WETLAND PREDICTORS OF AMPHIBIAN DISTRIBUTIONS AND DIVERSITY WITHIN THE SOUTHEASTERN U.S. COASTAL PLAIN

by

ANNA ELIZABETH LINER

(Under the Direction of Steven Castleberry)

ABSTRACT

I examined the relationship between habitat variables and the distribution of amphibian species in 29 isolated wetlands in southwestern Georgia, USA. Wetlands were sampled for amphibians in the winter, spring, and summer using aquatic traps, dipnetting, PVC pipe refugia, and automated frog call recording devices (frogloggers). Distributions of 6 amphibian species were associated with wetland type, and distributions of 3 species were negatively associated with predatory fish presence. Cypress-gum wetlands supported a different amphibian assemblage than cypress savannas or marshes. I contend that the different assemblage in cypress-gum wetlands is related to water chemistry, water temperature, food resource, and predator diversity differences that result from the dense canopy cover and long hydroperiod characteristic of this wetland type. I recommend a minimum combination of aquatic funnel traps and frogloggers for future amphibian surveys to effectively document species richness within isolated wetlands in the region.

INDEX WORDS: amphibian, amphibian community, wetland, isolated wetland, habitat use, distribution, Georgia, Southeast

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Seasonally flooded, hydrologically isolated wetlands are a prevalent part of the landscape of the Coastal Plain of the southeastern United States and provide breeding or primary habitat for 36 amphibian species (Moler and Franz 1987, Petranka 1998). The majority of these species also are dependant on adjacent uplands for some part of their life cycle (Semlitsch and Jensen 2001). However, isolated wetlands can vary in a number of factors that may affect the ability of amphibian species to successfully colonize and/or breed within them. Wetlands can vary in hydroperiod (the number of days in a year that a wetland holds standing water), size, the extent and type of vegetation, depth, water chemistry, and the presence of vertebrate and invertebrate predators (Eason and Fauth 2001, Hecnar and M'Closkey 1998, Rowe and Dunson 1993, Snodgrass et al. 2000a). In addition, certain landscape features, such as roads, rivers, and inhospitable land cover types, may act as barriers to amphibian movement and can limit the ability of amphibians to utilize upland habitats for foraging and hibernation, as well as hinder their dispersal to neighboring wetlands (Hecnar and M'Closkey 1998, Lehtinen et al. 1999, Semlitsch and Bodie 2003).

In addition to being highly variable habitats, isolated wetlands are highly productive biologically. In the southeastern United States, isolated wetlands have been linked with high plant, invertebrate, and amphibian biodiversity (Semlitsch et al. 1996, Sharitz 2003, Sutter and Kral 1994). In addition, these wetlands provide important habitat for federal and state protected species including: the federally threatened flatwoods salamander (*Ambystoma cingulatum*), the federally endangered pondberry (*Lindera melissifolia*) and American chaffseed (*Schwalbea americana*), and the Georgia protected striped newt (*Notophthalmus perstriatus*), among others. However, these biologically important habitats currently receive little legal protection. The SWANCC (*Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers*) ruling of the U.S. Supreme Court in 2001 removed almost all federal protection for isolated, intrastate wetlands. At this time, most states do not provide regulations that adequately protect the biological and hydrologic functions of these wetlands (Christie and Hausmann 2003). In Georgia, there are no state regulations that protect isolated wetlands, potentially placing these valuable habitats in jeopardy. Baseline information on amphibians and other taxa in unaltered isolated wetlands is needed in order to inform policy on these important and biologically productive habitats, as well as to serve as references for future wetland mitigation and restoration efforts.

In this study, I investigated the relationship between wetland and upland characteristics and amphibian diversity and distribution within 29 isolated wetlands in the southeastern Coastal Plain of the United States. The goals of this study were to: (1) provide baseline data on amphibian communities in isolated wetlands in southwestern Georgia, (2) determine which factors associated with isolated wetlands are most important in determining species richness and the presence/absence of individual species, and (3) evaluate the effectiveness of different capture techniques for future amphibian studies and monitoring programs.

