 26 September 2010 and from 26 January 2011 to 3 August 2011, which corresponded to the activity season. Weather variables examined in relation to amphibian movements included barometric pressure, cumulative precipitation, temperature and relative humidity. Several species used the ephemeral pond during the study but few successfully reproduced. Jefferson salamanders (*Ambystoma jeffersonianum*) and spotted salamanders (*A. maculatum*) were abundant and successful breeders and were the focus of this study. Breeding times between the two years varied for both species. Weather associations with prebreeding and postbreeding movements varied within and between years. Declines in barometric pressure were generally the best predictor of salamander movements but mean daily temperature and relative humidity were also associated with movements. Juvenile exiting movements also showed significant associations with cumulative precipitation. Detection of suitable weather reduces mortality from freezing and desiccation and can cause annual differences in breeding periods. Orientation of all prebreeding movements across years, sexes, and species were not statistically different from random, while orientation of postbreeding movements of some years and life stages were statistically different from random. Adult movements were generally oriented north of the pond while juveniles oriented in all directions. By being able to understand and predict habitat use and timing of amphibian breeding movements, better management practices can be implemented to reduce human-induced mortality during movements.

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I. INTRODUCTION

Many amphibian species are important in ecosystems because their reproductive and spatial ecology require both aquatic and forested habitats. Egg deposition and larval development occur in aquatic habitat (DiMauro and Hunter, 2002), while foraging and overwintering occurs in forested habitats (Rothermel and Semlitsch, 2002). Amphibians provide a large aquatic biomass that connects to terrestrial predators via food webs (Rittenhouse and Semlitsch, 2007). Habitat destruction and fragmentation affect amphibian spatial ecology and may reduce biomass available for predators (Lehtinen et al., 1999; Todd et al., 2009). Annual weather variation can also impact the reproductive and spatial ecology of amphibians. Expansion of current knowledge and understanding of amphibian reproductive and spatial ecology is required to enhance conservation of declining species and prevent future population declines.

Amphibian reproductive ecology involves movements through terrestrial habitats, and timing of these movements are generally associated with weather. Associations of temperature and precipitation with amphibian movements have been observed in several species (Roe and Grayson, 2008; Williams et al., 2009). Timm et al. (2007) observed varying response to weather between age classes, with rainfall and Julian day being the best predictors of movements, but mean temperature and drought periods also contributed to some timing of movements. Greenburg and Tanner (2004) observed spadefoot toad (*Scaphiopus holbrookii*) movements during breeding periods were most associated with rainfall and maximum change in barometric pressure, but prebreeding movements were more associated with rainfall and pond depth. Drying events early in the breeding season before metamorphosis can occur may limit dispersal events because of high larval and juvenile mortality (Semlitsch and Wilbur, 1988; DiMauro and Hunter, 2002; Morey and Reznick, 2004). Because response to weather might differ between species, age classes and activity periods, focal species need be observed throughout their life cycles to understand weather effects and accurately predict peak movement periods.

Weather patterns are important for predicting timing of amphibian movements; but studies of spatial ecology are important understanding patterns of movements into uplands (Richter et al., 2001; Gamble et al., 2006; Veysey et al., 2009). Semlitsch and Bodie (2003) determined a forested core habitat around breeding ponds was essential for some amphibian species. Forested habitat provides ground cover to escape from predators (Rothermel and Semlitsch, 2002), moist leaf litter to reduce desiccation (Popescu and Hunter, 2011), and mammal burrows to survive freezing temperatures (Douglas and Monroe, 1981; Madison, 1997; Faccio, 2003). Gibbs (1998) found some amphibian abundances declined near forested edges and forest roads while other species were not affected. Many species of amphibians frequently use forested habitat over open habitat, including wood frogs (*Rana sylvatica*; Baldwin et al., 2006), and American toads (*Bufo americanus*; Rothermel and Semlitsch, 2002). Differences in habitat preference may account for differences of orientation between species during breeding migrations and dispersal events.

By examining the orientation of amphibian breeding movements, the most frequently used habitat types can be identified (Greenburg and Tanner, 2004; Jenkins et al., 2006; Blomquist and Hunter, 2010). Roe and Grayson (2008) observed eastern newts (*Notophthalmus viridescens*) oriented toward and used forested habitat surrounding breeding ponds. DeMaynadier and Hunter (1999) observed wood frogs oriented more toward forested habitats than clear-cut areas, and Deguise and Richardson (2009) noted the same for western toads (*B. boreas*). Greenburg and Tanner (2004) observed eastern spadefoot toad movements were not always directed toward forested habitat. Because amphibian species vary in terrestrial habitat use, species of management concern need focal studies conducted to determine habitat preferences.

Reproductive and spatial ecology is better understood by examining populations over multiple years because amphibian response to weather and surrounding habitat use can vary among years (Richter et al., 2003; Brodman, 2004; Timm et al., 2007). Jenkins et al. (2006) found marbled salamander (*Ambystoma opacum*) movements were non-randomly oriented around several breeding ponds, but orientation at individual ponds differed between years. Walston and Mullins (2008) observed juvenile American toads, wood frogs and small-mouthed salamanders (*A. texanum*) always oriented in the same direction toward a large continuous forest block when exiting their breeding ponds. Timm et al. (2007) reported breeding periods of several amphibian species occurred in limited time frames; but between years, movement timing varied considerably as a result of differences in weather. Vasconcelos and Calhoun (2004) found associations of wood frog movements with precipitation and minimum, maximum, and mean daily temperature but response to each variable varied across years, sexes and age classes. Examining amphibian populations over multiple breeding seasons provides a more complete and realistic view of reproductive timing and movement in response to weather and terrestrial habitat.

Statement of Objectives

My objectives were to describe the environmental conditions that influence timing and orientation of adult and juvenile Jefferson salamander (*A. jeffersonianum*) and spotted salamander (*A. maculatum*) movement patterns across multiple years. My primary questions were: 1) What effect does weather have on the timing of adult and juvenile movements? 2) What effect does surrounding land use have on the orientation of adult and juvenile movements, and 3) How does timing and orientation of movements vary annually? I predicted timing of salamander movements to vary between species because of differences in life history characteristics (i.e., egg deposition time, larval development) and movement response to weather cues. Finally, I predicted movements to be oriented primarily toward areas of continuous forest as observed in previous studies (Rittenhouse et al., 2004; Jenkins et al., 2006; Guidugli, 2009).

II. MATERIALS AND METHODS

Study Site

My study site was a small (90.3 m^2), forested ephemeral pond located in a deciduous forest dominated by oaks at the Central Kentucky Wildlife Management Area (hereafter, Central Kentucky WMA; Figure 1) (37.623° N, 84.196° W), which is operated by the Kentucky Division of Fish and Wildlife Resources. Central Kentucky WMA is located within the eastern knobs of the Outer Bluegrass, Interior Plateau ecoregion in Madison County (Figure 2). The site is located southeast of Richmond, Kentucky and the Blue Grass Army Depot. When first visited in 2008, the pond was completely dry with signs of discolored leaf litter and soil suggesting the pond was ephemeral (Guidugli, 2009). Surrounding the forest patch is a regularly mowed field used for hay production, scattered wood lots (oak-hickory and cedar), and permanent ponds (Figure 1). Soils around the pond consisted primarily of poorly-to-somewhat-poorly drained Lawrence-Mercer-Robertsville soil (USDA, 1973).

Sampling Array

Amphibians were captured from 17 January 2010 to 26 September 2010 and from 26 January 2011 to 3 August 2011 using a circular drift fence that completely encircled the pond with 19 evenly spaced pairs of pitfall traps on each side of the fence (38 traps total). Pitfalls were placed approximately 3m apart and contained a wet sponge to

Figure 1. Aerial view of habitat surrounding breeding pond at the Central Kentucky Wildlife Management Area, Madison County, Kentucky

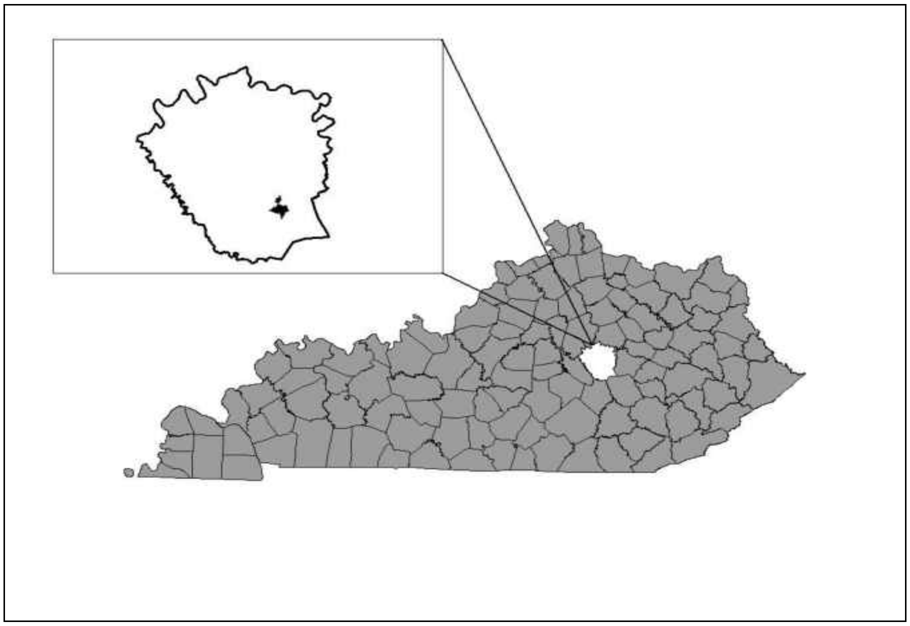

Figure 2. Boundary map of Kentucky counties, highlighting the Central Kentucky Wildlife Management Area, Madison County, Kentucky

prevent amphibian desiccation and a rope attached to the top of the bucket to reduce small mammal mortality (Karraker, 2001). Three small holes were drilled into the bottom of each bucket to keep buckets from overflowing (Walston and Mullins, 2008). Additionally, because of poorly draining Lawrence-Mercer-Robertsville soil, the holes prevented rising groundwater from pushing the pitfall traps out of the ground and biasing captures rates.

Pitfall traps were checked at least once every 24 hours starting before 0900 hours. Amphibians captured in pitfall traps while trying to enter the pond (prebreeding) were placed at the nearest pond edge. Amphibians captured exiting the pond (postbreeding) were placed on the outside of the fence 2m beyond the point of capture to reduce accidental recaptures (Graeter and Rothermel, 2007).

Salamander Measurements

Amphibians marked in a previous study by Guidugli (2009) were identified and released. New amphibians captured were marked by clipping the tip of the third toe on the rear right foot in 2010 and on the rear left foot in 2011. Individuals captured in multiple years were not reclipped. Toe clipping is assumed to not cause permanent damage to salamanders (McCarthy et al., 2009). Toe clips were collected using a pair of manicure scissors sterilized in 95% ethyl alcohol between each clip. Individuals with deformed appendages were not clipped but photos were taken for recapture identification. Salamanders were weighed using a Pesola 60 g spring scale and measured for total length (snout to tail) and snout-vent length (SVL).

Weather Data Collection

Several environmental characteristics were measured daily. Ambient temperature, relative humidity, barometric pressure and cumulative precipitation were collected from a weather station at the Blue Grass Army Depot (Tower 1, 37.732° N, 84.193° W) located 4 km north of the study pond. Pond depth was measured daily using a meter stick placed at the deepest point in the pond.

Statistical Analyses

Prebreeding and postbreeding movements were analyzed with a generalized linear model using SAS software, version 9.1 (SAS Institute, Inc.). Species do not move continually throughout the year, so weather data were analyzed only during movement periods and 5 days before and after movements. Minimum, maximum, maximum change and mean daily values were calculated for barometric pressure, temperature, and relative humidity. Adult movements were analyzed using weather data from the previous 24 hours and included cumulative precipitation. Statistical models of juvenile exiting movements also included pond depth as a potential explanatory factor. To avoid multicollinearity, some of the weather variables were removed prior to individual modeling. When weather variables were correlated with each other at $r \geq 0.70$, the variable most correlated with captures was retained. Generalized linear models were conducted separately for females, males and juveniles by species, year, and direction of travel. Using the GENMOD procedure, deviance divided by degrees of freedom (Dev/df) was used to determine which distribution type best fit the individual models, where Poisson was chosen if $\text{Dev/df} \leq 3$ or negative binomial if $\text{Dev/df} > 3$. Variables were removed from the models in a stepwise fashion by excluding the variable with the highest p value and rerunning the model. The process was repeated until all remaining variables in the model were at $p < 0.10$ with $p \leq 0.05$ being considered statistically significant.

Orientation of prebreeding and postbreeding movements were tested for a non-uniform distribution around the pond using Oriana software, version 3 (Kovach Computing Services) (Delisle and Grayson, 2011). A Rao's spacing test was preformed to ensure trap locations were non-biased and uniformly distributed around the pond. Separate circular-linear correlation analyses were conducted for females, males, and juveniles by species, year, and direction of travel.

III. RESULTS

Timing and Response of Movements to Weather

Adult Breeding Movements

Several amphibian species were captured at the drift fence, but few species reproduced successfully in the pond (Table 1). Analyses were focused on Jefferson and spotted salamanders, which were the only two species that reproduced and were in sufficient abundance. Although both bred successfully, there was variation in annual population sizes (Table 1). Timing of movements into and out of the pond varied across years, age classes, and species. Pond drying events took place on 22 September 2010 and 2 August 2011.

Table 1. Summary of adult and juvenile amphibian captures at the drift fence, respectively. *Ambystoma jeffersonianum* and *A. maculatum* in 2010 and 2011only, are separated by females, males and juveniles, respectively.

