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Treefrog (hyla Squirella) Responses To Rangeland And Management In Semi-tropical Florida, Usa

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TREEFROG (*HYLA SQUIRELLA*) RESPONSES TO RANGELAND MANAGEMENT IN SEMI-TROPICAL FLORIDA, USA

by

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ABSTRACT

As urban areas expand, agricultural lands become increasingly important habitat for many species. Compared to some types of agricultural land-use, ranchlands provide vast expanses of minimally modified habitat that support many threatened and endangered species. Conservation biologists can promote ecologically sound management approaches by quantifying the effects of agricultural practices on resident species. I examined the effects of pasture management, cattle grazing, and landscape characteristics on both adult and larval treefrogs in a ranchland in south-central Florida. I experimentally determined optimal deployment of artificial treefrog shelters constructed of polyvinylchloride (PVC) pipe to efficiently sample adult treefrogs (Chapter 1). Seventy-two shelters were hung on oak trees (*Quercus virginiana*) and cabbage palm trees (*Sabal palmetto*) with smooth trunks or boots (residual palm fronds), at all possible combinations of three heights (2, 3, and 4 m), four compass directions (N, S, E, and W) and two water levels (with or without 10 cm). Shelter residence was completely dominated by the Squirrel Treefrog, *Hyla squirella* (N = 65). Significantly fewer *H. squirella* were found in shelters on palms with boots than on smooth palms or oak trees (0.29 ± 0.21 [mean ± 1 SE hereinafter] versus 1.3 ± 0.21 and 1.1 ± 0.21, respectively), and shelters with water had slightly more *H. squirella* than those without (1.5 ± 0.19 versus 0.88 ± 0.19, respectively). Orientation and height did not affect the number of treefrogs encountered; thus, the optimal protocol is to deploy shelters on either smooth palms or oak trees, with water, at 2 m height for easy sampling, and in random compass orientations.

I used this protocol to sample *H. squirella* in woodlots surrounding twelve wetlands and examined how time, frog stage and sex, and landscape features influenced treefrog survival, recapture and site fidelity (Chapter 2). I deployed 15 shelters/ha of woodlot within a 100 m buffer around each wetland. I sampled shelters three times during the fall breeding season, removed all shelters to force frogs to overwinter in natural refugia, and replaced shelters for the final spring sampling. During sampling periods, I sexed, measured, and individually marked each frog using visual implant elastomer (VIE) tags. I used Program MARK to build linear models that included either gender group (female, male or juvenile) or life history stage (adult, juvenile) and either time (sampling interval 1, 2, or 3) or season (fall, spring). I used the most informative model as a null model to assess effects of landscape covariates on survival and recapture. Females had higher survival than either males or juveniles, for which estimates were similar (0.867 vs 0.741 and 0.783, respectively). Survival did not vary over time, although there was some support for an effect of season, with lower survival during the final over-wintering period than in the fall intervals (relative variable importance: group = 0.730; stage = 0.134; time = 0.200; season = 0.310). Adults had higher recapture rates than juveniles (average recapture 0.214 vs 0.102), and recapture for both stages varied over time, with highest recapture in sampling interval two (relative variable importance: group = 0.262; stage = 0.514; time = 0.513; season = 0.229). *Hyla squirella* was extremely site loyal; no individuals moved between sampling sites, and 95% of recaptured individuals were in their original shelter. Strong terrestrial site fidelity calls into question the traditional "ponds as patches" metapopulation view of treefrog population dynamics. Area of woodlot within 250 m was the most important landscape variable in explaining additional variation in both survival and recapture. Frogs had higher survival and lower recapture in larger woodlots, indicating that intact, contiguous woodlots are higher quality habitat than more fragmented woodlots. Neither survival nor recapture varied with wetland grazing treatments or between pasture types.

Finally, I experimentally assessed the effects of cattle grazing and pasture management on larval *H. squirella*. I selected four wetlands: two in semi-natural pastures (SN) and two in intensively managed pastures (IM). One wetland in each pasture type was fenced so that it was released from cattle grazing (R). I collected three clutches of *H. squirella* eggs (Clutches A, B, and C) and reared tadpoles in the laboratory until Gosner stage 25. In each wetland, I deployed a total of 50 tadpoles from each clutch into 105 L pens constructed of plastic laundry baskets and mesh window screening. Clutch significantly affected tadpole survival, with Clutch A having the highest percent survival, followed by Clutch B and finally Clutch C (41.66, 32.11 – 53.95 [mean, 95% confidence limits hereinafter]; 9.00, 6.76 – 11.88; 2.89, 2.02 – 4.01, respectively). Wetland type also affected survival, with SN wetlands supporting significantly higher survival than IM wetlands (SN-R: 53.95, 32.88 – 88.13; SN-G: 18.95, 11.30 – 31.36 vs IM-R: 7.32, 4.13 – 12.49; IM-G: 1.09, 0.29 – 2.39). Genetic variation in survival confirms the potential for *H. squirella* to adapt to rangeland management, but extremely low survival of some clutches indicates that few clutches may be able to survive in low quality wetlands, such as IM-G wetlands. Higher survival in SN pasture wetlands suggest this is a superior habitat and future management objectives should conserve semi-natural pastures and limit further modification of intensively managed pastures, including removing woodlots near wetlands.

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LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
CJS	Cormack-Jolly-Seber
df	Degrees of freedom
G	Grazed
GOF	Goodness of Fit
IM	Intensively managed
MAERC	MacArthur Agro-Ecology Research Center
NC	New capture
PVC	Poly-vinyl chloride
R	Released from grazing
RC	Recapture
SN	Semi-natural
SS	Sum of squares
VIE	Visible Implant Elastomer

GENERAL INTRODUCTION

Agriculture is among the largest drivers of habitat loss, degradation and fragmentation worldwide (Wilcove et al. 1998, Czech et al. 2000, Tilman et al. 2001). If human consumption and agricultural trends of the past 35 years continue, 10^9 ha of natural ecosystems – an area larger than the contiguous United States - will be converted to agriculture by 2050 (Tilman et al. 2001). Such massive loss of natural systems will disrupt ecosystem heterogeneity, reduce ecosystem services, increase eutrophication of aquatic ecosystems, shift food chain structure and accelerate extinctions (Tilman 1999, Tilman et al. 2001, Benton et al. 2003). Even in the United States, agriculture is among the top three causes of species endangerment, along with non-native species and urbanization (Czech et al. 2000). Rapidly increasing human populations and their associated food needs make it unlikely that agriculture will decrease in scale. However, as urban areas expand agricultural lands become increasingly important refuges for flora and fauna. Compared with harsh urban landscapes, agricultural lands in Florida support diverse communities including threatened and endangered species such as burrowing owls (*Athene cunicularia*), woodstorks (*Mycteria americana*), indigo snakes (*Drymarchon corais*), Florida grasshopper sparrows (*Ammodramus savannarum floridanus*) and the crested caracara (*Caracara cheriway*) (Morrison and Humphrey 2001, Boughton 2008, Bohlen et al. 2009). To preserve natural biodiversity and ecosystem processes while promoting economically viable agriculture, conservation biologists must understand how agriculture affects aquatic and terrestrial habitats and the species that inhabit them, and devise effective management plans.

I examined factors driving amphibian habitat use and demography in both aquatic and terrestrial habitats within a south-central Florida landscape modified for cattle grazing. Florida ranks 3rd in states east of the Mississippi River and 12th in the nation for production of beef calves, with sales totaling more than $443 million in 2004 (Florida Department of Agriculture 2007). Compared to many types of agricultural land-use, Florida ranchlands provide vast expanses of minimally modified habitat; statewide, over 3 million ha of non-federal land are grazed (USDA 2003). Many Florida cattle ranches have abundant small, isolated wetlands (Steinman et al. 2003) that serve a variety of ecosystem services (e.g., food sources and cooling for cattle) and provide habitat for local flora and fauna (Gibbons 2003, Jenkins et al. 2003). Small wetlands often are very species rich, contain species absent from larger wetlands (Snodgrass et al. 2000) and produce juvenile recruits for neighboring wetlands (Semlitsch and Bodie 1998). Therefore, small wetlands with short hydroperiods, which are common in agricultural landscapes, are important for maintaining biodiversity (Gibbons 2003).

Amphibians are among the world's most threatened taxa (Stuart et al. 2004). Global amphibian declines have been attributed to climate change, habitat fragmentation, introduced species, UV-B radiation, chemical contaminants and disease (from Young et al. 2001). Many amphibians depend on an aquatic habitat for breeding and larval stages and spend most of their adult life in terrestrial habitat (Wilbur 1980), so they are sensitive to perturbations in both environments. Combined with their moist, permeable skin, these attributes make amphibians potential bioindicators (Dunson et al. 1992, Lambert 1997, Welsh and Ollivier 1998). Amphibians also are highly philopatric (Gill 1978, Breden 1987, Berven and Grudzien 1990), play a significant role in trophic cycling (Dunson et al. 1992, Rowe and Dunson 1994) and are relatively long-lived compared to most fishes and macroinvertebrates (Plytycz and Bigaj 1993, Kumbar and Pancharatna 2001, Sinsch et al. 2001). Amphibians contribute to pest control through their insect-based diets (Young et al. 2001) and are an important link in food chains;

many larger animals are supported by an amphibian food base. For example, in southern Florida, frogs comprise 56% of the diet delivered to Swallow-tailed Kite (*Elanoides forficatus*) nestlings (Meyer et al. 2004).

Understanding how habitat loss and fragmentation affect amphibian populations requires examining the roles of multiple factors in species-specific, landscape-level investigations (Cushman 2006; see examples in Eason and Fauth 2001, Schurbon and Fauth 2003). In a series of three experiments, I examined how landscape structure and ranching practices affect both adult and larval amphibians. Specifically, I conducted two terrestrial experiments using PVC shelters to sample treefrogs (Boughton et al. 2000, Zacharow et al. 2003). I examined how tree species and morphology, shelter height and orientation, and water depth within a shelter affect treefrog use of PVC shelters (Chapter 1). I used the results of Chapter 1 in a subsequent study, where I estimated population characteristics of the squirrel treefrog (*Hyla squirella*) in woodlots adjacent to wetlands and examined how landscape features such as pasture management, area of woodlot, wetland availability, and connectivity through ditches affect survival, recapture, and site fidelity (Chapter 2). In addition, I conducted an aquatic experiment to assess effects of clutch, cattle grazing and pasture management on survival of larval *H. squirella* (Chapter 3). My research goals were to determine how amphibians respond to agriculturally-modified landscapes in both terrestrial and aquatic environments and to provide ranchland managers with valuable information that can promote ecologically sound agricultural practices.

STUDY SITE

My research was conducted at MacArthur Agro-Ecology Research Center (MAERC), a 4,170 ha working cattle ranch about 30 km northwest of Lake Okeechobee in south-central Florida. Roughly 3,000 cow-calf pairs grazed on MAERC pastures, which were categorized as intensively managed or semi-natural based on historical and ongoing ranch practices. Intensively managed pastures were heavily ditched, had few trees, and were regularly fertilized with NPK (nitrogen – phosphorus – potassium) fertilizer before 1987; since then, these pastures were fertilized with nitrogen only. Pasture grasses grow best at pH of 6.0 or higher, so ranchers commonly lime pastures to raise soil pH (Integrated Crop Management, Iowa State University). Lime has been intermittently added to intensively managed pastures at MAERC for the past 30 years at a rate of 1.1 to 3.4 $Mg*ha^{-1}$ (Capece et al. 2007). Intensively managed pastures were planted with introduced bahia grass (*Paspalum notatum*) and grazed most heavily in the wet summer season. Semi-natural pastures were less modified than intensively managed pastures; they have fewer ditches, more tree hammocks, and never were fertilized. Semi-natural pastures are dominated by native grasses such as bunchgrasses (eg, *Andropogon virginicus* and *Panicum spp.*) and grazed most heavily in the winter dry season. Both semi-natural and intensively managed pastures contained hardwood hammocks that are important habitat for adult frogs (Figure 1), including *Hyla squirella*, *H. cinerea*, *H. femoralis*, *H. gratiosa*, *Gastrophryne carolinensis*, *Lithobates sphenocephalus*, *L. grylio*, *Pseudacris ocularis*, *P. nigrita*, and *Anxyrus quercicus* (Babbitt et al. 2006). Hardwood hammocks are ecosystems unique to the southeastern United States, and consist of scattered patches of deciduous hardwoods and shrub species (Forest Encyclopedia Network). At MAERC, hammocks are

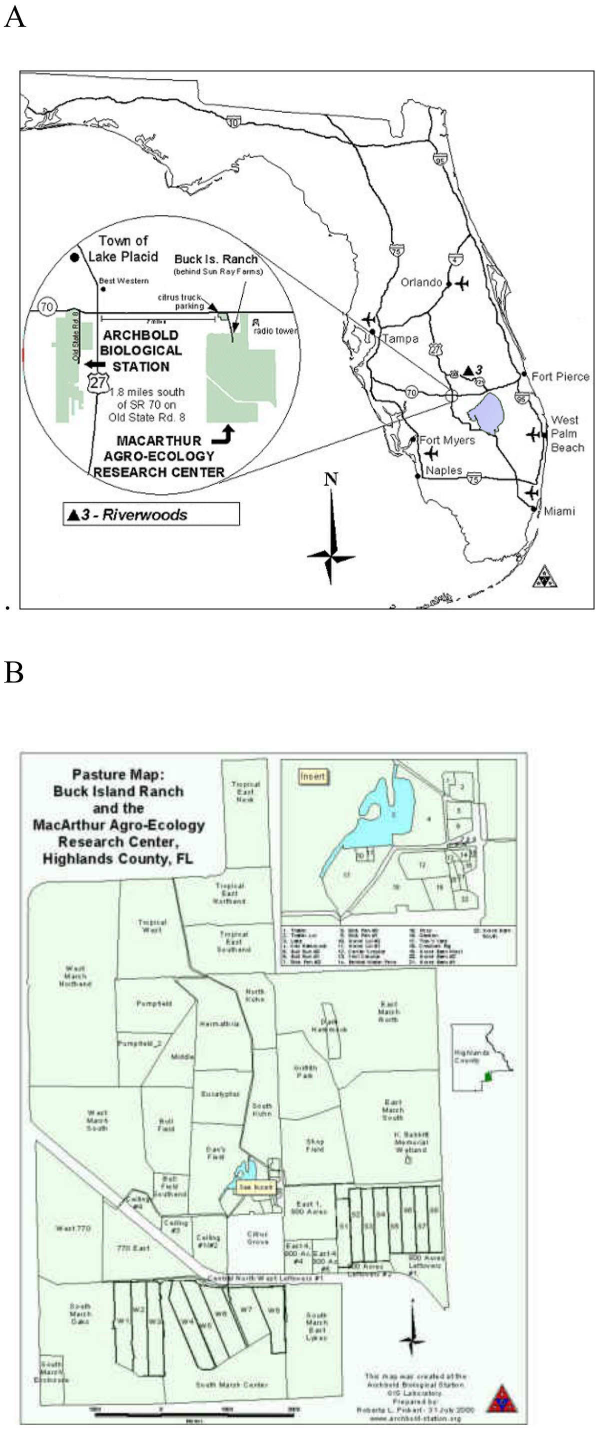

Figure 1. A) The MacArthur Agro-Ecology Research Center (MAERC) is located in Highlands County, south-central Florida, USA. B) Pasture map of MAERC. Images are from (A) http://www.maerc.net/ and B) http://www.maerc.org, accessed 30 January 2008.

dominated by oak (*Quercus virginiana*), cabbage palm (*Sabal palmetto*), and saw palmetto (*Serenoa repens*). I will use the term woodlot to refer to hammocks at MAERC.

Vegetation of wetlands embedded within intensively managed and semi-natural pastures differed greatly. Wetlands within intensively managed pastures typically were dominated in the shallower margins by rings of *Juncus effusus*, a common rush unpalatable to cattle. Several small water grasses, such as *Hydrochloa caroliniansis* and *Paspalum acuminatum*, were more abundant in wetlands within intensively managed pastures than wetlands within semi-natural pastures. Wetlands within semi-natural pastures typically had vegetation zones comprised of native grasses such as maidencane (*Panicum hemitomon*) and sedges (e.g., *Rhynchospora sp.* and *Eleocharis vivipara*). *Juncus* was not common in wetlands within semi-natural pastures. Emergent macrophytes such as *Pontederia cordata* and *Sagitaria lancifolia* were common to wetlands within both semi-natural and intensively managed pastures, especially in the deeper water areas (Boughton 2009).

My research was supported by a USDA-funded project, “Synergistic effects of grazing, fire, and pasture management on wetlands in cattle ranches” (hereinafter, USDA project). The USDA project involved forty MAERC wetlands that either were grazed or released from grazing (grazing treatment); burned or unburned (fire treatment); and in either semi-native or intensively managed pastures (pasture management). The forty wetlands comprised five replicates of each of all combinations of these three factors. My research was conducted simultaneously with the USDA project and some experiments used treatments applied in it.

CHAPTER 1: MAXIMIZING CAPTURES OF TREEFROGS USING PVC SHELTERS IN A FLORIDA RANGELAND

Introduction

Recently, herpetologists recognized the importance of identifying factors affecting terrestrial amphibian populations at both small scales (e.g., microhabitat choice, Johnson 2008) and landscape scales, by examining how landscape features shape populations (Chan-McLeod and Moy 2007, Pellet et al. 2004). Studying adult and juvenile amphibians that occupy terrestrial habitat is challenging because individuals often are inaccessible to traditional collecting methods. For example, treefrogs can climb out of pitfall traps deployed along drift fences (Dodd 1991, but see Murphy 1993) and are difficult to survey visually because they inhabit tall trees. Use of artificial treefrog shelters constructed of polyvinyl chloride (PVC) pipe is an increasingly popular method for sampling adult treefrogs. Treefrog shelters do not involve trapping individuals, which are free to enter or exit the shelter (Boughton et al. 2000, Zacharow et al. 2003). Instead, shelters provide refugia that mimic natural cavities. Treefrog shelters can be hung in trees or placed in the ground (Fogarty and Vilella 2002, Johnson 2005, Moulton et al. 1996, Pittman et al. 2008, Stewart and Pough 1983, Steward and Rand 1991, Zacharow et al. 2003). When both methods are used, frogs more frequently use tree-hung than ground-placed shelters (Boughton et al. 2000, Myers et al. 2007). Treefrog shelters are conducive to large-scale experimentation and monitoring because they require relatively little labor to construct and deploy and are easy to access. Studies often involve hundreds of shelters and result in hundreds or even thousands of captures (Boughton et al. 2000, Johnson et al. 2008, Zacharow et al. 2003).

Capture bias is a major concern when using treefrog shelters (Zacharow et al. 2003). The diameter of PVC used influences the frog species captured, with smaller species generally occurring in smaller diameter pipes and larger species being restricted to larger diameters (Baratreau 2004, Zacharow et al. 2003). Pipe diameter also influences the size of treefrog captured within a particular species, with the average size of individuals increasing with increasing diameter (Baratreau 2004). Male and female treefrogs may select tree-hung pipes based on tree characteristics. Johnson et al. (2008) found the size of captured female frogs was related to certain tree characteristics, such as diameter at breast height (DBH), whereas size of males was not. In addition to pipe diameter, researchers must consider other factors that influence use of treefrog shelters, such as shelter height and water depth within shelters (Boughton et al. 2000). When employing treefrog shelters in large-scale experiments, it is worthwhile to develop a hanging protocol appropriate for the system in question.

I examined use of tree-hung PVC shelters by hylid treefrogs in a landscape modified for cattle grazing in south-central Florida. Rangeland management can alter both terrestrial and aquatic habitats on which amphibians depend. Patchy habitats are created when trees are removed to create open pasture, decreasing suitable habitat and increasing woodlot fragmentation and isolation (Babbitt et al. 2006, Pellet et al. 2004). Artificial treefrog shelters are useful in determining population-level effects of agricultural fragmentation and detecting demographic shifts in treefrog populations. Because rangeland in south-central Florida is heterogeneous and consists of small, forested patches surrounded by open, treeless pastures, I needed to identify a protocol that captured the greatest number of treefrogs, to increase my chances of sampling frogs in sparsely-forested areas. I tested the null hypothesis that mean number of treefrogs in a shelter was independent of tree species and morphology, shelter height and orientation, water depth, and their interactions. I used this protocol to sample adult treefrog populations in a subsequent demographic study (Chapter 2).

Methods

Experimental design

Treefrog shelters were constructed of Schedule 40 PVC pipe (61 cm long x 3.8 cm diameter), with a nail hole drilled approximately 1 cm from the top of the pipe and a cap glued to the bottom. One-half of the shelters had a small hole drilled in the side of the pipe, 10 cm from the bottom, to allow excess water to drain. These shelters were filled with 10 cm of water before deployment. The remaining one-half of the shelters had small drainage holes drilled in the bottom of their caps to drain any water. These shelters were deployed with no water (0 cm).

Woodlots at MAERC consisted primarily of cabbage palm (*Sabal palmetto*) and oak trees (*Quercus virginiana*) that differ in morphology and height. I categorized trees by morphospecies: smooth palm trees, palms trees with boots and oak trees. Some palms (typically older trees) have smooth bark because they shed their “boots”: residual palm frond stalks that sometimes remain on the trunk. Boots also may be lost during fires. Other palms retain their boots, which provide numerous crevices suitable for treefrogs.

Different sides of a tree may be subject to varying amounts of light and heat, so I hung shelters on the north, south, east, or west sides of trees. Treefrogs use artificial refugia at varying heights on trees (Boughton et al. 2000), so I hung shelters at 2, 3, or 4 m above ground. I used a maximum height of 4 m because many palms with boots were just over 4 m tall, so shelters were hung directly under or slightly below the tree crown.

My experiment used a four-way, complete factorial design. I selected one woodlot in an intensively managed pasture that contained a fairly homogenous mixture of tree morphospecies. In many areas of MAERC, oaks occur in much smaller numbers than palm trees, so the study woodlot reflected a more even distribution of tree types. I deployed 72 treefrog shelters on an 80 m x 90 m grid, so that all shelters were 10 m apart. Each possible combination of tree morphospecies (smooth palm, palm with boots or oak), height (2.0, 3.0 or 4.0 m above ground), orientation (north, south, east or west), and water depth inside the shelter (0 cm or 10 cm) was represented in one of the 72 shelters. Shelters were sampled after three weeks, on 10 July 2007, from 1010-1415 h. Resident frogs were carefully emptied into a plastic bag and processed individually, as quickly as possible. I recorded the number, species and snout-vent length (SVL) of resident frogs, and then released them at the base of their tree of capture.

Statistical analysis

I used analysis of variance to determine the effects of tree morphospecies, shelter height and orientation, water depth, and their two- and three-way interactions on the mean number of treefrogs in a shelter. Because my design was unreplicated (Table 1), the four-way interaction term served as the error term. All statistical analyses were performed using JMP version 7.0 (SAS Institute 2007), with $\alpha = 0.05$.

Results

Artificial treefrog shelters efficiently sampled large numbers of adult treefrogs. In a single sampling session, I encountered 65 treefrogs in the 72 shelters, which required relatively little time to deploy and were easy to access and monitor. Shelter use was completely dominated by the Squirrel Treefrog (*Hyla squirella*), with all frogs belonging to this species. Based on call surveys, visual censuses and trapping of tadpoles, *Hyla squirella* was the most abundant treefrog at MAERC, although *H. cinerea*, *H. femoralis*, and *H. gratiosa* were present in lower numbers, and all four species use PVC refugia (Boughton et al. 2000, Zacharow et al. 2003, K. M. Windes, unpubl. data).

Only the main effect of tree morphospecies was statistically significant in the full model (Table 1). On average, shelters deployed on palms with boots had fewer treefrogs than those on smooth palms or oak trees (0.29 ± 0.21 [mean ± 1 SE hereinafter] versus 1.3 ± 0.21 and 1.1 ± 0.21, respectively). Height and orientation were non-significant in all models (full model: $F_{2,12} = 1.45$, $p = 0.27$ and $F_{3,12} = 0.44$, $p = 0.69$, respectively). Water depth was non-significant in the full model (Table 1) but was marginally significant in a reduced model in which palms with boots were excluded ($F_{1,6} = 6.047$, $p = 0.049$). In this sectored data set, shelters with water had more treefrogs on average than shelters without water (1.5 ± 0.19 versus 0.88 ± 0.19). No interaction terms were statistically significant in either the full or reduced models.

Of the 72 shelters, 35 were occupied. Eighteen (49%) of the empty shelters were on palms with boots, 12 (32%) on oaks and smooth palms without water, and the remaining 7 (19%) were on oaks and smooth palms with water (Figure 2). Logistic regression revealed that presence or absence of treefrogs was predicted by tree morphospecies ($p = 0.0021$) and the water depth x shelter height interaction (p = 0.0268). At 2 and 3 m, shelters with water were more likely to have treefrogs present than shelters without water, but the opposite trend existed for shelters hung at 4 m (Table 2).