This thesis is organized in manuscript style, with chapters 2 and 3 in the format of journal articles, which will be later submitted to scientific journals. Chapter 1 is an introduction to the study with a literature review. Chapter 2 is an investigation of the relationships between amphibian distributions and wetland habitat variables and will be submitted to the journal Wetlands. Chapter 3 is a comparison of the effectiveness of the different amphibian capture methods used during this study and will be submitted to the Journal of Applied Herpetology. Chapter 4 provides summaries and conclusions from the previous chapters.

LITERATURE REVIEW

Southeastern Amphibians and Isolated Wetlands

A total of 147 amphibians is known to live within the southeastern United States, making it the most diverse region in the nation for this group (Dodd 1997). Within the region, isolated wetlands of the Coastal Plain with a temporary hydroperiod are an especially species-rich habitat and provide principal breeding habitat for 10 anuran and 5 salamander species and are used facultatively by an additional 21 species (Moler and Franz 1987, Petranka 1998). However, while isolated wetlands are critical to the survival of many species in the Coastal Plain, most amphibians inhabit wetlands only during brief annual breeding periods and spend the remainder of the year in upland habitats foraging or hibernating (Semlitsch and Jensen 2001). In southwest Georgia, amphibians breed year-round, but individual species breed during particular times of the year. Little is known about the terrestrial phase of amphibian life cycles, because the majority of species spend this part of their life cycle underground and most research has focused on breeding amphibians, which are easier to detect and capture (Semlitsch and Jensen 2001).

Habitat Loss and Southeastern Reptiles and Amphibians

Since the mid-1980s, herpetologists have been concerned about apparent global declines in amphibian populations (Wake 2003). Recent research has implicated several factors in population declines, including: habitat destruction and alteration, climate change, chemical contaminants, diseases, parasites, invasive species, and commercial overexploitation (Semlitsch 2003). In a review of the literature regarding the declines of individual southeastern species, Dodd (1997) found that habitat alteration and loss were the most commonly implicated factors.

The reduction in the distribution of the longleaf pine ecosystem is a startling example of how the southeastern landscape has changed since European settlement. It is estimated that only 2 percent of the original 24 to 35 million ha of longleaf pine forest remains in the coastal plain (Noss 1989). Within Georgia, the extent of longleaf pine forest was reduced by 91 % between 1936 and 1997, leaving only 152,300 of the 1.7 million ha known to exist in the 1930s (Smith et al. 2000). In addition, Smith et al. (2000) predicted that the amount of longleaf pine forests in Georgia will continue to decrease because much of the remaining acreage is privately owned (83 %) and there are few incentives to maintain and plant longleaf pine.

Southeastern wetlands have suffered similar dramatic levels of decline. Hefner et al. (1994) estimated that approximately 900,000 ha of wetlands were lost between 1974 and 1983 in the region. In the continental United States, an estimated 50% of the wetlands present at the time of European colonization have since been destroyed (Dahl 1990). The effects of this extensive historical upland and wetland habitat loss on southeastern amphibian populations is unknown, and little baseline data on populations exists within the region to assess future losses (Dodd 1997).

Wetland Characteristics and Amphibian Distributions

The presence of amphibian species within individual wetlands can be highly variable, both spatially and temporally, in a landscape (Semlitsch et al. 1996, Skelly et al. 1999). However, due to the importance of both terrestrial and aquatic habitats to the life cycles of most wetland-associated amphibians in the Southeast, a variety of wetland and upland factors have the potential to affect amphibian distributions. Several studies have sought to determine the relative importance of different wetland and surrounding upland characteristics on amphibian community structure through observational studies. These studies have demonstrated that local wetland characteristics such as the presence of predatory amphibians (Knutson et al. 2004, Resetarits and Fauth 1998), canopy cover (Skelly et al. 1999, Werner and Glennemeier, 1999), water depth (Hecnar and M'Closkey 1998, Laan and Verboom 1990), fish presence/absence (Hecnar and M'Closkey 1997, Snodgrass et al. 2000a), hydroperiod (see Pechmann et al. 1989, Snodgrass et al. 2000b, among others), wetland size (Findlay and Houlahan 1997, Laan and Verboom 1990), and water chemistry variables, such as conductivity, pH, and metal concentrations (Eason and Fauth 2001, Hecnar and M'Closkey 1998, Rowe and Dunson 1993), have the potential to influence amphibian species richness and composition within wetland communities. In addition, species richness and presence/absence have been linked to terrestrial factors surrounding isolated wetlands such as the extent of the surrounding forest (Guerry and Hunter 2002, Herrmann et al. 2005, Porej et al. 2004) and surrounding agricultural habitat (Brodman et al. 2003), forest composition (Russell et al. 2002), distance to the nearest forest (Guerry and Hunter 2002, Knutson et al. 2004, Laan and Verboom 1990), paved road density (Findlay and Houlahan 1997, Findlay and Lenton 2001, Lehtinen et al. 1999), the distance to the nearest paved road (Hecnar and M'Closkey 1998), the distance to the nearest wetland (Lehtinen et al. 1999, Laan and

