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Maintaining biodiversity with a mosaic of wetlands: factors affecting amphibian species richness among small isolated wetlands in central Florida.

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Maintaining biodiversity with a mosaic of wetlands: factors affecting amphibian species
richness among small isolated wetlands in central Florida.

by

Jackie Guzy

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
College of Arts and Science
University of South Florida

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stepping-stone, wetland mosaic, ecological modeling, resource management,
reclamation

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Maintaining biodiversity with a mosaic of wetlands: factors affecting amphibian species richness among small isolated wetlands in central Florida

Jackie Guzy

Abstract

The biodiversity value of a wetland is linked not only to its position in the landscape relative to other wetlands, but also to its habitat characteristics. I monitored amphibian species richness among 12 small, isolated, and undisturbed wetlands (which occur on lands permitted for phosphate mining) in central Florida during the 2005 and 2006 breeding seasons. I used seven habitat and landscape variables to characterize the environments of the wetlands and generalized linear models to determine which of these variables had the greatest influence on the occurrence of seven amphibian species (*Anaxyrus terrestris*, *Gastrophryne carolinensis*, *Hyla gratiosa*, *Lithobates capito*, *L. catesbeianus*, *L. grylio*, and *Pseudacris nigrita verrucosa*). Significant models for each species incorporated six of the seven habitat and landscape variables: distance to permanent water (2 spp.), distance to nearest wetland (3 spp.), vegetation heterogeneity (2 spp.), hydroperiod (2 spp.), presence/absence of fish (1 sp.), and distance to canopy cover (1 sp.). I suggest that source/sink metapopulation and patchy population dynamics in a given year are affected in part by environmental variables of ephemeral wetlands as they affect individual amphibian species. I suggest that a diversity of environmental conditions among wetlands produces the greatest amphibian biodiversity in this system, and that conservation and restoration efforts should emphasize environmental heterogeneity.

Introduction

Amphibian declines are well documented (Blaustein and Wake 1990, Phillips 1994, Stuart et al. 2004); one-third of all amphibians are now considered threatened (Stuart et al. 2004) and 168 species have become extinct within the last two decades (Dodd 2009). These declines are no longer considered natural population fluctuations (Dodd 2009), but rather caused by a wide range of human-induced factors. This loss of biodiversity is of concern as it influences economics, ecosystem function, esthetics, and ethics (Noss and Cooperrider 1994, Groom et al. 2006).

Habitat loss and degradation are now considered among the greatest threats to amphibians worldwide (Cushman 2006, Dodd 2009). Among some of the most critical habitat to amphibians are small, isolated wetlands, which are used to support their biphasic life histories. Wetlands of all types are declining worldwide to facilitate draining or filling for human settlements and agriculture, and small, isolated wetlands are the least protected. As a result of a 2001 Supreme Court decision, *Solid Waste Agency of Northern Cook County (SWANCC) vs. U.S. Army Corps of Engineers*, a significant number of wetlands and other waters throughout the United States are no longer protected under the Clean Water Act (SWANCC 2001, Comer et al. 2005). The SWANCC decision eliminated reliance on the Migratory Bird Rule that included many geographically isolated wetlands within the jurisdiction of the Clean Water Act through their linkages to interstate commerce (Downing et al. 2003). In 2006, Court decisions in *Rapanos v. United States* and *Carabell v. Corps* further restricted federal authority over wetlands not directly connected (via surficial hydrologic connection) to “waters of the United States” further undermining remaining federal jurisdiction over isolated wetlands

(BenDor 2008). Thus, in Florida, where my study was conducted, federal regulation of impacts to wetlands is restricted to those greater than 1 acre which have significant connection to navigable waters of the state (e.g. rivers and streams). State regulation of alterations to natural, small, isolated wetlands in Florida varies by water management district and is generally restricted to those greater than one half acre [F.A.C. 62-340, South West Florida Water Management District (SWFWMD) 2009]. Thus, these critical amphibian habitats continue to be lost as development in Florida escalates.

One particular type of disturbance in central Florida is phosphate mining, which disturbs about 2,023-2,428 hectares of land annually; approximately 25-30% of these lands are isolated wetlands or wetlands hydrologically connected to navigable waters [Florida Institute for Phosphate Research (FIPR) 2010]. Florida provides approximately 75 percent of the USA's supply of phosphate fertilizer and about 25 percent of the world supply (FIPR 2010). The mining of phosphate for fertilizer is typically conducted using strip mining techniques which involves clearing the site of all vegetation, removal of soil, and mining the underlying phosphate matrix with draglines. Following extraction, the site is back-filled with sand tailings (FIPR 2010). Because of the large-scale clearing, mining and reclamation in central Florida, recent emphasis has been on improvement of reclamation techniques for the purpose of maintaining a diverse flora and fauna after mining (Durbin et al. 2008, FIPR 2010). State law requires that land disturbed by phosphate mining must be restored to a useful condition, and sometimes to where ecological systems function as they did before the mining (FIPR 2010). In the legislation creating the Florida Institute for Phosphate Research is the mission that includes the study of reclamation alternatives and technologies. Goals of FIPR include developing methods to improve wildlife habitat on reclaimed mined lands and facilitate recolonization by wildlife. Thus, it is vital to identify the factors of native wetlands that support amphibian diversity to assist resource managers.

Small, isolated wetlands are critical for amphibians because these wetlands dry throughout the year and thus cannot support predatory fish and perhaps support a lesser abundance and diversity of invertebrate predators that may consume amphibian larvae (Morin 1983, Wilbur 1987, Semlitsch et al. 1996). Most amphibians are regarded as highly philopatric and because dispersal distance is generally <0.3 km (Gibbs 1993, Semlitsch 1998, Semlitsch and Bodie 1998, Semlitsch and Bodie 2003) they are generally considered to have poor dispersal abilities (Marsh et al. 1999, Semlitsch 2000, Smith and Green 2005) despite evidence of long-distance movement (1.0-1.6 km) in some frogs and toads (Lemckert 2004). Furthermore, these wetlands harbor large numbers of species of other taxa that are less mobile than birds and mammals (Semlitsch and Bodie 1998) and are more affected by their loss; species include wetland plants such as sundew (*Drosera* spp) and pitcher plants (*Sarracenia* spp.; Sharitz and Gibbons 1982), microcrustaceans (Mahoney et al. 1990), and aquatic insects (Kondratieff and Pyott 1897, Sharitz and Gibbons 1982, Gaddy 1994).

Perhaps most important is the small, isolated wetlands aggregate role in protecting wetland-dependant species through either source-sink dynamics (metapopulations) and/or patchy populations. A metapopulation is a collection of partially isolated breeding habitat patches, connected by occasionally dispersing individuals where each patch exists with a substantial extinction probability; long-term persistence occurs only at the regional level of the metapopulation (Smith and Green 2005). Because each wetland in an area may fluctuate in the number of individuals of a species it contains, at times a wetland may act as a sink when the population of a species dies out locally from that wetland, or it may be a source that produces surplus individuals, which can colonize a nearby sink wetland (Semlitsch 2000). An alternative to metapopulation structure at the local level is the existence of patchy populations that treat local wetlands as habitat patches. Patchy populations often occur where many

wetlands are in close proximity to one another and facilitate adaptive habitat switching; movements between wetlands occur at such high rates that local wetland populations do not develop a significant degree of demographic independence (Harrison 1991, McCullough 1996, Smith and Green 2005, Petranka and Holbrook 2006).

Regardless of how amphibian populations are structured, small, isolated wetlands are critical for breeding success of many species. Because these wetlands are more affected by disturbance, and thus more vulnerable than larger wetlands, consequences to losing them include alterations to metapopulation or patchy population dynamics; two main effects include the reduction of individuals dispersing and the increase in dispersal distances (Gibbs 1993). This loss reduces the total number of sites in which wetland-breeding amphibians can reproduce and successfully recruit juveniles (Semlitsch and Bodie 1998) and ultimately can reduce the number of source populations because juvenile recruitment is related to hydroperiods that favor the periodic drying characteristic of small wetlands (Pechmann et al. 1989). Despite support in the literature for the biological importance of small, isolated wetlands (e.g. Semlitsch and Bodie 1998, Gibbs 2000, Snodgrass et al. 2000, Paton and Crouch 2002, Comer et al. 2005), they remain unprotected from disturbance.