Species	2009	2010	2011
Acris crepitans	4; 0	0; 0	0; 0
Ambystoma barbouri	4; 0	1; 0	0; 0
A. jeffersonianum	78; 507	40; 33; 86	43; 26; 60
A. maculatum	468; 37	316; 86; 50	138; 107; 112
A. opacum	5; 1	2; 0	0; 0
Bufo americanus	2; 0	4; 0	1; 0
B. fowleri	4; 0	0; 0	0; 0
Notophthalmus viridescens	11; 0	3; 0	4; 0
Plethodon glutinosus	0; 0	1; 0	0; 0
Pseudacris crucifer	0; 0	11; 0	2; 0
Rana catesbeiana	8; 0	186; 1	20; 0
R. clamitans	3; 0	53; 7	30; 1
R. palustris	4; 0	1; 0	0; 0

Timing of female Jefferson salamander prebreeding and postbreeding movements varied annually (Figures A-1 and A-2). Earliest prebreeding movements occurred in late

January 2010 during precipitation events above freezing temperatures, and a second prebreeding movement peak occurred in mid-March during precipitation events (Figure A-1). The generalized linear model resulted in a significant negative association of mean daily relative humidity with female Jefferson salamander movements (mean ± stdev for days moved: 84.7 ± 9.18%; Table 2; Figure B-1). In 2011 an initial prebreeding wave occurred during precipitation events in early February (Figure A-1). Days prior to the second wave were large precipitation events during near-freezing temperatures, but prebreeding movements in 2011 were not significantly associated with any weather variables. The earliest postbreeding movements occurred in mid-January 2010 with the highest proportion of movements in March (Figure A-2). The peak movement period was preceded by several days of precipitation events at low temperatures. In 2011 movements occurred over a shorter period than 2010, with the highest proportion of postbreeding movements in late February, coinciding with multiple precipitation events above 10° C. Postbreeding movements in 2010 and 2011 were not significantly associated with any measured weather variables.

Timing of male Jefferson salamander prebreeding and postbreeding movements varied throughout the study (Figures A-3 and A-4). Initial prebreeding movements in 2010 occurred during mid-to-late January during large precipitation events and were significantly and positively associated with mean daily temperature (mean ± stdev for days moved: 8.59 ± 4.10° C; Table 2; Figures A-3 and B-2). In 2011 movements occurred over a month, but 75% of movements occurred on 2 February. Prior to movements were

Table 2. Model selection and significant weather associations with adult *Ambystoma jeffersonianum* breeding movements.

Sex	Direction	Year	Model	Parameter	Estimate	Standard Error	Z	p value
Female	Entering	2010	Poisson	Intercept	-6.41	3.01	-2.13	0.03
				Mean daily relative humidity	0.07	0.03	2.01	0.02
Male	Entering	2010	Poisson	Intercept	-0.98	0.34	-2.86	<0.01
				Mean daily temperature	0.15	0.04	4.08	0.04
Male	Exiting	2011	Poisson	Intercept	96.20	37.08	2.59	<0.01
				Mean daily barometric pressure	-0.10	0.04	-2.60	0.04

freezing precipitation events, but the day before movement temperatures were above 10° C. The model, however, did not result in significant associations with any weather variables. Postbreeding movements for both years started in February and subsided in March (Figure A-4). During the highest proportion of 2010 postbreeding movements were multiple precipitation events around 10° C, but were not significantly associated with weather. Postbreeding movements in 2011 were negatively associated with mean daily barometric pressure (mean ± stdev for days moved: 981.25 ± 5.60mb; Table 2; Figure B-3).

Timing of female spotted salamanders prebreeding and postbreeding movements varied annually during the study (Figures A-5 and A-6). Prebreeding movements in 2010 began the latest in mid-March after multiple days of precipitation above 10° C, the first continuous period of precipitation above 10° C since the end of January (Figure A-5). Prebreeding movements in 2010 were significantly and negatively associated with mean daily barometric pressure (mean ± stdev for days moved: 974.42 ± 4.81mb; Table 3; Figure B-4). The only continuous precipitation events above 10° C in February occurred

Table 3. Model selection and significant weather associations with *Ambystoma maculatum* breeding movements. Negbin represents models using a negative binomial distribution.

Sex	Direction	Year	Model	Parameter	Estimate	Standard Error	Z or Chi	p value
Female	Entering	2010	Negbin	Intercept	215.59	72.14	8.93	0.01
				Mean daily pressure	-0.22	0.07	8.86	<0.01
	Exiting	2010	Negbin	Intercept	117.58	47.59	6.10	0.01
				Minimum barometric pressure	-0.12	0.05	6.25	0.01
				Maximum change in barometric pressure	0.25	0.09	7.32	0.01
		2011	Negbin	Intercept	-5.37	2.20	5.97	0.01
				Maximum change temperature	0.22	0.10	5.14	0.02
				Mean daily relative humidity	0.06	0.03	5.13	0.03
Male	Entering	2011	Negbin	Intercept	211.63	98.25	4.64	0.03
				Minimum barometric pressure	-0.22	0.10	4.70	0.04
				Maximum change barometric pressure	0.09	0.05	2.84	0.09
	Exiting	2010	Poisson	Intercept	130.93	45.56	2.81	<0.01
				Mean daily barometric pressure	-0.13	0.05	-2.82	0.04
				Maximum change barometric pressure	0.26	0.06	4.18	0.06
				Mean daily relative humidity	-0.05	0.02	-2.40	0.07
		2011	Negbin	Intercept	121.59	57.61	4.45	0.03
				Mean daily barometric pressure	-0.14	0.06	5.43	0.02
				Maximum change temperature	0.19	0.11	3.10	0.08
				Mean daily relative humididty	0.10	0.03	11.61	<0.001
				Maximum change relative humidity	0.05	0.03	3.14	0.07

in 2011, during the earliest spotted prebreeding movements of the study. No significant weather associations were found for 2011 prebreeding movements. Postbreeding movements in 2010 predominantly took place at the end of March; preceding precipitation events near 10° C, and were negatively associated with minimum daily barometric pressure (mean ± stdev for days moved: 970.04 ± 4.67mb), and positively associated with maximum change in daily barometric pressure (mean ± stdev for days moved: 10.17 ± 3.30mb; Table 3; Figures A-6, B-5, and B-6, respectively). Peak 2011 postbreeding movements took place between February and March during intermittent precipitation events and mean daily temperatures above 10° C. Postbreeding 2011 movements were negatively associated with maximum change in daily temperature (mean ± stdev for days moved: 12.02 ± 3.71° C) and mean daily relative humidity (mean ± stdev for days moved: 72.97 ± 12.19%; Table 3; Figures A-6, B-7, and B-8, respectively).

Male spotted salamanders showed annual variation in timing of prebreeding and postbreeding movements (Figures A-7 and A-8). Highest proportion of movements in 2010 occurred in late March, immediately after a large precipitation event with temperatures around 10° C (Figure A-7). Earliest 2011 prebreeding movements occurred in late February during continuous precipitation events around 10° C and had a significant negative association with minimum daily barometric pressure (mean ± stdev for days moved: 973.14 ± 4.67mb; Table 3; Figure B-9). Postbreeding movements in 2010 began in March and ended in late April, while 2011 postbreeding movements occurred from late February to early April (Figure A-8). Precipitation events with several days above 10° C coincided with postbreeding movements. Postbreeding movements in 2010 and 2011 had a significant negative association with mean daily barometric pressure (mean ± stdev for days moved: 976.60 ± 4.77mb and 976.61 ± 4.86mb, respectively); and 2011 movements had a positive association with mean daily relative humidity (mean ± stdev for days moved: 75.34 ± 3.58%; Table 3; Figures B-10, B-11, and B-12, respectively). A summary of significant weather associations with adult prebreeding and postbreeding movements can be found in Tables 4 and 5, respectively.

Table 4. Summary of significant weather associations with adult *Ambystoma jeffersonianum* and *A. maculatum* prebreeding movements. Negative symbols represent a negative association and a positive symbol represents a positive association with the weather variable.

Species	Sex	Year	Barometric pressure	Temperature	Relative humidity	Precipitation
Ambystoma jeffersonianum	F	2010			(+)	
	M	2010		(+)		
A. maculatum	F	2010	(-)			
	M	2011	(-)			

Table 5. Summary of significant weather associations with adult *Ambystoma jeffersonianum* and *A. maculatum* postbreeding movements. Negative symbols represent a negative association and a positive symbol represents a positive association with the weather variable.

Species	Sex	Year	Barometric Pressure	Temperature	Relative humidity	Precipitation
Ambystoma jeffersonianum	M	2011	(-)			
A. maculatum	F	2010	(-) (+)			
	M	2010	(-)			
	F	2011		(+)	(+)	
	M	2011	(-)		(+)	

Juvenile Exiting Movements

Timing and response of juvenile Jefferson and spotted salamander exiting movements varied annually (Figures A-9 and A-10). In 2010 a high proportion of juvenile Jefferson salamanders exiting movements occurred during a 12-day period with recurring precipitation events below 26° C, but movements were not significantly associated with weather (Figure A-9). Exiting movements in 2011 were more dispersed and had significant positive associations with maximum change in barometric pressure and cumulative precipitation (mean ± stdev for days moved: 3.71 ± 1.24mb and 7.97 ± 12.36mm, respectively), and negative associations with mean daily barometric pressure and mean daily temperature (mean ± stdev for days moved: 979.91 ± 2.30mb and 22.72 ± 1.97° C, respectively; Table 6; Figures B-13, B-14, B-15, and B-16). Juvenile spotted salamanders exiting movements took place from the end of June to September in 2010 and were significantly negatively associated with minimum barometric pressure (mean ± stdev for days moved: 979.36 ± 2.50 mb; Table 6; Figures A-10 and B-17). Movements in 2011 had a significant positive association with cumulative precipitation (mean ± stdev for days moved: 8.93 ± 6.66mm) and a negative association with mean daily temperature (mean ± stdev for days moved: 22.70 ± 1.97 ° C; Table 6; Figures B-18 and B-19, respectively). A summary of significant weather associations with juvenile exiting movements can be found in Table 7.

Table 6. Model selection and significant weather associations with juvenile *Ambystoma jeffersonianum* and *A. maculatum* exiting movements. Negbin represents models using a negative binomial distribution.

Species	Year	Model	Parameter	Estimate	Standard Error	Z or Chi Square	p value
Ambystoma jeffersonianum	2011	Poisson	Intercept	261.29	71.63	3.65	<0.001
			Mean daily barometric pressure	-0.26	0.07	-3.46	0.03
			Maximum change barometric pressure	-0.50	0.14	-3.47	0.01
			Cumulative precipitation	0.01	-0.01	1.8	0.03
			Mean daily temperature	-0.34	-0.48	-4.5	<0.01
A. maculatum	2010	Poisson	Intercept	220	63.67	3.47	<0.001
			Minimum barometric pressure	-0.23	-0.35	-3.47	0.04
	2011	Negbin	Intercept	-50.26	42.18	1.42	0.23
			Cumulative precipitation	0.26	0.11	5.47	<0.01
			Mean daily temperature	-0.61	0.26	5.42	<0.01
			Maximum relative humidity	0.67	0.47	2.05	0.07

Table 7. Summary of significant weather associations with juvenile *Ambystoma jeffersonianum* and *A. maculatum* exiting movements. Negative symbols represent a negative association and a positive symbol represents a positive association with the weather variable.

Species	Year	Barometric pressure	Temperature	Relative humidity	Precipitation
Ambystoma jeffersonianum	2011	(-) (+)	(-)		(+)
A. maculatum	2010	(-)			
	2011		(-)		(+)

Orientation of Salamander Movements

Adult Breeding Movements

Orientation of female Jefferson salamanders during prebreeding and postbreeding movements varied annually (Figures C-1 and C-2). Prebreeding and postbreeding movements in 2010 were not statistically different from random, but orientation was not observed toward the west-southwest (Table 8; Figures C-1 and C-2). During 2011, prebreeding movements were not statistically different from random, and movements were not observed from the west-southwest (Table 8; Figure C-1). Postbreeding movements in 2011 were significantly different from random (p= 0.04, R= 0.446; Table 8; Figure C-2).

Table 8. Orientation of adult *Ambystoma jeffersonianum* breeding movements.

Sex	Year	Direction	p value	R
Adults	2009	Entering	0.049	0.432
		Exiting	NS	NS
Female	2010	Entering	0.195	0.319
		Exiting	0.096	0.382
	2011	Entering	0.702	0.149
		Exiting	0.04	0.446
Male	2010	Entering	0.082	0.394
		Exiting	0.038	0.45
	2011	Entering	0.828	0.109
		Exiting	0.001	0.633

Male Jefferson salamanders showed annual variation in the orientation of prebreeding and postbreeding movements (Figures C-3 and C-4). In 2010, male prebreeding movements were not statistically different from random, but postbreeding movements were statistically different from random and oriented primarily toward the north-northeast (p= 0.038, R= 0.45; Table 8; Figure C-4). Prebreeding orientation in 2011 was not statistically different from random but the highest proportion of movements were oriented north-northeast (Table 8; Figure C-3). Postbreeding movements in 2011 were statistically different from random and were not oriented toward the north-northeast, west-northwest or south-southwest ($p < 0.001$, $R = 0.633$; Table 8; Figure C-4).

Orientation of female spotted salamanders during prebreeding and postbreeding movements varied from year-to-year (Figures C-5 and C-6). During 2010, prebreeding and postbreeding movements were not statistically different from random with orientation primarily in the north (Table 9; Figures C-5 and C-6). In 2011, prebreeding movements were not significantly different from random, but postbreeding movements were statistically different from random and oriented primarily in the north ($p < 0.001$, $R = 0.733$; Table 9; Figures C-5 and C-6).

Table 9. Orientation of adult *Ambystoma maculatum* breeding movements.