Table 1: Model I (fixed factor) ANOVA. Columns give sources of variation, degrees of freedom (df), sum of squares (SS), F-ratio, and p-value; * indicates significant F-ratio. Full model R^2 = 0.871.

Source	**df**	**SS**	**F-ratio**	**p**
Tree morphospecies (T)	2	14.19	6.59	0.011*
Shelter height (S)	2	3.11	1.45	0.273
Orientation (O)	3	1.60	0.49	0.693
Water depth (W)	1	4.01	3.73	0.077
T x S	4	3.64	0.85	0.523
T x O	6	5.03	0.78	0.602
T x W	2	2.69	1.25	0.320
S x O	6	4.78	0.74	0.628
S x W	2	5.78	2.68	0.109
O x W	3	1.38	0.43	0.738
T x S x O	12	15.47	1.20	0.380
T x O x W	6	9.42	1.46	0.272
T x S x W	4	4.64	1.08	0.410
S x O x W	6	11.67	1.81	0.181
Error	12	12.92		
Total	71	100.33		

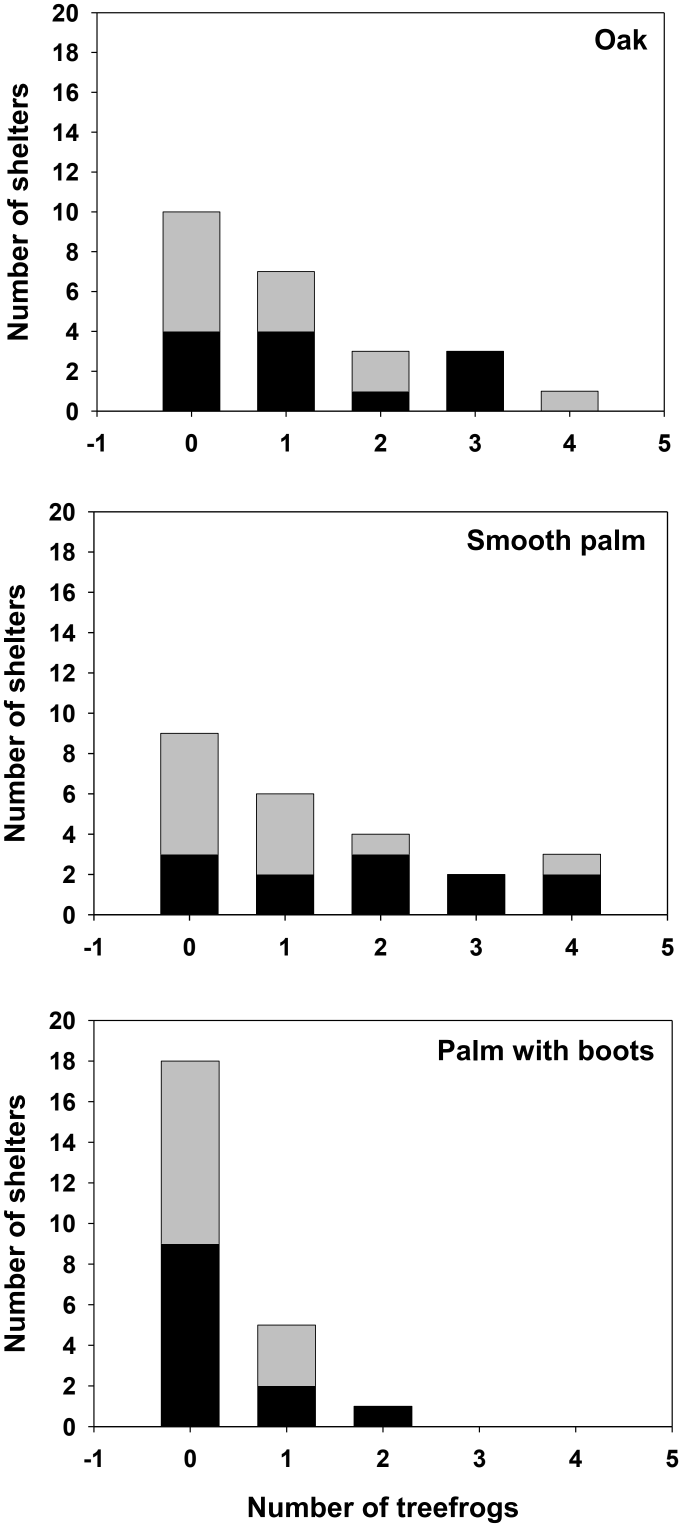

Figure 2: Numerical distribution of treefrogs within shelters. Black shading represents treefrog shelters deployed with water; gray shading represents shelters deployed without water.

Table 2. Experiment 1: Trend in water depth x shelter height interaction from logistic regression. Shelters were hung at either 2, 3, or 4 m and with either 0 cm or 10 cm water. Values in cells represent the number of shelters that had ≥ 1 treefrog.

		Shelter height		
		2 m	**3 m**	**4 m**
Water depth	**0 cm**	4	4	7
	10 cm	9	6	5

Discussion

At my study site, the protocol that maximized captures was to hang treefrog shelters on either palm trees with smooth trunks or oak trees. Shelters hung at 2 m can be sampled easily without using a ladder. Orientation should be random and equal (assign approximately equal numbers of each cardinal direction at each site, but randomize which shelter receives which direction) to avoid potential capture differences between sites. Because water depth was significant in the reduced model, shelters should be deployed with water to prevent desiccation during longer deployment. Shelters with water had slightly more treefrogs than shelters without water, indicating that frogs select refugia for moisture. Another study (Boughton et al. 2000) also found treefrogs used PVC shelters containing water more frequently than those without.

I found fewer treefrogs in shelters on palm trees with boots, likely because boots provide natural crevices for treefrogs to inhabit, thus decreasing the number of individuals selecting artificial shelters. Alternatively, treefrogs may avoid palms with boots. I found equivalent numbers of treefrogs in shelters hung at 2, 3, and 4 m, indicating that treefrogs do not restrict refugia selection to certain vertical areas of trees. Although treefrogs also colonize PVC pipes anchored to the ground or placed in shrubs (Boughton et al. 2000, Schurbon and Fauth 2003, Zacharow et al. 2003), potential trampling by cattle precluded my use of ground-based pipes. Orientation did not affect the number of treefrogs sampled. Variables such as tree position in a woodlot and proximity to other trees likely affect heat and moisture retention in a shelter; orientation may not reflect this variation.

Because treefrogs are selective in their use of artificial refugia, some researchers suggested that PVC refugia may be of limited use when monitoring treefrog populations (Zacharow et al. 2003). I often encountered several *H. squirella* in the same shelter, so they may crowd or outcompete larger species such as *H. cinerea* and *H. gratiosa*. Further research is needed to assess this prediction (Zacharow et al. 2003). Larger species also may seek larger refugia. I used shelters 3.8 cm in diameter, but in another study that examined shelters of varying diameters (1.9 cm, 5.1 cm, 7.7 cm), *H. squirella* was found more frequently in smaller diameter pipes and *H. cinerea* in larger pipes (Zacharow et al. 2003). In subsequent research conducted at MAERC, I encountered *H. cinerea*, *H. femoralis*, and *H. gratiosa* in shelters of the same design, albeit in much lower numbers than *H. squirella*. Sampling using artificial treefrog shelters may be particularly useful in mark-recapture studies because it allows access to large numbers of individuals. Careful attention must also be paid when using mark-recapture methods. Amphibians exhibit varying degrees of pipe fidelity (Boughton et al. 2000, Cohen and Alford 1996, Zacharow et al. 2003, K. M. Windes, unpubl. data); this can violate one of the critical assumptions of many mark-recapture models that all individuals in a population (both marked and unmarked) have an equal probability of capture. When this assumption is violated, other models must be used. For example, the Cormack-Jolly-Seber method assumes that only marked individuals have an equal probability of recapture, but this model does not estimate population size. Other population parameters such as apparent survival are calculated, and the total number of unique captures can be used as a conservative estimate of population size. Recent amphibian declines (Stuart et al. 2004, Young et al. 2001) and continuing large scale land-use changes necessitate a better understanding of amphibian population demography, and few sampling methods permit such efficient access to large numbers of individuals as artificial treefrog shelters.

While potential capture biases may make estimating hylid population size difficult, much information can be gained from treefrog shelters. *Hyla squirella* and *H. cinerea* are not threatened or endangered; it is less important to calculate extremely accurate population sizes than to detect trends in population demography and the factors that influence those trends. Detecting trends allows better management of landscapes and development of conservation objectives for amphibians, including threatened and endangered species. However, careful attention should be paid to potential capture biases and pilot studies conducted to determine appropriate hanging protocol for the species and system in question (Zacharow et al. 2003). The hanging protocol presented here (shelters on smooth palm trees or oak trees, at 2 m, with water, in random orientations) is appropriate for use in rangeland in Florida and similar semi-tropical systems, and is effective for sampling adult and juvenile *Hyla squirella*. I used this protocol to further examine how agriculturally modified landscape features influence *H. squirella* population demography in Chapter 2.

CHAPTER 2: LANDSCAPE FEATURES AFFECT TREEFROG POPULATION DEMOGRAPHY AND SITE FIDELITY

Introduction

Global amphibian declines necessitate a better understanding of amphibian autecology (Alford and Richards 1999). Effective conservation measures are built on knowledge of underlying population dynamics and how they interact with the environment in question. Many studies support the hypothesis that amphibians exist in metapopulations, where suitable habitat patches are occupied, become extinct, and are recolonized by other nearby patches (Gulve 1994, Carlson and Edenhamn 2000). However, an overwhelming majority of research on metapopulation dynamics is conducted at breeding sites (e.g., using aquatic sampling or calling censuses) and reports the presence or absence of a species from a particular pond (Pellet et al. 2004, Schmidt and Pellet 2005, Zanini et al. 2008). In other words, a "ponds as patches" view largely has been adopted in metapopulation spatial dynamics (Marsh and Trenham 2001).

Comparatively little is known about how amphibians use terrestrial, non-breeding habitat, although adults of many species spend most of their time in upland habitat. Mark-recapture studies in terrestrial habitats can estimate population survival and recapture and determine how landscape features affect these parameters. In addition, mark-recapture data allow researchers to measure degree of site fidelity and trends in dispersal. Some researchers have used mark-recapture data to examine differences in growth, development and movement, but have not reported estimates of demographic parameters such as survival and recapture (Berven and Grudzien 1990, Altwegg 2003, Smith and Green 2006). Many authors report population abundance estimates but do not calculate other parameters that can be compared among groups (e.g., stage or sex) or related to environmental variables (Gittins 1983, Measey et al. 2003, Nelson and Graves 2004). Only a few mark-recapture studies estimated amphibian population parameters outside of abundance, and these focused on individuals collected either in ponds or as they migrated to breeding ponds. Holenweg Peter (2001) reported higher survival of *Rana lessonae* than *R. esculenta* adults captured in breeding ponds and higher recapture of males than females; recapture also varied over time. Wood et al. (1998) collected *R. grylio* in wetlands and reported higher survival of females than males or juveniles, which were similar to each other. The problem with collecting individuals only in breeding habitat is that, especially for some species, it increases the chance that some groups will be missed (i.e., are in unobservable states), such as juveniles or non-breeding adults (Bailey et al. 2004). Almost no data is available on amphibian population parameters calculated from terrestrial sampling methods.

I used mark-recapture data to model survival and recapture parameters for the squirrel treefrog, *Hyla squirella*, in a landscape modified for cattle ranching in south-central Florida. Agricultural lands are important in the conservation of many species because these lands often retain large areas of native habitat and associated species, especially compared to urban or commercial land (Boughton 2008, Bohlen et al. 2009). Central Florida ranches support species-rich and abundant amphibian assemblages (Babbitt and Tanner 2000, Babbitt et al. 2006). However, extensive landscape modifications during ranchland construction and maintenance greatly affect amphibians, which are sensitive to perturbations in both aquatic and terrestrial environments due to their complex life cycle and semi-permeable skin. Ditches that drain or irrigate pastures increase connectivity between wetlands and provide a route for predatory fish to invade (Babbit and Tanner 2000). Fish are major tadpole predators and many amphibians avoid laying eggs in fish-inhabited water (Brönmark and Edenhamn 1993, Binckley and Resetarits 2002, Petranka and Holbrook 2006). Runoff from fertilizer and nutrients from cattle urine and feces alter water chemistry in wetlands (Day and Detling 1990, Hobbs 1996, Frank and Groffman 1998), which may affect amphibian growth and development.

Modifications to terrestrial habitat create a harsh matrix in which suitable upland habitat and breeding sites are interspersed in relatively treeless, open pasture, where amphibians risk predation and desiccation (Steinman et al. 2003, Pellett et al. 2004, Babbitt et al. 2006). Highly fragmented environments affect amphibian population processes. For example, amphibian occurrence can be predicted by forest patch proximity (Babbitt et al. 2006) and area (Knutson et al. 1999, Kolozsvary and Swihart 1999) and proximity of wetlands (Vos and Stumpel 1995, Kolozsvary and Swihart 1999), indicating that both wetland and upland characteristics affect population demography. Fragmentation adversely affects migratory success of juvenile spotted salamanders (*Ambystoma maculatum*) and American toads (*Bufo americanus*), where migration success is primarily a function of distance to nearest forest (Rothermel 2004). In a metapopulation of pool frogs (*Rana lessonae*), probability of extinction increases with increasing inter-population distance (Sjögren 1991). Fragmentation may have other adverse effects on breeding ecology; female tungara frogs have decreased opportunity for mate choice with increasing inter-pond distance (Marsh et al. 2000). In addition, habitat fragmentation may affect amphibian populations simply by decreasing habitat quality (Marsh and Pearman 1997). The relatively low mobility of amphibians combined with strong site fidelity may hinder re-colonization of habitat patches after local extinction (Blaustein et al. 1994), so even modest habitat fragmentation may negatively affect amphibian subpopulations (Marsh and Pearman 1997). Because habitat fragmentation increases inter-pond distances, site fidelity may increase in more isolated, fragmented woodlots. If amphibians exhibit strong site fidelity, such fragmentation and isolation may affect population persistence.

To identify effective conservation and agricultural management strategies, it is important to understand how landscape features influence amphibian population demography and habitat use (Pope et al. 2000, Bosch et al. 2004, Van Buskirk 2005, Babbitt et al. 2006). "Area-informed isolation metrics," such as amount of suitable habitat in concentric buffer areas (Bender et al. 2003), are more informative for predicting population dynamics than distance-based measures (e.g., nearest-neighbor distances). Area informed metrics are particularly important in agricultural areas where wetlands are situated in variable and often highly modified landscapes. For example, some wetlands may have many nearby, neighboring wetlands but be devoid of suitable upland habitat due to agricultural modification. Recent studies adopted concentric buffer areas to examine effects of landscape features on amphibian population dynamics (Pellet et al. 2004a,b, Chan-McLeod and Moy 2007, Otto et al. 2007).

I collected mark-recapture data of *H. squirella* in a Florida cattle ranch over a nine month sampling period. Using Program MARK, I estimated differences in survival and recapture over time and among frog stage and sex. I then examined how concentric landscape features influenced survival and recapture, and measured the strength site fidelity using encounter history records and recapture rate as a proxy for site fidelity. These data reveal how treefrogs use terrestrial habitat and could be use to aid in landscape-level management recommendations.

Methods

Experimental design

I selected six wetlands in semi-natural pastures (three grazed and three released from grazing) and six wetlands in intensively managed pastures (three grazed and three released from grazing) from the USDA experiment (Figure 3). Using ArcMap 9.1 (ESRI Inc., Redlands, CA), I created a 100 m buffer around each focal wetland. Any woodlot within this 100 m buffer was considered a focal woodlot (Figure 4). I assessed landscape features within the initial 100 m focal woodlot, and also at increasingly large, non-nested buffers of 100 – 150, 150 – 200, and 200 – 250 m (Figure 4). In each concentric buffer, I calculated woodlot area (ha), number of wetlands, wetland area (ha), Index of Wetland Availability (Wetland Index; Equation 1), and Ditch Index (Equation 2).

Wetland Index = $\sum$ (area of wetland x distance to center of focal wetland)/100 (Equation 1)

Ditch Index = $\sum$ (ditch length x top width x depth)*1000 (Equation 2)

I also determined area and Northing and Easting coordinates (UTM) of the focal wetland, and included July 2007 water depths of each focal wetland. There were 26 total landscape variables (Table 3).

To sample treefrogs, in July 2007 I deployed 30 PVC shelters/ha of focal woodlot using the optimal tree morphospecies, height, orientation, and water depth combinations determined in Chapter 1. I placed shelters at randomly selected points at least 10 m from any other shelter

Figure 3. Location of Chapter 2 focal wetlands shown in red.

within the focal woodlot, for a total of 265 treefrog shelters across the twelve sites. I monitored shelters three times in the fall breeding season: in August, October, and November 2007 (the end of the wet season), and then removed all shelters to force treefrogs to overwinter in natural refugia. By removing shelters, I ensured that overwintering survival was influenced as little as possible, because artificial shelters may provide a superior refuge to natural refuges. In

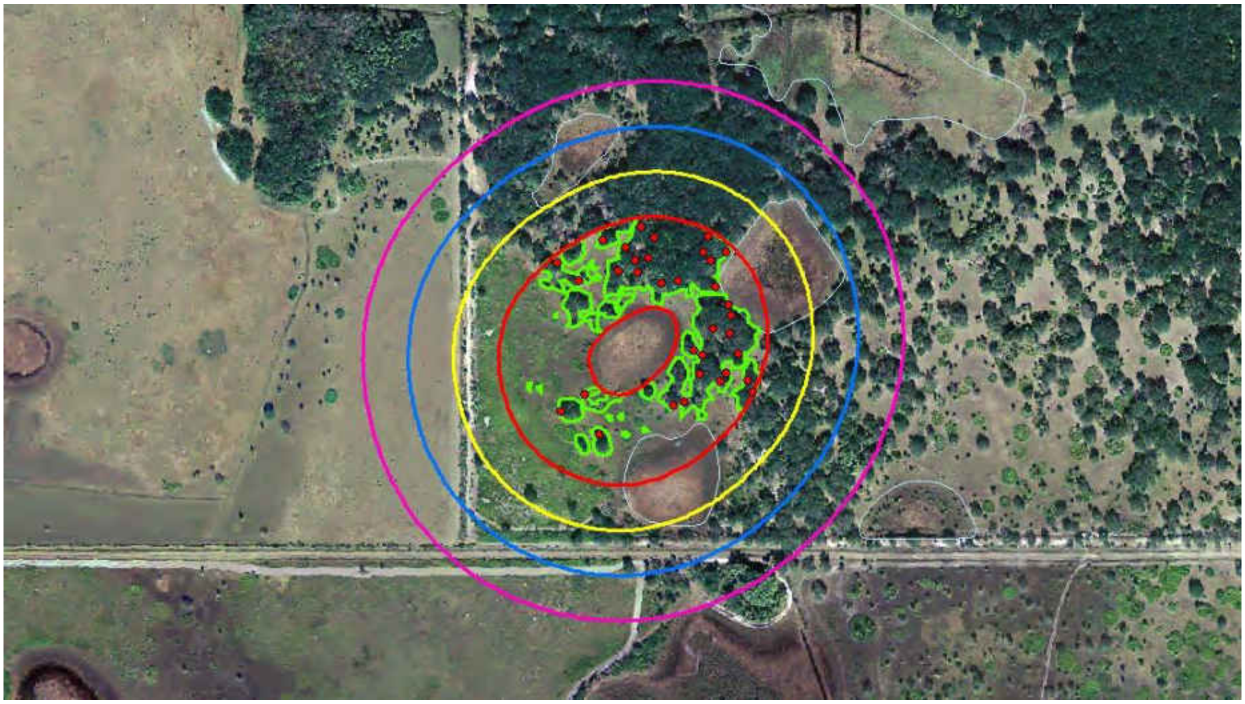

Figure 4. Chapter 2 – Experimental design. Center red circle delineates experimental wetland 597. Focal woodlot is outlined in green within the first 100 m buffer (red). Red dots indicate randomly selected locations of PVC shelters. Subsequent lines represent buffers of 100-150 (yellow), 150-200 (blue), and 200-250 m (purple).

Table 3. List of landscape variables assessed for all focal wetlands.

Independent (landscape) variables	
Pasture management (Semi-natural, Intensively managed)	Wetland area 100 (ha)
Grazing (Grazed, Relased from grazing)	Wetland area 150 (ha)
Focal wetland area (ha)	Wetland area 200 (ha)
Easting (m)	Wetland area 250 (ha)
Northing (m)	Wetland Index 100
July water depth (cm)	Wetland Index 150
Woodlot area 100 (ha)	Wetland Index 200
Woodlot area 150 (ha)	Wetland Index 250
Woodlot area 200 (ha)	Ditch Index 100
Woodlot area 250 (ha)	Ditch Index 150
Number of wetlands 100	Ditch Index 200
Number of wetlands 150	Ditch Index 250
Number of wetlands 200	
Number of wetlands 250	

April, I re-hung all shelters in their original location, and added 50% more new ones at each site, to compare recapture rates of old versus new location shelters. With the addition of 136 new shelters, there were 401 total shelters across the twelve sites in April 2008. To determine which mark-recapture model best fit my data, I compared recapture rates in old vs. new shelters. If rates were similar, both marked and unmarked individuals had equal capture probability and I could use the standard Jolly-Seber (JS) model, which allows estimation of population size. If individuals displayed strong site fidelity, then new shelters would have fewer recaptures, thus violating the necessary JS assumptions, and I would proceed with the Cormack-Jolly-Seber (CJS) model, which assumes only that marked individuals have equal capture probability.

I monitored all shelters (old and new) in late May 2008 to estimate overwintering survival and growth. During all monitoring periods, I sexed, measured (SVL) and uniquely marked each frog, and identified re-captured frogs during subsequent visits. Individuals 2.2 cm and larger were sexed, while individuals under 2.2 cm were recorded as juveniles, due to the difficulty and uncertainty in sexing small individuals. I chose 2.2 cm because that was the minimum size at which I observed obvious characteristics of a sexually mature individual (i.e., a gravid female or a male with an enlarged, yellow throat sac). Marks were administered using visible implant elastomer (VIE) tags (Hand Injection Kit, Northwest Marine Technology, Inc., Shaw Island, WA). To generate a sufficiently large list of unique marks, I used eight elastomer colors and four potential marking locations: right thigh, right calf, left thigh, and left calf (Figure 5). To minimize the total number of marks frogs received, I eliminated combinations comprised of four marks (i.e., I only used combinations that consisted of 1, 2 or 3 marks). Frogs were transported in plastic bags from their shelter of capture to various along the focal wetland edges, where I processed and released them.

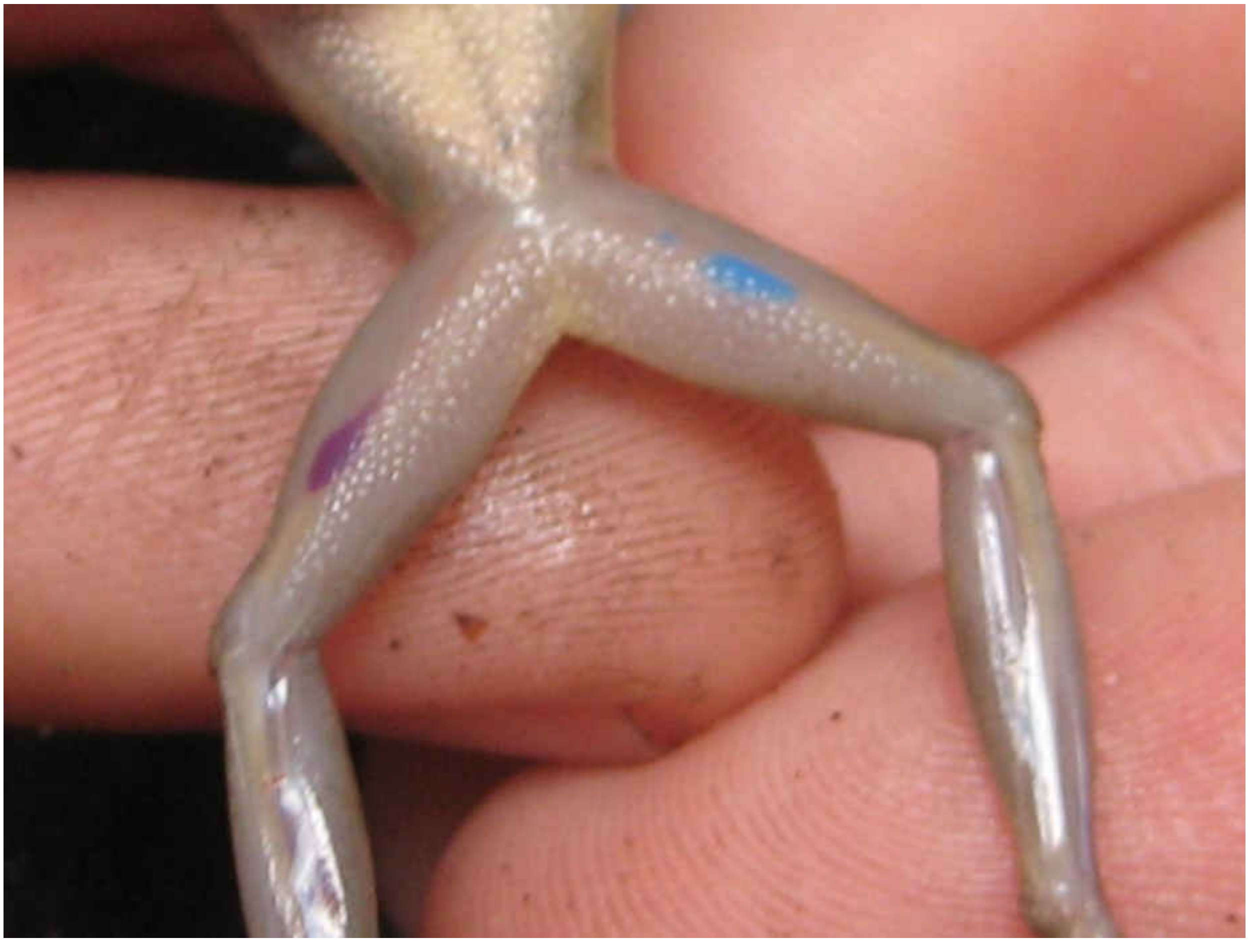

Figure 5. Squirrel treefrog (*Hyla squirella*) marked with combination purple, none, blue, none.