Landscape ecology, conservation biology, and restoration ecology aim to promote better management of natural resources including biodiversity and a large literature (e.g. Wiens and Moss 2005; Lindenmayer and Fischer 2006) has resulted. Many studies have focused on individual patches of habitat or sites within those patches, but patch size effects cannot be divorced from other critical issues such as the role of patch mosaics, a topic poorly understood (Bennett et al. 2006). I suggest that wetland and amphibian conservation would be best guided by landscape conservation that includes a mosaic approach rather than an individual site or patch approach.

Gibbs (1993, 2000) emphasizes the necessity of evaluating wetland resources as a mosaic rather than as isolated entities; as human populations shift from rural to urban landscapes, wetland spatial patterns go from many clustered wetlands (2-5 wetlands/km², 0.2-0.4 km apart) to fewer, more isolated wetlands (<1 wetland, >0.5 km apart). Gibbs found that wetland mosaics could withstand only modest losses and still provide wetland densities that are minimally sufficient to maintain wetland biota; wetland mosaics characterized by <1 wetland per km² and >0.5 km from other wetlands were not able to sustain metapopulations of wetland-dependent animals.

Present understanding of the traits of wetland mosaics important to sustaining metapopulations or patchy populations of wetland organisms and how those traits are altered by mounting wetland destruction and by regulations intended to restrict it is minimal (Semlitsch and Bodie 1998, Gibbs 2000). Previous studies have explored the importance of the density and distribution of wetlands (Laan and Verboom 1990, Gibbs 1993, Semlitsch and Bodie 1998, Marsh et al. 1999), but only two exist that focus on the structure of an entire network or mosaic of wetlands in an area and its role in amphibian persistence. Fortuna et al. (2006) found that the observed spatial structure of ponds in Spain is robust to drought, allowing the movement of amphibians to and between flooded ponds, and hence, increasing the probability of reproduction even in dry seasons. Gómez-Rodríguez et al. (2009) investigated spatial and temporal variation in amphibian breeding habitats in Spain during two different hydrologic cycles and found that a large and diverse network of ponds provides different habitat opportunities each year, favoring the long-term persistence of the whole amphibian community.

There have been a limited number of studies (Bennett et al. 2006) that present empirical data on the response of one or more faunal groups to agricultural land mosaics (an area of land containing multiple different landuses). Studies on faunal responses to land mosaics in forested (McGarigal and McComb 1995, Edenius and Elmberg 1996,

Jokimaki and Huhta 1996, Hargis et al. 1999, Gjerde et al.2005), and experimental model landscapes (Collins and Barrett 1997; Collinge and Forman 1998, Parker and MacNally 2002, With et al. 2002) are very limited and all studies are of insects, birds, and mammals. In this study, a mosaic is defined as a group of small, isolated wetlands with different landscape and wetland characteristics.

Functioning as stepping stones, wetland mosaics are important buffers against yearly environmental variation. Ephemeral wetlands act as stepping stones during years with less rainfall, and can link a large number of dry wetlands with short hydroperiods to those with longer hydroperiods that contain water, and thus favor amphibian persistence and/or dispersal. Thus, I suggest preservation of the mosaic with a range of differing ephemeral wetlands intermingled in the landscape is essential to maintain the biodiversity which the network of wetlands supports.

My study is designed to elucidate the landscape and wetland characteristics of amphibian breeding habitats (small, isolated wetlands) in west-central Florida which yield the greatest species richness. Given the high rate of wetland disturbance and/or elimination of small, isolated wetlands in Florida, I investigate which types of wetlands sustain the highest species richness and present them as a target for preservation and/or restoration goals. I hypothesize that while some of the wetlands have lower richness in a given year, the overall high species richness observed at these sites is a result of the presence of a mosaic of small, isolated wetlands with varying landscape and physical characteristics which act as buffers to breeding amphibians against yearly environmental variation.

I studied seven wetland and landscape variables including (1): major structuring factors of wetland communities such as area (Beja and Alcazar 2003, Burne and Griffin 2005, Werner et al. 2007), fish presence (e.g. Heyer et al. 1975, Hecnar and M'Closkey 1997), vegetation heterogeneity (Atauri and Lucio 2001, Tews et al. 2004), and

hydroperiod (Beja and Alcazar 2003, Snodgrass et al. 2000, Gonzales 2004, Werner et al. 2007) and (2) landscape features important to metapopulations/patchy populations including distance to canopy (deMaynadier and Hunter 1999, Herrmann and Babbitt 2005), distance to permanent water (Dickman 1987, McComb et al. 1993, Semlitsch and Bodie 2003), and distance to nearest wetland (e.g. Vos and Stumpel 1995, Halley et al. 1996, Semlitsch 2000).

Methods

The study areas are located in west-central Florida (Hillsborough and Hardee Counties, Figure 1), an area of high-diversity of amphibians that supports 18 of the 31 species of anurans native to the state [Florida Museum of Natural History (FMNH) 2010]. I surveyed 12 native, ephemeral wetlands ranging from 0.1-3.3 acres which occur on lands permitted for phosphate mining.

Automated Frog Call Recorders (frogloggers) were installed in each wetland (Barichivich 2003) to monitor frog-calling activities during the summer and winter breeding seasons of 2005 and 2006. At the onset of wetland flooding frogloggers were set to record anuran calls for one minute each evening hour between 1800 – 0600 hours, each night from 8 June - 23 August (2005) and 28 June - 4 September (2006) for a total of 140 sampling nights (70 sampling nights each year). This timeframe encompasses the breeding season for all species occurring in the study area [North American Amphibian Monitoring Program (NAAMP) 2010]. The majority of recordings (90%) were interpreted by me and the remaining 10% were interpreted by two others also trained in Central Florida frog vocalizations and experienced with biology of amphibians. Calling male anurans were identified and their choruses were placed into one of four size categories according to according to the North American Amphibian Monitoring Program (NAAMP 2010). A calling index of zero indicated that no individuals were heard. An index of one indicated that individuals could be counted but there was time between calls. A calling index of two indicated that calls of individuals could be counted, but there was some overlap, and a calling index of three indicated that there was a full chorus of constant and overlapping calls. To ensure that frogloggers were

detecting the frequency range for calls of all species, wetlands were visited 3-5 times late in the evening during peak breeding season each for five minutes. Data were compared to that collected on froglogger cassette tapes. No additional species were heard during these visits and anuran choruses were comparable to those captured on the frogloggers.

Amphibian assemblages within a given wetland are highly dynamic from year to year (Hecnar and M'Closkey 1996) and the nature of this study permitted collection of data during two hydrologic extremes with differing rainfall amounts and timing seasonal extremes. The 2005 study season was characterized by heavy rain and elevated water levels, resulting from a particularly severe Hurricane Season influencing the study area in 2004 [National Oceanic and Atmospheric Administration (NOAA) 2010], while the 2006 season was characterized by infrequent rains and the beginning of a two year drought which had the driest back-to-back calendar years Florida has experienced, since 1932 (FDEP 2010).

Wetlands were characterized using seven habitat variables (Table 1) including area, distance to canopy, distance to permanent water, distance to nearest wetland, fish presence, vegetation heterogeneity, and hydroperiod. To obtain landscape variables, I used georeferenced digital 1:100,000 USGS geological Orthophoto Quarter Quadrangle maps (based on 2004 aerial photographs) along with National Wetlands Inventory and Florida Rivers shapefiles, each obtained from the Southwest Florida Water Management District (SWFWMD 2010) to build a geographical information system in ArcMap 9.3.1 [Environmental Systems Research Institute (ESRI) 2009]. Hydroperiod was determined from weekly site visits to each wetland and is considered to be the length of time surface water inundates the wetland. Fish presence was determined using active and passive methods. Each month, using D-frame dip nets, five 1-m sweeps were conducted in each microhabitat proportional to the fraction of the total area of the wetland that each

microhabitat covers (Mushinsky et al. 2004). Passive sampling was performed monthly, using four unbaited minnow traps placed haphazardly throughout each of the wetlands for a period of 24 hours. Vegetation heterogeneity was determined after extensive surveys by placing each wetland in one of three categories based on plant species that occur within and immediately surrounding the wetland; categories include: herbaceous, herbs and shrubs, and herbs, shrubs, and trees.