Sex	Year	Direction	p value	R
Adults	2009	Entering	0.003	0.591
		Exiting	<0.001	0.662
Female	2010	Entering	0.099	0.379
		Exiting	0.08	0.396
	2011	Entering	0.201	0.316
		Exiting	<0.001	0.733
Male	2010	Entering	0.209	0.312
		Exiting	0.01	0.53
	2011	Entering	0.502	0.207
		Exiting	0.108	0.372

As with the orientation of female spotted salamander movements, males of the species also exhibited changes in orientation (Figures C-7 and C-8). During 2010, prebreeding movements were not significantly different from random; while postbreeding movements were statistically different from random, with no movements occurring in the south-southwest (p= 0.01, R= 0.53; Table 9; Figure C-7 and C-8). In 2011, prebreeding and postbreeding movements were not statistically different from random with movements oriented in all directions (Table 9; Figures C-7 and C-8).

Juvenile Exiting Movements

After metamorphosis, orientation of exiting juvenile Jefferson and spotted salamanders varied annually (Figures C-9 and C-10). Juvenile Jefferson salamander exiting movements were not statistically different from random, with movements oriented in all directions (Table 10; Figures C-9). Postbreeding movements in 2011 were statistically different from random with low orientation towards the west-southwest and north-northwest (p= 0.27, R= 0.652; Table 10; Figure C-9). Juvenile spotted salamander exiting movements in 2010 and 2011 were not statistically different from random (Table 10). Exiting movements in both years were oriented in all directions, but in 2010 orientation was proportionately higher in the west-southwest (Figure C-10).

Table 10. Orientation of juvenile *Ambystoma jeffersonianum* and *A. maculatum* exiting movements.

Species	Year	p value	R
Ambystoma jeffersonianum	2009	NS	NS
	2010	0.1	0.378
	2011	0.027	0.472
A. maculatum	2009	<0.001	0.652
	2010	0.261	0.189
	2011	0.457	0.221

IV. DISCUSSION

Annual Variation of Timing and Response of Movements to Weather

Adult Breeding Movements

Timing of movements is an important factor for persistence of pond-breeding amphibians. Several studies have examined the timing of ambystomatid salamander breeding movements, but were limited to a single year (Harris, 1980; Douglas and Monroe, 1981). Without examining several years, annual variation in breeding times cannot be addressed. For example, Guidugli (2009) observed movements within one year were shifted an entire month compared to my study. Other researchers have examined breeding populations over multiple years to detect annual variation in breeding times, but these studies focused on a single permanent pond (Sexton et al., 1990; Brodman, 1995; Delisle and Grayson, 2011). Drying events in ephemeral ponds may have an influence on the breeding period and juvenile exiting movements. This study is unique because to my knowledge it is the first to examine annual variation in timing and weather response of ephemeral pond breeding adult and juvenile ambystomatid salamander movements.

Timing of ambystomatid breeding periods in this study varied by species and across years. Similar to Harris (1980) and Sexton et al. (1990), spotted salamanders in this study had a breeding period that lasted two to three months. In contrast, Brodman (1995) and Guidugli (2009) found much shorter breeding periods, a few days and one month, respectively. Although timing of Jefferson salamander breeding movements varied between years, the patterns I observed were similar to other studies in 2010 (Williams, 1973; Douglas and Monroe, 1981; Smith, 1983; Minton, 2011) and 2011 (Brodman, 1995; Guidugli, 2009; Delisle and Grayson, 2011). In this study female Jefferson salamander movements occurred in distinct breeding waves, similar to findings from other studies for Jefferson (Guidugli, 2009) and spotted salamanders (Harris, 1980; Sexton et al., 1990).

Breeding in waves can have mixed effects on salamander survival. Intraspecies competition for egg deposition sites and mate selection is reduced with lower salamander densities. Harris (1980) observed later breeding spotted salamanders had higher survival rates than early breeders because of early freezing events that increase egg and adult mortalities. However, spotted salamanders breeding later in the season can have increased larval mortality from predation and desiccation if drying events take place before metamorphosis can occur (Smith and Petranka, 1987; Brodman, 1996; Brodman, 2004).

Because Jefferson and spotted salamanders use similar habitat and resources, the presence of one species potentially affects the other's behavior and movements (Douglas and Monroe, 1981; Faccio, 2003; Homan et al., 2007). Brodman and Jaskula (2002) found spotted salamander larvae increased time spent in refuge when Jefferson larvae were present. A high proportion of adult Jefferson salamander postbreeding movements took place on the same day or the following day of high proportioned spotted salamander prebreeding movements. Density dependent factors could lead to Jefferson salamanders exiting the pond as spotted salamanders began to enter and limit the available terrestrial and aquatic habitat. Overlapping movements could also result from these time periods having optimal weather conditions for movements of both species.

Although no measured weather variable was significantly associated with all ambystomatid movements, some patterns were apparent. Unlike Guidugli (2009), generally only one or two weather variables were significantly associated with adult movements and were more associated with barometric pressure than temperature and relative humidity. Response to weather cues varied between female and male Jefferson salamanders and between prebreeding and postbreeding movements. Female and male spotted salamanders responded more similarly to weather cues than female and male Jefferson salamanders. Changes in weather cues between years may be crucial for detecting periods with sufficient moisture and temperatures but might be missed by studies lasting only one or two years (Madison, 1997; Vasconcelos and Calhoun, 2004; Guidugli, 2009; Veysey et al., 2009). I suggest more research is needed over multiple breeding seasons to thoroughly understand the relationships between weather and movements.

Barometric pressure seemed to be the best indicator for ambystomatid movements across years, sexes and species. Barometric pressure has been observed to affect frog chorus activity (Brooke et al., 2000; Oseen and Wassersug, 2002), but only two known studies have examined associations of barometric pressure with amphibian movements. Greenburg and Tanner (2004) observed eastern spadefoot breeding movements were associated with maximum change in barometric pressure and precipitation, and Guidugli (2009) found barometric pressure and other weather variables were associated with

Jefferson and spotted salamander movements. Rapid and severe changes in barometric pressure generally coincide with changes in temperature or precipitation events, which are ideal conditions for *Ambystoma* movements. Detection of these changes might help individuals move during optimal conditions.

Cumulative precipitation was not significantly associated with any adult breeding movements. Rainfall has been a consistent predictor of ambystomatid salamander movements in several studies (Sexton et al., 1990; Brodman, 1995; Vasconcelos and Calhoun, 2004; Guidugli, 2009). Although both species were seen moving during or closely following precipitation events, no statistical associations were detected. Veysey et al. (2009) found weekly precipitation was more positively correlated with amphibian movements than daily cumulative precipitation. At my study site, soils surrounding the pond are poorly-drained and remained saturated for multiple days after precipitation events. Presence of saturated soil and leaf litter may have provided sufficient moisture to support salamander movements and reduce precipitation effects in the models. Other studies have found precipitation combined with temperature is a better indicator of adult salamander movements (Sexton et al., 1990; Vasconcelos and Calhoun, 2004; Todd and Winne, 2006; Guidugli, 2009). Freezing precipitation events may have also altered the effect of precipitation in the models. For example in 2009 when adult movements were associated with precipitation there was a lower total cumulative freezing precipitation compared to 2010 and 2011 (Guidugli, 2009).

Juvenile Exiting Movements

Annual variation in occurrence and timing of drying events can have effects on timing of exiting juvenile ambystomatid salamanders. Similar to Guidugli (2009), Jefferson salamander movements into the pond generally occurred at least two weeks earlier than spotted salamanders. Larval spotted salamanders might have an increased risk of mortality if drying events occur before metamorphosis. Similar to previous studies, juvenile spotted salamanders exited the pond from July to autumn (Wilson, 1976; Windmiller, 1996; Delisle and Grayson, 2011). Unlike my population, DiMauro and Hunter (2001) observed juvenile spotted salamanders began exiting ponds in August, but over 80% of their study ponds dried before metamorphosis occurred. In contrast to my results, Guidugli (2009) observed juvenile Jefferson salamanders ended their exiting movements in autumn. This suggests that if a drying event does not occur annually, larval and juvenile Jefferson salamanders might forage longer to increase body size before exiting ponds. Although Rothermel and Semlitsch (2002) found juveniles that weighed more before exiting had an increased probability of survival, there is a trade-off in terms of increased larval mortality from ranid adults, other salamanders, and raccoons (*Procyon lotor*) for individuals remaining in the pond.

Although significant weather associations with juvenile ambystomatid salamander movements varied across time and species, negative associations with barometric pressure and temperature occurred in both species. Studies on the effects of weather on juvenile spotted salamanders are limited, and Guidugli (2009) is the only other study to examine the effects of weather on juvenile Jefferson salamanders. Similar to my results, Guidugli (2009) found barometric pressure had a significant association with movements of juvenile Jefferson and spotted salamanders. Associations of movements with temperature and precipitation have also been associated with adult (Sexton et al., 1990; Vasconcelos and Calhoun, 2004) and juvenile (Timm et al., 2007b; Guidugli, 2009) spotted salamander movements.

Similar to previous studies, significant weather associations with movement varied between life stages of both species but general trends were observed (Greenburg and Tanner, 2004; Timm et al., 2007). Juvenile exiting movements took place during precipitation events below 26° C, suggesting movements were limited by hotter temperatures, as opposed to adult movements which were limited by freezing temperatures. Adult movements were not associated with precipitation, possibly due to increased freezing precipitation events earlier in the year, and because sufficient moisture was retained in the soil and leaf litter on days where movements occurred. Juvenile exiting movements always shared at least one significant weather association with adult exiting movements for the same year; suggesting age classes respond to similar weather variables, but movement response varies based on age and additional weather cues. Movement timing of both species and life stages, with the exception of female Jefferson salamanders, had negative associations with barometric pressure. These finding suggests more amphibian studies are needed to examine annual effects of weather, especially barometric pressure, on timing of amphibian movements between sexes and life stages.

Annual Variation of Orientation of Salamander Movements

Adult Breeding Movements

Despite orientation of adult ambystomatid breeding movements in this study varying across time, sexes and species, general trends were observed. Adult movements tended to be directed north, which is toward the largest forested area (Figure 1). Orientation toward forested habitat over agricultural or open areas has been observed in several field studies (Madison, 1997; Jenkins et al., 2006; Homan et al., 2008) and in the laboratory (Rittenhouse et al., 2004). Forested habitats provide canopy cover, leaf litter and coarse woody debris, which reduce desiccation during movements (Popescu and Hunter, 2011), and mammal burrows, which are used by salamanders to survive freezing events (Madison, 1997; Faccio, 2003; Regosin et al., 2004).

Orientation of adult ambystomatid breeding movements varied between direction of travel (i.e. into the pond or out of the pond) and within and between sexes. Throughout this study, Jefferson and spotted salamander prebreeding movement orientations were not statistically different from random. This finding differs from several studies in which prebreeding movement orientation was always statistically different from random (Homan et al., 2008; Guidugli, 2009; Delisle and Grayson, 2011). Orientation of some postbreeding movements were significantly different from random, similar to Guidugli (2009), for spotted salamanders but different from Jefferson salamanders. Dissimilar to Delisle and Grayson (2011), Jefferson salamander postbreeding movements were not always randomly oriented. Variation within sexes was observed with male Jefferson salamanders shifting from a northern orientation to a southern orientation in 2011 and also varied between sexes as females in 2011 oriented north. Movement from foraging locations to overwintering sites might affect observed orientation of prebreeding and postbreeding movements. Individuals skipping breeding years and not entering the pond might also affect overall orientation of breeding movements (Homan et al., 2007; Delisle and Grayson, 2011).

Adult Jefferson and spotted salamander breeding movements were oriented the least toward the west-southwest and south-southeast. A small forest patch is oriented west-southwest of the pond; but just beyond is heavily managed open habitat. Orientation away from open areas is consistent with previous findings for ambystomatid salamanders (Madison, 1997; Jenkins et al., 2006; Homan et al., 2008). Movements in this study oriented away from (i.e. in other directions) the south-southeast might be directly affected by biotic factors. In the very open area located south-southeast of the study site there is a large permanent lake and a small permanent pond, both of which support aquatic predators. Movements toward these habitats would potentially increase salamander predation and desiccation.

Juvenile Exiting Movements

Exiting orientation of juvenile Jefferson and spotted salamanders in this study varied across time and among species. Guidugli (2009) observed a similar path of random orientation of juvenile Jefferson exiting movements, but in contrast she observed a statistically non-random exiting orientation of juvenile spotted salamanders with apparent movements toward forested habitat. Delisle and Grayson (2011) also observed a random orientation of exiting juvenile Jefferson salamanders. Similar to adult breeding orientation, biotic factors may have limited movements in this study toward the east-southeast. Drying events in 2010 and 2011 could have triggered faster exiting movements than in 2009 when a drying event did not occur (Guidugli, 2009). As the pond dried, available aquatic habitat in 2010 and 2011 was reduced into small separated puddles. Individuals might have exited toward the closest pond edge from their respective puddles and then reoriented once entering the surrounding habitat beyond the drift fence.

Forest edges can also contribute to the orientation of salamander movements. Rittenhouse and Semlitsch (2006) observed translocated spotted salamanders ventured into open areas but remained within a few meters from forest edges. Walston and Mullins (2008) and Popescu and Hunter (2011) observed forest edges acted as a dispersal barrier to juvenile amphibians. Amphibians at forest edges may reorient once the edge is reached, changing initial observed orientations and thereby avoiding dispersal through open habitat. Although open areas can be detrimental to salamanders, they do not always act as movement barriers (Montieth and Paton, 2006; Rittenhouse and Semlitsch, 2006; Veysey et al., 2009). Because of fragmented conditions of my study site, immigration to new breeding locations generally can only be accomplished through movements in non-forested habitat, so the ability to traverse open habitat appears essential to maintaining connected populations.