Statistical analysis

I used JMP version 8.0 (SAS Institute) to examine correlations among landscape variables. I used Program MARK (White and Burnham 1999) to estimate treefrog survival and recapture rate as linear functions of time and season, treefrog stage, sex and size, and selected landscape variables. Program MARK uses mark-recapture data to estimate apparent survival (Φ): the probability that an animal survived from time i to time i+1 and was available for recapture. Program MARK also estimates recapture probability (p): the probability that an animal is re-encountered, given that it survived the previous interval. Survival and recapture parameters are assessed for consecutive cohorts over time (Figure 6).

I assessed goodness of fit (GOF) using two methods available within Program MARK: bootstrapping and median ĉ. Both bootstrapping and median ĉ provide an estimate that quantifies the degree of overdispersion in the data (the variance inflation factor, or ĉ). Bootstrapping runs multiple simulations with observed parameter estimates for the model in question to construct a series of encounter histories that meet model assumptions. The original model is then fit to the simulated data, generating simulated model deviance and ĉ. There are two ways to calculate ĉ using bootstrap results: ĉ (deviance) = observed model deviance/mean simulated deviance, and ĉ (observed ĉ) = observed model ĉ /mean simulated ĉ, where observed ĉ = observed model deviance/deviance df. The median ĉ approach calculates the value of ĉ for which the number of simulated deviance ĉ above and below the observed value are equal.

Model selection analysis was a two-part process based on the Quasi-likelihood corrected form of the Akaike Information Criterion coefficient (QAICc). I first determined the best underlying model using combinations of either gender group (Juvenile, Male, Female) or life history stage (Juvenile, Adult) and either time (where each sampling interval was considered separately, i.e., interval 1, 2 and 3) or season (intervals 1 and 2 [Fall], interval 3 [Spring]). I used these variables to determine the best underlying model for treefrog survival and recapture; this model served as the null model in phase two of the analysis, where I applied landscape variables and treefrog size to the null model as individual covariates.

If my data best fit a JS model, then I would use Program MARK to examine how group, time, and landscape variables influenced population size, as described above. If my data best fit a CJS model, I would use the number of unique captures at each site to determine density of treefrogs and use model selection based on Akaike's Information Criterion (AIC) to determine the effect of landscape variables on frog density.

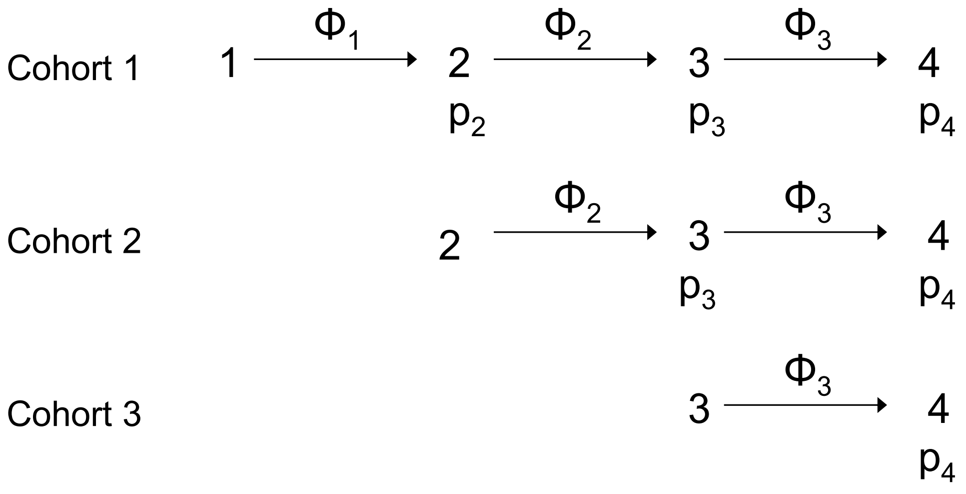

Figure 6. Apparent survival (Φ) and recapture (p) parameters for three release cohorts and four sampling occasions.

Results

Landscape variables

Focal wetland area averaged 0.80 ha and ranged from 0.46 – 1.18 ha. Maximum center depths were recorded, but four of the 12 wetlands (33.3%) did not hold any water during the study due to drought conditions. Focal wetlands varied greatly in the area of surrounding woodlot. Wetlands had an average of 1.45 ha of woodlot in the first 100 m buffer, but values ranged from as little as 0.15 ha at wetland 205 (IM-R) to 4.37 ha at wetland 597 (SN-R). Wetland number and area tended to increase with increasing buffer size, although buffers were non-nested. The Wetland Index varied among sites, with some sites (e.g., site 123 [SN-R]) having high values even for larger buffers due to extremely large, nearby wetlands that most likely connect to the focal wetland during very wet periods. Most IM sites had high Ditch Index values and most (but not all) SN sites had relatively low Ditch Index values (although site 79 [SN-R] had a relatively high index). A complete list of values for all variables in all buffers is presented in Table 4.

To eliminate strong correlations between landscape variables, I selected a reduced set of variables. All measures of woodlot area were significantly correlated with one another, so I used one woodlot variable that represented the area of woodlot from 0 – 250 m. The new woodlot variable was negatively correlated with Northing (because larger woodlots in this study were in the south of MAERC), so I excluded Northing from the set of candidate variables. Ditch Index was negatively correlated with Woodlot 0 – 250, so I excluded Ditch Index. Wetland Index measures were correlated with one another and with wetland area and number of wetlands, so I used one Wetland Index that included all wetlands from 0 – 250 m. The reduced set of variables used for phase two of the Program MARK analysis is presented in Table 5.

Table 4. Experiment 2 landscape variables by site. (Top) Pond No. = site number of focal wetland; Past = pasture type, SN = semi-natural, IM = intensively managed; Graze = grazing treatment, R = released from grazing, G = grazed; Pd area = area (ha) of focal wetland; Depth = July depth (cm) of focal wetland; Woodlot area = area (ha) of woodlot per buffer; Wetland number = number of wetlands per buffer. (Bottom) Wetland area = area of wetland (ha) per buffer; Wetland Index = total Wetland Index per buffer (Equation 1); Ditch Index = total Ditch Index per buffer (Equation 2). Buffers are: 100 = 0 – 100 m from focal wetland, 150 = 100 – 150 m, 200 = 150 – 200 m, 250 = 200 – 250 m.

					Woodlot AREA (ha)				**Wetland NUMBER**			
Pond No.	**Past**	**Graze**	**Pd area (ha)**	**Depth (cm)**	**100**	**150**	**200**	**250**	**100**	**150**	**200**	**250**
49	SN	R	0.82	32	1.77	0.85	0.69	0.83	2	3	5	4
66	SN	R	0.46	0	0.72	0.06	0.08	0.12	1	2	3	2
79	SN	G	0.65	25	1.60	0.90	1.82	2.29	7	6	7	5
123	SN	G	0.60	16	0.57	0.15	0.06	0.20	1	4	6	6
196	IM	R	0.67	0	1.44	0.86	1.20	0.94	2	3	3	4
205	IM	G	0.98	61	0.15	0.28	0.23	0.24	0	1	2	3
245	IM	G	1.03	40	2.96	1.27	0.77	0.29	1	2	4	4
271	IM	R	0.75	0	0.72	0.15	0.18	0.19	1	1	4	5
310	IM	R	0.71	0	0.46	0.34	0.13	0.30	0	5	9	4
336	IM	G	1.18	24	0.36	0.47	0.25	0.62	2	5	7	5
595	SN	G	1.10	12	4.37	2.50	3.21	2.90	1	3	3	2
597	SN	R	0.65	40	2.28	2.16	3.04	3.85	2	2	3	1

	Wetland AREA (ha)				**Wetland INDEX**				**Ditch INDEX**			
Pond ID	**100**	**150**	**200**	**250**	**100**	**150**	**200**	**250**	**100**	**150**	**200**	**250**
49	1.02	0.93	0.76	1.13	10.07	5.79	3.77	4.56	0.00	8.12	10.39	11.02
66	0.08	0.33	0.85	1.30	0.66	2.45	4.33	5.56	0.00	0.00	36.33	42.61
79	0.83	1.11	1.43	1.89	11.13	8.93	7.10	8.38	10.02	5.37	27.56	21.40
123	1.43	2.02	3.55	2.76	24.49	13.97	18.50	11.39	12.06	15.12	13.22	15.60
196	0.30	0.61	0.47	0.98	3.02	4.04	2.32	3.89	18.28	11.59	56.09	40.67
205	0.00	0.08	0.90	1.49	0.00	0.43	4.37	5.95	13.16	21.18	15.45	16.47
245	0.06	0.83	1.68	2.19	0.43	5.25	8.06	8.53	0.00	0.25	2.36	6.04
271	0.00	0.22	0.42	1.14	0.01	1.56	1.90	4.58	9.94	42.03	30.83	29.98
310	0.00	0.47	1.37	0.50	0.00	2.82	6.92	2.06	2.60	12.63	11.43	38.73
336	1.58	2.28	1.97	1.12	16.23	14.71	9.33	4.27	11.10	5.95	48.12	55.31
595	0.14	0.42	0.62	0.62	0.98	2.55	2.99	2.48	0.00	9.65	5.60	4.84
597	0.63	1.08	0.84	0.15	6.07	7.56	4.30	0.62	0.00	0.00	10.68	4.71

Table 5. Reduced landscape variables selected for model building.

Variable
Pasture management (Semi-natural, Intensively managed)
Grazing (Grazed, Released from grazing)
Easting (m)
Focal wetland area (ha)
July water depth (cm)
Woodlot area (ha) 0 – 250 m
Wetland Index 0 – 250 m

Summary of treefrog captures

In total, there were 1,875 treefrog captures. Nearly all captures (1,854) were *Hyla squirella*; I captured only one *Hyla gratiosa*, seven *H. femoralis*, and thirteen *H. cinerea* during my study. None of these congeners was ever recaptured. In the final sampling occasion, shelter status and capture status were not independent ($\chi^2 = 44.002$, $p < 0.0001$); old shelters had a recapture percentage nine times greater than new shelters (Table 6). Therefore, marked and unmarked individuals did not have equal probability of capture and the data did not conform to JS assumptions. Instead, I used CJS to estimate survival and recapture. I excluded new shelter captures to ensure that data used in analyses were consistent across all sampling periods.

Table 6. Captures of *Hyla squirella* in new and old shelters during the last capture session; May, 2008. TC = total captures, NC = new captures, RC = recaptures, %RC = percent recaptures. $\chi^2 = 44.002$, $p < 0.0001$.

	TC	**NC**	**RC**	**%RC**
New shelters	133	130	3	2.26
Old shelters	241	191	50	20.75

There were 1,721 total captures of *H. squirella* in old shelters, representing 1,547 unique individuals. Of the individuals recaptured, 132 were captured twice, and 20 were captured three times. No individuals were encountered on all four occasions. Fifty individuals were encountered at least once in the fall sampling occasions and then recaptured in the final spring sampling (i.e., are known to have survived the 6 month winter interval). Percent recapture increased with every sampling occasion (Table 7), and varied substantially among sites (Table 8). Most captures were adult frogs, with a total of 638 (41.2%) females, 683 (44.1%) males, and only 226 (14.6%) juveniles.

Table 7. Captures of *H. squirella* by sampling occasion. TC = total captures, NC = new captures, RC = recaptures, %RC = percent recapture.

Occasion	**Date**	**TC**	**NC**	**RC**	**% RC**
1	08 - 2007	220	220		
2	10 - 2007	365	345	20	5.80
3	11 - 2007	895	792	103	13.01
4	05 - 2008	241	191	50	26.18

Site fidelity

Individuals of *H. squirella* exhibited extreme site fidelity. Of the 152 individuals recaptured, 145 (95.4%) were encountered in their original shelter of capture. The seven individuals that were encountered in shelters other than their original shelter were encountered only twice, and moved 10 – 175 m between shelters (Table 9). Over one-half (4/7) were female frogs that moved sometime during the six month over-wintering period. The larger distances almost always required moving across open pasture to reach the second shelter. The smaller distances consisted of movements within the same patch of trees.

Table 8. Captures of *H. squirella* by sites at the MacArthur Agro-Ecology Research Center. N shelters = number of treefrog shelters deployed, TC = total captures, NC = new captures, RC = recaptures, %RC = percent recapture, Avg. frogs/shelt = average number of treefrogs per shelter over all four sampling occasions.

Site	N shelters	TC	NC	RC	% RC	Avg frogs/shelt
49	27	56	55	1	1.79	2.1
66	11	61	59	2	3.28	5.5
79	24	65	58	7	10.77	2.7
123	9	15	15	0	0.00	1.7
196	22	149	132	17	11.41	6.8
205	5	64	55	9	14.06	12.8
245	44	618	562	56	9.06	14.0
271	11	111	98	13	11.71	10.1
310	7	41	34	7	17.07	5.9
336	5	17	17	0	0.00	3.4
595	66	265	241	24	9.06	4.0
597	34	259	222	37	14.29	7.6

Table 9. Treefrogs that moved between shelters. Sex of frog: F = female; M = male; First occasion = occasion on which individual was first encountered; Second occasion = occasion on which individual was recaptured; Distance = distance traveled between shelters.

Site	Sex	First occasion	Second occasion	Distance (m)	Open pasture traversed?
196	F	3	4	109.4	Yes
196	F	3	4	10.6	No
205	M	2	3	13.5	No
245	F	3	4	168.1	Yes
245	J	2	3	99.0	Yes
595	J	1	4	171.4	Likely
597	F	3	4	175.6	Yes

Program MARK

I used standard Cormack Jolly Seber (CJS), live recaptures only to model survival and recapture of *H. squirella*. I assessed GOF on the fully time-dependent CJS model {Phi(g*t) p(g*t)} using two applications available within Program MARK. Bootstrapping with 100 simulations gave ĉ (deviance) = 1.88; ĉ (observed ĉ) = 2.78; results similar with 500 simulations: ĉ (deviance) = 1.87; ĉ (observed ĉ) = 2.80. Using the median ĉ approach, ĉ = 2.49. Because the median ĉ yielded an estimate just slightly larger than the mid-way point of the bootstrapping estimates, and because median ĉ performs well with CJS data and typically produces relatively small mean squared error (Cooch and White 2009), ĉ was adjusted to the median ĉ estimate in the analysis.

Phase 1

Because the analysis was exploratory in nature, I ran all possible combinations of gender group and time models. I then incorporated models including either life history stage or season in place of group and time. When Δ AIC < 2, models are not substantially different (Burnham and Anderson 1998). The top seven models had a Δ QAICc ≤ 2 and are presented in Table 10. There was no support for any interactive effects.

Relative variable importance was calculated for each parameter by adding model weights of all models that contained a particular variable (Table 11). Gender group was the most important explanatory variable for apparent survival (Φ). In models containing group, Female survival was consistently higher than Male or Juvenile survival, for which estimates were similar. There was relatively little support for effects of life history stage or time in explaining apparent survival (Φ). Some evidence existed for an effect of season; in models containing season, survival was lower for all groups in the final time interval (i.e., the over-wintering period) than in the fall intervals.

Table 10. Top models from phase 1 of Program MARK analysis. Phi = apparent survival (Φ), p = recapture rate. Variables are: g (gender group: Juvenile, Male, Female), stage (life hiostry stage: Juvenile, Adult), t (time: interval 1, 2, 3), and season (Fall, Spring). QAICc = quasi-likelihood corrected form of Akaike Information Criterion; ΔQAICc = difference between the top model and the model in question; QAICc Wgt = model weight; Likelihood = model likelihood; No. Par = number of parameters; QDev = model deviance.

Model	**QAICc**	**Δ QAICc**	**QAICc Wgt**	**Likelihood**	**No. Par**	**QDev.**
1 {Phi(g) p(stage+t)}	441.621	0.000	0.1135	1.000	7	427.544
2 {Phi(g) p(t)}	441.930	0.310	0.0972	0.857	6	429.873
3 {Phi(g) p(stage)}	442.750	1.125	0.0647	0.570	5	432.705
4 {Phi(g+season) p(stage+t)}	442.882	1.261	0.0604	0.532	8	426.784
5 {Phi(t) p(g)}	443.424	1.804	0.0461	0.406	6	431.367
6 {Phi(g) p(g+t)}	443.600	1.983	0.0421	0.371	8	427.506
7 {Phi(g+season) p(stage)}	443.820	2.200	0.0378	0.333	6	431.763

Table 11. Relative importance of phase 1 variables in Program MARK analysis. Φ = apparent survival; p = recapture. Variables are: g (gender group: Juvenile, Male, Female), stage (life history stage: Juvenile, Adult), t (time: interval 1, 2, 3), and season (Fall, Spring).

Variable	**Φ**	**p**
Group	0.7294	0.2620
Stage	0.1343	0.5135
time	0.1996	0.5126
Season	0.3104	0.2288

Life history stage and time were equally important in estimating recapture (p), and they were about twice as important as either gender group or season (Table 11). In models containing stage, Adult recapture was consistently higher than Juvenile. In models containing a group effect rather than stage, whether Male or Female recapture was estimated to be higher varied. However, both adult groups had consistently higher recapture estimates than Juveniles, indicating that stage is in fact a better predictor of recapture. Recapture was highest on the third sampling occasion (ie, time 3) in all models containing time.

Although the top model did not have a very high QAICc weight (Table 10), it reflected the results of the relative variable importance for both parameters. Most subsequent models were simply nested versions of the top model, except for the presence of season in models four and seven and inclusion of group rather than stage in the recapture parameter in some models. Therefore, the top model {Phi(g) p(stage+t)} was selected as the null model for phase two of the analysis.

Phase 2

I applied the reduced set of landscape variables (Table 5) and treefrog size to the null model as individual covariates. First, each covariate was added as a single additive effect to Φ, p, or both Φ and p. This allowed me to assess the relative contribution of each variable to both parameters. Models with size, pasture or July depth ranked below the null model; in other words, they did not explain any additional variation in either Φ or p, so they were excluded in the following step. I next examined additive effects of the remaining variables in sets of two on Φ, p or both Φ and p. This allowed me to examine whether multiple additive effects explained substantially more variation than models with single effects. Woodlot, Wetland, and Easting were important in explaining Φ, and Woodlot and Easting were important in explaining p, so I ran a small subset of models with varying combinations of these effects.

I selected a subset of biologically meaningful two-way interactions from the possible two-way interactions of all eight covariates. Interactive models were built for each parameter separately, and I compared these models to those that had only additive effects of the two particular variables as a direct test for an interactive effect (Table 12). No interactive models were substantially different from the additive only models; most interactive models ranked much lower.

Table 12. Interactive effects tested in phase 2 of Program MARK analysis.

Interactive model	**Additive model for comparison**
Size+Pasture+Size*Pasture	Size+Pasture
Size+Woodlot+Size*Woodlot	Size+Woodlot
Size+Wetland+Size*Wetland	Size+Wetland
Pasture+Grazing+Pasture*Grazing	Pasture+Grazing
Pasture+Woodlot+Pasture*Woodlot	Pasture+Woodlot
Pasture+Wetland+Pasture*Wetland	Pasture+Wetland
Woodlot+Wetland+Woodlot*Wetland	Woodlot+Wetland

The top ten models had a Δ QAICc ≤ 2 (Table 13). The top two models had approximately equal (although relatively low) weight. Relative variable importance was calculated for each parameter by adding model weights of all models that contained a particular variable (Table 14). Woodlot was the most important variable in estimating Φ, with survival of all groups increasing with increasing area of woodlot (Figure 7). There was some evidence for effects of Wetland and Easting on Φ, but predicted trends for Easting were inconsistent; some models predicted a positive effect of Easting on Φ while others predicted a negative effect.

Survival decreased with increasing Wetland Index. However, most models had at least some β estimates for which the 95% confidence intervals overlapped zero. All other covariates were essentially unimportant in estimating Φ.

Woodlot area also was the most important variable in estimating p, but less so than for Φ (Table 14). Easting was almost equally important in estimating p, with recapture decreasing both with increasing woodlot area (Figure 7) and increasing Easting. The top two covariate models were similar in structure and carried approximately equal weight; estimates of survival and recapture are given for these models (Table 15, Table 16).

Population density

Because CJS does not provide an estimate of population size, I used the number of unique captures at each site to determine density of *H. squirella* in focal woodlots (Table 17). I used model selection based on AIC to determine the relationship between density and the reduced set of landscape variables. The 10 top models are presented in Table 18; only the top two models have a ΔAICc < 2 and are not substantially different. Pasture type and July depth were the most informative variables in explaining variation in frog density, with IM woodlots having much higher density of *H. squirella* than SN woodlots (Table 19), and focal wetlands with more water having a greater surrounding density of frogs. Backward stepwise regression also revealed a significant effect of July depth and Pasture type on treefrog density ($Y = \beta_0 + 0.590*X_{\text{July depth}} + 0.524*X_{\text{Pasture type}}$). There was no relationship between density and treefrog size ($r^2 = 7.483 \times 10^{-5}$, $p = 0.9787$).

Table 13. Top models from phase 2 of Program MARK analysis. Phi = apparent survival (Φ), p = recapture rate. Variables are: Wood = area of woodlot (ha) within 250 m; Wet = area of wetland (ha) within 250 m; East = easting (m); Graze = grazing treatment (grazed or released from grazing). QAICc = quasi-likelihood corrected form of Akaike Information Criterion; ΔQAICc = difference between the top model and the model in question; AICc Wgt = model weight; Likelihood = model likelihood; No. Par = number of parameters; QDev = model deviance.

Model	**QAICc**	**Δ QAICc**	**QAICc Wgt**	**Likelihood**	**No. Par**	**QDev**
{Phi(g)Wood+Wet p(stage+t)Wood+East}	438.183	0.000	0.0739	1.000	11	416.002
{Phi(g)Wood+East p(stage+t)Wood+East}	438.255	0.073	0.0713	0.964	11	416.075
{Phi(g)Woodlot p(stage+t)Woodlot}	439.050	0.867	0.0479	0.648	9	420.927
{Phi(g) p(stage+t)East}	439.337	1.154	0.0415	0.562	8	423.239
{Phi(g)East+Woodlot p(stage+t)}	439.608	1.425	0.0362	0.490	9	421.485
{Phi(g)East p(stage+t)}	439.672	1.490	0.0351	0.475	8	423.574
{Phi(g)Woodlot p(stage+t)}	439.746	1.564	0.0338	0.458	8	423.648
{Phi(g)Wood+Wet p(stage+t)Wood}	439.902	1.720	0.0313	0.423	10	419.750
{Phi(g)Wood+Wet+East p(stage+t)Wood+East}	440.169	1.987	0.0274	0.370	12	415.956
{Phi(g)Graze+Woodlot p(stage+t)}	440.461	2.278	0.0237	0.320	9	422.338

Table 14. Relative variable importance for covariates in phase 2 of Program MARK analysis. Φ = apparent survival, p = recapture.