For calling amphibians, detection of a species is indicative of “presence,” but non-detection of the species is not equivalent to absence. Detection probability varies because certain species are not conspicuous and also because of seasonal behavior patterns, changing environmental conditions, habitat quality, and sampling techniques; thus, it is necessary to estimate the proportion of sites occupied when species detection probabilities are less than one (MacKenzie et al. 2002, Bailey 2004). I used the mark-recapture-like approach of MacKenzie et al. (2002) as implemented in the program PRESENCE (available for download from <http://www.proteus.co.nz/>) to estimate the proportion of sites occupied by each species, accounting for imperfect detection. Because sampling occasions were so numerous ($n=140$; 70 each for 2005 and 2006), presence data were sparse relative to absence data. This sparseness often occurs from over-sampling, and even when collapsing/pooling sampling occasions, estimates are unreliable. Therefore, I ran the simplest occupancy and detection model ($\psi(\cdot), p(\cdot)$) for each species to retain the most basic estimates of occupancy given detection; this model assumes the probability of occupancy and detection for each sampling night is the same. Any estimates over 50% were considered in further modeling. For example, if a species was estimated to occur at a site with a 65% chance, and it likely occurred there based on its biology and my extensive site knowledge, I added the species to the site.

I used generalized linear models (GLZM) to determine which landscape and wetland variables (Table 1) had the greatest influence on individual amphibian species

occurrence. Models were fit by maximum-likelihood and the significance of individual parameters was tested with likelihood ratio tests based on Type III (non-order dependant) sums-of-squares using STATISTICA 7.1 (StatSoft, Inc 2005). Individual amphibian species occurrence was analyzed using a binomial regression (used with presence/absence data) and logarithmic-link function (McCullagh and Nelder 1989). In multiple regression, collinearity between predictor variables can confound their independent effects; therefore, prior to our regression analysis I calculated Pearson correlation coefficients for all pairwise combinations of independent variables (Hair et al. 1998, Knapp et al. 2003). Correlation coefficients for three of the seven variables ranged between -0.46-0.51 and thus were included in subsequent modeling. Distance to permanent water and fish presence were strongly correlated ($r=0.82$) as were area of wetland and average hydroperiod ($r=0.62$). During model building (see below), if either pair of these correlated variables was shown to be important, the stronger of the two was selected.

Exploratory univariate GLZM's were run to assess the importance of measured habitat variables at each wetland. The resulting models for each species included all possible combinations of the top three covariates with the lowest or significant p-values ($p \leq 0.05$). Because my sample size was limited to twelve wetlands, adding more than three variables would have overparameterized the models (Doherty and Grubb 2002). Thus, for each species, a resulting seven candidate models were obtained from all possible combinations of the top three covariates with low or significant p-values. I followed a model selection approach based on Akaike's information criterion (AIC), as Mazerolle (2006) recommends for herpetological studies; models with lower AIC values are assumed to explain variation in data better (Burnham and Anderson 1998). I selected the models with substantial empirical support given the data (model AIC— $\text{minAIC}/2$, following Burnham and Anderson 2002). For each species, only models with

AIC values that differed (Δ AIC) by less than 2.0 were considered in model selection; in models with very close Δ AIC, I chose the one with the fewest parameters (most parsimonious) as the one best explaining the data (Burnham and Anderson 1998).

Results

Frogloggers installed in 12 native, ephemeral wetlands recorded a total of 17,760 minutes of frog calls during peak breeding season in 2005 and 2006 (Table 2). Because of equipment failure, 11% of minutes recorded were unusable, so 15,756 minutes were analyzed. Sampling nights averaged 123 per wetland and ranged from 66-135 and frogloggers functioned between 73-94% of the time (Table 2).

Fourteen amphibian species were present at the study sites from June 2005-September 2006 (Table 3). Amphibian species richness among wetlands ranged from 8-13. Six species occurred at all wetlands: the southern cricket frog (*Acris gryllus dorsalis*), oak toad (*Anaxyrus quercicus*), green treefrog (*Hyla cinerea*), pinewoods treefrog (*Hyla femoralis*), southern leopard frog (*Lithobates spehnocephela*), and little grass frog (*Pseudacris ocularis*). Another common species was the squirrel treefrog (*Hyla squirella*); initially occurring at 11 of 12 wetlands. Because occupancy estimates obtained from PRESENCE indicated a 95% chance of occupancy, which I found biologically probable, it was assumed present at all wetlands. All other occupancy estimates obtained from PRESENCE ranged from 5-36% and combined with the intense sampling of each wetland, warranted confidence that species were not present. Species not occurring at every wetland (Table 3), and thus included in modeling, were the southern toad (*Anaxyrus terrestris*), eastern narrow-mouth toad (*Gastrophryne carolinensis*), barking treefrog (*Hyla gratiosa*), gopher frog (*Lithobates capito*), bullfrog (*Lithobates catesbeianus*), pig frog (*Lithobates grylio*), and southern chorus frog (*Pseudacris nigrita verrucosa*).

Landscape and wetland variable measurements differed markedly between wetlands. With the exception of one outlier in distance to canopy, there was even spread among all variables. Distance to permanent water averaged 0.64 km and ranged from 0.1-1.35 km. Distance to canopy cover averaged 145.6 m and ranged from 3-853m. Wetland area averaged 0.48 hectares with a range between 0.04-1.34 acres. Distance to nearest wetland averaged 261 m and ranged 44-765 m (see Appendix 1).

Among wetlands, seven (58%) contained fish and five (42%) did not. Wetland hydroperiod during the breeding season averaged 6.42 weeks and ranged from 2-10 weeks (see Appendix 1). Vegetation heterogeneity within wetlands ranged from 1-3 with five wetlands earning a score of 1 (herbaceous cover), three wetlands earning a 2 (herbaceous and shrub cover), and four wetlands earning a score of 3 (herbs, shrubs, and tree coverage). Wetlands had a high diversity and abundance of herbaceous groundcover species including grasses, sedges, and flowers (e.g. various species of *Andropogon*, *Panicum*, *Spartina*, *Juncus*, *Ilex*, *Xyris*, *Rhynchospora*, *Eleocharis*, *Aesclepias*, *Rhexia*, *Drosera*, *Sagittaria*, *Pontedaria*, *Cladium*, and *Cyperus*). Shrubs included *Serenoa repens*, *Hypericum* spp., *Baccharis halimifolia*, *Cephalanthus occidentalis*, *Ludwigia* spp, and *Myrica cerifera*. Trees within wetlands were few and limited to individuals of *Nyssa sylvatica* and *Quercus laurifolia*; distance to canopy coverage was measured and tree species included those of xeric and mesic hardwood hammocks, predominantly *Quercus* spp.

For six of the seven species, the best model selected was significantly better than the intercept-only model ($p < 0.05$, Table 4). The remaining species (pig frog) was marginally significant ($p = 0.058$). Although AIC is a robust method for model selection (Burnham and Anderson 1998), I also employed Type 3 likelihood ratio tests to test which of the three selected factors (for each species) significantly affected the model (Table 5). For five species (*Anaxyrus terrestris*, *Gastrophryne carolinensis*, *Hyla*

gratiosa, *Lithobates capito*, and *L. grylio*), the factors composing the best model significantly affected the model; for *Pseudacris nigrita verrucosa*, only one of the two factors in the best model also significantly affected the model (Table 5).

The best model for the southern toad was one that incorporated distance to permanent water, distance to nearest wetland, and vegetation heterogeneity (Table 4). All other models had $\Delta AIC > 2.0$. A likelihood ratio test found all factors in the best model were also significant ($p \leq 0.038$, Table 5). Response plots were created for these significant factors and the resulting direction of the relationship suggests that southern toad occupancy decreases with increasing distance from permanent water (Table 5 and Appendix 1). While vegetation heterogeneity and distance to nearest wetland appear to affect occupancy in conjunction with distance to permanent water, there is no clear positive or negative relationship.