Orientation mechanisms of amphibians, especially ambystomatid salamanders, are not well understood but are important in their reproductive and spatial ecology. Patrick et al. (2007) observed juvenile wood frogs oriented east-northeast from their natal ponds, and from translocated locations at foreign ponds; suggesting they used indirect cues for orientation. Phillips (1986) manipulated magnetic fields of enclosures and found eastern newts to orient themselves based on the given magnetic field. Schlegel and Renner (2007) observed alpine newts (*Triturus alpestris*) in dark conditions spontaneously reoriented themselves using the earth's magnetic field. McGregor and Teska (1986) observed spotted salamanders selected the scent of their natal pond over a foreign pond scent. Madison and Shoop (1970) found displaced Jordan's salamanders (*Plethodon jordani*) frequently climbed vegetation and substrate; suggesting they were orienting their movements by detecting olfactory cues from natal ponds. Olfactory cues might also orient salamander movements toward important microhabitat such as leaf litter and mammal burrows (Madison, 1997; Faccio, 2003). Orientation mechanisms may also involve visual cues to orient toward breeding or foraging habitat. Regardless of the mechanism, knowledge concerning amphibian movement orientation needs to be expanded because orientation affects detection of natal ponds during migrations, foreign ponds during dispersal events, and optimal microhabitat during all types of movements.

V. MANAGEMENT IMPLICATIONS

The continuing decline of amphibian populations coupled with habitat destruction and fragmentation means conservationists need to further their understanding of spatial and reproductive ecology of focal species across multiple years in order to optimize conservation efforts. This study furthers the understanding of amphibian reproductive ecology and increases our understanding of the understudied Jefferson salamander. Findings in this study support limiting management activities such as mowing and prescribed burnings in central Kentucky during peak movements of adult (mid-January to early April) and juveniles (June to September or the first drying event). Alternatively, if management activities need to occur during these time frames, land managers should undergo these activities when movements are least likely to occur in relation to weather (Sexton et al., 1990; Timm et al., 2007; Guidugli, 2009). I recommend reforesting the core forested habitat around my study pond to a distance of at least 164m (Semlitsch and Bodie, 2003). Re-establishing the forested core, would provide more habitat for the populations and connect nearby linear habitat as corridors, which would greatly facilitate migration and dispersal movements of salamanders into the surrounding habitat.

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APPENDIX A:

Timing of Adult Breeding Movements and Juvenile Exiting Movements

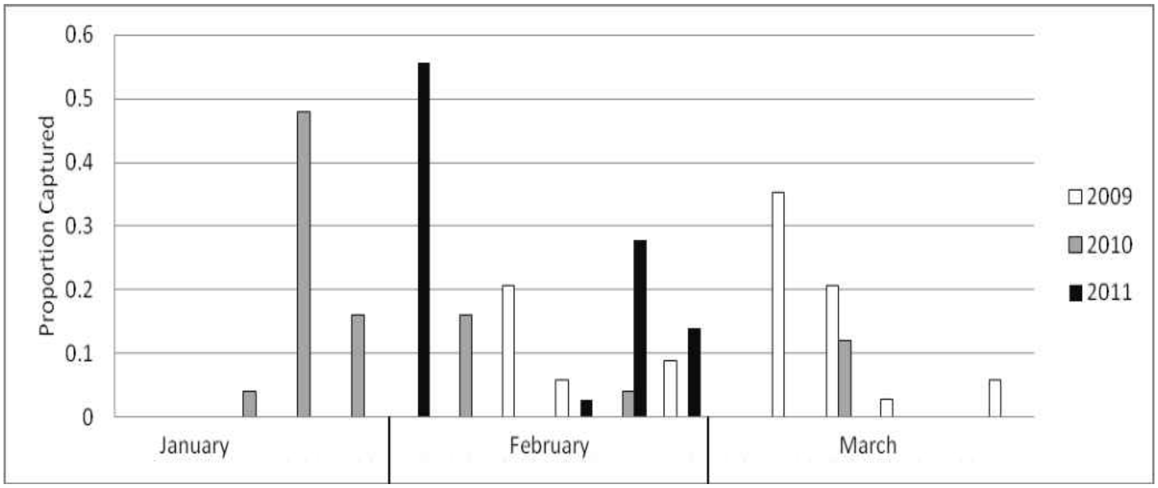

Figure A-1. Timing of female *Ambystoma jeffersonianum* prebreeding movements. Bars on the X axis represent movements over 5-day periods.

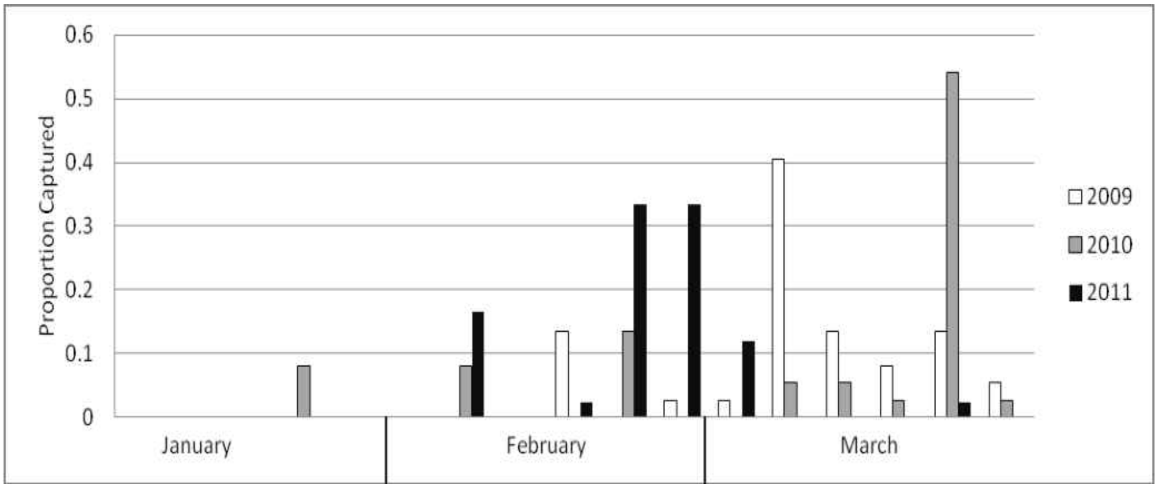

Figure A-2. Timing of female *Ambystoma jeffersonianum* postbreeding movements. Bars on the X axis represent movements over 5-day periods.

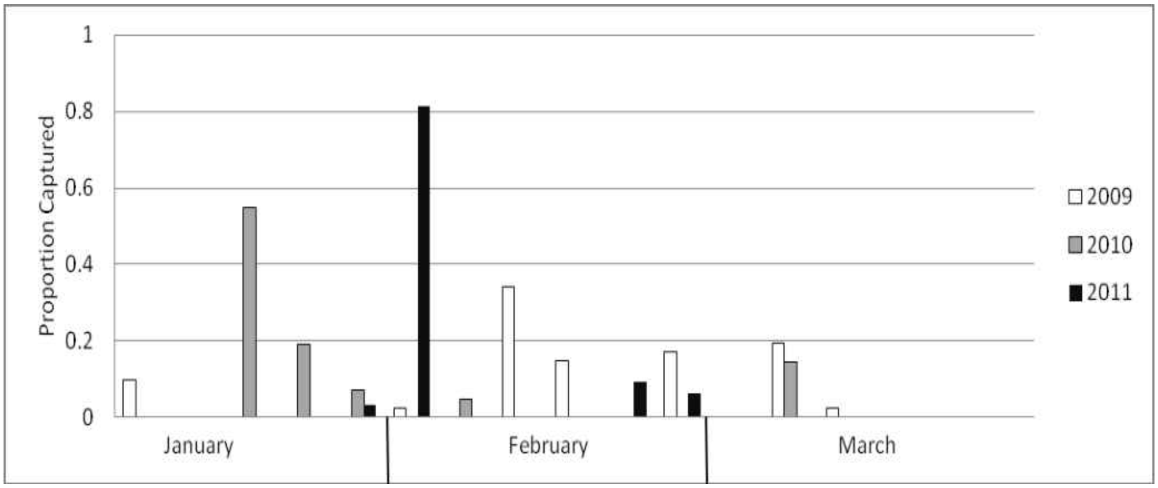

Figure A-3. Timing of male *Ambystoma jeffersonianum* prebreeding movements. Bars on the X axis represent movements over 5-day periods.

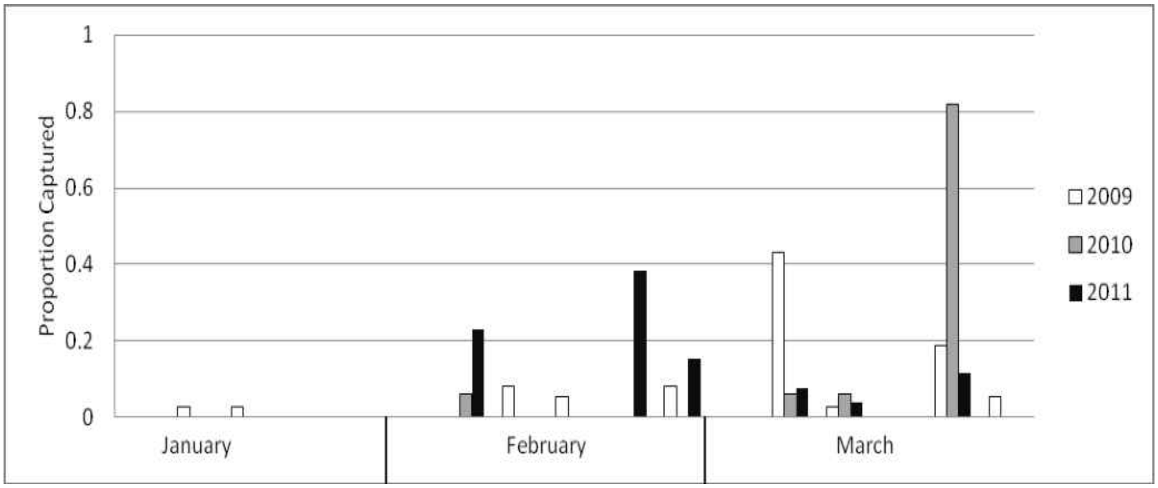

Figure A-4. Timingof male *Ambystoma jeffersonianum* postbreeding movements. Bars on the X axis represent movements over 5-day periods.

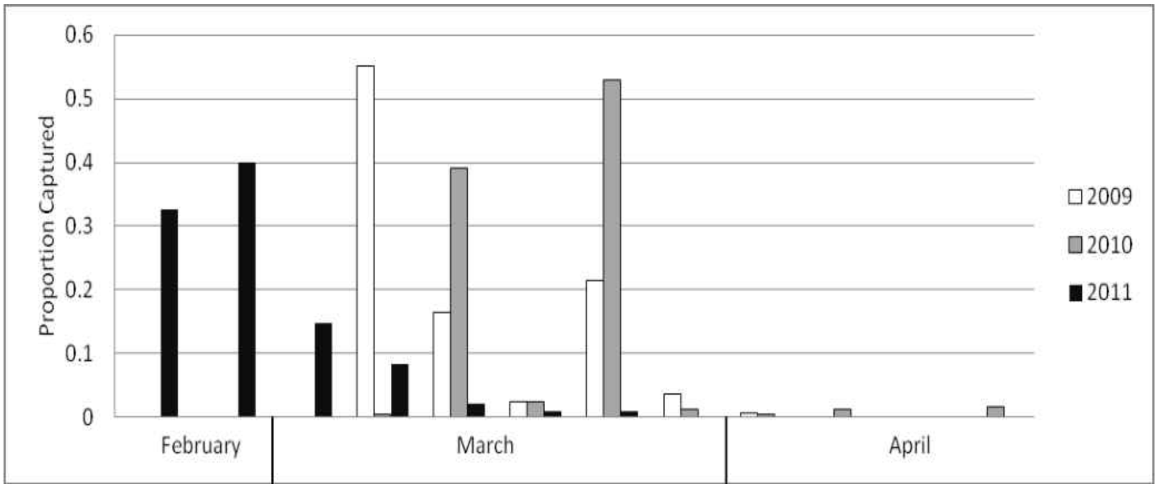

Figure A-5. Timing of female *Ambystoma maculatum* prebreeding movements. Bars on the X axis represent movements over 5-day periods.

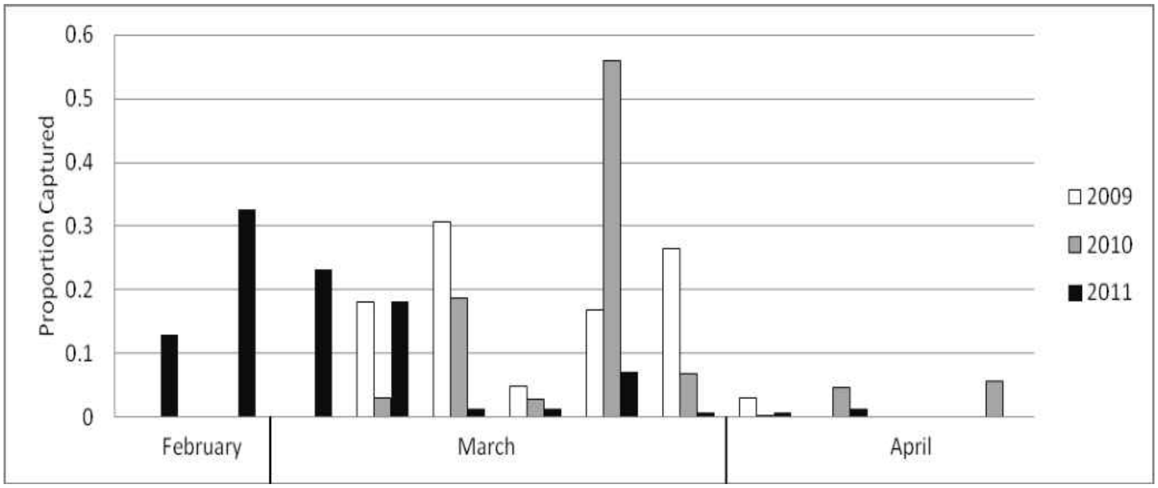

Figure A-6. Timing of female *Ambystoma maculatum* postbreeding movements. Bars on the X axis represent movements over 5-day periods.