Variable	**Φ**	**p**
Woodlot	0.4416	0.3296
Wetland	0.2757	0.0789
Size	0.0413	0.0221
Pasture	0.0671	0.0437
Grazing	0.0724	0.0839
Easting	0.2591	0.3123
Pond area	0.0644	0.0718
July depth	0.0018	0.0067

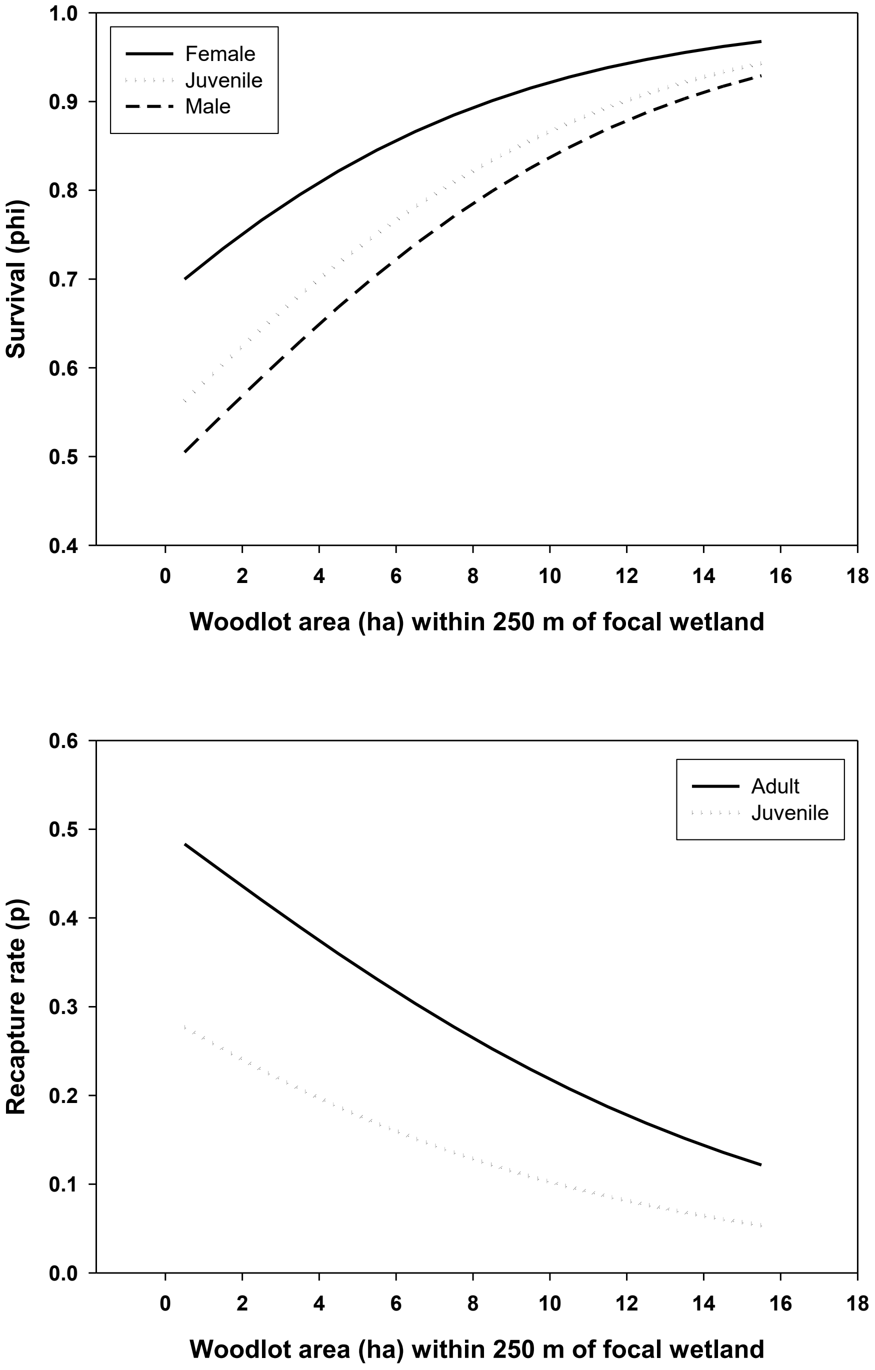

Figure 7. Effect of woodlot area on apparent survival (top) and recapture rate (bottom) of *Hyla squirella* at the MacArthur Agro-Ecology Research Center. Modeled using top covariate model: Phi(g)woodlot+wetland p (stage+t)woodlot+easting.

Table 15. Apparent survival (Phi) estimates for top two covariate models. g = gender group; t = time.

Model	**Group**	**Phi**	**SE**
Phi(g)Woodlot+Wetland p(stage+t)Woodlot+Easting	Juvenile	0.78280	0.09457
	Male	0.74055	0.06668
	Female	0.86713	0.05432
Phi(g)Woodlot+Easting p(stage+t)Woodlot+Easting	Juvenile	0.77650	0.09453
	Male	0.73522	0.06096
	Female	0.86483	0.05263

Table 16. Recapture (p) estimates for top two covariate models. g = gender group; t = time [time 2 = sampling occasion 2; time 3 = sampling occasion 3; time 4 = sampling occasion 4].

Model	**Stage**	**Time**	**p**	**SE**
Phi(g)Woodlot+Wetland p(stage+t)Woodlot+Easting	Juvenile	2	0.07140	0.03232
		3	0.15054	0.05222
		4	0.08380	0.04624
	Adult	2	0.15821	0.03778
		3	0.30225	0.04103
		4	0.18272	0.07625
Phi(g)Woodlot+Easting p(stage+t)Woodlot+Easting	Juvenile	2	0.07056	0.03216
		3	0.14944	0.05220
		4	0.08428	0.04672
	Adult	2	0.15781	0.03782
		3	0.30248	0.04082
		4	0.18511	0.07624

Table 17. Minimum Density of *Hyla squirella* per site. N captures = number of unique captures; focal woodlot = area of woodlot (ha) within 100 m buffer of focal wetland.

Wetland	**N captures**	**Focal woodlot (ha)**	**Minimum Density (frogs/ha)**	**Average size (cm)**
49	55	1.77	31.12	2.75
66	59	0.72	81.66	2.47
79	58	1.60	36.29	2.72
123	15	0.57	26.28	2.61
196	132	1.44	91.42	2.82
205	55	0.15	368.59	2.84
245	562	2.96	189.58	2.41
271	98	0.72	135.47	2.78
310	34	0.46	73.35	2.91
336	17	0.36	47.47	2.93
595	241	4.37	55.10	2.68
597	222	2.28	97.17	2.84

Table 18. Top 10 models from analysis of selected landscape variables on treefrog density. Model variables are: July depth = July water depth of focal wetland (cm); Pasture = pasture type (intensively managed, semi-natural); Wetland = wetland index; Woodlot = woodlot index; Pond area = area of focal wetland (ha); Ditch = ditch index; Easting (m). Remaining columns are: R^2 = multiple correlation coefficient; RMSE = root mean squared error; AICc = corrected form of Akaike Information Criterion; ΔAICc = difference between top model and model in question.

Model	**R^2**	**RMSE**	**AICc**	**ΔAICc**
July depth, Pasture	0.623	65.210	144.579	0.000
July depth	0.348	81.324	146.429	1.850
July depth, Pasture, Wetland	0.713	60.326	147.583	3.004
Pasture	0.275	85.794	147.713	3.134
July depth, Woodlot	0.450	78.727	149.100	4.521
July depth, Pasture, Pond area	0.673	64.375	149.456	4.877
July depth, Ditch	0.434	79.901	149.539	4.960
July depth, Pasture, Easting	0.662	65.449	150.320	5.741
Pasture, Ditch	0.391	82.833	150.492	5.913
July depth, Easting	0.383	83.427	150.553	5.974

Table 19. Mean density of *Hyla squirella* by pasture type. LCL = lower 95% confidence limit; UCL = upper 95% confidence limit.

Pasture type	**Average density (frogs/ha)**	**LCL**	**UCL**
Semi-natural	54.60	24.07	85.14
Intensively managed	150.98	27.37	274.59

Discussion

There is a paucity of information on treefrog demography, particularly in terrestrial stages. To create effective conservation plans, it is necessary to fill this gap in knowledge. Pham et al. (2007) estimated population size of one population of *Hyla cinerea* in an urban environment using data collected from individuals marked with VIE tags. Mark-recapture data can be used to calculate much more informative parameters, such as survival and recapture rate. Waddle et al. (2008) used Program MARK to examine the effect of toe clipping on apparent survival and recapture rate of *H. cinerea* and *H. squirella*. My study is the first to estimate apparent survival and recapture for different groups (e.g., sex and stage) of a treefrog species and to examine how those parameters are influenced by landscape features.

In the general models, treefrog survival (Φ) was best explained by gender group (juvenile, male, female), and recapture (p) was best explained by life history stage (juvenile, adult) and time (time 2, 3, 4). The model predictions follow predictions based on anuran biology. Females had higher survival than males and juveniles; there was enough difference in male and female survival that the parameter was better explained by group than stage effects. Males are conspicuous to predators during calling and juvenile anurans likely disperse from home sites, risking predation and desiccation in the process (Gill 1978a, Berven and Grudzien 1990). My data are comparable in trend and survival estimates to mark-recapture data for *Rana grylio* collected in northern Florida wetlands: females in that study had higher survival than males and juveniles, for which estimates were similar (mean Φ: 0.83, 0.75, 0.72, respectively; Wood et al. 1998). There was some evidence for effect of season on survival, with all groups experiencing lower survival in the final time interval, i.e., the six month over-wintering period. Resources were likely lower during this long time interval, as the Fall 2007 – Spring 2008 time period was characterized by drought conditions (NOAA 2008); wetlands did not fill again until Summer 2008. Treefrogs also were forced to overwinter in natural refugia, which may be poorer quality than artificial shelters. I used estimates generated by the top model (Table 15) for my nine month sampling period to predict annual apparent survival rates for juveniles, males and females (annual Φ = 0.71, 0.65, and 0.82, respectively).

Recapture rate varied by life history stage. The lower recapture rate for juveniles may have occurred because as juveniles migrate away from their pond of emergence, they are less likely to be recaptured. Adult anurans are site-loyal to breeding ponds; for example, *Rana sylvatica* adults were 100% faithful to the ponds in which they first bred, while a portion of juveniles dispersed from their home sites (Berven and Grudzien 1990).

Hyla squirella was extremely site loyal, both to sampling site (no individuals moved between sites) and to particular treefrog shelters. Almost 95% of recaptures were in their original shelter of capture every time they were encountered. Of the 50 individuals encountered in one of the fall sampling occasions and then recaptured in the final spring sampling (i.e., individuals known to survive the 6 month over-wintering period), 45 were in their original shelter. This is particularly impressive because shelters were removed during the last fall sampling in November and were not re-hung until the following April. My data suggest that while individuals of *H. squirella* likely use larger areas of terrestrial woodlot for foraging and certainly migrate to ponds for breeding events, they return to a relatively small area that can be considered “home base”, perhaps to a particular tree or small group of trees.

My data confirm that adults also are more site loyal within the terrestrial environment than are juveniles. Because frogs were site loyal, recapture rate increased over time during the fall samplings as shelters became more colonized and frogs moved into woodlots to over-winter. Recapture rate dropped slightly for the final spring sampling, as individuals had to “re-colonize” shelters that were removed over the winter.

The strong terrestrial site fidelity exhibited by *H. squirella* has implications for population dynamics. Amphibians commonly are thought to exist in metapopulations, with patches blinking in and out over time (Figure 8, top). However, metapopulation structure sometimes is only apparent when considering ponds as patches, but the structure is not conserved when terrestrial habitat use is included (Marsh and Trenham 2001). Metapopulation studies that consider only the presence or absence of a particular species in a pond may misrepresent population structure. If suitable upland habitat is nearby and if adults are site-loyal, absence of a species from a pond does not mean it is absent from the site entirely; adults may use permanently occupied terrestrial habitat and migrate to alternative breeding sites depending on environmental conditions such as water levels and presence of competitors and predators (Pechmann et al. 1989, Resetarits and Wilbur 1989, Binckley and Resetarits 2002, Babbitt et al. 2003; Figure 8, bottom).

Woodlot area was the most important landscape covariate in explaining additional variation in both survival and recapture rates of *H. squirella*. All models predicted a positive relationship between survival and woodlot area, indicating that large areas of woodlot are critical for survival of *H. squirella*. Ranch managers would need to conserve 6.5 – 7.5 ha of woodlot within 250 m of wetlands to maintain estimated survival rates for all groups (Table 15). While many semi-natural wetlands have close to 6.5 ha of woodlot within 250 m, most intensively managed wetlands have much less; many IM wetlands at MAERC have less than 1 ha of woodlot within 250 m. On average, the SN wetlands in my study had 2.5 times more surrounding woodlot than IM wetlands.

Distributions of many amphibians are related to woodlot area surrounding breeding sites. At MAERC, anuran species composition in wetlands is affected by proximity to woodlot; habitat specialists such as *Hyla gratiosa*, *H. femoralis*, and *Bufo quercicus* only bred in wetlands with nearby woodlots (Babbitt et al. 2006). In temperate North America, occurrence of redback salamanders (*Plethodon cinereus*) in forests and nearby wetlands was positively associated with area of the forest patch (Kolozsvary and Swihart 1999), and wetlands occupied by carpenter frogs (*Lithobates virgatipes*) had higher proportions of surrounding forest cover than unoccupied ponds (Otto et al. 2007).

Recapture rates of *H. squirella* decreased with increasing woodlot area, indicating that site fidelity was stronger in smaller woodlots. However, models must be interpreted with caution, as the confidence intervals for many models overlapped zero. The trend of increasing site fidelity with decreasing woodlot area is particularly important in landscapes such as rangeland and other agricultural lands, where the habitat matrix often consists of small patches of suitable habitat surrounded by a harsh matrix of open pasture. Further upland habitat modification (e.g., removing trees to create open pasture) may severely affect the ability of amphibians to persist long-term. Recapture rate also decreased with Easting, representing an

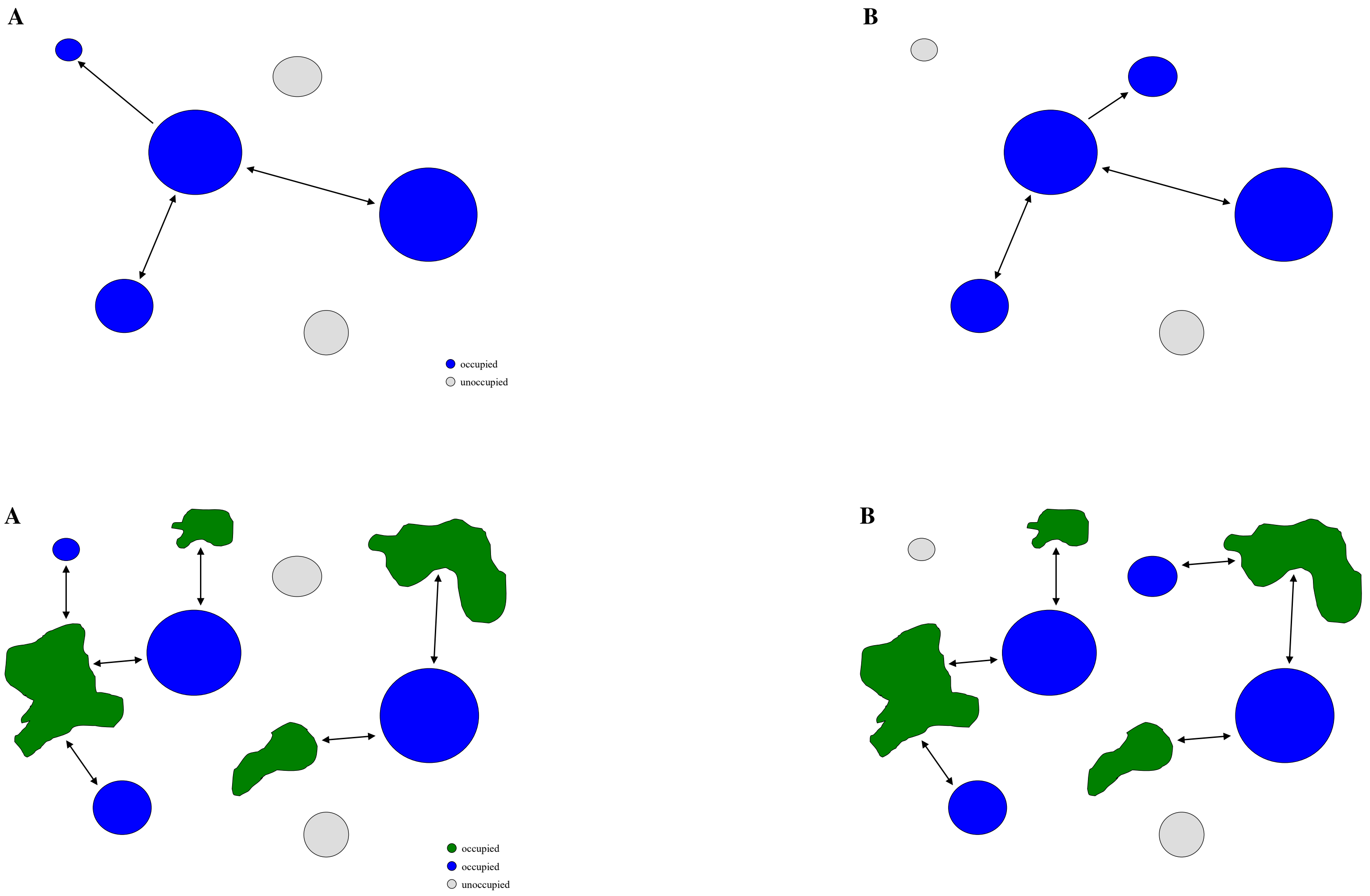

Figure 8. (Top) Classic metapopulation dynamics, with ponds as patches (A), where unoccupied ponds are re-colonized by occupied ponds (B). (Bottom) Terrestrial habitat occupancy model, where individuals migrate to breeding ponds from continuously occupied terrestrial patches (A), and unoccupied ponds are colonized from terrestrial patches, for example at different times during the breeding season (B).

environmental gradient not captured by the landscape variables measured. Eastern pastures at MAERC are mostly semi-natural pastures with relatively large areas of woodlot, but there was not support for an effect of pasture type on either survival or recapture. Models were inconsistent in predicting the relationship of Easting and survival, and confidence intervals largely overlapped zero.

Models consistently predicted a negative relationship between apparent survival and Index of Wetland Availability. I expected a positive relationship between survival and availability of breeding habitat. However, conditions were extremely dry throughout the study, as 2007 was a drought year and ponds did not refill until Summer 2008. The Wetland Index was simply a measure of available wetland habitat and did not take into account whether the wetlands held water during the study period. Given the severity of the drought, the Wetland Index essentially may have been a measure of open pasture. The effect of Wetland Index on survival was likely heavily influenced by study wetlands in the northeastern corner of MAERC. The three wetlands in this area (49, 79, and 123) had high Wetland Index values, but low treefrog captures; there were no recaptures at wetland 123 and no captures at all on the final sampling occasion. There was only one recapture at pond 49.

Pasture type and July water depth of focal wetlands affected minimum treefrog density. Density of *H. squirella* was greater in intensively managed woodlots than in semi-natural woodlots. On average, intensively managed pastures had less available woodlot than semi-natural pastures; therefore, frogs had to crowd within the available habitat. In semi-natural pastures, frogs had larger areas of woodlot available and could move more freely through the terrestrial habitat. Wetlands that had greater July water depths supported a higher density of *H.*

squirella. This is not surprising given the habitat requirements of amphibians, and especially given the prolonged dry conditions that characterized the study period.

My results highlight the importance of terrestrial habitat in amphibian spatial population dynamics and conservation. When species are extremely site-loyal to terrestrial habitat, a traditional metapopulation model using "ponds as patches" may not accurately reflect population structure and patterns of movement. Decreased survival and increased site fidelity in smaller woodlots highlight the importance of quality (i.e., large or contiguous) woodlot habitat for treefrog persistence. Intensively managed pastures at MAERC typically have less intact woodlot than semi-natural pastures and have higher densities of *Hyla squirella*. Because intensively managed pastures have less woodlot but greater frog densities, the two pasture types likely support approximately equal numbers of treefrogs. Intensively managed pastures at MAERC support a minimum of 22,788 *H. squirella*, and semi-natural pastures support a minimum of 26,753 *H. squirella* (Appendix B). *H. squirella* was extremely site loyal; therefore, capture density in my artificial shelters reflect only a small proportion of the population, so my estimates of population density are conservative in nature. Actual density may be orders of magnitude higher than my estimates. Because *H. squirella* exhibited strong site fidelity, even small modifications to the landscape can affect the ability of populations to persist over time. Ranchland managers interested in conserving biodiversity should maintain contiguous woodlots and avoid unnecessary tree removal near pasture wetlands.

CHAPTER 3: RESPONSES OF LARVAL TREEFROGS TO CATTLE GRAZING AND PASTURE MANAGEMENT: GENETIC AND ENVIRONMENTAL VARIATION IN *HYLA SQUIRELLA*

Introduction

Amphibians are the most threatened vertebrate taxa and their global declines are of substantial concern to scientists and conservationists worldwide (Houlahan et al. 2000, Young et al. 2001, Stuart et al. 2004). Declines are attributed to a variety of factors, including climate change, disease, introduced species, UV-B radiation, chemical contaminants, and habitat fragmentation and degradation (Young et al. 2001). Large-scale land-use practices such as rangeland management contribute heavily to some of these factors and introduce others (e.g., cattle grazing), whose effects are just beginning to be quantified (Schmutzer et al. 2008). About one-half of the planet's usable land is already exploited for pastoral or agricultural purposes (Tilman et al. 2001), an amount likely to increase as the global human population increases 50% by 2050, and as global grain demand doubles (projections from Alexandratos 1999, Cassman 1999). In the United States, rangeland accounts for a significant amount of land cover, with 233 million hectares of non-federal land grazed nation-wide (USDA 2003). Pastures in some grazing regions are rich in wetlands that provide breeding sites for adult amphibians and habitat for larval stages (Babbitt et al. 2006). Understanding how specific landscape modifications affect amphibian growth and survival could lead to better management practices and could help reduce or halt widespread population declines.

Anthropogenic modifications that create and maintain grazing pasture affect both aquatic and terrestrial habitats necessary to complete the amphibian life cycle. Extensive ditching alters wetland hydrology (Babbit and Tanner 2000), pesticides and nitrogenous fertilizers alter development and survival of both larval and adult amphibians (Oldham et al. 1997, Marco and Blaustein 1999, Rouse et al. 1999, Schuytema and Nebeker 1999, Relyea 2005), and removing trees to create open pasture increases habitat fragmentation and reduces suitable habitat for adult amphibians (Pellet et al. 2004, Babbitt et al. 2006). Large herbivores induce changes in pond vegetation, topography and water quality that may have important ramifications for larval stages of amphibians (Boyer and Grue 1996, Babbitt and Jordan 1996, Babbitt and Tanner 1997, Babbitt and Tanner 1998, Marco and Blaustein 1999, Rouse et al. 1999). Cattle frequently use wetlands for cooling and forage, resulting in heavily trampled wetlands with high turbidity (Belsky et al. 1999, Schmutzer et al. 2008). Grazers remove vegetation, which decreases feeding sites available for tadpoles because most anurans scrape algae from vegetative surfaces (Duellman and Trueb 1986). Cattle deposit 13 – 27 $kg*d^{-1}$ of wet feces (Azevedo and Stout 1974), creating nitrogen surpluses that eutrophy aquatic systems, especially at high cattle stocking densities (Carpenter et al. 1998).

Understanding how amphibians respond to agricultural modifications is critical for developing appropriate conservation and management strategies. I examined how pasture management and cattle grazing affected growth and survival of three sibships of larval *Hyla squirella* in a Florida ranchland. Amphibians often experience high mortality, particularly in the larval stages (Werner 1986), so identifying stressors that affect larval growth and survival is critical for conservation. Larvae that develop faster and larger are able to escape gape-limited predators (Caldwell et al. 1980, Semlitsch and Gibbons 1988, Richards and Bull 1990, Babbitt and Tanner 1998), are more likely to survive when ponds dry (Semlitsch 1987, Newman 1988, Denver 1997), and reproduce earlier or at a larger size (Smith 1987, Semlitsch et al. 1988, Berven 1990). However, amphibians also have adaptive changes in larval and metamorphic characteristics (Wilbur and Collins 1973, Wilbur 1980, Werner 1986) that can be attributed to genetic variation or phenotypic plasticity (Travis 1980, 1981, Van Buskirk and Relyea 1998, Van Buskirk and McCollum 1999, Relyea and Werner 2000, Relyea 2001). Genetic differences among sibships account for some variation in metamorphic traits and differential response to environmental stressors (Newman 1988, Semlitsch 1993, Bridges and Semlitsch 2000).

Assessing the response of different sibships to agriculturally modified wetlands allows me to quantify the potential of amphibians to adapt to local conditions created by rangeland management. These data are useful in determining the sensitivity of amphibians to rangeland modifications and identifying management strategies that minimize mortality during the larval stage.