The best model for the eastern narrow mouth toad was one that incorporated only the average hydroperiod between the two sampling years (Table 4). This factor was also significant when using a likelihood ratio test ($p = 0.017$, Table 5). The next best significant model within $\Delta AIC < 2.0$ incorporated distance to permanent water with hydroperiod; this factor, however, was not significant with a likelihood ratio test ($p = 0.72$). The direction of the relationship suggests that eastern narrow mouth toad occupancy increases when hydroperiod is relatively short (2-8 weeks; Table 5 and Appendix 1).

The distance to nearest wetland was the only factor included in the best model for the barking treefrog (Table 4). All other models had $\Delta AIC > 2.0$. This factor was also significant when using a likelihood ratio test ($p = 0.034$, Table 5). The direction of the relationship suggests barking treefrog occupancy increases when distance to the next wetland is short (within 160 m; Table 5 and Appendix 1).

The best model for the Florida gopher frog was one that included distance to nearest wetland and fish presence/absence as factors (Table 4). All other models had

$\Delta AIC > 2.0$. A likelihood ratio test found all factors in the best model were also significant ($p \leq 0.001$, Table 5). The direction of the relationship suggests that Florida gopher frog occupancy increases when wetlands are nearer to other wetlands (within 160 m; Table 5 and Appendix 1). While fish presence appears to affect occupancy in conjunction with distance to nearest wetland, there is no clear positive or negative relationship.

Distance to canopy coverage (with and without the outlier at wetland G, Appendix 1) was the only factor included in the best model for the bullfrog (Table 4). This factor was not significant when using a likelihood ratio test ($p = 0.22$, Table 5). The next best significant model within $\Delta AIC < 2.0$ incorporated fish presence/absence along with distance to canopy coverage; this factor, however, was also not significant with a likelihood ratio test ($p = 0.18$). The direction of the relationship suggests a trend for the bullfrog to be positively associated with wetlands that are closer to canopy and support fish populations because the AIC method found these factors to be significantly better than the intercept-only model.

The distance to permanent water was the only factor included in the best model for the pig frog (Table 4), however the model was marginally significantly better than the intercept-only model ($p = 0.058$). Conversely, this factor was significant when using a likelihood ratio test ($p = 0.016$, Table 5). The direction of the relationship suggests pig frog occupancy increases with increasing distance (> 0.4 km; Appendix 1) to permanent water (Table 5).

The best model for the southern chorus frog was one that incorporated only the average hydroperiod between the two sampling years and vegetation heterogeneity (Table 4). Only vegetation heterogeneity was significant when using a likelihood ratio test ($p = 0.004$, Table 5). The next best significant model within $\Delta AIC < 2.0$ incorporated distance to nearest wetland with hydroperiod and vegetation heterogeneity (Figure 4); this additional factor, however, was not significant with a likelihood ratio test ($p = 0.59$;

Table 5). The direction of the relationship for the significant model suggests that southern chorus frog occupancy increases with increasing vegetation heterogeneity.

Discussion

My study suggests that a range of wetland and landscape characteristics resulting in a mosaic of wetlands are important in supporting amphibian diversity through a stepping-stone array. The models developed provide insight to the limited knowledge-base on the structure of a mosaic of wetlands in an area and its role in the factors influencing amphibian occupancy of wetlands. Species not occurring in all habitat types can be very informative when quantifying habitat value, and in this particular study, of the 14 frog species observed, seven were absent from four or more wetlands.

The southern toad appears to be influenced negatively by increasing distance to permanent water. Of the twelve wetlands, the southern toad was found at seven wetlands, four of which were 0.1-0.19 km from a permanent water source; the remaining three wetlands were 0.42-1.11 km and toads were not present at wetlands 0.97-1.35 km from permanent water. In part, proximity to permanent water appears important to the toad, perhaps because of its life history. They breed in both temporary and permanent aquatic habitats (Gibbons and Semlitsch 1991) and are unpalatable or toxic to many potential predators, including fish (e.g. Lefcort 1998). Following transformation and prior to emigration, juvenile southern toads forage for several weeks around the edge of the pond from which they emerged (Beck and Congdon 1999). Southern toad home range may encompass an area 1.6 km wide (Bogert 1947); they can travel further distances than frogs as they are better able to regulate water loss. Perhaps given their unpalatability and migration/dispersal abilities, they can afford to occupy wetlands closer to permanent water sources and risk occasional fish invasion during sheet-overflow events because of the advantage conferred by water permanency.

Eastern narrow mouth toad occupancy was significantly influenced by shorter hydroperiods. Female *G. carolinensis* deposit a small sheet of eggs on the water's surface in highly ephemeral pools of water (Wright 1932, Wright and Wright 1949, Gibbons and Semlitsch 1991). Larval development is rapid and complete metamorphosis has been reported to occur in 6–10 days (Anderson 1951) but can also occur 20–70 days after egg deposition (Wright 1932, Martof et al. 1980) and has been also been reported to reported complete metamorphosis in 30 days (Donnelly 1997). *G. carolinensis* is the only species in this study to metamorph so quickly and also the only one to be significantly affected by shorter hydroperiods. The eight wetlands occupied by breeding *G. carolinensis* had hydroperiods ranging from 14-56 days, five of which held water less than 35 days (Appendix 1), which coincides with its breeding phenology.

Barking treefrog occupancy was significantly negatively influenced by increasing distance to next nearest wetland. In part, distance to next nearest wetland appears important to the frog, likely because of its life history. Adult *H. gratiosa* do not migrate seasonally, but remain in the vicinity of breeding wetlands when not engaged in calling or reproduction in water (Neill 1952, 1958). Murphy (1994) reported movements of 100 m between breeding ponds by several males in Florida; of the twelve wetlands in my study, *H. gratiosa* only occurred where distance to next wetland was within 160 m. Murphy et al. (1993) suggest multiple ponds in the landscape should be protected to allow dispersal because *H. gratiosa* migrate among breeding sites.

Gopher frogs are considered Endangered, Threatened, or of Special Concern in all of the states within their range (Mount 1975, Martof et al. 1980, Moler 1992, Levell 1997). In thus study, *L. capito* occupancy was significantly negatively influenced by increasing distance to nearest wetland. Several migrations may occur throughout the breeding season resulting in the use of multiple wetlands for breeding, with males

arriving at reproductive sites prior to females and remaining there longer (Bailey 1991). While *L. capito* have consistently been reported to move long distances from breeding wetlands to upland retreats which is important for conservation efforts (one individual moved 2 km, Franz et al. 1988, see also Roznik et al. 2009), during the breeding season they may move among ponds in close proximity, which has been observed in other pond-breeding amphibians (Semlitsch 2008). Roznik et al. (2009) found support for this hypothesis in their study where radio-tagged adult frogs oriented toward breeding ponds within 300 m and an adult frog captured at one wetland was recaptured at a nearby pond the next year. *L. capito* in our study were only present at wetlands within 160 m of another wetland and our modeling results suggests that during the breeding season, *L. capito* occupancy increases in part when wetlands are nearer to other wetlands (within 160 m). Perhaps this is due to a confluence of unexplained reasons; *L. capito* might be affected at the within-pond level and thus if a wetland isn't suitable it would be beneficial to have other wetlands nearby.

Distances to canopy cover and fish presence were incorporated in the best models for the bullfrog; however, these factors were not significant when using a likelihood ratio test. Trend in the data exists however, for the *L. catesbeianus* to be positively associated with wetlands that are closer to canopy (generally within 20 m; Appendix 1) and also support fish populations. This finding could be explained by the increased transpiration rates of wetlands with high hardwood density nearby; if wetlands can withstand high transpiration rates and still support fish populations, the hydrology is likely also suitable for *L. catesbeianus* tadpoles. The time to metamorphosis for these frogs is among the longest (to confer greater fitness through larger sizes) and varies from a few months in the south in temporary wetlands to 3 yr in Michigan and Nova Scotia (Collins 1979, Bury and Whelan 1984) where they must over winter. Unlike many other frogs, bullfrogs can coexist with predatory fishes (Hecnar 1997) as tadpoles are

relatively immune to fish predation because of unpalatability (e.g. Walters 1975, Werner and McPeck 1994) and are one of only a few species likely to persist after fish invasion (Seale 1980).