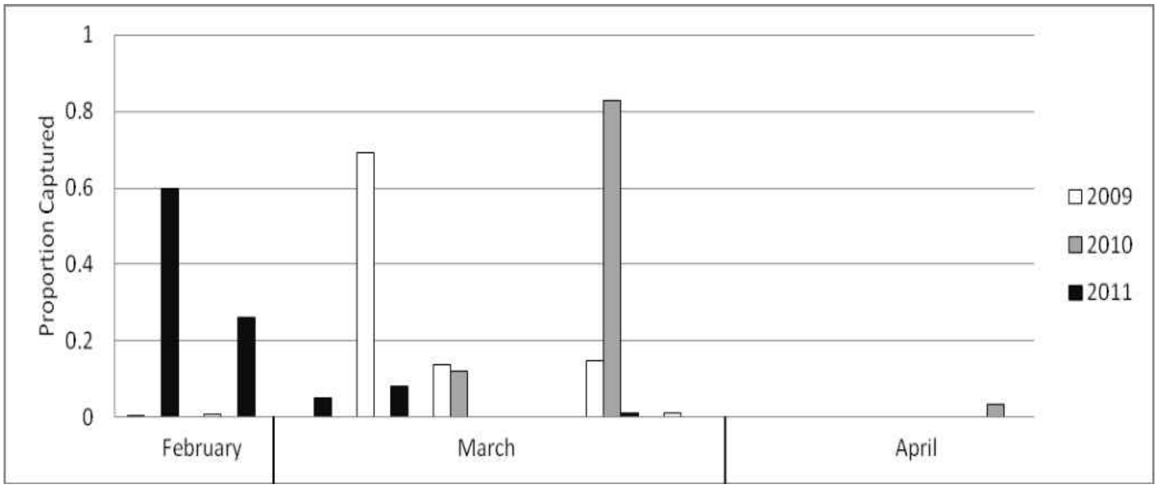

Figure A-7. Timing of male *Ambystoma maculatum* postbreeding movements. Bars on the X axis represent movements over 5-day periods.

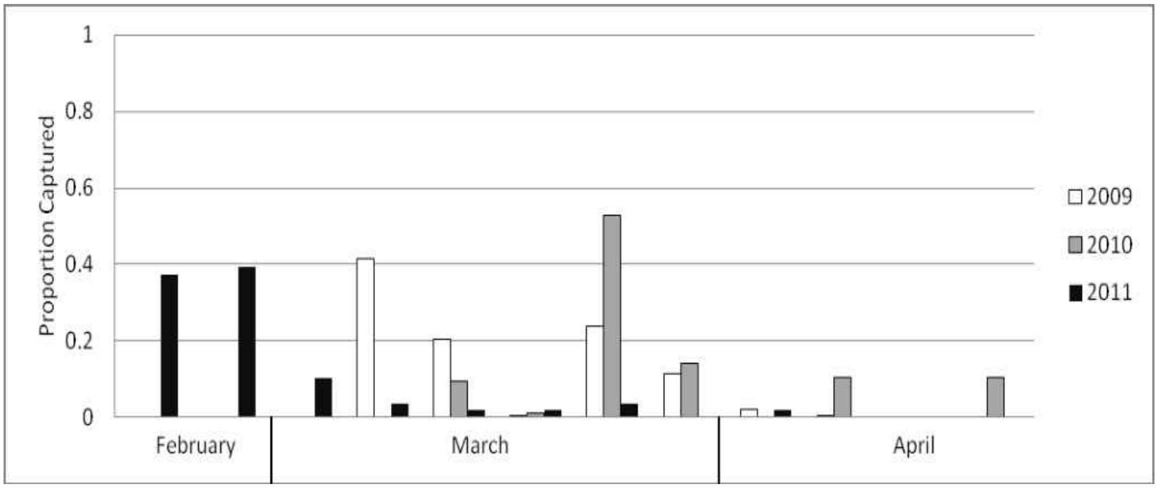

Figure A-8. Timing of male *Ambystoma maculatum* postbreeding movements. Bars on the X axis represent movements over 5-day periods.

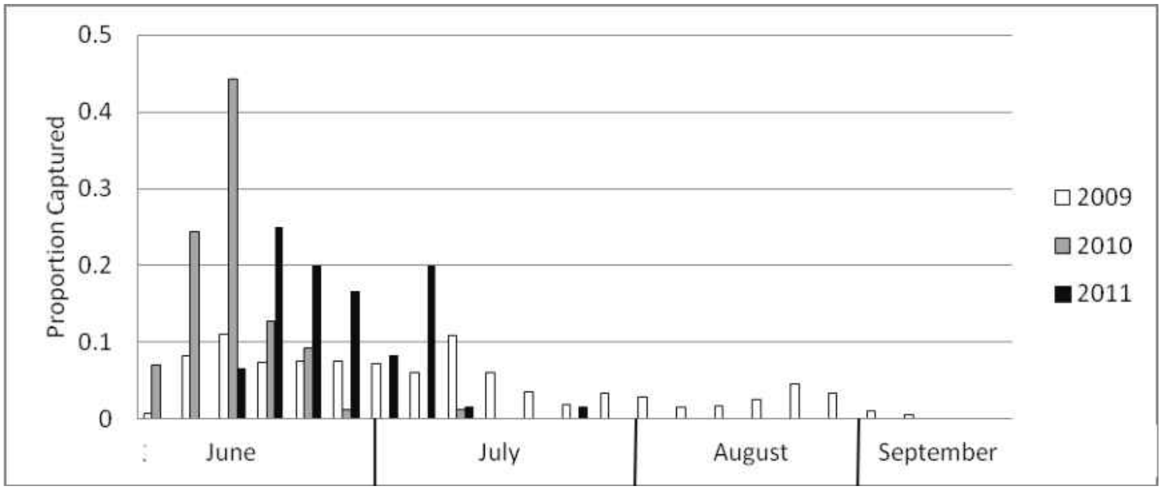

Figure A-9. Timing of juvenile *Ambystoma jeffersonianum* exiting movements. Bars on the X axis represent movements over 5-day periods.

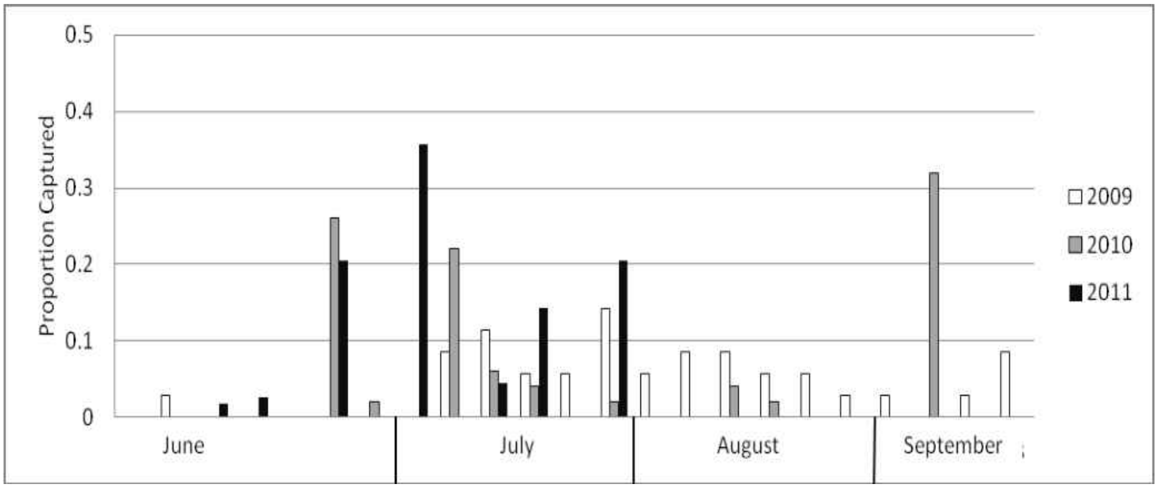

Figure A-10. Timing of juvenile *Ambystoma maculatum* exiting movements. Bars on the X axis represent movements over 5-day periods.

APPENDIX B:

Significant Associations of Weather with Adult and Juvenile Salamander Movements

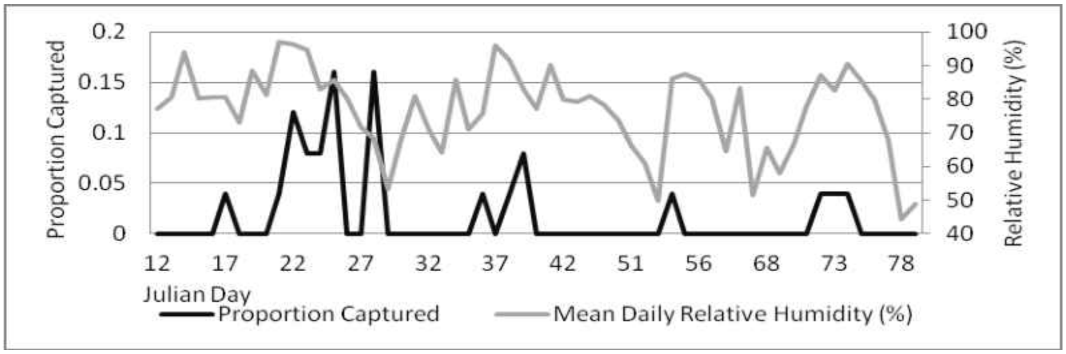

Figure B-1. Timing of female *Ambystoma jeffersonianum* 2010 prebreeding movements and mean daily relative humidity. Proportion captured is identified by the black line (right y axis) and mean daily relative humidity by the grey line (left y axis).

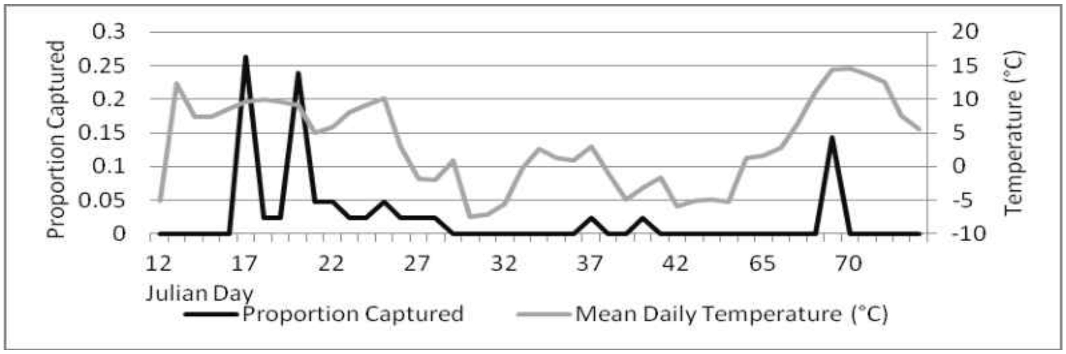

Figure B-2. Timing of male *Ambystoma jeffersonianum* 2010 prebreeding movements and mean daily temperature. Proportion captured is identified by the black line (right y axis) and mean daily temperature by the grey line (left y axis).

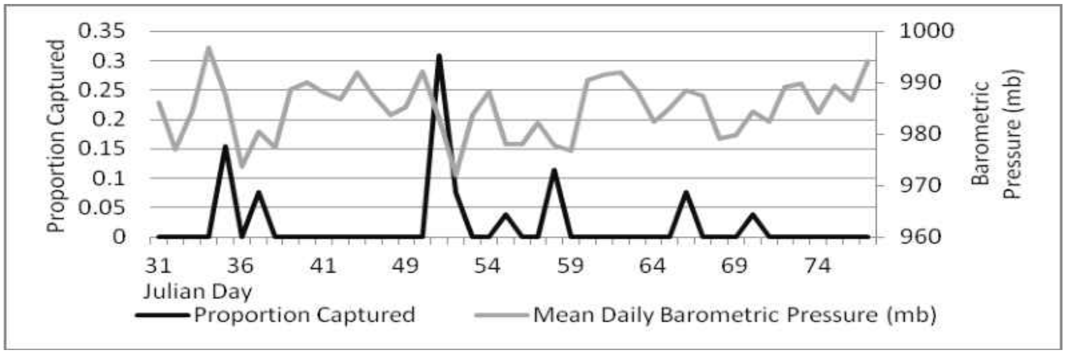

Figure B-3. Timing of male *Ambystoma jeffersonianum* 2011 postbreeding movements and mean daily barometric pressure. Proportion captured is identified by the black line (right y axis) and mean daily barometric pressure by the grey line (left y axis).

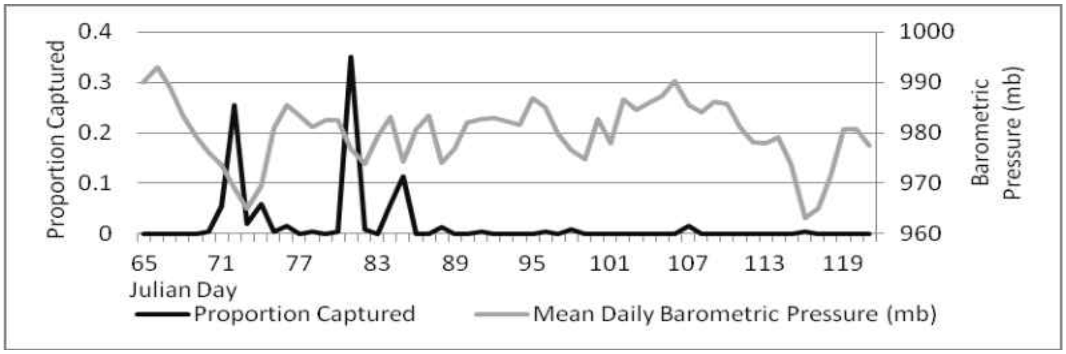

Figure B-4. Timing of female *Ambystoma maculatum* 2010 prebreeding movements and mean daily barometric pressure. Proportion captured is identified by the black line (right y axis) and mean daily barometric pressure by the grey line (left y axis).