Methods

Experimental design

I selected four wetlands at MAERC: two within semi-natural (SN) pasture, and two within intensively managed (IM) pasture. I selected wetlands that had ample water at the beginning of the wet season to ensure sufficient depth throughout the experiment. One wetland from each pasture type was completely fenced since April 2007 to exclude cattle grazing as part of an ongoing study assessing effects of grazing on wetland biodiversity. This resulted in four wetland types that comprised a 2 x 2 factorial design (Figure 9): one each of a semi-natural pasture, grazed wetland (SN-G); semi-natural pasture, released from grazing wetland (SN-R); intensively managed pasture, grazed wetland (IM-G); and an intensively managed pasture, released from grazing wetland (IM-R).

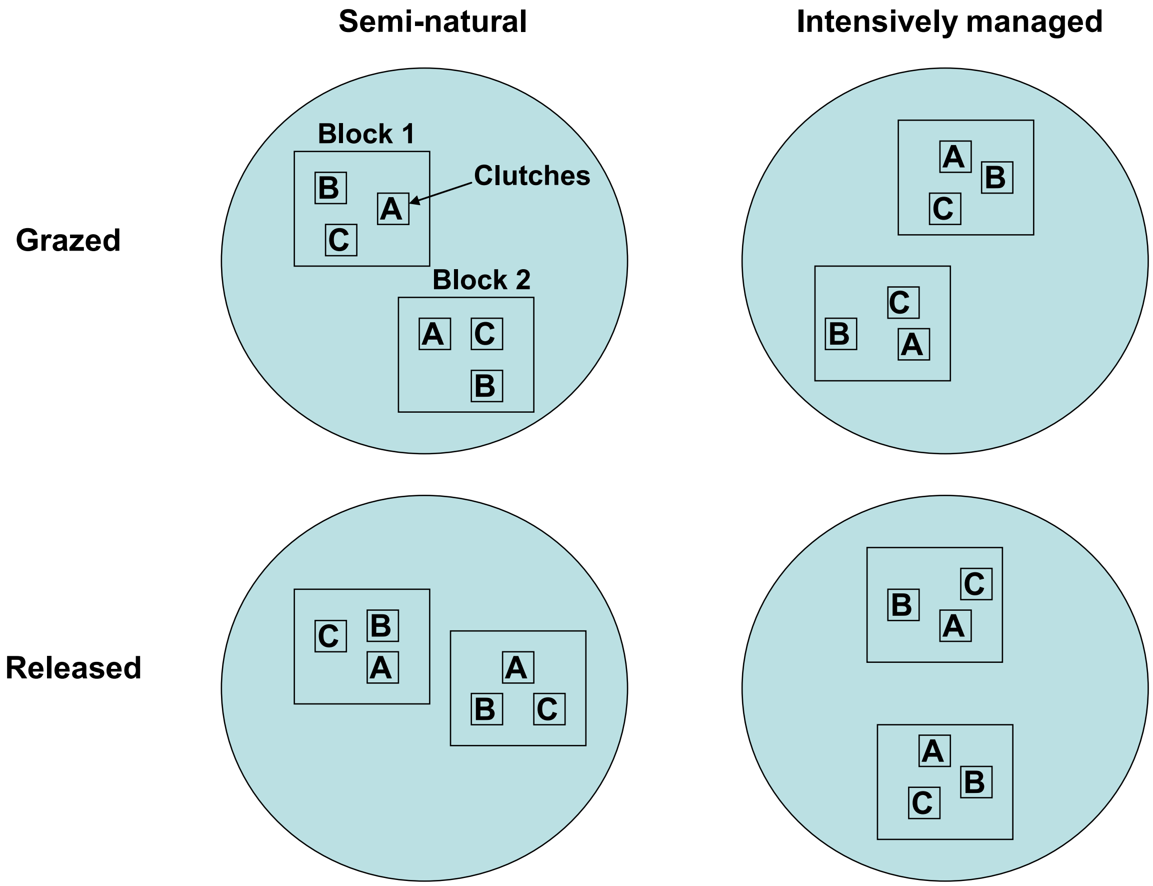

Figure 9. Chapter 3 experimental design. Pasture type (semi-natural, intensively managed) is represented by column and grazing treatment (grazed, released from grazing) is represented by row. Each block was a cage constructed of metal fencing panels. Each clutch (A, B, C) was contained in a separate pen.

In each wetland, I constructed two cages using metal fencing panels (2.4 m x 2.4 m) to exclude large animals. Cages were placed at random compass bearings from the center of each wetland and served as experimental blocks. Blocks were placed in approximately equal water depths (~26 – 32 cm) in each wetland. Within each block, I deployed three pens to house experimental tadpoles. Pens consisted of a plastic laundry basket (50 cm x 35 cm x 60 cm) fitted internally with a mesh liner and externally with a mesh lid, both made out of standard 1 mm fiberglass window screening. The lining mesh confined tadpoles to the inside of the basket and excluded potential invertebrate predators. Pens were secured to metal t-posts staked inside each block (Figure 10). The pens were deployed on 1 August 2009, to allow time for algae to grow and provide a food source for tadpoles.

Figure 10. Experimental pens housing *Hyla squirella* tadpoles. Pens were constructed of plastic laundry baskets fitted with mesh liners made of 1 mm window screening.

To quantify environmental differences among wetlands, I recorded temperature (ºC), pH, conductivity (µS/cm), DO (mg/L), and water depth (cm) in each block during each of the four monitoring occasions, except DO was not recorded during the first monitoring session. I also had access to data for concentrations of nitrogen and phosphorus in the surface water for the experimental wetlands from 2006 – 2009 (P. Bohlen, unpublished data).

I collected breeding pairs of *Hyla squirella* in an IM pasture at MAERC on 28 July, 2009, after a heavy rain. I captured amplectant pairs by hand near the ranch laboratory, enclosed them in plastic containers (55 cm x 40 cm x 17 cm) with water and plant debris and left them overnight to allow females to oviposit egg masses. The next morning, I released adults and transported eggs to the laboratory. I kept the three clutches that had the highest hatching success (hereinafter, clutches A, B, and C) and reared tadpoles in approximately equal densities in water collected from a wet pasture at MAERC. Every 2 – 3 d, I changed the water and fed tadpoles frozen chopped spinach and commercial rabbit food pellets.

I randomly assigned 25 tadpoles from each clutch to one of the three pens in each block on 12 August 2009 (13 d post-hatch, Gosner stage 25; Gosner 1960). I monitored tadpoles four times over the next several weeks, taking size measurements on surviving tadpoles. I halted data collection when the first metamorphs were seen experiment-wide; this occurred in the IM-R wetland on 27 August 2009, 28 d post-hatch (Table 20). I infer that smaller tadpoles at that date would have metamorphosed either later or at a smaller size than larger surviving tadpoles (Wilbur and Collins 1973, Collins 1979, Travis 1984).

Statistical analysis

I used nested analysis of variance to test the null hypothesis that percent survival of *H. squirella* was independent of wetland type, block, or clutch (Table 21). I used *a priori* contrasts to partition variation among wetland types (SN vs IM, G vs R and pasture type x grazing). To correct for non-normally distributed residuals, I $\log_{10}$-transformed percent survival as (log[percent survival +1]). All means and standard errors reported are back-transformed. Complete loss of clutch C in two wetlands and loss of almost all tadpoles in one wetland in particular (IM-G) precluded analysis of tadpole size data (Table 20). Instead, I present growth trajectories in Figure 11. I used individual correlations to assess the relationship between Total N and P and tadpole survival, and regression to examine the relationship between all other environmental variables and survival. All statistical analyses were performed using JMP version 7.0 (SAS Institute 2007), with $\alpha = 0.05$.

Table 20. Percent survival and mean size of *Hyla squirella* tadpoles at the conclusion of the experiment.

(Wetland number) Wetland type	**Block**	**Clutch**	**% survival**	**Mean length (cm), 28 d post-hatch**
(210) Semi-natural, released	1	A	64	2.43
	1	B	56	2.97
	1	C	16	2.95
	2	A	100	2.68
	2	B	56	2.53
	2	C	76	2.60
(226) Semi-natural, grazed	1	A	60	2.64
	1	B	48	3.03
	1	C	36	3.12
	2	A	44	2.20
	2	B	12	2.73
	2	C	0	.
(127) Intensively managed, released	1	A	96	3.15
	1	B	8	3.25
	1	C	0	.
	2	A	72	3.27
	2	B	4	2.30
	2	C	0	.
(205) Intensively managed, grazed	1	A	4	3.60
	1	B	0	.
	1	C	0	.
	2	A	16	2.78
	2	B	0	.
	2	C	0	.

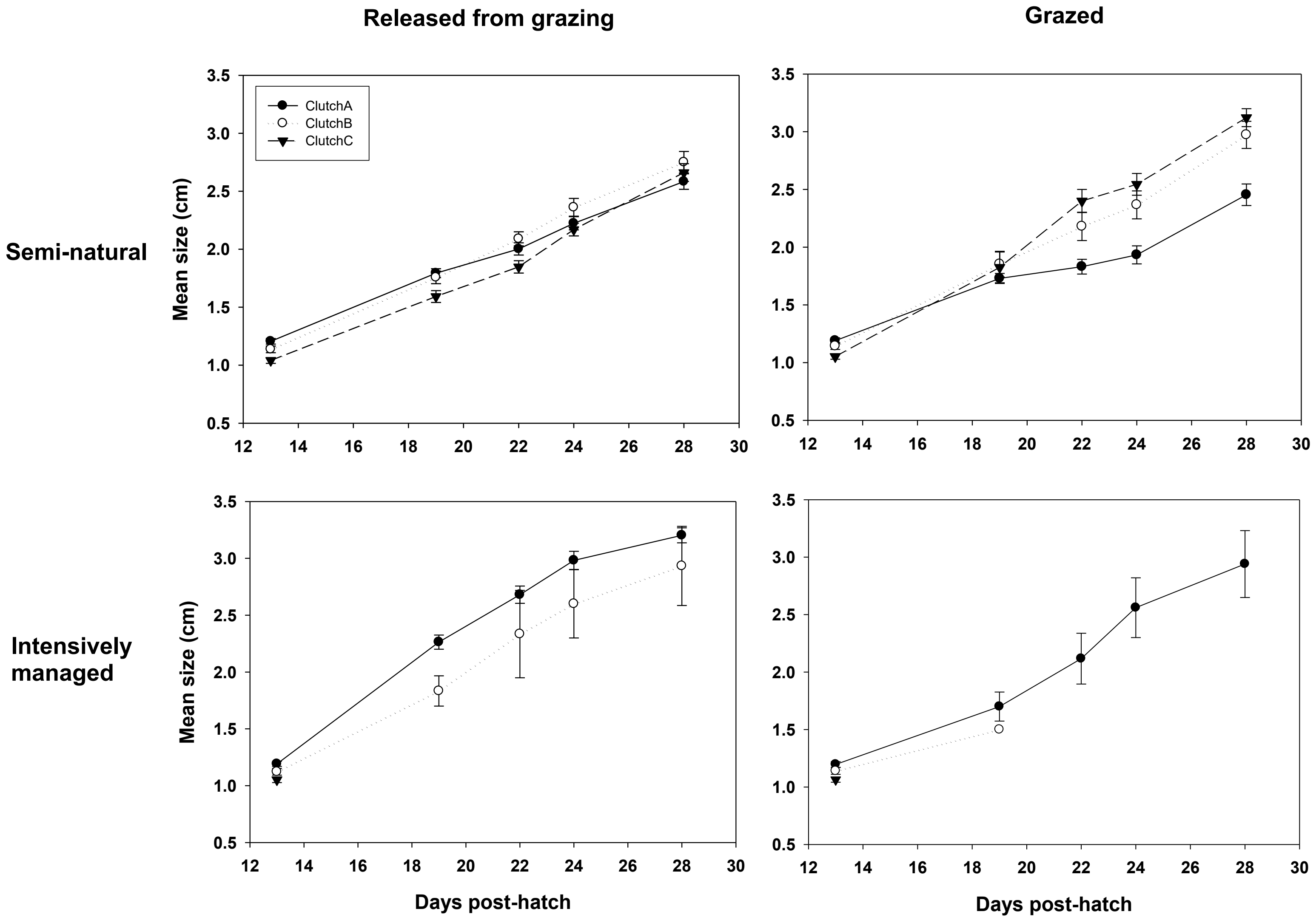

Figure 11. Mean (± 1SE) growth trajectories of three clutches of *Hyla squirella* tadpoles. Wetland pasture type (semi-natural, intensively managed) is represented by row, and grazing treatment (grazed, released from grazing) is represented by column.

Results

Wetland type significantly affected percent survival of *H. squirella*, with SN-R and SN-G wetlands having higher mean survival than IM-R and IM-G (Table 21, Table 22). *A priori* contrasts of wetland types revealed a significant difference between intensively managed and semi-natural pasture wetlands (Table 21), with higher tadpole survival in SN wetlands than IM wetlands. The difference between fenced and grazed wetlands neared significance, with R wetlands having slightly higher survival than G wetlands. The interaction between pasture type and fencing was not significant.

Table 21. Nested ANOVA for effects of wetland type (fixed), block (random) and clutch (random) on percent survival of larval *Hyla squirella*. Columns give sources of variation, numerator and denominator degrees of freedom (df), sum of squares (SS), F-ratio, and p-value; * indicates significant F-ratio. Full model $R^2 = 0.947$.

Source	**df**	**SS**	**F**	**p**
Wetland type	3,4	6.52	5.05	0.0425*
SN vs IM	1,4	4.88	18.51	0.0126*
G vs R	1,4	1.61	6.09	0.0691
Pasture x grazing	1,4	0.04	0.14	0.7279
Block(wetland)	4,8	1.05	2.76	0.1037
Clutch	2,6	4.42	8.43	0.0181*
Clutch x wetland	6,8	1.58	2.75	0.0939
Error	8	0.76		
Total	23			

I concluded the experiment on 27 August, 2009, when five metamorphs from clutch A were observed in the IM-R wetland. Of the surviving tadpoles in IM-R, 60% were in Gosner stage 36 or above; they had well-developed hind limbs and could have reached metamorphosis in a few days. Ninety-six percent of these tadpoles were from clutch A. Tadpoles in the remaining wetlands were farther from metamorphosis (Figure 12): in the IM-F wetland, 20% of surviving tadpoles were in stage 36 or above, SN-U had 10%, and SN-F had 0%.

Clutches also varied significantly in mean survival, with clutch A surviving significantly better than clutch B, and clutch B better than clutch C (Table 21, Table 22). The interaction of clutch and wetland type was not significant.

Table 22. Mean percent survival and upper and lower 95% confidence limits (CL) for experimental treatments. Values are back-transformed (inverse log – 1).

Treatment	**Mean % survival**	**Upper 95% CL**	**Lower 95% CL**
Semi-natural, released	53.95	88.13	32.88
Semi-natural, grazed	18.95	31.36	11.30
Intensively managed, released	7.32	12.49	4.13
Intensively managed, grazed	1.09	2.39	0.29
Clutch A	41.66	53.95	32.11
Clutch B	9.00	11.88	6.76
Clutch C	2.89	4.01	2.02

Wetlands varied in mean values of recorded environmental variables. The IM wetlands had higher total N and much higher total P than SN wetlands. The G wetlands had slightly higher N and P levels than the corresponding R wetlands (Table 23). Principal Components Analysis (PCA) of environmental variables resulted in two fundamental axes explaining 95% of the variance. All four experimental wetlands varied substantially in environmental parameters, with one pond falling in each quadrat in the fit of Principal Component 2 by Principal Component 1 (Figure 13). IM wetlands occupy the right hand side of the figure, with higher pH, conductivity, DO, total N, and total P. Temperature accounted for most of the variance in PC2, with warmer ponds (IM-G and SN-R) occupying the top of the figure.

Overall survival was not significantly correlated with total N and total P, although both variables showed a clear trend (Total N, $r^2_{1,3} = 0.826$, $p = 0.091$; Total P, $r^2_{1,3} = 0.812$, $p = 0.099$); wetlands with higher N and P had lower overall tadpole survival. To reduce variance inflation factors, DO was removed from the regression model. Regression analysis by block revealed a significant effect of pH, conductivity and temperature in tadpole survival that explained virtually all of the among-block (>99%) variation (Table 24). There was a negative relationship between survival and mean pH and mean temperature and a positive relationship between survival and mean conductivity.

Table 23. Mean values (± 1 standard error) of selected environmental parameters of wetlands used in the experiment at MacArthur Agro-Ecology Research Center.

(Wetland number) Wetland type	**Temperature (C)**	**pH**	**Conductivity (μ/S)**	**DO (mg/L)**	**Total N (ppm)**	**Total P (ppm)**
(127) Intensively managed, released	27.92 ± 0.38	5.20 ± 0.36	184.35 ± 6.39	3.27 ± 0.60	1.92 ± 0.09	0.20 ± 0.04
(205) Intensively managed, grazed	28.83 ± 0.52	4.61 ± 0.22	49.52 ± 2.65	3.89 ± 0.63	2.28 ± 0.22	0.38 ± 0.10
(210) Semi-natural, released	28.72 ± 0.46	3.42 ± 0.36	23.98 ± 1.30	2.44 ± 0.34	1.52 ± 0.08	0.04 ± 0.00
(226) Semi-natural, grazed	28.11 ± 0.38	4.02 ± 0.26	25.47 ± 1.41	1.53 ± 0.38	1.59 ± 0.09	0.06 ± 0.01

Table 24. ANOVA table for regression of environmental variables and tadpole survival. Source = source of variation (mean environmental variables by block); SS = sum of squares; F-ratio; p value. *indicates significant p value. Full model $R^2 = 0.990$.

Source	**df**	**SS**	**F-ratio**	**p**
Temperatue	1	131.11	12.13	0.0253*
pH	1	4088.05	378.09	<0.0001*
Conductivity	1	1425.99	131.89	0.0003*
Error	4	43.25		
Total	7	4369.78		

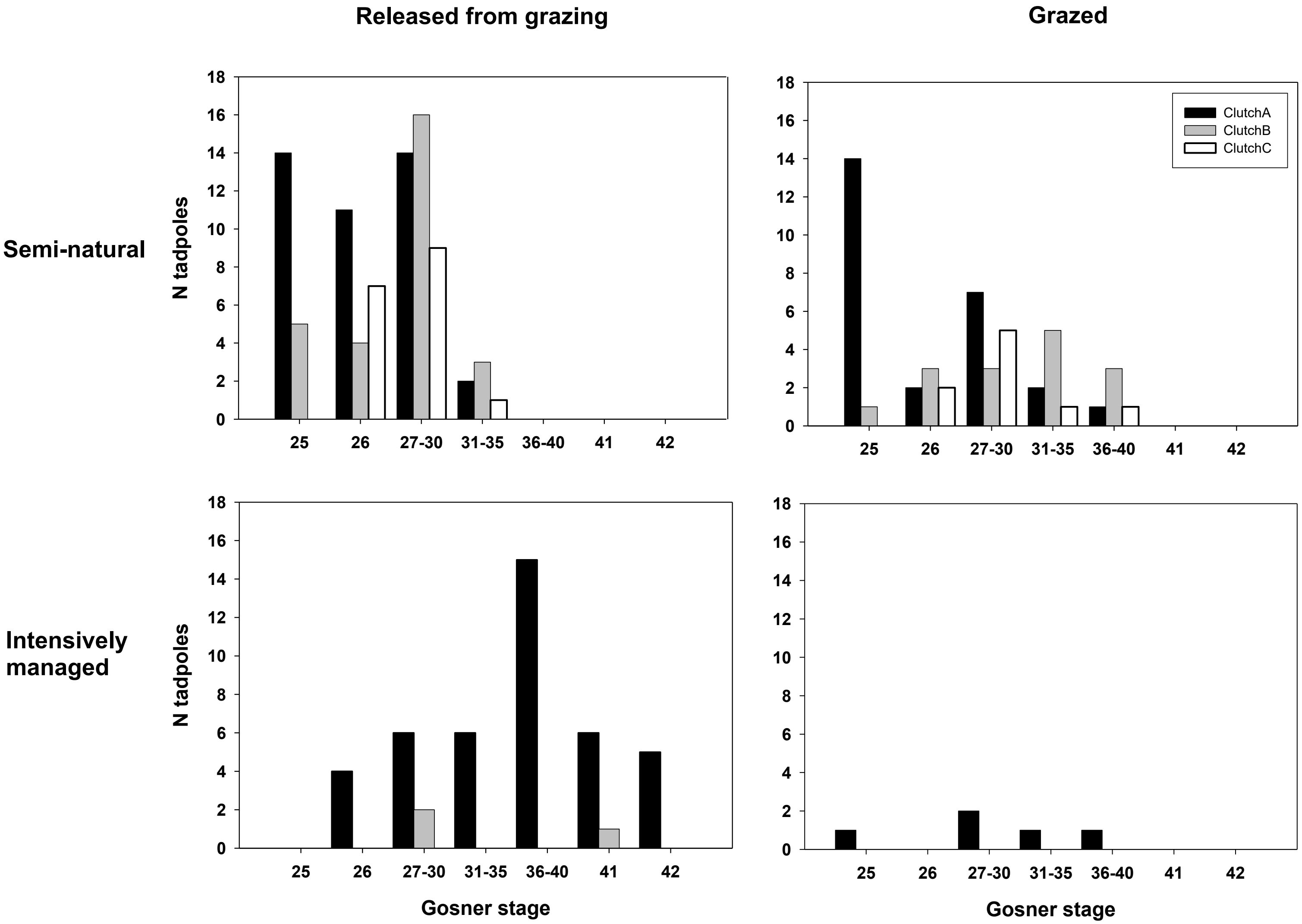

Figure 12. Distribution of Gosner stages of surviving tadpoles at 28 d post-hatch. Wetland pasture type is represented by row (semi-natural, intensively managed), and grazing treatment is represented by column (released from grazing, grazed). An individual was classified as a metamorph when forelimbs appeared (Gosner stage 42).

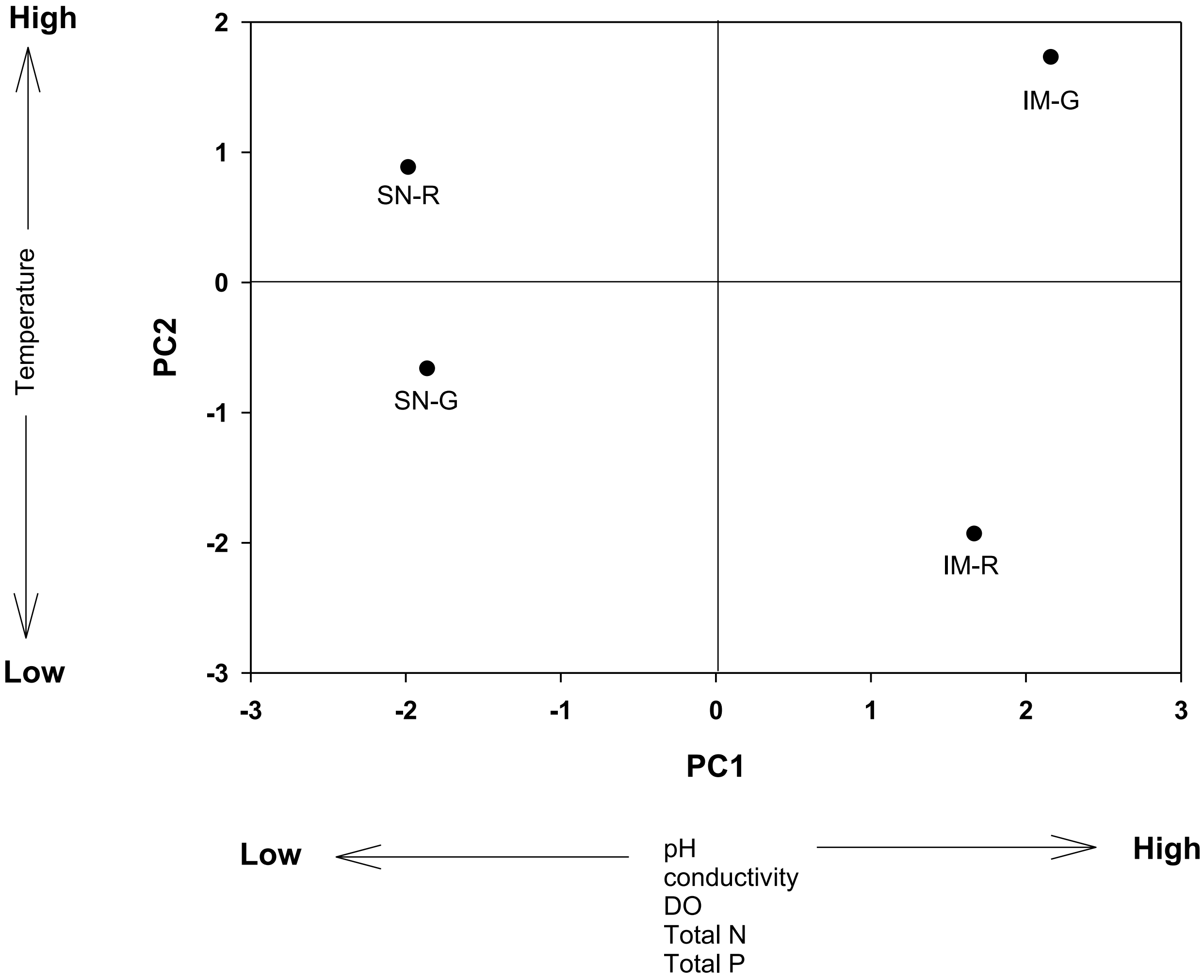

Figure 13. Plot of wetlands on Principal Component 2 (PC2) by Principal Component 1 (PC1). Intensively managed pasture (IM) wetlands occupy the right side of the figure, indicating high values for environmental parameters listed on the PC1 axis. The semi-natural (SN) released from grazing (R) wetland and IM grazed (G) wetland had higher mean temperatures than the remaining two ponds.