The distance to permanent water was the only factor included in the best model for the pig frog and while only marginally significantly better than the intercept-only model, this factor was significant in a likelihood ratio test. A trend suggests pig frog occupancy increases with increasing distance (>0.4 km; Appendix 1) to permanent water. While *L. grylio* opportunistically use ephemeral wetlands, they are largely aquatic, typically remaining within permanent water habitats throughout the year (Wright 1932, Wright and Wright 1949, Lamb 1984) and tadpoles require comparatively longer to metamorphose [up to 365 days in Florida; (Donnelly 1997) and 365-730 days further north (Wright 1932, Wright and Wright 1949, Dundee and Rossman 1989)]. Wood et al. (1998) found that pig frogs tend to remain in one location when food and water conditions are suitable, but that substantial movement is possible when water conditions change. Thus, the importance of increasing distance to permanent water is perhaps just an artifact of expected natural fluctuations of amphibian populations and a prolonged drought especially during the latter stages of the study.

Southern chorus frog occupancy of wetlands was significantly positively influenced by an increasing degree of vegetative heterogeneity. At our study area, wetlands with the highest vegetative heterogeneity score were those with high diversity and abundance of herbaceous groundcover species including grasses, sedges, and flowers (e.g. *Andropogon* spp., *Spartina* spp., *Juncus* spp., *Rhynchospora* spp., *Eleocharis* spp., *Aesclepias* spp., *Rhexia* spp., *Drosera* spp., and *Cyperus* spp.), and presence of shrubs (e.g. *Serenoa* spp., *Hypericum* spp., *Baccharis* spp., *Cephalanthus* spp., *Ludwigia* spp., and *Myrica* spp.) within or directly surrounding the wetland, and presence of trees immediately adjacent to the wetland. Males of *P. n. verrucosa* are

secretive and call with their heads protruding above the water from locations where the vegetation is most dense, generally at the bases of grass tussocks or under overhanging grass and shrubs on the edges of wetlands (Einem and Ober 1956, Duellman and Schwartz 1958, Mount 1975, Gartside 1980). This preference contrasts with ornate chorus frogs (*Pseudacris ornata*) who call from open, exposed situations in the same locations (Schwartz 1957).

Ecosystem models aim to characterize the major dynamics of ecosystems, to understand systems and to allow predictions of their behavior (whether generally or in response to particular changes). No single natural scale at which ecological phenomena should be studied exists; systems generally show characteristic variability on a range of spatial, temporal, and organizational scales and life history adaptations such as dispersal and dormancy alter the perceptual scales of the species and the observed variability. Developing predictive models of these systems for habitat and species management is important, thus it is necessary to interface the disparate scales of interest of researchers studying these problems at different levels (Levin 1992). My study has investigated amphibian occurrence at wetlands using a combination of ecosystem scale (wetland variables) and broad scale (landscape level) characteristics and provided information from species life histories to explain the resulting significant ecological models.

In Florida, isolated wetlands are used as breeding habitat by at least 28 species of amphibian (Sudol et al. 2009). Of these, 14 species are obligates, meaning they breed exclusively in isolated wetlands. The presence of isolated wetlands is essential for these species to breed successfully. The remaining species use isolated wetlands opportunistically and have the ability to breed elsewhere. Increasing pressure placed on wetlands caused by low-density, sprawl-style urban development, agriculture, and

phosphate mining have severely reduced the number of wetlands in the United States and particularly Florida.

Under recent changes to federal regulations, many isolated wetlands that are hydrologically separated from waterways either by berms or great distances are no longer under federal protection. As a result of two Supreme Court decisions, a significant number of isolated wetlands throughout the United States lost protection under the Clean Water Act's Migratory Bird Rule stipulation (SWANCC 2001, Comer et al. 2005) and even more lost protection when federal authority over wetlands not directly connected (via surficial hydrologic connection) to "waters of the United States" were restricted (BenDor 2008). These narrow readings by the court increase pressure on local governments forcing them to plan for and regulate the effects of wetland conversions and subsequent relocations, often through the form of local or countywide stormwater ordinances (BenDor et al. 2008). This situation has increased the importance of well-formulated wetland regulations and ordinances at the state and local scale.

A major disturbance to isolated wetlands in central Florida is phosphate mining (FIPR 2010). The mining of phosphate for fertilizer is typically conducted using strip mining techniques including clearing the site of all vegetation, removal of soil, and mining the underlying phosphate matrix with draglines. Enormous draglines dig 10 m into the earth to get at the phosphate; strip mining may leave 20 m deep valleys interspersed with piles of cast earth, and the resulting landscape must be reclaimed (FIPR 2010). Following extraction of phosphate, the site is back-filled with sand separated from the phosphate ore. Because of this large-scale clearing, mining, and reclamation in central Florida, improvement of reclamation techniques is critical. State law requires that land disturbed by phosphate mining be restored to a useful condition, and sometimes reclamation where the ecological systems function as they did before the

mining (FIPR 2010). In the legislation creating the Florida Institute for Phosphate Research (FIPR) is the mission to study reclamation alternatives and technologies. Goals of FIPR include developing methods to improve wildlife habitat on reclaimed mined lands and facilitate recolonization by wildlife. To date, reclamation practices include contouring (land is reshaped to resemble pre-mining topography and drainage) and revegetation (replacement of plant communities which also support agricultural opportunities). Under current practice there is not a standardized, post-release, quantitative assessment of phosphate mine reclamation and restoration projects, but each is considered on a case by case basis according to the conditions contained in the permits (FIPR 2010). Establishing conservation and restoration goals that provide for high quality wetland and upland heterogeneity as a condition for reclamation release is critical.

In a given year, individual species metapopulation or patchy population dynamics are affected in part by environmental variables of ephemeral wetlands. Where and when species occupy areas of the landscape is of great importance to conservation biology, particularly when identifying areas for protection and management. The number of species within an area results from a complex interaction of resource availability, habitat complexity, biogeography, land-use history, and phylogenetic history (Dodd 2009). Because it is logistically challenging to estimate changes in absolute amphibian abundance across large areas over time, an excellent option is to measure the presence or absence of the species at a number of wetlands which is the proportion of area occupied (MacKenzie et al. 2006). Because small, isolated wetlands support a diverse array of amphibian species, produce large numbers of metamorphosing juveniles, and can function as stepping stones for dispersal and recolonization of extinct populations (Moler and Franz 1987, LaClaire and Franz 1991, Semlitsch and Bodie 1998), I have

attempted to elucidate the factors affecting individual species occupancy of a range of native, small, isolated wetlands in central Florida where wetland disturbance is high.

With the worldwide decline in amphibian species richness, conservation targets for amphibians have been a priority for resource managers and are well discussed in the literature. Amphibian conservation requires an integrated landscape approach to management, rather than solely a species-oriented approach (Dodd 2009) because of their complicated biphasic life-cycle. When attempting to conserve amphibian habitat, wetland breeding sites (core habitat), retreat sites, dispersal corridors, and meta/patchy population structure must be considered. Semlitsch and Jensen (2001) advanced the idea of core habitats for wetland breeding amphibians and suggest a core wetland should be surrounded by three areas of protection including the aquatic buffer zone, core habitat plus aquatic buffer zone, and a terrestrial buffer zone that is critical for feeding, growth, maturation, and maintenance of the juvenile and adult population, some of which lay eggs and overwinter in this zone. Dodd (2009) suggested this concept could also be expanded to include unique habitat including caves, rock faces, steeply sided slopes, and areas that restrict populations including waterfall spray zones and mountain tops.