Verboom 1990, Russell et al. 2002), percentage of surrounding wetland habitat (Houlahan and Findlay 2003), and the number of surrounding wetlands (Brodman et al. 2003, Hecnar and M'Closkey 1998, Porej et al. 2004).

Recent studies have looked at wetland-specific and landscape-level factors simultaneously (Hecnar and M'Closkey 1998, Herrman et al. 2005, Knutson et al. 2004, Kolozsvary and Swihart 1999, Laan and Verboom 1990, Lehtinen et al. 1999, Weyrauch and Grubb 2004), but these have yielded conflicting results suggesting regional differences in factors regulating amphibian distributions. For example, in a study in southwestern Minnesota, Lehtinen et al. (1999) found a significant correlation between amphibian species richness and distances between wetlands, whereas a study in southwestern Ontario (Hecnar and M'Closkey 1998) did not. Similarly, Eason and Fauth (2001) found that anuran species richness in temporary ponds within the Francis Marion National Forest, South Carolina, was related to a different set of factors (pH, hydroperiod, and fish diversity) than was found for a similar set of wetlands 250 km away in North Carolina (hydroperiod, interspecific competition, and salamander predation). In addition, some studies have found wetland-level factors to be most important (Knutson et al. 2004, Weyrauch and Grubb 2004), while other studies (Lehtinen et al. 1999) have determined that landscape-level factors are more important in influencing amphibian communities. Given the apparent regional differences in these factors and their importance in managing wetlands and surrounding uplands for amphibian diversity, I investigated the nature and scope of relationships between wetland-specific and landscape-level factors and amphibian distributions within a group of southeastern wetlands.

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CHAPTER 2

AMPHIBIAN DISTRIBUTIONS IN ISOLATED WETLANDS WITHIN A LONGLEAF PINE-DOMINATED LANDSCAPE[1]

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[1] Liner, A.E., L.L. Smith, S.B. Castleberry, S.W. Golladay, and J.W Gibbons. To be submitted to Wetlands.

ABSTRACT

We examined the relationship between wetland habitat variables and the distribution of amphibian species in 29 relatively undisturbed isolated wetlands in southwestern Georgia, USA. Wetlands were sampled for amphibians in the winter, spring, and summer using aquatic traps, dipnetting, PVC pipe refugia, and automated frog call recording devices (frogloggers). Mean amphibian species richness among study wetlands was 12.7 ± 2.7 species (range 7-18). Principal components analysis revealed strong correlations between wetland types and habitat variables suggesting that wetland types varied fundamentally in hydroperiod, size, depth, numbers of amphibian predators, densities of surrounding paved roads, percentage of surrounding forest, and wetland isolation. Distributions of 6 amphibian species were associated with wetland type, a designation based on wetland vegetation and soil characteristics. Distributions of 3 species were negatively associated with predatory fish presence. Detrended correspondence analysis of amphibian species compositions revealed that one wetland type, cypress-gum wetlands, supported a different amphibian assemblage than cypress savannas or marshes. Our research highlights the importance of wetland variation in promoting amphibian diversity in the region. Future amphibian monitoring and research efforts in Georgia should account for both wetland type and fish presence when conducting amphibian surveys.