Discussion

Wetland type significantly affected tadpole survival, with tadpoles surviving better in wetlands within semi-natural pasture (SN) than intensively managed pastures (IM). Collectively, wetlands in SN pastures supported 68 tadpoles/m^2 in the experimental pens at the conclusion of the experiment, compared to only 24 tadpoles/m^2 in IM wetlands. Before 1987, intensively managed pastures at MAERC were fertilized with NPK fertilizer, and with nitrogen only since 1987. Consequently, wetlands in IM pastures had slightly higher nitrogen levels than those in SN pastures, but phosphorus levels over three times higher (P. Bohlen, unpubl. data). Long-term or excess fertilization can lead to differences in water quality (Carpenter et al. 1998) that affect development and survival of larval stages of amphibians (Oldham et al. 1997, Marco and Blaustein 1999, Rouse et al. 1999, Schuytema and Nebeker 1999, Relyea 2005). Although the correlations between overall survival and total N and P were not significant, wetlands with higher nutrient levels (IM pastures) had lower overall survival than wetlands with lower nutrient levels (SN pastures).

Principle Components Analysis of environmental variables highlights environmental differences between wetlands in IM and SN pastures (Figure 13). Wetlands in IM pastures had higher pH, conductivity, DO, total N, and total P, indicative of poor-quality environments. Tadpole survival decreased with increasing pH. Pond acidity can interact with many factors such as UVB radiation, tadpole density, nitrate, and chemical pollutants to decrease tadpole survival (Warner et al. 1983, Horne and Dunson 1995, Long et al. 1995, Hatch and Blaustein 2000, Macias et al. 2007). Wetlands with high conductivity had high tadpole survival. Conductivity may be a measure of productivity; ponds with high conductivity may have more organic matter available for tadpole consumption. Tadpole survival also decreased with increasing temperature, indicating that high temperature may be an additional stressor for tadpoles.

Intensively managed pastures also were more heavily grazed than semi-natural pastures, which leads to vegetation differences in both terrestrial and aquatic habitats (Boughton et al. 2010). For example, wetlands in IM pastures were dominated by zones of *Juncus effusus*, a rush unpalatable to cattle (Boughton 2009). In contrast, wetlands in semi-natural pastures generally supported more native plant species (Boughton et al. 2010), and were dominated by native grasses and sedges (*Panicum hemitomon* and *Rhynchospora sp*). Fenced wetlands were enclosed for only two years, so the IM-R wetland still had vegetation characteristic of wetlands in intensively managed pasture wetlands, including dense stands of *J. effusus*. Variation in vegetation and leaf-litter quality may lead to differences in algal food availability (Cattaneo et al. 1998, Hart and Lovvorn 2000) and the abundance and diversity of invertebrates (Voights 1976, Webb et al. 1984, Sanderson et al. 1995, Morrison and Bohlen unpubl. data). Aquatic insects are common predators of tadpoles (Caldwell et al. 1980, Formanowicz 1986, Peterson and Blaustein 1992), so association between particular vegetation types and insect predators may affect habitat quality for amphibians. Mesh enclosures in my experiment prevented direct predation by aquatic invertebrates on experimental tadpoles. While larval amphibians can alter morphological development in response to chemical cues from invertebrate predators (McCollum and Leimberger 1997, Smith and Van Buskirk 1995), there were no differences in invertebrate community structure between wetlands in SN and IM pastures (Medley et al., unpubl. data).

Pasture modification also alters amphibian species richness and community composition. At MAERC, amphibian species richness was higher in wetlands within SN pastures than IM pastures (Babbitt et al. 2009, Fauth and Windes, unpubl. data). Wetlands in SN pastures favor habitat specialists such as treefrogs (e.g., *Hyla squirella, H. gratiosa,* and *H. femoralis*), while IM pastures are favorable for others, including exotics such as *Lithobates catesbeiana* (Fauth and Windes, unpubl. data). In general, SN pastures had greater area of hardwood hammock than IM pastures. Babbitt et al. (2006) found proximity to woodlot affected amphibian species composition at MAERC, with habitat specialists such as *H. gratiosa, H. femoralis,* and *Anaxyrus quercicus* found only in wetlands near woodlots.

The *a priori* contrast between wetlands released from grazing (R) versus grazed (G) was not statistically significant, but released wetlands had slightly higher tadpole survival than grazed wetlands. Positive responses of amphibian assemblages to fencing led several researchers to recommend excluding cattle from aquatic environments (Schmutzer et al. 2008). Amphibian species richness typically is lower in grazed (G) wetlands than released (R) wetlands (Fauth and Windes, unpubl. data, Jansen and Healey 2003, Knutson et al. 2004, Schmutzer et al. 2008). The effect of grazing also may be species-specific. Burton et al. (2009) captured more green frogs (*Lithobates clamitans*) in released wetlands than grazed wetlands, but the opposite trend existed for American toads (*Anaxyrus americanus*). At MAERC, southern leopard frogs (*Lithobates sphenocephala*) are more than three times as likely to occur in R wetlands than G wetlands (Fauth and Windes, unpubl. data).

Clutch significantly affected tadpole survival (Table 21), with clutch A having the greatest survival, followed by clutch B and finally clutch C, which experienced relatively low survival experiment-wide. Of the surviving tadpoles from clutch A, 25% were in Gosner stage 36 or above; they had well developed hind limbs and could have reached metamorphosis within a few days. Comparatively, only 9% of surviving clutch B tadpoles and 4% of clutch C tadpoles were in stage 36 or above. Experiment-wide, tadpoles from all clutches were smaller and less developed in ponds with higher survival rates than in ponds with low survival, a typical density-dependent response: as the density of larvae increases, mean size decreases (Wilbur 1980, Morin 1983, Wilbur et al. 1983, Scott 1990, Altwegg 2003).

Genetic variation in survival among clutches confirms the potential for *H. squirella* to adapt to locally modified rangeland conditions such as pasture management. However, I did not observe a clutch x wetland type interaction; poor conditions were equally detrimental (or even lethal) to all three clutches. Lack of phenotypic plasticity in larval *H. squirella* makes it particularly important to identify and manage high quality aquatic habitat conditions. While genotype affects survival, it is unpredictable; the effect of environment on survival can be predicted and environmental conditions can be manipulated through management strategies that promote tadpole growth.

Larval amphibians are excellent bioindicators, and their higher survival in semi-natural wetlands indicates these were a superior habitats; I therefore recommend preserving or restoring semi-natural conditions to Florida rangelands. Pastures currently categorized as semi-natural should be maintained as such, without addition of ditches, fertilizers, or replacement of native vegetation. Intensively managed pastures can be managed to support higher amphibian survival by reducing fertilizer application and excluding cattle from wetlands by fencing. Other studies report positive effects of cattle exclusion on amphibians (Fauth and Windes, unpubl. data, Jansen and Healey 2003, Knutson et al. 2004, Schmutzer et al. 2008, Burton et al. 2009); a prudent management strategy is to exclude grazing in some wetlands. Long-term fencing of intensively managed pasture wetlands may be necessary to return semi-natural vegetation, improve water quality, and restore the topography of heavily trampled pond basins. Stocking density also could be reduced in pastures with large numbers of wetlands (Schumtzer et al. 2008), but reduced stocking rates have a direct negative impact on ranch economics and may not be a feasible strategy for most ranchers (Arthington et al. 2007, Swain et al. 2007). Alternatively, cattle could be moved into fenced wetlands for short periods, a technique termed “flash grazing” (Weltz et al. 1989). Fencing can be expensive to install and maintain, so ranchers would likely need to fence wetlands through cost share programs, such at the United States Department of Agriculture’s Wildlife Habitat Enhancement Program. Being able to defer grazing in wetland may increase ranchers’ ability to maintain favorable forage species in wetland habitats on ranches, and so may benefit multiple ecosystem services. Management strategies that minimize amphibian mortality are necessary to preserve the biotic integrity of wetland ecosystems and effectively conserve a taxon already in global decline.

GENERAL CONCLUSION

Rapid increases in global food demands require improved understanding of how agriculture affects resident species. Current agricultural practices attempt to maximize yield and largely ignore the need for biologically intact ecosystems. Rangeland management alters both terrestrial and aquatic environments through landscape-level modifications (e.g., tree removal and ditching), cattle grazing, and fertilizers (Day and Detling 1990, Hobbs 1996, Frank and Groffman 1998, Babbitt and Tanner 2000, Pellett et al. 2004, Babbitt et al. 2006). Ranches in south Florida support large numbers of rare, threatened and endangered species and provide a variety of ecosystem services that are critical to conservation priorities in the region (Bohlen and Swain 2009, Bohlen et al. 2009). Conservation biologists must identify rangeland and pasture practices that pose the least threat possible to ecosystems while still supporting economic viability. The MacArthur Agro-Ecology Research Center provided the opportunity to experimentally determine appropriate rangeland management practices. The MacArthur Agro-Ecology Research Center is a working cattle ranch situated in the framework of an ecological research center in south-central Florida and is home to a species-rich amphibian assemblage.

Amphibians are ideal indicators of ecosystem responses to rangeland management because they are sensitive to perturbations in both terrestrial and aquatic environments (Figure 14) and are a key link in many food chains (Meyer et al. 2004). I examined responses of both adult and larval amphibians to rangeland management in both aquatic and terrestrial habitats at MAERC. My results highlight the importance of semi-natural conditions and minimally altered habitat for amphibian survival. Adult treefrog survival was positively associated with area of woodlot and larval treefrog survival was higher in wetlands within semi-natural pastures than within intensively managed pastures. It is critical to examine multiple life history stages and habitats of organisms with complex life cycles to provide complete information to ranchland managers.

Using amphibians as indicator species, my results indicate that managers should strive to maintain semi-natural conditions and avoid further woodlot fragmentation to promote amphibian survival and preserve the integrity of rangeland ecosystems. Ecologically informed rangeland management benefits diverse assemblages, including many threatened and endangered species. For example, ranchlands are critical habitat for the crested caracara (*Caracara cheriway*); in south-central Florida, most active nesting sites are on privately-owned cattle ranches, and reproductive success is higher on private ranches compared to nests on other land-use types (Morrison and Humphrey 2001). Maintaining semi-natural conditions also benefits livestock; trees provide shade and cover for cattle, and native wetland vegetation such as maidencane (*Panicum hemitomon*) is high quality forage (Kalmbacher et al. 2002). Semi-native pastures also provide valuable winter forage for cattle and native grasses survive better during cold freezes when Bahia grass dies back (E. Boughton, pers. comm.). By implementing ecologically sound landscape management, ranchland managers can preserve biodiversity while benefitting their cattle operation.

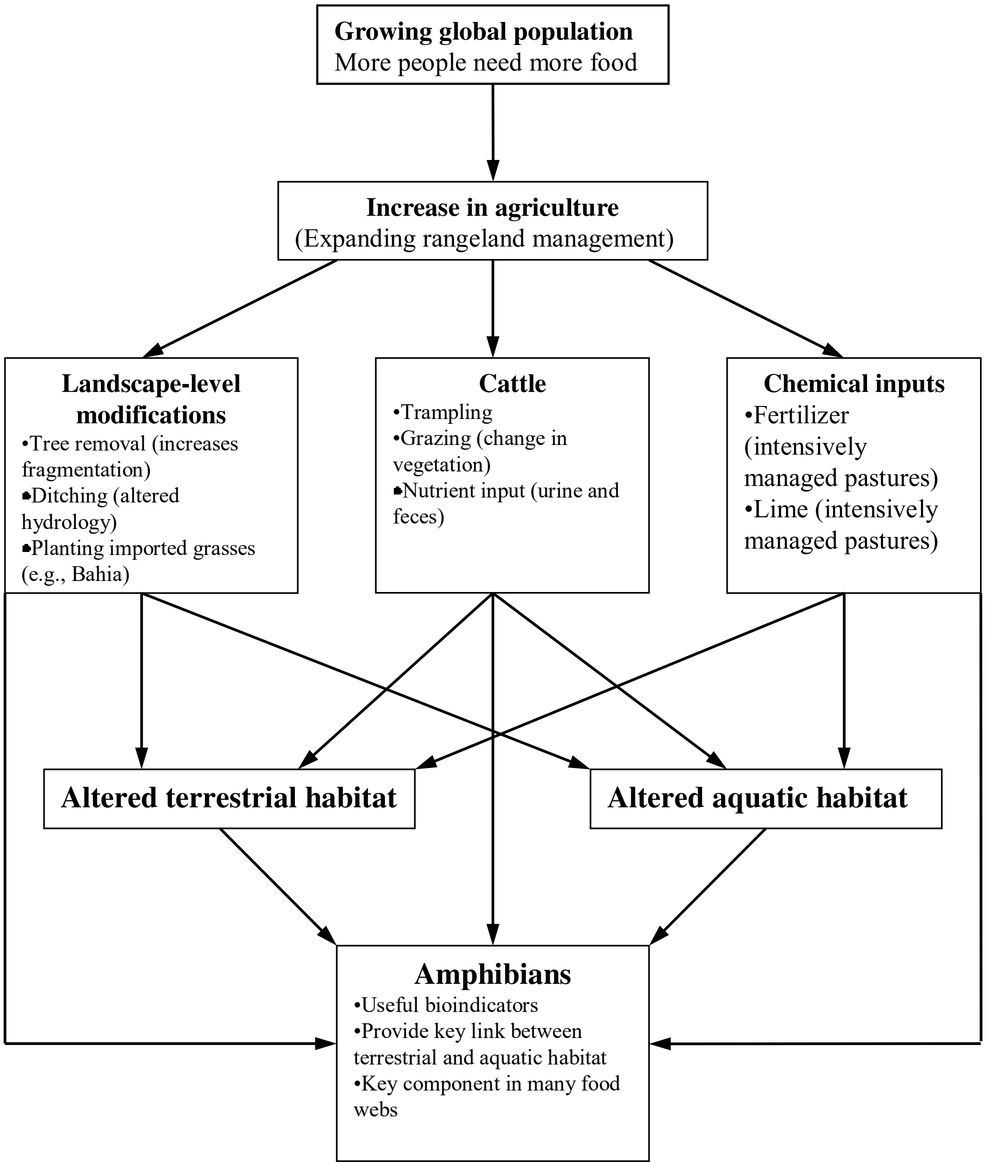

Figure 14. Amphibians are bioindicators for effects of rangeland management.

APPENDIX A: CHAPTER 2 EXPERIMENTAL WETLANDS

Appendix A: Chapter 2 Experimental Wetlands

The twelve experimental wetlands from Chapter 2 are presented in the following figures. In each figure, the focal wetland is in the center, colored in pale green. Concentric buffers are represented in red (0 – 100 m), yellow (100 – 150 m), blue (150 – 200 m), and purple (200 – 250 m). The focal woodlot is outlined in red within the first 100 m buffer. Subsequent woodlot is outlined in primary colors corresponding to the buffer in which it is located. Green dots in the focal woodlot indicate randomly selected locations of the old PVC shelters; blue dots indicate randomly selected locations of the new PVC shelters (used in the spring sampling only). Surrounding wetlands are colored in pastel colors corresponding to the buffer in which they are located. Each site is categorized as either semi-natural (SN) or intensively managed (IM) and as either grazed (G) or released from grazing (R).

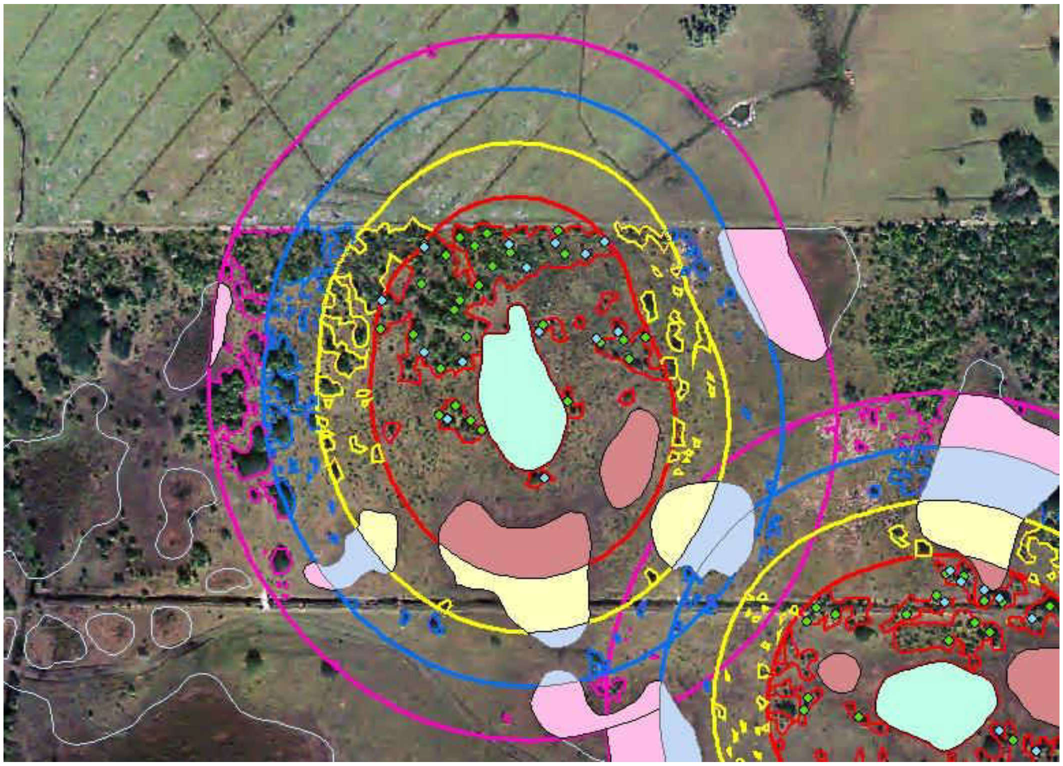

Figure 15. Wetland 49: SN-R. Wetland 79 can be seen in bottom right of figure.

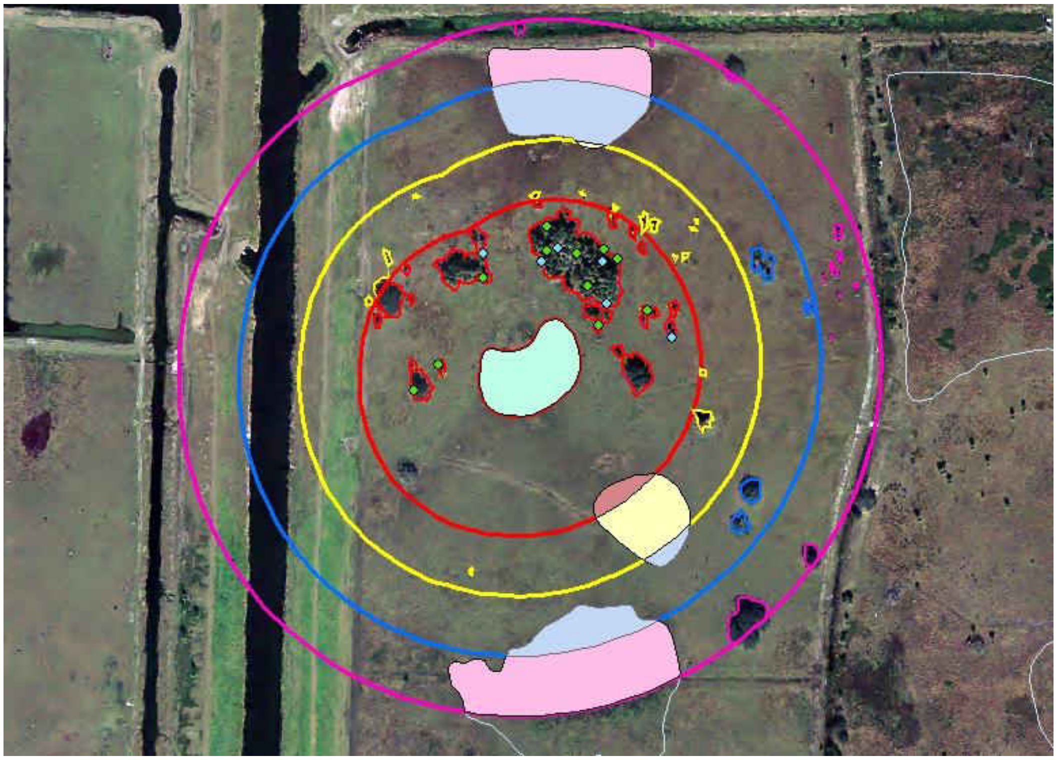

Figure 16. Wetland 66: SN-R.

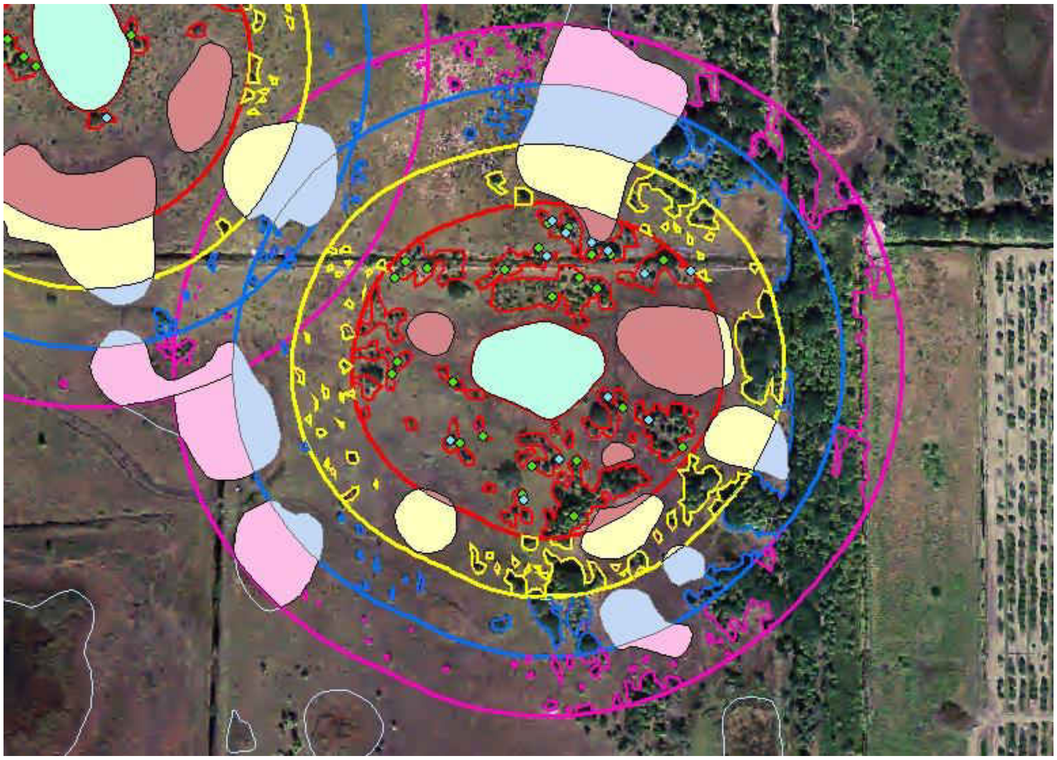

Figure 17. Wetland 79: SN-G. Wetland 49 can be seen in upper left of figure.