Semlitsch (2000) suggested that as the distance between wetlands increases, the potential for migration and recolonization by amphibians decreases as well as the chance for recolonization by source populations from nearby wetlands. Furthermore, many pond-breeding amphibians show high site fidelity and return each breeding season to the same pond (Shields 1982) and do not emigrate long distances. In addition to considerations of distance to neighboring wetlands, it is important for regulatory agencies interested in protecting pond-breeding amphibians to consider wetland isolation and hydroperiod (Paton and Crouch 2002).

Beyond individual wetland conservation goals, however, should be considerations that include a mosaic of wetlands with different wetland and landscape characteristics, including several of the factors I measured in our study (distance to permanent water, hydroperiod, distance to nearest wetland, and vegetation heterogeneity). In average years, amphibians are equipped to handle specific breeding environments (e.g. whether it is a short hydroperiod, contains fish, near a permanent water source, or is far from neighboring wetlands). With unavoidable environmental variability, however, amphibians must work harder to find suitable breeding sites. Some amphibians require a variety of vegetative structure around a wetland (structure composition often more important than species composition); some require elevated calling sites, shallow emergent vegetation for cover, or woody debris to deposit eggs (Dodd 2009). Canopy cover is often important as it affects thermal regimes and many species do not breed in enclosed canopy. Spatial and temporal variations in rainfall patterns can have significant effects on amphibian breeding success since dry years reduce the chance of larval amphibians developing to metamorphosis, whereas excessively wet years increase the connectivity among wetlands and allow occupation by predatory fish (Babbitt and Tanner 2000, Barber 2001). Rainfall in Florida during 2004 was extensive, with four major named hurricanes (Hurricanes Charlie, Frances, Ivan, and Jeanne; NOAA 2010) passing over Florida, and slightly above average during 2005 when the study began. The following year, 2006, was characterized by infrequent rains and was the beginning of a severe two-year drought comprising two of the driest back-to-back calendar years Florida has experienced, dating back to 1932 (FDEP 2010). Thus, preserving or creating a mosaic of wetlands with varying wetland and landscape characteristics acts as a buffer to breeding amphibians during environmental fluctuations. Important for preserving and especially when restoring wetlands, it is necessary to implement designs that accommodate adult anti-predator behaviors and

adaptive habitat shifting (Petranka and Holbrook 2006); this data shows that this can be achieved by arrays of wetlands that vary markedly in hydroperiod, vegetative heterogeneity (structure) and spatial proximity. This mosaic approach is especially relevant to practices that disturb large areas where mitigation and restoration goals could include restoration of wetlands that provide each resident species with many potential breeding sites. Sites that contain one or only a few wetlands with similar characteristics (e.g. hydroperiod) may severely constrain the ability of adults to seek out high-quality habitats that have low densities of predators. Thus, a diverse array of wetlands on site increases spatiotemporal variability in predation risk and increases the likelihood that juveniles will be recruited annually into the adult population, which should enhance the long-term persistence of (patchy) populations (Petranka and Holbrook 2006).

Wetland-breeding amphibians have often been characterized as having strong site fidelity, low vagility, and metapopulation structure (Alford and Richards 1999, Smith and Green 2005). Although conservation guidelines have emphasized the need to establish habitats to support metapopulations (e.g. Semlitsch 2000), emerging research suggests some amphibians are more vagile and less philopatric than previously suspected (Petranka et al. 2004, Smith and Green 2005). An alternative to metapopulation structure at the local level is the existence of patchy populations where movements between wetlands occur at such high rates that local wetland populations do not develop a significant degree of demographic independence (Harrison 1991, McCullough 1996, Smith and Green 2005). Thus, when restoring wetlands, ecologists must decide on the appropriate number and spatial arrangement of habitats, which is strongly influenced by the nature of population organization at the local level. According to Petranka and Holbrook (2006) at sites where wetlands are in close proximity (e.g. <500 m apart), restoration success may be enhanced by creating spatial arrays of

wetlands that are designed to support patchy populations rather than metapopulations. For example, a metapopulation design would likely entail the installation of relatively few wetlands that are spaced the maximum distance apart to increase demographic independence. In contrast, a patchy population design would likely incorporate more wetlands, with many in close proximity to one another to facilitate adaptive habitat switching. At this scale, metapopulation designs will likely fail to establish local metapopulations (Smith and Green 2005). Instead metapopulation- or landscape-level conservation, in general, should be focused on dispersal among populations at spatial scales >1–10 km, longer periods of time, and on the importance of pond density and distributions, terrestrial connectivity, and isolation effects due to land use (Marsh and Trenham 2001, Semlitsch 2008).

Conclusions

My study suggests that a diverse range of wetland and landscape characteristics resulting in a mosaic of wetlands provides different habitat opportunities each year, favoring the long-term persistence of amphibian diversity. The models developed in this study provide insight to the limited empirical knowledge-base on the structure of a mosaic of wetlands in an area and its role in the factors influencing amphibian occupancy of wetlands. I concur with Snodgrass et. al. (2000) and Paton and Crouch (2002) that regulatory agencies should strive to maintain a diversity of wetlands with varying hydroperiods and minimal nearest-neighbor distances among wetlands and also with Petranka and Holbrook (2006) who advocate restoring wetlands as arrays that vary markedly in hydroperiod and spatial proximity to one another. Further, I suggest preservation and restoration of mosaics of wetlands with a wider variety of landscape and wetland characteristics including distance to permanent water and vegetation heterogeneity. In this system, the diversity of amphibian species supported by small, isolated, ephemeral wetlands probably relies on the wide environmental gradient the wetlands encompass.

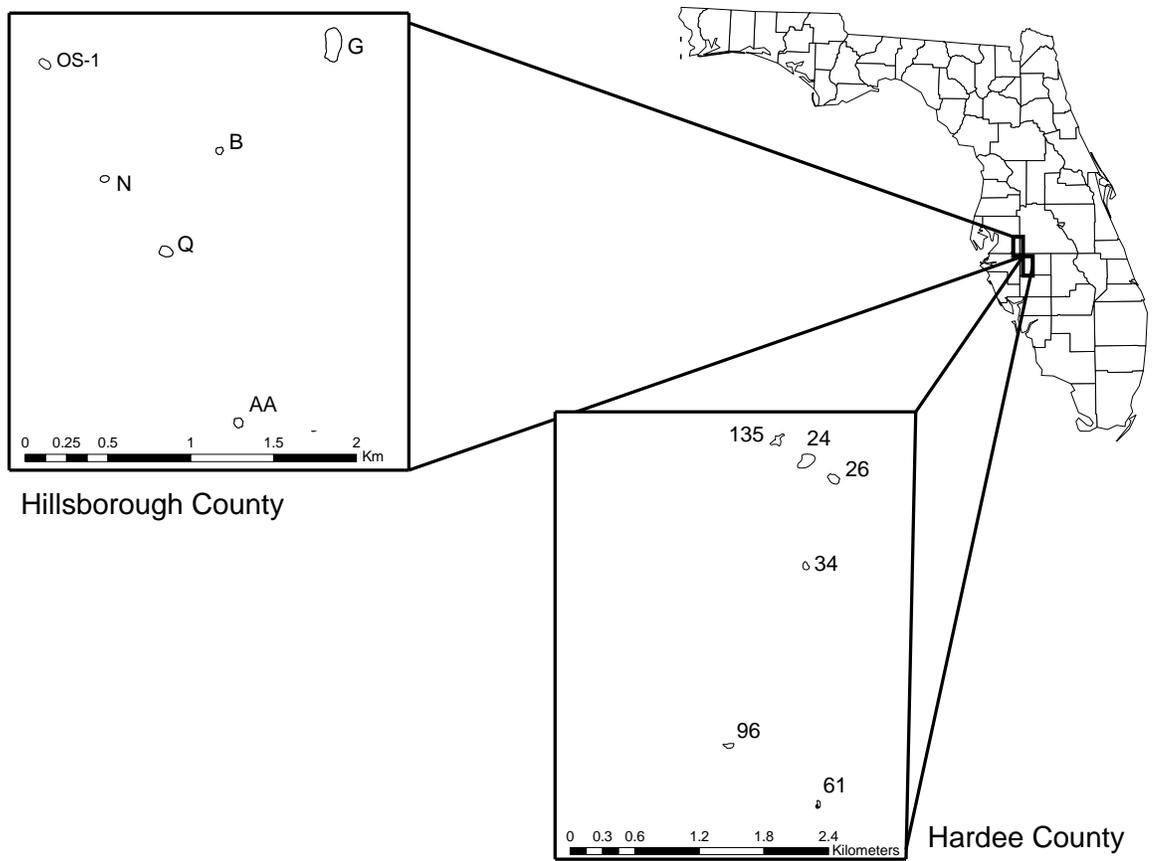


Figure 1. Map of study wetlands located in Hillsborough and Hardee Counties, Florida