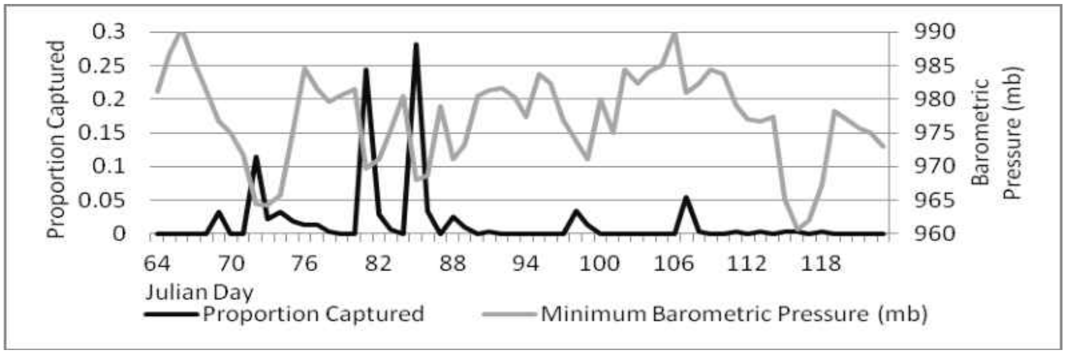

Figure B-5. Timing of female *Ambystoma maculatum* 2010 postbreeding movements and minimum daily barometric pressure. Proportion captured is identified by the black line (right y axis) and minimum daily barometric pressure by the grey line (left y axis).

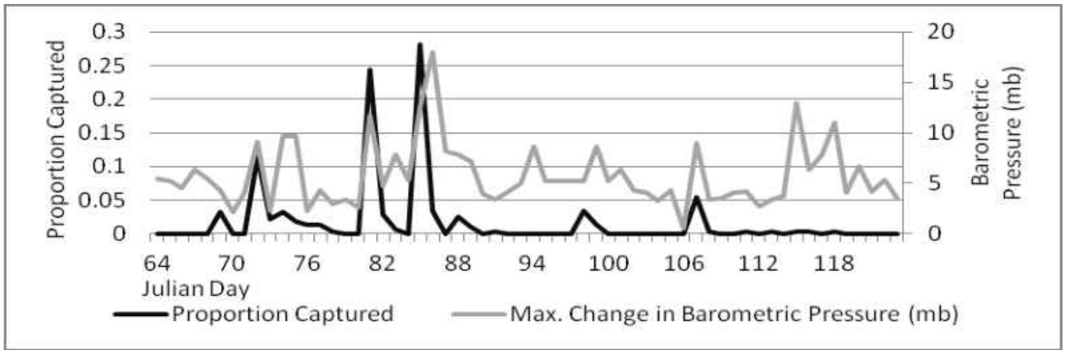

Figure B-6. Timing of female *Ambystoma maculatum* 2010 postbreeding movements and maximum change in daily barometric pressure. Proportion captured is identified by the black line (right y axis) and maximum change in daily barometric pressure by the grey line (left y axis).

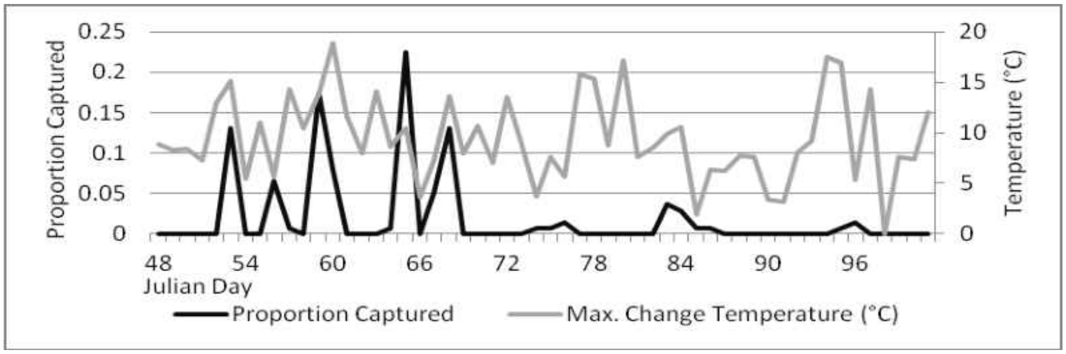

Figure B-7. Timing of female *Ambystoma maculatum* 2011 postbreeding movements and maximum change in daily temperature. Proportion captured is identified by the black line (right y axis) and maximum change in temperature by the grey line (left y axis).

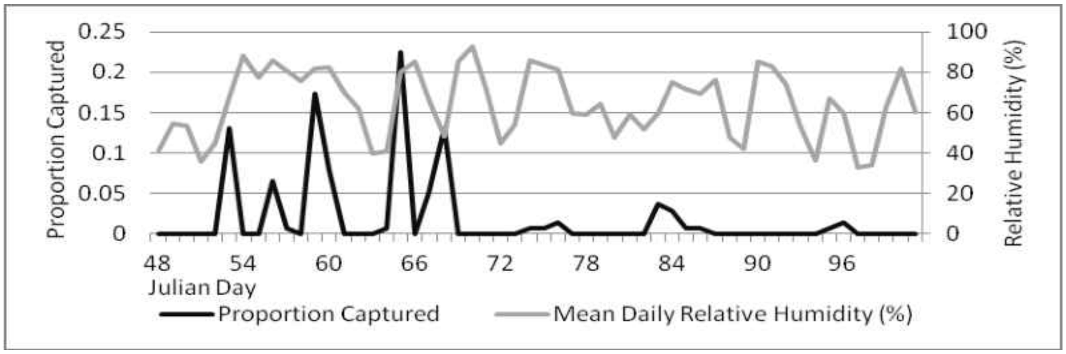

Figure B-8. Timing of female *Ambystoma maculatum* 2011 postbreeding movements and mean daily relative humidity. Proportion captured is identified by the black line (right y axis) and mean daily relative humidity by the grey line (left y axis).

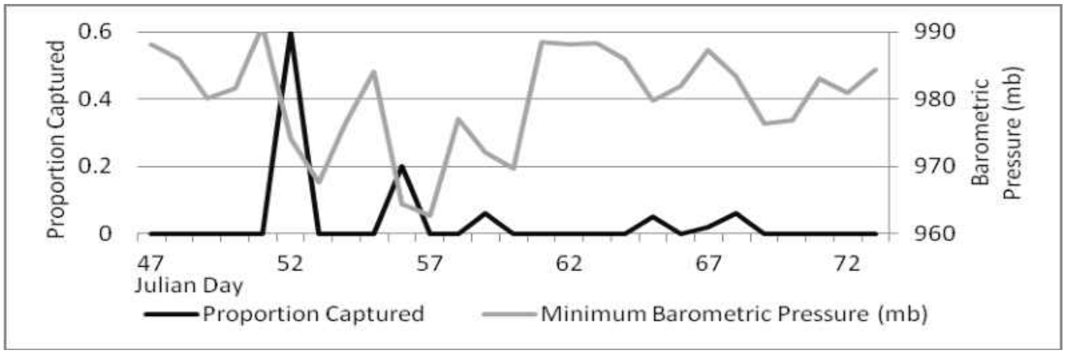

Figure B-9. Timing of male *Ambystoma maculatum* 2011 prebreeding movements and minimum daily barometric pressure. Proportion captured is identified by the black line (right y axis) and minimum daily barometric pressure by the grey line (left y axis).

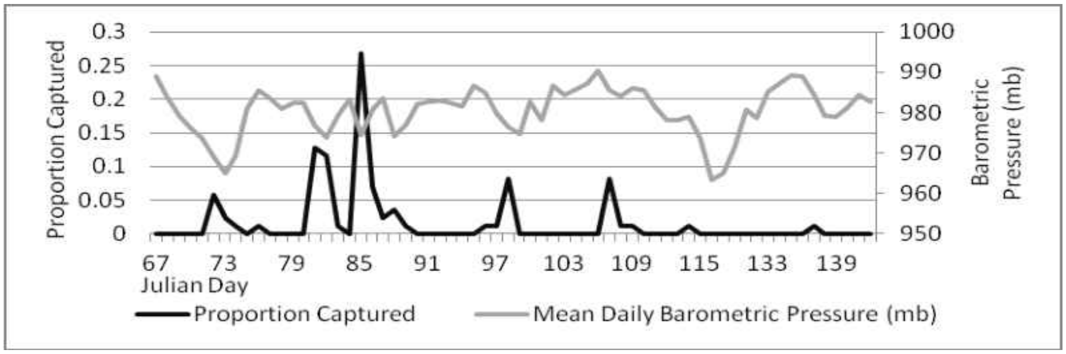

Figure B-10. Timing of male *Ambystoma maculatum* 2010 postbreeding movements and mean daily barometric pressure. Proportion captured is identified by the black line (right y axis) and mean daily barometric pressure by the grey line (left y axis).

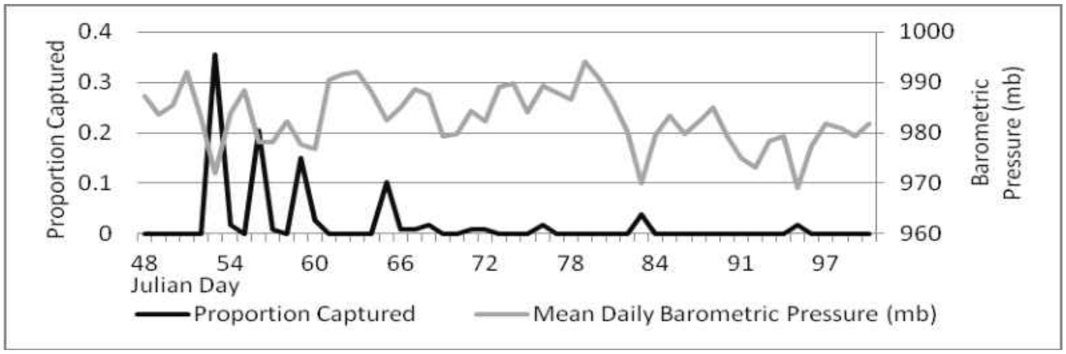

Figure B-11. Timing of male *Ambystoma maculatum* 2011 postbreeding movements and mean daily barometric pressure. Proportion captured is identified by the black line (right y axis) and mean daily barometric pressure by the grey line (left y axis).

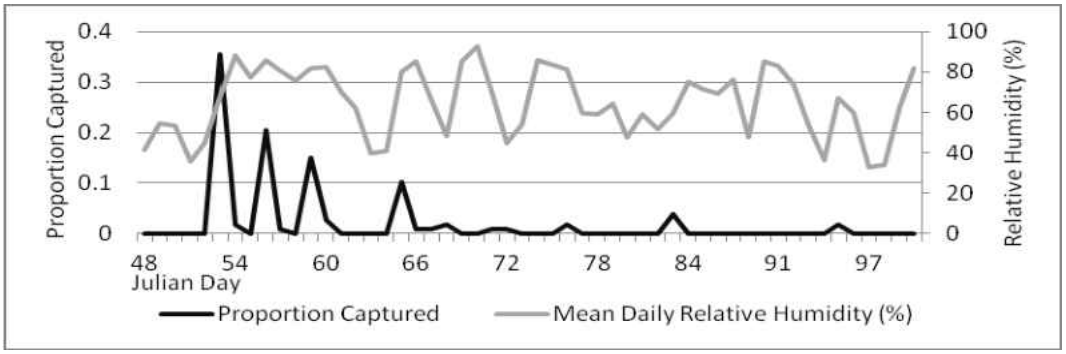

Figure B-12. Timing of male *Ambystoma maculatum* 2011 postbreeding movements and mean daily relative humidity. Proportion captured is identified by the black line (right y axis) and mean daily relative humidity by the grey line (left y axis).

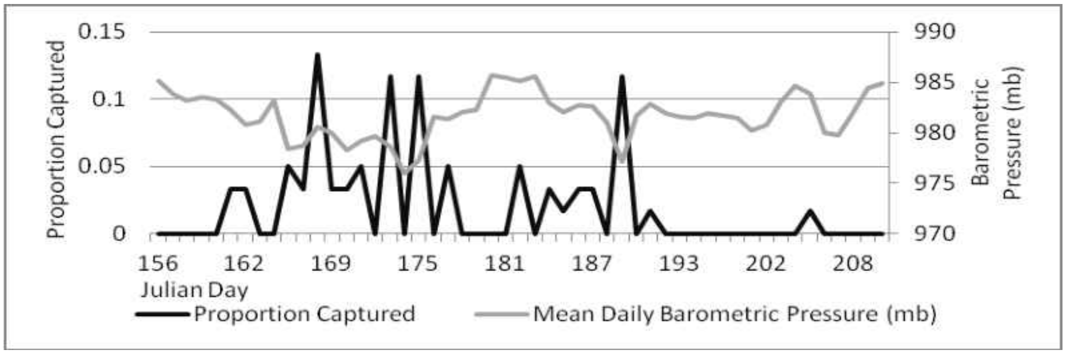

Figure B-13. Timing of juvenile *Ambystoma jeffersonianum* 2011 exiting movements and mean daily barometric pressure. Proportion captured is identified by the black line (right y axis) and mean daily barometric pressure by the grey line (left y axis).