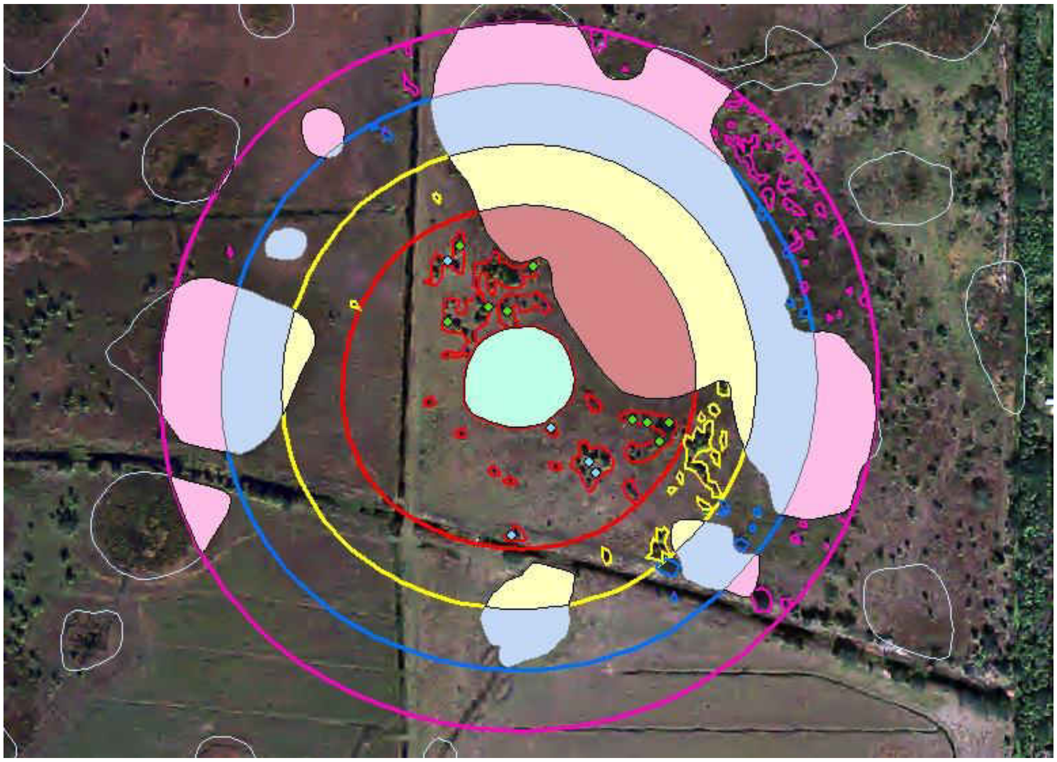

Figure 18. Wetland 123: SN-G.

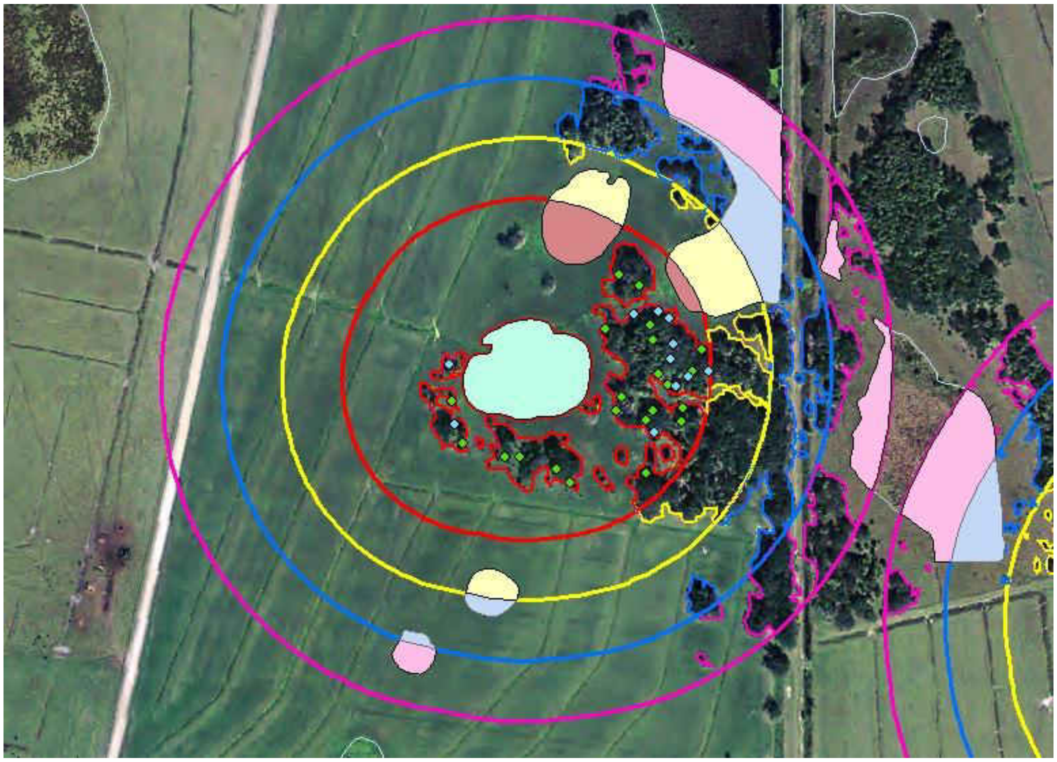

Figure 19. Wetland 196: IM:R.

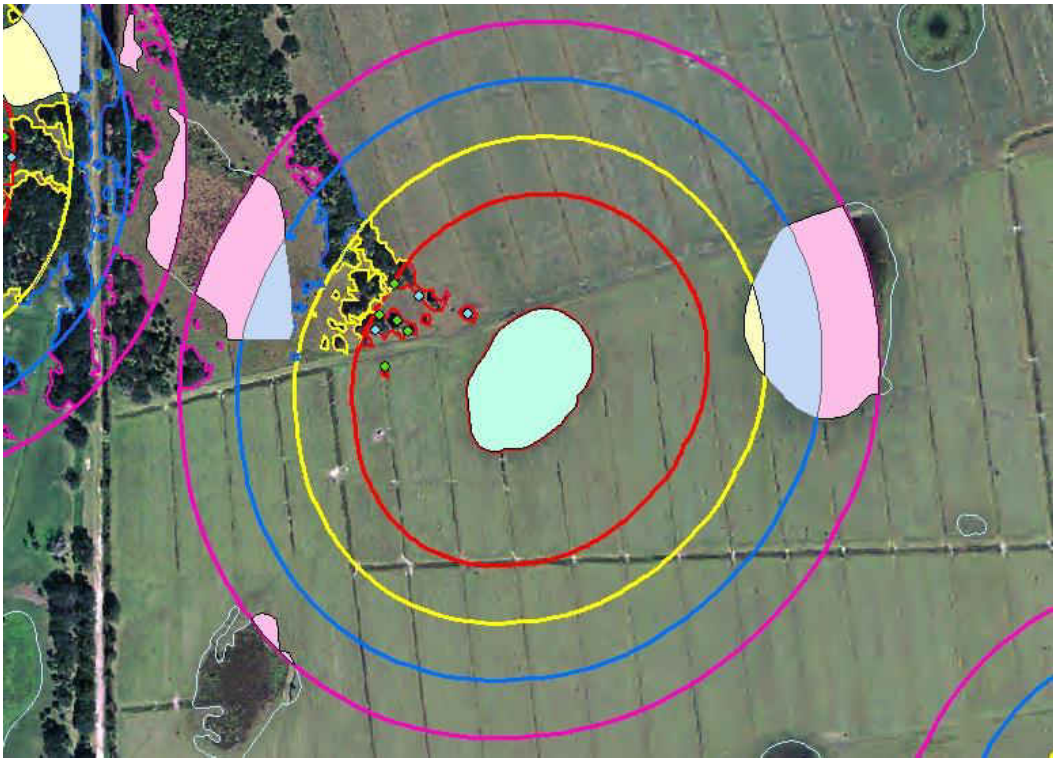

Figure 20. Wetland 205: IM-G.

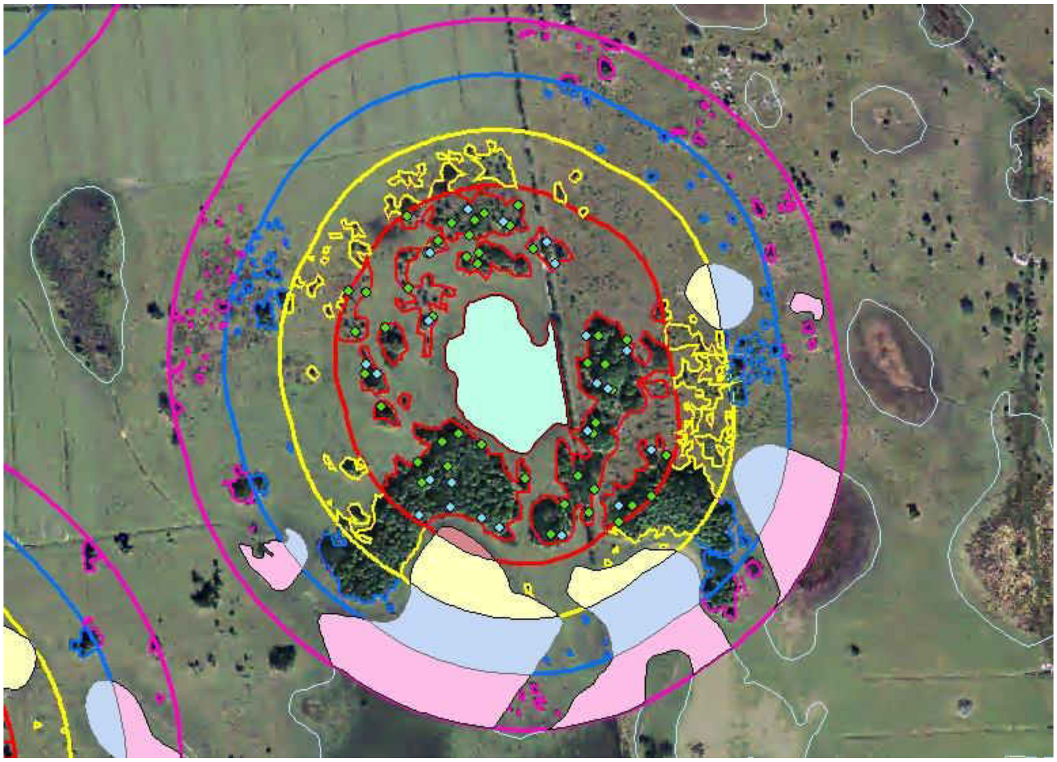

Figure 21. Wetland 245: IM-G.

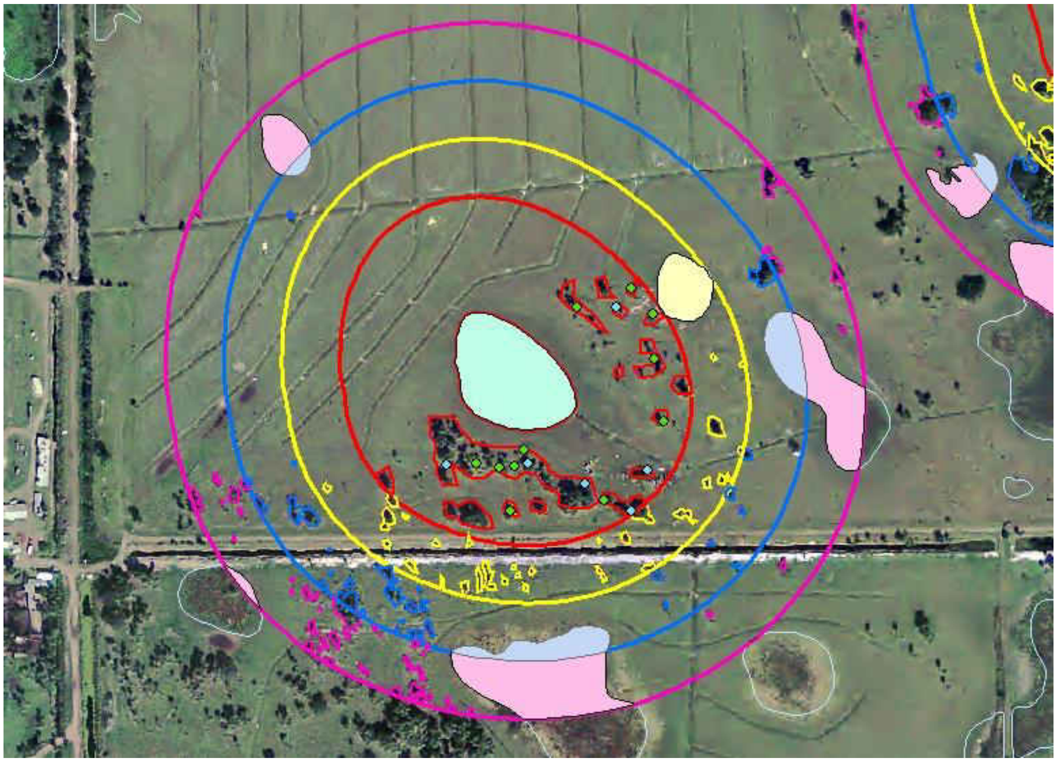

Figure 22. Wetland 271: IM-R.

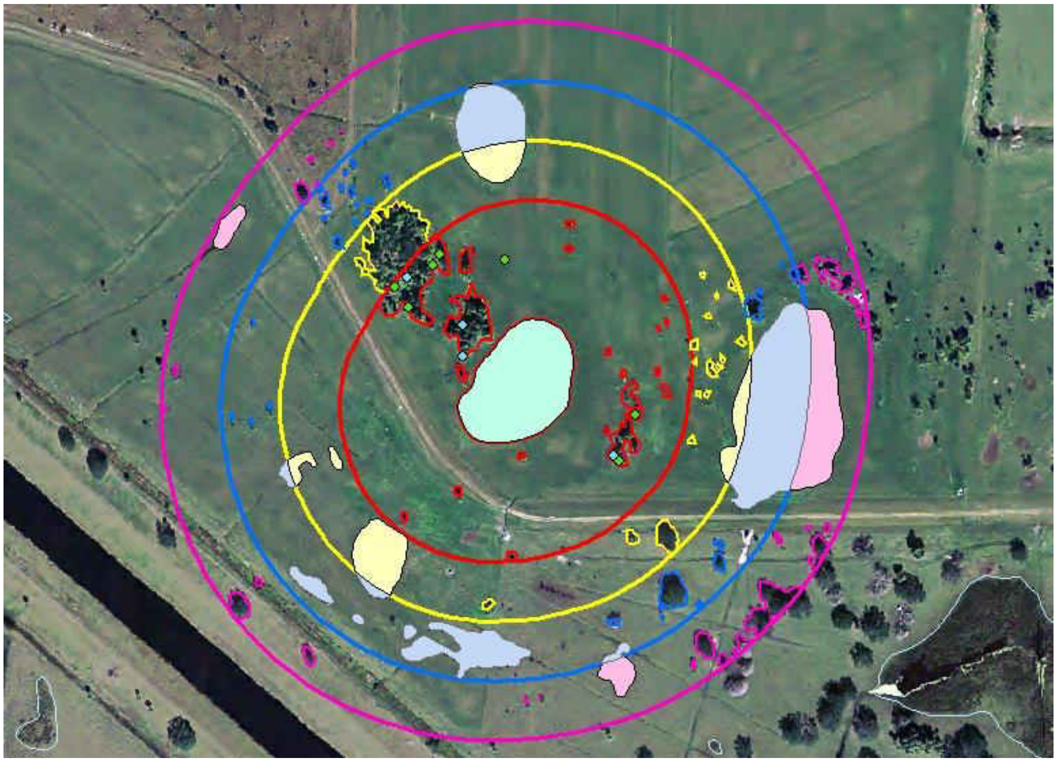

Figure 23. Wetland 310: IM-R.

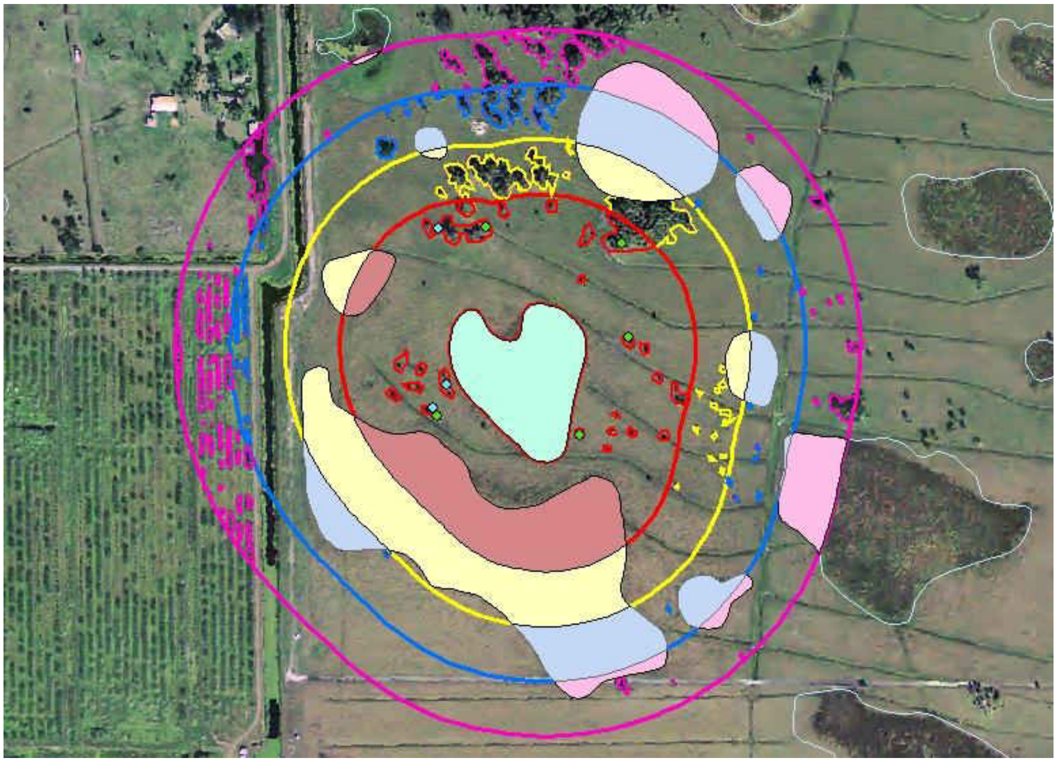

Figure 24. Wetland 336: IM-G.

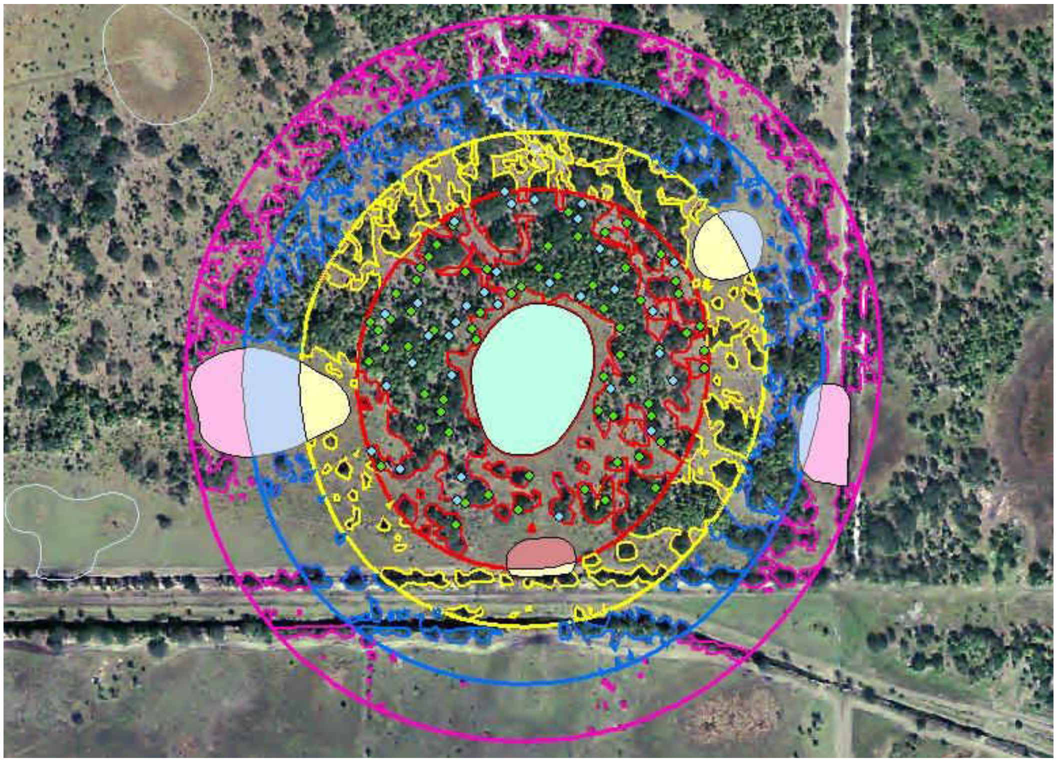

Figure 25. Wetland 595: SN-G.

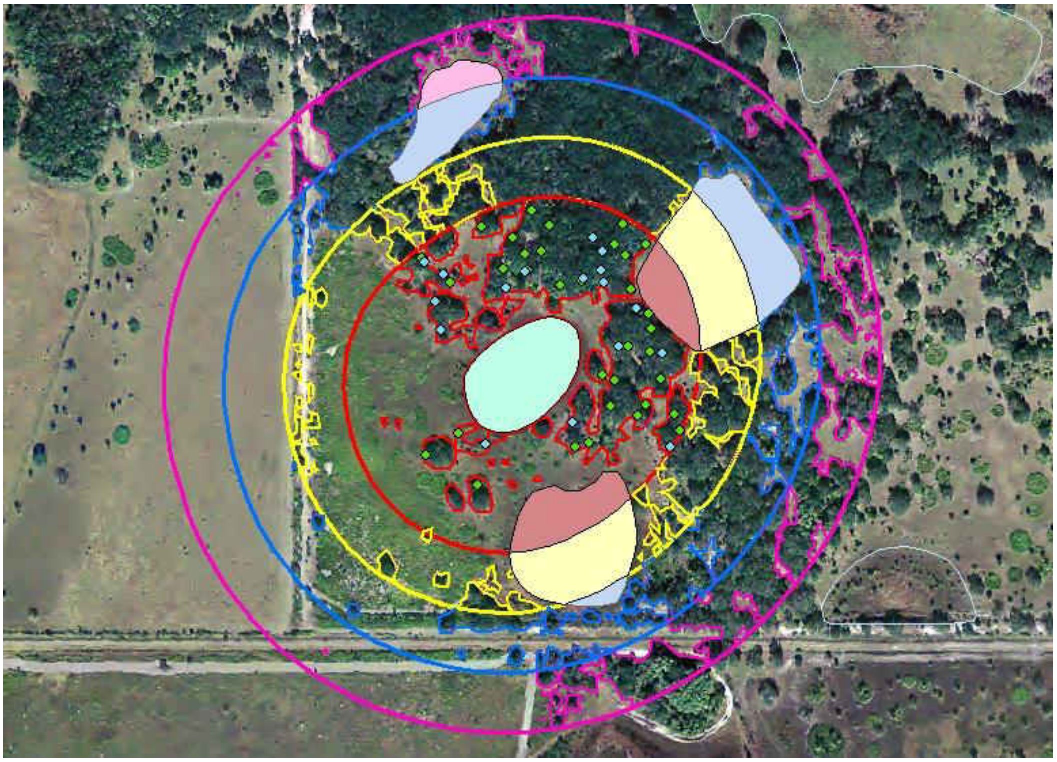

Figure 26. Wetland 597: SN-R.

APPENDIX B: ADDITIONAL CALCULATIONS

Appendix B: Additional calculations

Table 25. Fraction of woodlot by site. Pasture type: SN = semi-native, IM = intensively managed; Area (ha) 250 m = total hectares in the 250 m buffer of each focal wetland; Woodlot (ha) 250 m = total hectares of woodlot in the 250 m buffer of each wetland; Fraction woodlot = (Woodlot (ha) 250 m)/(Area (ha) 250 m)

Wetland	Pasture type	Area (ha) 250 m	Woodlot (ha) 250 m	Fraction woodlot
49	SN	29.755	4.135	0.139
66	SN	26.554	0.979	0.037
79	SN	27.802	6.616	0.238
123	SN	27.134	0.981	0.036
196	IM	27.873	4.452	0.160
205	IM	29.702	0.889	0.030
245	IM	30.714	5.296	0.172
271	IM	28.446	1.245	0.044
310	IM	28.172	1.233	0.044
336	IM	31.626	1.692	0.053
595	SN	30.188	12.980	0.430
597	SN	27.738	11.340	0.409

Table 26. Estimated number of *Hyla squirella* supported by each pasture type. Past = pasture type: SN = semi-natural, IM = intensively managed; Total ha = hectares of each pasture type at MAERC; Avg. fract woodlot = average fraction of woodlot, calculated from Fraction woodlot values in Table 24. Est woodlot = estimated woodlot (Total ha x Avg fract woodlot). Avg density = average density of *H. squirella* in frogs per ha (number of unique captures/area of focal woodlot); Est number frogs = estimated number of *H. squirella* (Est woodlot x Avg density).