Table 1. Wetland and landscape covariates used in modeling amphibian species occurrence.

| Variable name | Code | Description |
|-------------------------------|------|---|
| Area (ac) | Area | Area of each study wetland |
| Distance to Canopy (m) | Can | Linear distance from each wetland to a forested tree line |
| Permanent water distance (km) | PH20 | Linear distance from each study wetland to the nearest body of permanent water (river) |
| Nearest wetland distance (m) | NWL | Linear distance from each study wetland to the nearest non-study wetland |
| Fish presence/absence | Fish | Presence/absence of fish as determined using passive (unbaited traps) and aggressive (dip net) sampling |
| Vegetation | Veg | Level of vegetative heterogeneity within each study wetland. 1=herbs, 2=herbs and shrubs, and 3=herbs, shrubs, and trees |
| Hydroperiod | HP | Length of time surface water inundated each study wetland during the breeding season, averaged across study years |

Table 2. Number of successful sampling nights, percent of time frogloggers functioned, and total number of minutes of amphibian breeding vocalizations recorded per wetland.

| Site | Total # of sampling nights | Successful sampling evenings | Void sampling nights due to equipment failure | % void sampling nights | % of time recorders functioned | Total # of minutes recorded during peak breeding |
|-------|----------------------------|------------------------------|---|------------------------|--------------------------------|--|
| AA | 70 | 66 | 4 | 5.7% | 94.3% | 792 |
| B | 135 | 127 | 8 | 5.9% | 94.1% | 1524 |
| G | 66 | 48 | 18 | 27.3% | 72.7% | 576 |
| N | 135 | 110 | 25 | 18.5% | 81.5% | 1320 |
| OS-1 | 135 | 127 | 8 | 5.9% | 94.1% | 1524 |
| Q | 134 | 115 | 19 | 14.2% | 85.8% | 1380 |
| 24 | 135 | 121 | 14 | 10.4% | 89.6% | 1452 |
| 26 | 134 | 126 | 8 | 6.0% | 94.0% | 1512 |
| 34 | 134 | 112 | 22 | 16.4% | 83.6% | 1344 |
| 61 | 134 | 121 | 13 | 9.7% | 90.3% | 1452 |
| 96 | 135 | 119 | 16 | 11.9% | 88.1% | 1428 |
| 135 | 133 | 121 | 12 | 9.0% | 91.0% | 1452 |
| Total | 1480 | 1313 | 167 | | | 15756 |
| Ave | 123 | | | | 88.3% | |

Table 3. Presence or absence of each amphibian species at study wetlands, from June 2005-September 2006.

| Scientific Name | Common Name | AA | B | G | N | OS-1 | Q | 24 | 26 | 34 | 61 | 96 | 135 |
|-------------------------------------|---------------------------|-----------|-----------|----------|----------|----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| <i>Acris gryllus dorsalis</i> | Southern cricket frog | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Anaxyrus quercicus</i> | Oak toad | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Anaxyrus terrestris</i> | Southern toad | X | X | | X | | X | X | | | X | X | |
| <i>Gastrophryne carolinensis</i> | Eastern narrow-mouth toad | X | X | | | X | X | | | X | X | X | X |
| <i>Hyla cinerea</i> | Green treefrog | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Hyla femoralis</i> | Pinewoods treefrog | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Hyla gratiosa</i> | Barking treefrog | X | | X | | | X | | X | | | | |
| <i>Hyla squirella</i> | Squirrel treefrog | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Lithobates capito</i> | Florida gopher frog | | X | | | | | X | X | | | | |
| <i>Lithobates catesbeianus</i> | Bullfrog | | | | | | X | X | | X | X | X | X |
| <i>Lithobates grylio</i> | Pig frog | | X | | | | X | X | X | X | X | | X |
| <i>Lithobates sphenoccephala</i> | Southern leopard frog | X | X | X | X | X | X | X | X | X | X | X | X |
| <i>Pseudacris nigrita verrucosa</i> | Southern chorus frog | | | | X | X | X | X | | | | X | X |
| <i>Pseudacris ocularis</i> | Little grass frog | X | X | X | X | X | X | X | X | X | X | X | X |
| Total Number of Species | | 10 | 11 | 8 | 9 | 9 | 13 | 12 | 11 | 10 | 11 | 11 | 11 |

Table 4. Candidate models constructed from a generalized linear model of top three covariates against presence/absence of each species.

| Candidate Models | df | AIC | Δ AIC | L.Ratio | Chi ² | p |
|--|----------|--------------|-------------|--------------|------------------|---|
| <i>Anaxyrus terrestris</i> (southern toad) | | | | | | |
| PH2O+NWL+Veg | 4 | 10.00 | 0.00 | 16.30 | 0.003 | |
| PH2O+Veg | 3 | 12.30 | 2.30 | 12.00 | 0.007 | |
| PH2O | 1 | 15.27 | 5.27 | 5.03 | 0.025 | |
| Veg | 2 | 15.50 | 5.50 | 6.80 | 0.033 | |
| NWL+Veg | 3 | 16.44 | 6.44 | 7.86 | 0.049 | |
| PH2O+NWL | 2 | 16.91 | 6.91 | 5.39 | 0.068 | |
| NWL | 1 | 20.04 | 10.04 | 0.26 | 0.608 | |
| <i>Gastrophryne carolinensis</i> (eastern narrow mouth toad) | | | | | | |
| Ave HP | 1 | 11.82 | 0.00 | 7.46 | 0.006 | |
| PH2O+Ave HP | 2 | 13.69 | 1.87 | 7.59 | 0.022 | |
| NWL+Ave HP | 2 | 13.82 | 2.00 | 7.46 | 0.024 | |
| PH2O+NWL+Ave HP | 3 | 15.68 | 3.86 | 7.59 | 0.055 | |
| PH2O | 1 | 18.16 | 6.34 | 1.11 | 0.291 | |
| NWL | 1 | 18.53 | 6.71 | 0.75 | 0.387 | |
| PH2O+NWL | 2 | 19.39 | 7.57 | 1.88 | 0.390 | |
| <i>Hyla gratiosa</i> (barking treefrog) | | | | | | |
| NWL | 1 | 13.79 | 0.00 | 5.48 | 0.019 | |
| NWL+Ave HP | 2 | 15.79 | 2.00 | 5.48 | 0.064 | |
| NWL+Fish | 2 | 15.79 | 2.00 | 5.48 | 0.064 | |
| NWL+Ave HP+Fish | 3 | 17.79 | 4.00 | 5.48 | 0.140 | |
| Fish | 1 | 18.56 | 4.77 | 0.71 | 0.399 | |
| Ave HP | 1 | 18.90 | 5.11 | 0.37 | 0.541 | |
| Ave HP+Fish | 2 | 20.27 | 6.48 | 1.01 | 0.604 | |
| <i>Lithobates capito</i> (Florida gopher frog) | | | | | | |
| NWL+Fish | 2 | 6.00 | 0.00 | 13.50 | 0.001 | |
| NWL+Fish+Ave HP | 3 | 8.00 | 2.00 | 13.50 | 0.004 | |
| NWL | 1 | 15.11 | 9.11 | 2.38 | 0.123 | |
| Fish | 1 | 16.47 | 10.47 | 1.02 | 0.312 | |
| NWL+Ave HP | 2 | 17.08 | 11.08 | 2.42 | 0.298 | |
| Ave HP | 1 | 17.37 | 11.37 | 0.13 | 0.723 | |
| Ave HP+Fish | 2 | 18.24 | 12.24 | 1.26 | 0.534 | |
| <i>Lithobates catesbeianus</i> (bullfrog) | | | | | | |
| Can | 1 | 15.93 | 0.00 | 4.71 | 0.030 | |
| Can+Fish | 2 | 15.96 | 0.04 | 6.67 | 0.036 | |
| Fish | 1 | 17.38 | 1.46 | 3.26 | 0.071 | |
| NWL+Fish | 2 | 17.45 | 1.53 | 5.18 | 0.075 | |
| NWL | 1 | 17.67 | 1.75 | 2.96 | 0.085 | |
| Can+NWL | 2 | 17.70 | 1.77 | 4.94 | 0.085 | |
| Can+NWL+Fish | 3 | 17.92 | 1.99 | 6.72 | 0.081 | |
| <i>Lithobates grylio</i> (pig frog) | | | | | | |
| PH2O | 1 | 16.71 | 0.00 | 3.59 | 0.058 | |
| PH2O+Ave HP | 2 | 17.20 | 0.49 | 5.10 | 0.078 | |
| Ave HP | 1 | 19.93 | 3.22 | 0.37 | 0.545 | |
| PH2O+Ave HP+Veg | 4 | 19.99 | 3.28 | 6.31 | 0.177 | |
| PH2O+Veg | 3 | 20.48 | 3.77 | 3.82 | 0.282 | |
| Veg | 2 | 22.09 | 5.38 | 0.21 | 0.902 | |
| Ave HP+ Veg | 3 | 23.85 | 7.13 | 0.45 | 0.929 | |
| <i>Pseudacris nigrita verrucosa</i> (southern chorus frog) | | | | | | |
| Ave HP+Veg | 3 | 11.87 | 0.00 | 12.43 | 0.006 | |
| NWL+Ave HP+Veg | 4 | 13.58 | 1.71 | 12.72 | 0.013 | |
| NWL+Veg | 3 | 14.63 | 2.76 | 9.67 | 0.022 | |
| Veg | 2 | 14.82 | 2.95 | 7.48 | 0.024 | |
| Ave HP | 1 | 18.61 | 6.74 | 1.69 | 0.194 | |
| NWL | 1 | 20.10 | 8.23 | 0.20 | 0.655 | |
| NWL+Ave HP | 2 | 20.58 | 8.71 | 1.72 | 0.423 | |