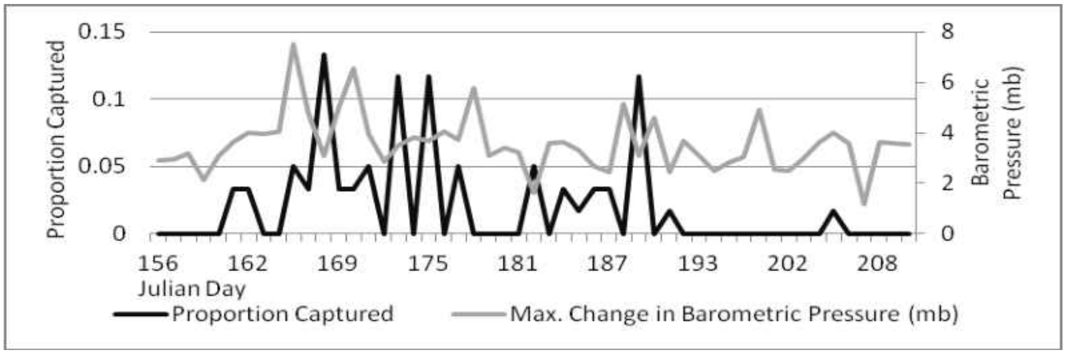

Figure B-14. Timing of juvenile *Ambystoma jeffersonianum* 2011 exiting movements and maximum change in daily barometric pressure. Proportion captured is identified by the black line (right y axis) and maximum change in barometric pressure by the grey line (left y axis).

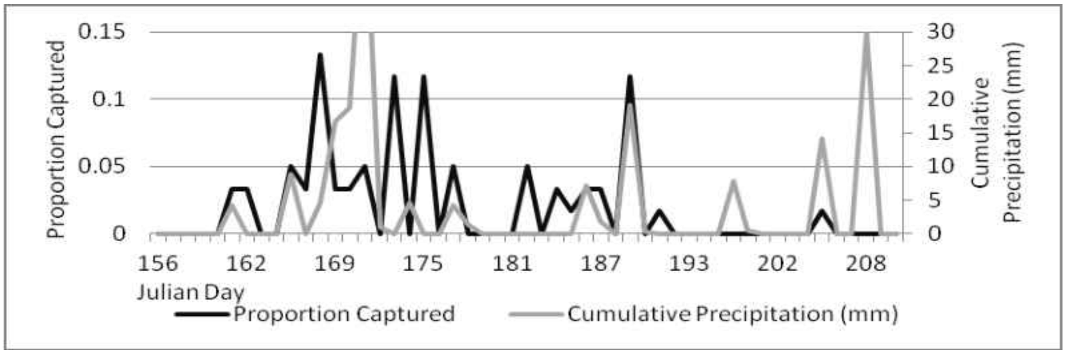

Figure B-15. Timing of juvenile *Ambystoma jeffersonianum* 2011 exiting movements and daily cumulative precipitation. Proportion captured is identified by the black line (right y axis) and daily cumulative precipitation by the grey line (left y axis).

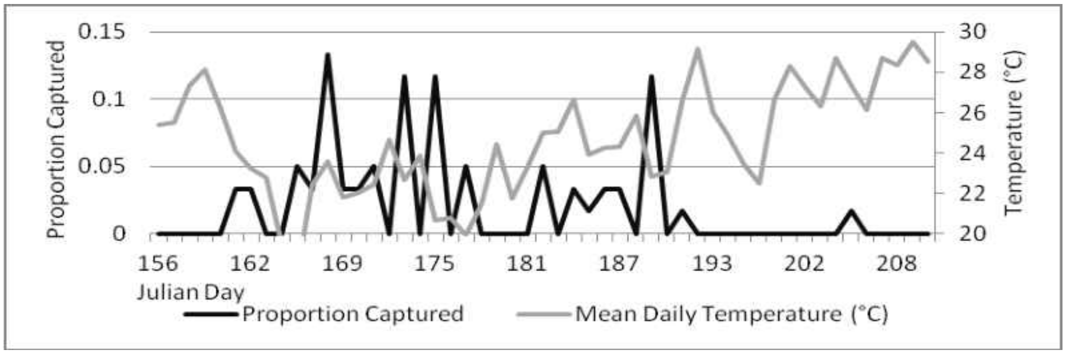

Figure B-16. Timing of juvenile *Ambystoma jeffersonianum* 2011 exiting movements and mean daily temperature. Proportion captured is identified by the black line (right y axis) and mean daily temperature by the grey line (left y axis).

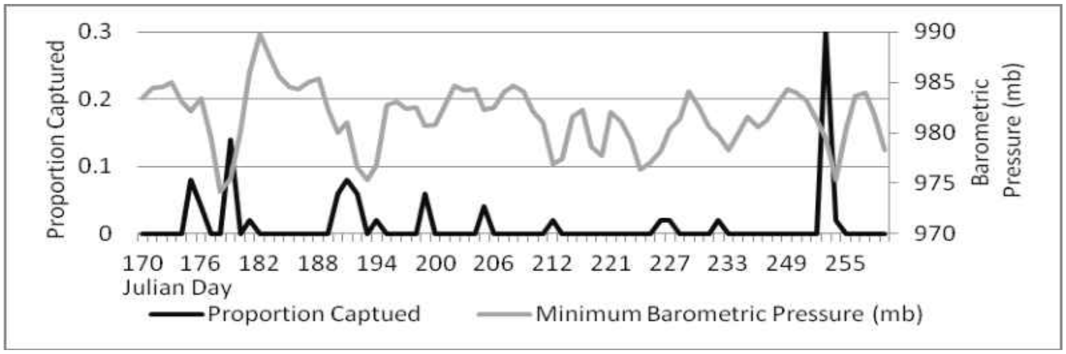

Figure B-17. Timing of juvenile *Ambystoma maculatum* 2010 exiting movements and minimum daily barometric pressure. Proportion captured is identified by the black line (right y axis) and minimum daily barometric pressure by the grey line (left y axis).

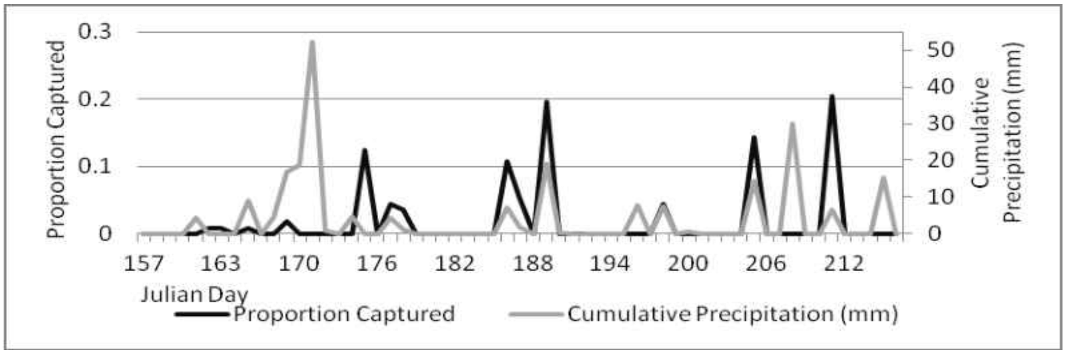

Figure B-18. Timing of juvenile *Ambystoma maculatum* 2011 exiting movements and daily cumulative precipitation. Proportion captured is identified by the black line (right y axis) and daily cumulative precipitation by the grey line (left y axis).

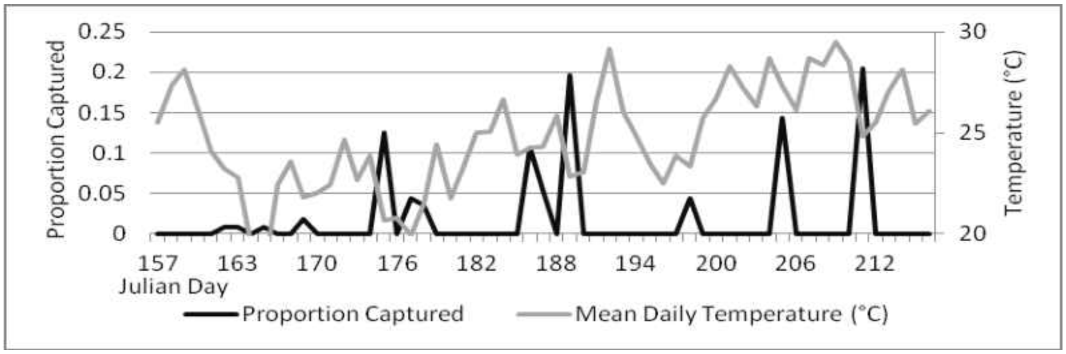

Figure B-19. Timing of juvenile *Ambystoma maculatum* 2011 exiting movements and mean daily temperature. Proportion captured is identified by the black line (right y axis) and mean daily temperature by the grey line (left y axis).

APPENDIX C:

Orientation of Adult Breeding Movements and Juvenile Exiting Movements

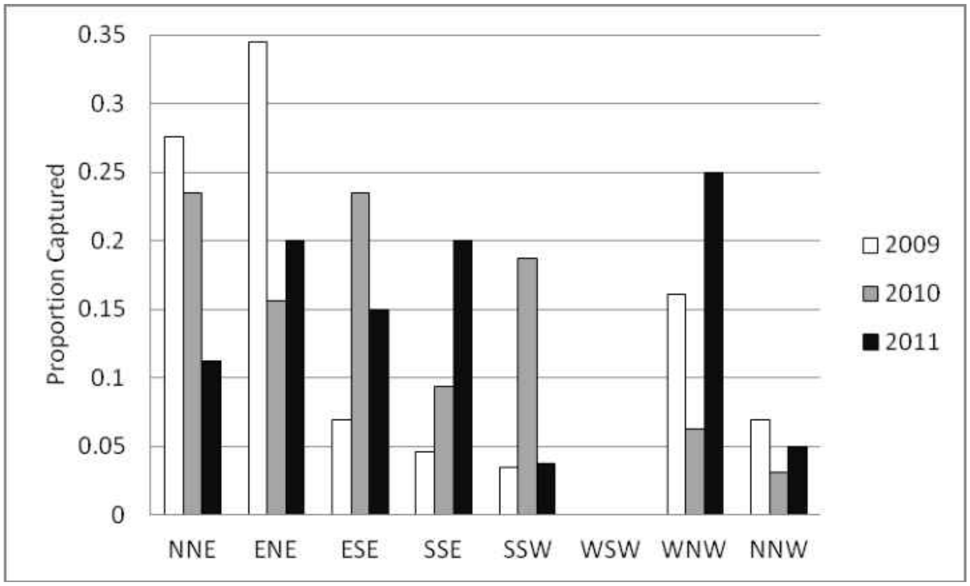

Figure C-1. Orientation of female *Ambystoma jeffersonanium* prebreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

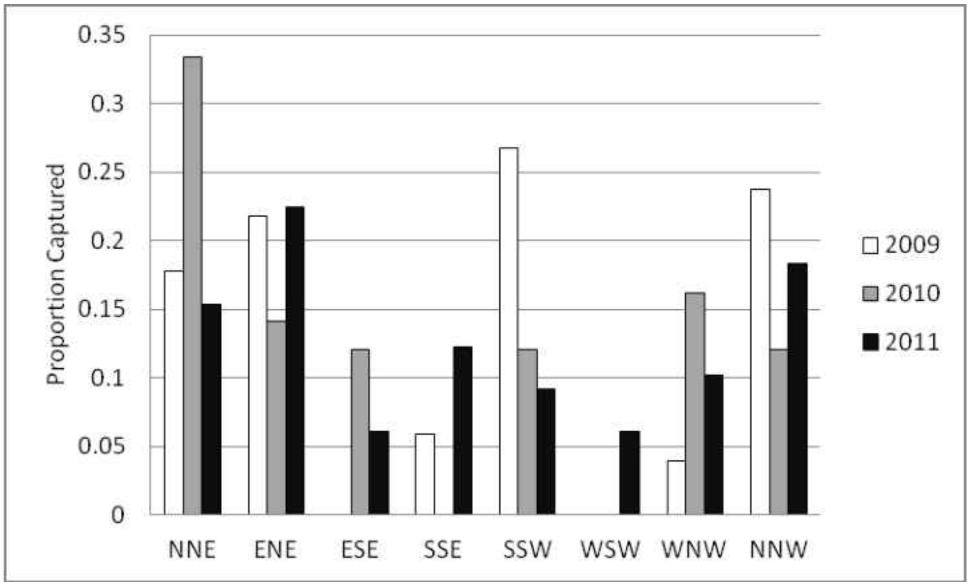

Figure C-2. Orientation of female *Ambystoma jeffersonanium* postbreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

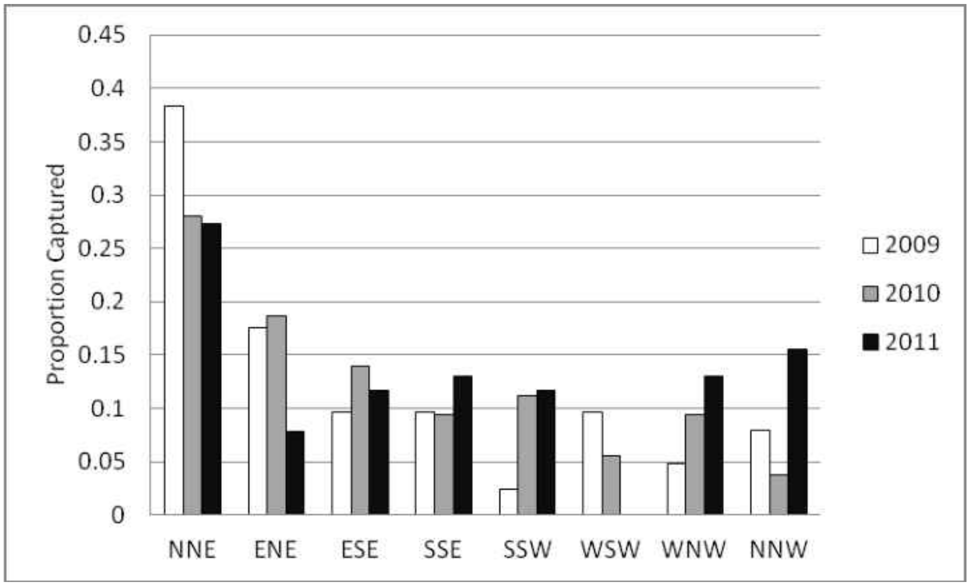

Figure C-3. Orientation of male *Ambystoma jeffersonanium* prebreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