Past	Total ha	Avg fract woodlot	Est woodlot	Avg density (frogs/ha)	Est number frogs
SN	2,281	0.215	489.938	54.605	26,752.839
IM	1,800	0.084	150.936	150.979	22,788.143
				Total	49,540.982

LIST OF REFERENCES

Alford, R. A. 1986. Effects of parentage on competitive ability and vulnerability to predation in *Hyla chrysoscelis* tadpoles. Oecologia 68:199-204.

Alford, R.A., and S.J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30:133-165.

Altwegg, R. 2003. Multistage density dependence in an amphibian. Oecologia 136:46-50.

Arnett, E. B., and J. P. Hayes. 2000. Bat use of roosting boxes installed under flat-bottom bridges in western Oregon. Wildlife Society Bulletin 28:890-894.

Arthington, J. D., F. M. Roka, J. J. Mullahey, S. W. Coleman, L. O. Lollis, and R. M.Muchovej. 2007**.** Integrating ranch forage production, cattle performance and economics in ranch management systems. Rangeland Ecology and Management 60:12-18..

Azevedo, J. , and P. R. Stout. Farm animal manures: an overview of their role in the agricultural environment. California Agric. Exp. Station Extension Service. Manual 44. Ag. Publication. University of California Berkeley, California.

Babbitt, K. J., M. J. Baber, and L. A. Brandt. 2006. The effect of woodland proximity and wetland characteristics on larval anuran assemblages in an agricultural landscape. Canadian Journal of Zoology 84:510-519.

Babbitt, K. J., M. J. Baber, and T. L. Tarr. 2003. Patterns of larval amphibian distribution along a wetland hydroperiod gradient. Canadian Journal of Zoology 81:1539-1552.

Babbitt, K. J, and F. Jordan. 1996. Predation on *Bufo terrestris* tadpoles: effects of cover and predator identity. Copeia 1996:485-488.

Babbitt, K. J., and G. W. Tanner. 1997. Effects of cover and predator identity on predation of *Hyla squirella* tadpoles. Journal of Herpetology 31:128-130.

Babbitt, K. J., and G. W. Tanner. 1998. Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. Oecologia 111:258-262.

Babbitt, K. J., and G. W. Tanner. 2000. Use of temporary wetlands by anurans in a hydrologically modified landscape. Wetlands 20:313-322.

Bailey, L. L., W. L. Kendall, D. R. Church, and H. M. Wilbur. 2004. Estimating survival and breeding probability for pond-breeding amphibians: a modified robust design. Ecology 85:2456-2466.

Bartareau, T. M. 2004. PVC pipe diameter influences the species and sizes of treefrogs captured in a Florida coastal oak scrub community. Herpetological Review 35:150-152.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences in stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419-431.

Bender, D. J, L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18:17-39.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology and Evolution 18:182-188.

Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71:1599-1608.

Berven, K. A., and T. A. Grudzien. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44:2047-2056.

Binckley, C. A., and W. J. Resetarits, Jr. 2002. Reproductive decisions under threat of predation: squirrel treefrog (*Hyla squirella*) responses to banded sunfish (*Enneacanthus obesus*). Oecologia 130:157-161.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8:60-71.

Bohlen, P.J., S. Lynch, L. Shabman, M. Clark, S. Shulka, and H. Swain. 2009. Paying for environmental services from agricultural lands: an example from the northern Everglades. Frontiers in Ecology and the Environment 7:46-55.

Bohlen, P. J. and H. M. Swain. 2009. Conceptual model for integrating ecological and economic sustainability in agroecosystems: an example from subtropical grazing lands. In P. J. Bohlen and G. House (eds.), Sustainable agroecosystem management: integrating ecology, economics and society, p. 235-257. CRC Press, Boca Raton, FL

Boone, M. D., and C. M. Bridges. 1999. The effect of temperature on the potency of carbaryl for survival of tadpoles of the green frog (*Rana clamitans*). Environmental Toxicology and Chemistry 18:1482 – 1484.

Bosch, J., L. Boyero, and I. Martinez-Solano. 2004. Spatial scales for the management of amphibian populations. Biodiversity and Conservation 13:409-420.

Boughton, E. H. 2008. Florida ranchlands: areas of conservation value and opportunities for restoration. The Palmetto 25:12-15.

Boughton, E.H. 2009. Understanding plant community composition in agricultural wetlands: context dependent effects and plant interactions. Dissertation, University of Central Florida.

Boughton, R. G., J. Staiger, and R. Franz. 2000. Use of PVC refugia as a sampling technique for hylid treefrogs. American Midland Naturalist 144:168-177.

Boyer, R. and C. E. Grue. 1995. The need for water quality criteria for frogs. Environmental Health Perspectives 103:352-367.

Breden, F. 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. Copeia 1987:386-395.

Bridges, C. M., and R. D. Semlitsch. 2000. Variation in pesticide tolerance of tadpoles among and within species of Ranidae and patterns of amphibian decline. Conservation Biology 14:1490-1499.

Bridges, C. M., and R. D. Semlitsch. 2001. Genetic variation in insecticide tolerance in a population of southern leopard frogs (*Rana sphenocephala*): Implications for amphibian conservation. Copeia 2001:7-13.

Brönmark, C,. and P. Edenhamn. 1994. Does the presence of fish affect the distribution of tree frogs (*Hyla aborea*)? Conservation Biology 8:841-845.

Burton, E. C., M. J. Gray, A. C. Schmutzer, and D. L. Miller. 2009. Differential responses of postmetamorphic amphibians to cattle grazing in wetlands. Journal of Wildlife Management 73:269-277.

Caldwell, J. P., J. H. Thorpe, and T. O. Jervey. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. Oecologia 46:285-289.

Capesce, J. C., K. L. Campbell, P. J. Bohlen, G. A. Graetz, K. M. Portier. 2007. Soil phosphorus, cattle stocking rates, and water quality in subtropical pastures in Florida, USA. Rangeland Ecology and Management 60:19-30.

Carlson, A., and P. Edenhamn. 2000. Extinction dynamics and the regional persistence of a treefrog metapopulation. Proceedings of the Royal Society of London. 267:1311-1313.

Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface water with phosphorus and nitrogen. Ecological Applications 8:559-568.

Cattaneo, A., G. Galanti, S. Gentinetta, and S. Romo. 1998. Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. Freshwater Biology 39:725-740.

Chan-McLeod, A. C. A., and A. Moy. 2007. Evaluating residual tree patches as stepping stones and short-term refugia for red-legged frogs. Journal of Wildlife Management 71:1838-1834.

Cohen, M. P., and R. A. Alford. 1996. Factors affecting diurnal shelter use by the cane toad, *Bufo marinus*. Herpetologica 52:172-181.

Collins, J. P. 1973. Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog, *Rana catesbeiana*. Ecology 60:738-749.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128:231-240.

Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. BioScience 50:593-601.

Day, T. A., and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180-188.

Denver, J. D. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. American Zoologist 37:172-184.

Dodd, C. K. 1991. Drift fence-associated sampling bias of amphibians at a Florida sandhills temporary pond. Journal of Herpetology 25:296-301.

Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. The John Hopkins University Press. Baltimore, Maryland, USA.

Dunson, W. A., R. L. Wyman, and E. S. Corbett. 1992. A symposium on amphibian declines and habitat acidification. Journal of Herpetology 26:349-352.

Eason, G.W., Jr., and J.E. Fauth. 2001. Ecological correlates of anuran species richness in temporary pools: a field study in South Carolina, USA. Israel Journal of Zoology 47:346-365.

Fogarty, J. H., and F. J. Vilella. 2002. Population dynamics of *Eleutherodactylus coqui* in cordillera forest reserves of Puerto Rico. Journal of Herpetology 36:193-201.

Formanowicz, D. R., Jr. 1986. Anuran tadpole/aquatic insect predator-prey interactions: tadpole size and predator capture success. Herpetologica 42:367-373.

Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grassland of Yellowstone National Park. Ecology 79:2229-2241.

Gibbons, J. W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands 23:630-635.

Gill, D. E. 1987a. Effective population size and interdemic migration rates in a metapopluation of the red spotted newt, *Notopthalmus viridescens* (Rafinesque). Evolution 32:839-849.

Gill, D. E. 1978b. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48:145-166.

Girish, S., and S. K. Saidapur. 1999. The effects of kinship and density on growth and metamorphosis of the bronze frog (*Rana temporalis*) tadpoles. Acta Ethologica 2:61-66.

Gittins, S. P. 1983. Population dynamics of the common toad (*Bufo bufo*) at a lake in Mid-Wales. Journal of Animal Ecology 52:981-988.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologia 16:183-190.

Gulve, P. S. 1994. Distribution and extinction patterns in a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75:1357-1367.

Hart, A. E. and J. R. Lovvorn. 2000. Vegetation dynamics and primary production in saline lacustrine wetlands of a Rocky Mountain basin. Aquatic Botany 66:21-39.

Hatch, A. C., and A. R. Blaustein. 2000. Combined effects of UVB, nitrate, and low pH reduce the survival and activity level of larval cascades frogs (*Rana cascadae*). Archives of Environmental Contamination and Toxicology 39:494-499.

Hatch, A. C., and A. R. Blaustein. 2003. Combined effects of UV-B radiation and nitrate fertilizer on larval amphibians. Ecological Applications 13:1083-1093.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695-713.

Holenweg Peter, A.-K. 2001. Survival of adults in the water frog *Rana lessonae* and its hybridogenetic associate *Rana esculenta*. Canadian Journal of Zoology 79:652-661.

Holomuzki, J.R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. Ecology 67:737-748.

Horne, M. T., and W. A. Dunson. 1995. Effects of low pH, metals, and water hardness on larval amphibians. Archives of Environmental Contamination and Toxicology 29:500-505.

Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyers, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian declines. Nature 404:752-755.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics 22:477-503.

Integrated Crop Management, Iowa State University, University Extension. www.ipm.iastate.edu

Jansen, A., and M. Healey. 2003. Frog communities and wetland condition: relationships with grazing and domestic livestock along an Australian floodplain river. Biological Conservation 109:207-219.

Jenkins, D. G., S. Grissom, and K. Miller. 2003. Consequences of prairie wetland drainage for crustacean biodiversity and metapopulations. Conservation Biology 17:158-167.

Johnson, J. R. 2005. A novel arboreal pipe-trap designed to capture the gray treefrog (*Hyla versicolor*). Herpetol. Rev. 36:274-277.

Johnson, J. R., R. D. Mahan, and R. D. Semlitsch. 2008. Seasonal terrestrial microhabitat use by gray treefrogs (*Hyla versicolor*) in Missouri oak-hickory forests. Herpetologica 64:259-269.

Kalmbacher, R. S., I. V. Ezenwa, and J. Vendramini. 2002. Managing South Florida range for cattle. Florida Forage Handbook. University of Florida Institute of Food and Agricultural Sciences Extension. http://edis.ifas.ufl.edu.

Knutson, M. G., J. R. Sauer, D. A. Olsen, M. J. Mossman, L. M. Hemesath, and M. J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. Conservation Biology 13:1437-1446.

Knutson, M. G., W. B. Richardson, D. M. Reineke, B. R. Gray, J. R. Parmelee, and S. E. Weick. 2004. Agricultural ponds support amphibian populations. Ecological Applications 14:669-684.

Kolozsvary, M. B., and R. K. Swihart. 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. Canadian Journal of Zoology 77:1288-1299.

Kumbar, S. M., and K. Pancharatna. 2001. Determination of age, longevity and age at reproduction of the frog *Microhyla ornata* by skeletochronology. Journal of Biosciences 26:265-270.

Lambert, M. R. K. 1997. Environmental effects of heavy spillage from a destroyed pesticide store near Hargeisa (Somaliland) assessed during the dry season, using reptiles and amphibians as bioindicators. Archives of Environmental Contamination and Toxicology 32:80-93.

Long, L. E., L. S. Saylor, and M.E. Soule. 1995. A pH/UV-B synergism in amphibians. Conservation Biology 9:1301-1303.

Macias, G., A. Marco, and A. R. Blaustein. 2007. Combined exposure to ambient UVB radiation and nitrite negatively affects survival of amphibian early life stages. Science of the Total Environment 385:55-65.

Marco, A., and A. R. Blaustein. 1999. The effects of nitrite on behavior and metamorphosis in cascades frogs (*Rana cascadae*). Environmental Toxicology and Chemistry 18:946-949.

Marsh, D. M., and P. B. Pearman. 1997. Effects of habitat fragmentation on the abundance of two species of leptodactylid frogs in an Andean montane forest. Conservation Biology 11:1323-1328.

Marsh, D. M., A. S. Rand, and M. J. Ryan. 2000. Effects of inter-pond distance on the breeding ecology of tungara frogs. Oecologia 122:505-513.

Marsh, D. M., and P. C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40-49.

Measey, G. J., D. J. Gower, O. V. Oommen, and M. Wilkinson. 2003. A mark-recapture study of the caecilian amphibian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) in southern India. Journal of Zoology, London 261:129-133.

Meyer, K. D., S. M. McGehee, and M. W. Collopy. 2004. Food deliveries at swallow-tailed kite nests in southern Florida. The Condor 106:171-176.

Meyers, C. H., L. Eigner, J. A. Harris, R. Hilman, M. D. Johnson, R. Kalinowski, J. J. Muir, M. Reyes, and L. E. Tucci. 2007. A comparison of ground-based and tree-based polyvinyl chloride pipe refugia for capturing *Pseudacris regilla* in northwestern California. Northwestern Naturalist 88:147-154.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87-105.

Moore, R. D., B. Newton, and A. Sih. 1996. Delayed hatching as a response of streamside salamander eggs to chemical cues from predatory sunfish. Oikos 77:331-335.

Morin, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:120-138.

Morrison, J. L. and S. R. Humphrey. 2001. Conservation value of private lands for crested caracaras in Florida. Conservation Biology 15:675-684.

Moulton, C. A., W. J. Flemming, and B. R. Nerney. 1996. Use of PVC pipes to capture hylid frogs. Herpetological Review 27:186-187.

Murphy, C. G. 1993. A modified drift fence for capturing treefrogs. Herpetological Review 24:143-145.

Nelson, G. L., and B. M. Graves. 2004. Anuran population monitoring: comparison of the North American Amphibian Monitoring Program's calling index with mark-recapture estimates for *Rana clamitans*. Journal of Herpetology 38:355-359.

Newman, R. A. 1988. Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. Evolution 42:774-783.

NOAA. 2008. National Oceanic and Atmospheric Administration, National Climatic Data Center. Annual 2008 Report: Regional Drought Overview. www.ncdc.noaa.gov.

Noy-Meir, I., M. Gutman, and T. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. Journal of Ecology 77:290-310.

Oldham, R. S., D. M. Latham, D. Hilton-Brown, M. Towns, A. S. Cooke, and A. Burn. 1997. The effect of ammonium nitrate fertiliser on frog (*Rana temporaria*) survival. Agriculture, Ecosystems, and Environment 61:69-74.

Otto, C. R. V., D. C. Forester, and J. W. Snodgrass. 2007. Influences of wetland and landscape characteristics on the distribution of carpenter frogs. Wetlands 27:261-269.

Pechmann, J. H. K., D. E. Scott, J. W. Gibbons, and R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3-11.

Pellet, J., A. Guisan, and N. Perrin. 2004. A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. Conservation Biology 18:1599-1606.

Pellet, J., S. Hoehn, and N. Perrin. 2004. Multiscale determinants of tree frog (*Hyla arborea* L.) calling ponds in western Switzerland. Biodiversity and Conservation 13:2227-2235.

Peterson, J. A., and A. R. Blaustein. 1992. Relative palatabilities of anuran larvae to natural aquatic insect predators. Copeia 1992:577-584.

Petranka, J. W., and C. T. Holbrook. 2006. Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? Restoration Ecology 14:404-411.

Pham, L., S. Boudreaux, S. Kharbet, B. Price, A. S. Ackleh, J. Carter, and N. Pal. 2007. Population estimates of *Hyla cinerea* (Schneider) (Green Treefrog) in an urban environment. Southeastern Naturalist 6:203-216.

Pittman, S. E., A. L. Jendrek, S. J. Price, and M. E. Dorcas. 2008. Habitat selection and site fidelity of Cope's gray treefrog (*Hyla chrysoscelis*) at the aquatic-terrestrial ecotone. Journal of Herpetology 42:378-385.

Plytycz, B., and J. Bigaj. 1993. Studies on the growth and longevity of the yellow-bellied toad, *Bombina variegata*, in natural environments. Amphibia-Reptilia 14:35-44.

Pope, S. E., L. Fahrig, and H. G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498-2508.

Relyea, R. A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82:523-540.

Relyea, R. A. 2005. The lethal impact of Roundup on aquatic and terrestrial amphibians. Ecological Applications 15:1118-1124.

Relyea, R. A., and N. Mills. 2001. Predator-induced stress makes the pesticide carbaryl more deadly to gray treefrog tadpoles (*Hyla versicolor*). Proceedings of the National Academy of Sciences 98:2491-2496.

Relyea, R. A., and E. E. Werner. 2000. Morphological plasticity in four larval anurans distributed along an environmental gradient. Copeia 2000:178-190.

Resetarits, W. J., Jr., and H. M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. Ecology 70:220-228.

Richards, S. J., and C. M. Bull. 1990. Size-limited predation on tadpoles of three Australian frogs. Copeia 1990:1041-1046.

Rothermel, B. 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecological Applications 14:1535-1546.

Rouse, J. D., C. A. Bishop, and J. Struger. 1999. Nitrogen pollution: an assessment of its threat to amphibian survival. Environmental Health Perspectives 107:799-803.

Rowe, C. L., and W. A. Dunson. 1994. The value of simulated pond communities in mesocosms for studies of amphibian ecology and ecotoxicology. Journal of Herpetology 28:346-356.

Sanderson, R. A., S. P. Rushton, A. J. Cherrill, and J. P. Byrne. 1995. Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. Journal of Applied Ecology 32:506-518.

Schmidt, B. R., and J. Pellet. 2005. Relative importance of population process and habitat characteristics in determining site occupancy of two anurans. The Journal of Wildlife Management 69:884-893.

Schmutzer, A. C., M. J. Gray, E. C. Burton, and D. L. Miller. 2008. Impacts of cattle on amphibian larvae and the aquatic environment. Freshwater Biology 53:2613-2625.

Schurbon, J.M., and J.E. Fauth. 2003. Effects of prescribed burning on amphibian diversity in a southeastern U.S. national forest. Conservation Biology 17:1338-1349.

Schuytema, G. S., and A. V. Nebeker. 1999. Comparative toxicity of ammonium and nitrate compounds to Pacific treefrog and African clawed frog tadpoles. Environmental Toxicology and Chemistry 18:2251-2257.

Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. Ecology 71:296-306.

Semlitsch, R. D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia 1987:61-69.

Semlitsch, R. D. 1993. Adaptive genetic variation in growth and development of tadpoles of the hybridogenetic *Rana esculenta* complex. Evolution 47:1805-1818.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129-1133.

Semlitsch, R. D., and J. W. Gibbons. 1988. Fish predation in size-structured populations of treefrog tadpoles. Oecologia 75:321-326.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184-192.

Semlitsch, R. D., C. M. Bridges, and A. M. Welch. 2000. Genetic variation and a fitness tradeoff in the tolerance of gray treefrog (*Hyla versicolor*) tadpoles to the insecticide carbaryl. Oecologia 125:179-185.

Sih, A., and R. D. Moore. 1993. Delayed hatching of salamander eggs in response to enhanced larval predation risk. American Naturalist 142:947-960.

Sinsch, U., I. E. Di Tada, and A.L. Martino. 2001. Longevity, demography, and sex-specific growth of the Pampa de Anchala toad, *Bufo achalensis* CEI, 1972. Studies on Neotropical Fauna and Environment 36:95-104.

Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnean Society 42:135-147.

Skelly, D. K. 2001. Distributions of pond-breeding anurans: an overview of mechanisms. Israel Journal of Zoology 47:313-332.

Smith, D. C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. Ecology 68:344-350.

Smith, G. R. 1999. Among family variation in tadpole (*Rana catesbeiana*) response to density. Journal of Herpetology 33:167-169.

Smith, M. A., and D. M. Green. 2006. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110-128.

Snodgrass, J. W., M. J. Komoroski, A. L. Bryan Jr., and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulation. Conservation Biology 14:414-419.

Steinman, A. D., J. Conklin, P. J. Bohlen, and D. G. Uzarski. 2003. The influence of cattle grazing and pasture land use on macroinvertebrate communities in freshwater wetlands. Wetlands 23:877-889.

Stewart, M. M., and A. S. Rand. 1991. Vocalizations and the defense of retreat sites by male and female frogs, *Eleutherodactylus coqui*. Copeia 1991:1013-1024.

Stewart, M. M., and F. H. Pough. 1983. Population density of tropical forest frogs: relation to retreat sites. Science 221:570-572.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.

Swain, H. M., P. J. Bohlen, K. L. Campbell, L. O. Lollis, and A. D. Steinman. 2007. Integrated ecological and economic analysis of ranch management systems: an example from south central Florida. Rangeland Ecology and Management 60:1-11.

Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. Proceedings of the National Academy of Sciences 96:5995-6000.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science 292:281-284.

Travis, J. 1980. Phenotypic variation and the outcome of interspecific competition in hylid tadpoles. Evolution 32:40-50.

Travis, J. 1981. Control of larval growth variation in a population of *Pseudacris triseriata* (Anura: Hylidae). Evolution 35:423-432.

Travis, J. 1983a. Variation in development patterns of larval anurans in temporary ponds. Evolution 37:496-512.

Travis, J. 1983b. Variation in growth and survival of *Hyla gratiosa* larvae in experimental enclosures. Copeia 1983:232-237.

Travis, J. 1984. Anuran size at metamorphosis: experimental test of a model based on intraspecific competition. Ecology 65:1155-1160.

USDA. 2003. National resources inventory. United States Department of Agriculture Natural Resource Conservation Service. Washington, D.C. http://www.nrcs.gov

Van Buskirk, J. 2005. Local and landscape influence on amphibian occurrence and abundance. Ecology 86: 1936-1947.

Van Buskirk, J., and S. A. McCollum. 1999. Plasticity and selection explain variation in tadpole phenotype between ponds with different predator composition. Oikos 85:31-39.

Van Buskirk, J., and R. A. Relyea. 1998. Selection for phenotypic plasticity in *Rana sylvatica* tadpoles. Biological Journal of the Linnean Society 65:301-328.

Voights, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. American Midland Naturalist 95:313-322.

Vos, C. C., and A. H. P. Stumpel. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla aborea*). Landscape Ecology 11:203-214.

Waddle, J. H., K. G. Rice, F. J. Mazzotti, and H. F. Percival. 2008. Modeling the effect of toe clipping on treefrog survival: beyond the return rate. Journal of Herpetology 42:467-473.

Walls, S. C., and A. R. Blaustein. 1994. Does kinship influence density dependence in a larval salamander? Oikos 71:459-468.

Warner, S. C., J. Travis, and W. A. Dunson. 1983. Effect of pH variation on interspecific competition between two species of hylid tadpoles. Ecology 74:183-194.

Webb, N. R., R. T. Clarke, and J. T. Nicholas. 1984. Invertebrate diversity on fragmented calluna-heathland: effects of surrounding vegetation. Journal of Biogeography 11:41-46.

Welsh, H. H., Jr., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. Ecological Applications 8:1118-1132.

Weltz, M., M. K. Wood, and E. E. Parker. 1989. Flash grazing and trampling: Effects on infiltration rates and sediment yield on a selected New Mexico range site. Journal of Arid Environments 16:95-100.

Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. American Naturalist 128:319-341.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplemental): 120-138.

Wilbur, H. M. 1980. Complex life cycles and community organization in amphibians. Annual Review of Ecology and Systematics 11:67-93.

Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science 182:1305-1214.

Wilbur, H. M., P. J. Morin, and R. N. Harris. 1983. Salamander predation and the structure of experimental communities: anuran responses. Ecology 64:1423-1429.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Loso. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607-615.

Wood, K. V., J. D. Nichols, H. F. Percival, and J. E. Hines. 1998. Size-sex variation in survival rates and abundance of pig frogs, *Rana grylio*, in Northern Florida wetlands. Journal of Herpetology 32: 527-535.

Young, B. E., K. R. Lips, J. K. Reaser, R. Ibáñez, A. W. Salas, J. Rogelio Cedeño, L. A. Coloma, S. Ron, E. La Marca, J. R. Meyer, A. Muñoz, F. Bolaños, G. Chaves, and D. Romo. 2001. Population declines and priorities for amphibian conservation in Latin America. Conservation Biology 15:1213-1223.

Zacharow, M., W. J. Barichivich, and C. K. Dodd, Jr. 2003. Using ground-placed PVC pipes to monitor hylid treefrogs: capture biases. Southeastern Naturalist 2:575-590.

Zanini, F., A. Klingemann, R. Schlaepfer, and B. R. Schmidt. 2008. Landscape effects on anuran pond occupancy in an agricultural countryside: barrier based buffers predict distributions better than circular buffers. Canadian Journal of Zoology 86:692-699.