PH2O - distance to permanent water Fish - presence/absence of fish Can - distance to canopy
 Ave HP - wetland hydroperiod length VEG - vegetation heterogeneity NWL - distance to nearest wetland

Bold models represent significant values as tested from Likelihood Type 3 tests

Table 5. Direction of the relationship [positive (+); no relationship (nr); negative (-)] for each covariate as it relates to individual species and the Likelihood Type 3 tests for top three covariates used in building candidate models.

| | Direction of Relationship | df | Log-Likelihood | Chi-Square | p |
|---|---------------------------|----|----------------|---------------|------------------|
| <i>Anaxyrus terrestris</i> (southern toad) | | | | | |
| Dist. to permanent water (m) | - | 1 | -4.222 | 8.444 | 0.003 |
| Vegetation heterogeneity | nr | 2 | -5.456 | 10.913 | 0.004 |
| Dist. to nearest wetland (m) | + | 1 | -2.151 | 4.302 | 0.038 |
| <i>Gastrophyne carolinensis</i> (eastern narrow mouth toad) | | | | | |
| Average Hydroperiod | - | 1 | -6.697 | 5.710 | 0.017 |
| Dist. to permanent water (m) | - | 1 | -3.908 | 0.133 | 0.715 |
| Dist. to nearest wetland (m) | + | 1 | -3.843 | 0.003 | 0.959 |
| <i>Hyla gratiosa</i> (barking treefrog) | | | | | |
| Dist. to nearest wetland (m) | - | 1 | -7.134 | 4.476 | 0.034 |
| Average Hydroperiod | + | 1 | -4.896 | 0.001 | 0.977 |
| Fish presence | - | 1 | -4.896 | 0.000 | 0.985 |
| <i>Lithobates capito</i> (Florida gopher frog) | | | | | |
| Dist. to nearest wetland (m) | - | 1 | -6.120 | 12.241 | <0.001 |
| Fish presence | nr | 1 | -5.538 | 11.077 | 0.001 |
| Average Hydroperiod | nr | 1 | 0.000 | 0.000 | 1.000 |
| <i>Lithobates catesbeianus</i> (bullfrog) | | | | | |
| Dist. to canopy (m) | - | 1 | -5.726 | 1.535 | 0.215 |
| Fish presence | + | 1 | -5.848 | 1.780 | 0.182 |
| Dist. to nearest wetland (m) | + | 1 | -4.982 | 0.048 | 0.827 |
| <i>Lithobates grylio</i> (pig frog) | | | | | |
| Dist. to permanent water (m) | + | 1 | -7.924 | 5.854 | 0.016 |
| Average Hydroperiod | - | 1 | -6.241 | 2.488 | 0.115 |
| Vegetation heterogeneity | nr | 2 | -5.601 | 1.209 | 0.546 |
| <i>Pseudacris nigrita verrucosa</i> (southern chorus frog) | | | | | |
| Vegetation heterogeneity | + | 2 | -7.291 | 10.998 | 0.004 |
| Average Hydroperiod | + | 1 | -3.317 | 3.051 | 0.081 |
| Dist. to nearest wetland (m) | - | 1 | -1.936 | 0.288 | 0.592 |

Bold values are significant

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Appendix 1. Wetland and landscape covariate values used in modeling amphibian species occurrence at twelve wetlands across west-central Florida, 2005 and 2006

| Wetland | Area (hectares) | Distance to canopy (m) | Distance to permanent water (km) | Distance to nearest wetland (m) | Fish presence | Vegetation heterogeneity ¹ | Hydroperiod ² (weeks) |
|---------|-----------------|------------------------|----------------------------------|---------------------------------|---------------|---------------------------------------|----------------------------------|
| AA | 0.21 | 127 | 0.19 | 87 | 0 | 1 | 5 |
| B | 0.1 | 152 | 0.42 | 44 | 0 | 1 | 5 |
| G | 1.3 | 853 | 0.97 | 82 | 0 | 1 | 10 |
| N | 0.14 | 46 | 0.19 | 358 | 0 | 3 | 9.5 |
| OS-1 | 0.51 | 183 | 0.40 | 200 | 0 | 2 | 6 |
| Q | 0.43 | 61 | 0.10 | 48 | 0 | 3 | 7 |
| 24 | 1.32 | 192 | 1.11 | 140 | 1 | 1 | 9.5 |
| 26 | 0.68 | 96 | 1.01 | 160 | 1 | 3 | 6 |
| 34 | 0.27 | 13 | 1.01 | 500 | 1 | 2 | 2 |
| 61 | 0.2 | 16 | 0.79 | 765 | 1 | 1 | 5 |
| 96 | 0.04 | 3 | 0.10 | 581 | 0 | 3 | 4 |
| 135 | 0.56 | 5 | 1.35 | 168 | 1 | 3 | 8 |

¹ vegetation heterogeneity of wetland; 1=herbaceous, 2=herbaceous and shrub coverage, 3=herbs, shrubs, and trees

² average hydroperiod (length of time surface water inundates the wetland) between June-September 2005 and 2006

About the Author

Jackie Guzy is from Chicago, IL and earned a B.S. Degree in Biology (marine science concentration) from the University of Tampa where she participated in honors research travel in Honduras (coral reefs) and Costa Rica (tropical ecology and conservation). At UT she published her research on effects of groundwater withdrawal on amphibians at Morris Bridge Wellfield. She obtained a M.S. Degree in Biology (ecology and evolution concentration) from the University of South Florida where she worked as a research assistant studying amphibian populations among wetlands affected by varying degrees of urbanization. She has twice presented research at the international Joint Meeting of Ichthyologists and Herpetologists conference and been recognized for “Outstanding Teaching by a Graduate Student”.