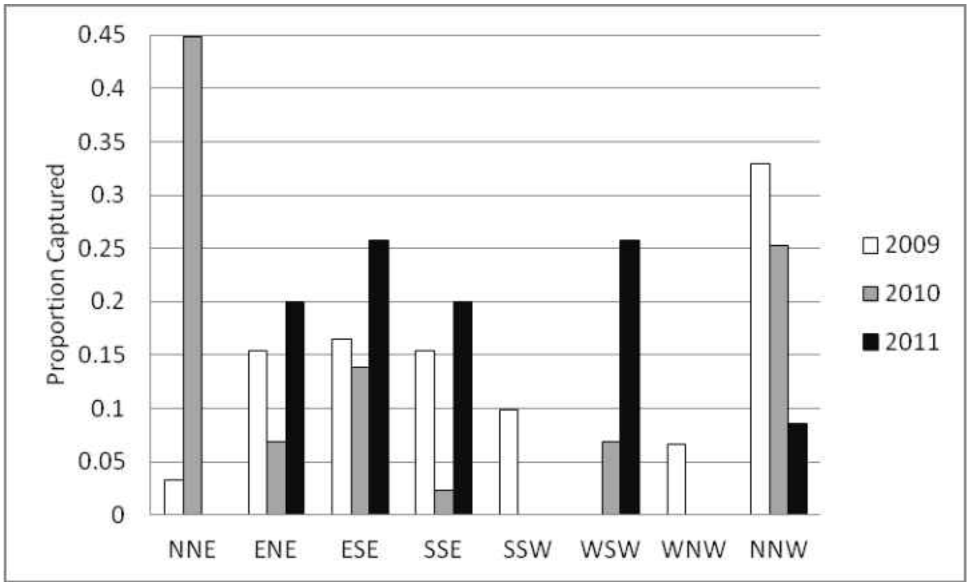

Figure C-4. Orientation of male *Ambystoma jeffersonanium* postbreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

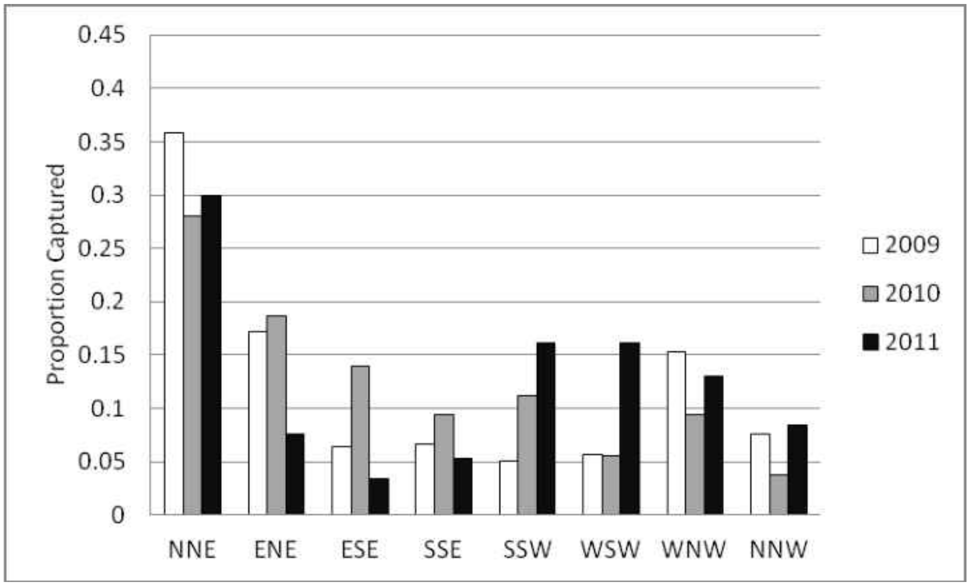

Figure C-5. Orientation of female *Ambystoma maculatum* prebreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

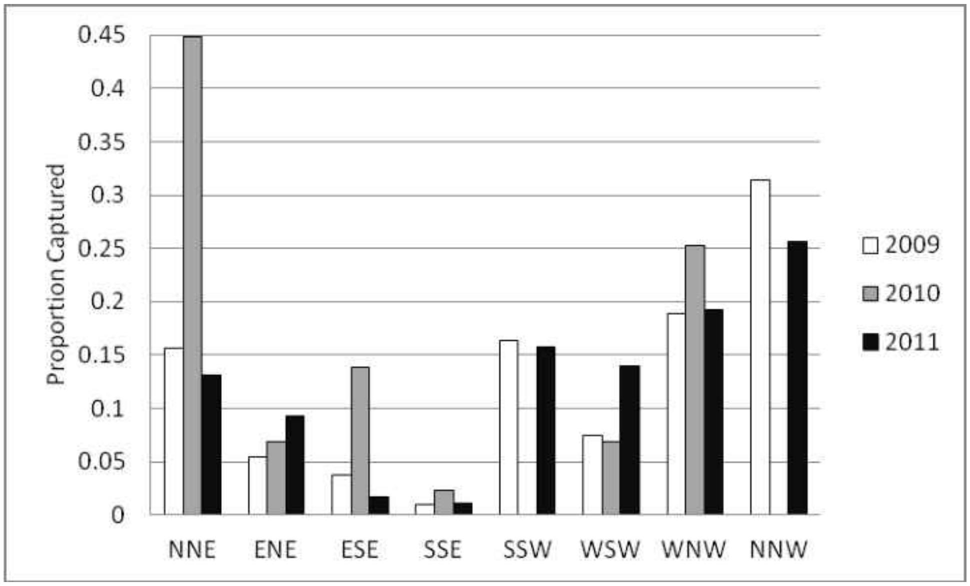

Figure C-6. Orientation of female *Ambystoma maculatum* postbreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

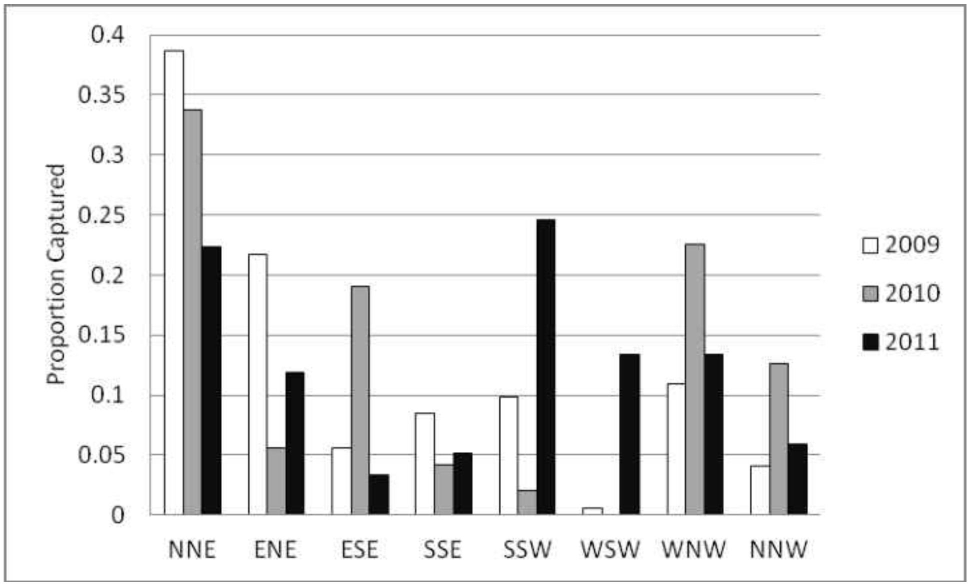

Figure C-7. Orientation of male *Ambystoma maculatum* prebreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

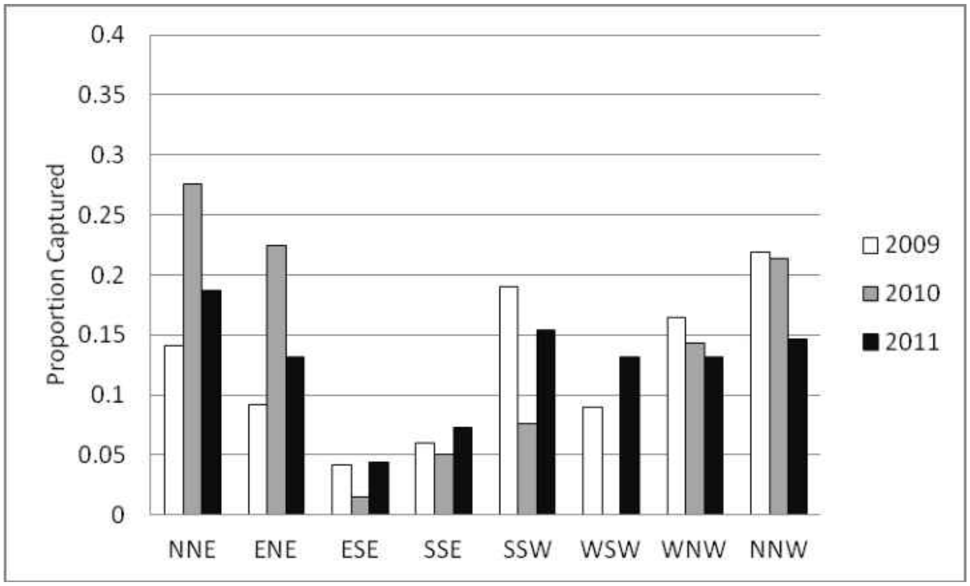

Figure C-8. Orientation of male *Ambystoma maculatum* postbreeding movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

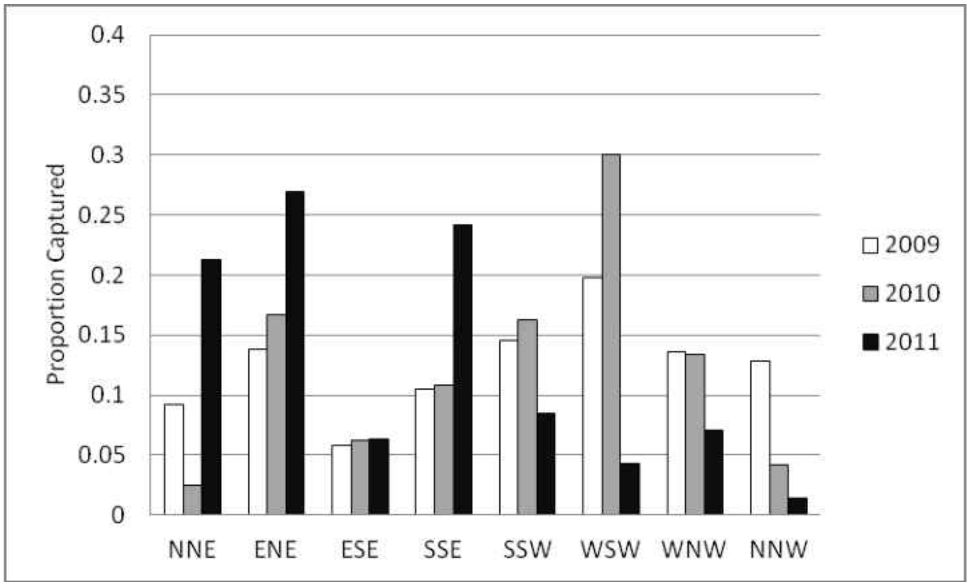

Figure C-9. Orientation of juvenile *Ambystoma jeffersonanium* exiting movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

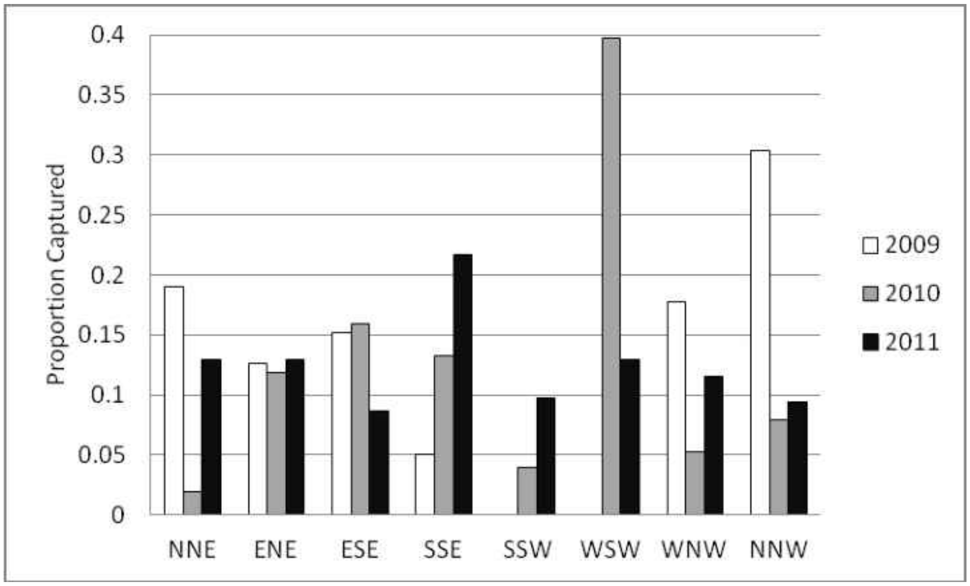

Figure C-10. Orientation of juvenile *Ambystoma maculatum* exiting movements. Bars on the X axis represents catch per unit effort of movements oriented from the pond.

VITA

Christopher J. St. Andre was born in Dorchester, Massachusetts on November 18, 1987. He attended elementary school at Frank E. Holt (Whitman) and graduated from Whitman Hanson Regional High School in May 2005. The following September, he entered Bridgewater State College, and in May 2009 received the degree of Bachelor of Science in Environmental Biology. He attended Eastern Kentucky University the following September, and in May 2012 received the degree of Master of Science in Biology. He is currently seeking employment with government and non-profit organizations working with amphibians and reptiles.