Key Words: amphibians, isolated wetlands, community composition, Georgia, longleaf pine

INTRODUCTION

Seasonally flooded, hydrologically isolated wetlands are a prevalent feature of the landscape of the Coastal Plain of the southeastern United States (Sutter and Kral 1994). Isolated wetlands within this region support a large number of plant and animal species, including a unique and diverse amphibian fauna, providing critical breeding habitat for 10 anuran and 5 salamander species (Moler and Franz 1987, Semlitsch et al. 1996, Sharitz 2003, Sutter and Kral 1994). Southeastern Coastal Plain isolated wetlands are also used facultatively by at least 21 additional amphibian species (Moler and Franz 1987, Petranka 1998). However, isolated wetlands are a highly threatened habitat, receiving little legislative protection and high levels of development pressure (Christie and Hausmann 2003, Tiner 2003). Wetland loss has been particularly pronounced in the Southeast, and has accounted for the majority of national wetland loss in recent decades (Hefner and Brown 1985). The extent of isolated wetland loss in the region is unknown (Sutter and Kral 1994), however, it has undoubtedly been extensive, as these wetlands have historically been afforded less legal protection than coastal and larger inland water bodies (Petrie et al. 2001, Semlitsch 2003, Semlitsch and Bodie 1998).

In addition to wetland habitat loss, amphibians in many parts of the world are threatened by upland habitat loss and fragmentation. Isolated wetlands within the southeastern Coastal Plain were historically surrounded by longleaf pine (*Pinus palustris*) forests (LaClaire 1997). Longleaf pine forest is considered one of the most critically endangered ecosystems in the United States, and it is estimated that only 2% of the original 24 to 35 million ha of forest remains (Noss 1989). In the United States, the majority of wetland-breeding amphibians exhibit a biphasic lifestyle, requiring aquatic habitats for breeding and terrestrial habitats for foraging and overwintering (Dodd 1997, Semlitsch 1998, Semlitsch 2003). In addition, it is hypothesized that amphibian populations in isolated wetlands exist in complex metapopulations in which infrequent dispersals from neighboring wetlands promote genetic exchange and recolonization after local extinctions (Semlitsch 2003, but see Smith and Green 2005). Thus, while little is known about the impacts of this extensive wetland and upland habitat loss on southeastern amphibian populations, it is likely that they have been far reaching (Dodd 1997).

A variety of wetland and upland factors have the potential to affect amphibian distributions. For instance, any factor that separates amphibians from either wetland or upland habitats, or limits the extent of suitable terrestrial habitat available has the potential to directly impact amphibian survival (Semlitsch 2003). Roads can directly reduce amphibian mobility in a landscape through increased mortality (Fahrig et al. 1995), and may act indirectly as a movement barrier by behavioral road avoidance (Gibbs 1998). Certain habitat types also can serve as barriers to movement due to the susceptibility of amphibians to desiccation. For example, Rothermel and Semlitsch (2002) found that dispersing juvenile spotted (*Ambystoma maculatum*) and small-mouthed (*Ambystoma texanum*) salamanders exhibited greater water loss and moved shorter distances in experimental runs in field habitats than in forest habitats, suggesting that fields were a more stressful environment for juveniles emigrating from natal wetlands. In addition to the connectivity of the surrounding landscape, the number of wetlands in an area and the distances between them can directly influence the distributions and persistence of amphibian populations by creating more opportunities for immigration (Berven and Grudzien 1990, Joly et al. 2001, Laan and Verboom 1990, Reh and Seitz 1990). Futhermore, local wetland characteristics such as amphibian predators and competitors (Knutson et al. 2004; Morin 1981, 1983; Resetarits and Fauth 1998), depth (Hecnar and M'Closkey 1998, Laan and Verboom 1990), hydroperiod (see Pechmann et al. 1989, Snodgrass et al. 2000a, among others), wetland size (Findlay and Houlahan 1997, Laan and Verboom 1990), and water chemistry variables such as conductivity, pH, and metal concentrations (Eason and Fauth 2001, Hecnar and M'Closkey 1998, Rowe and Dunson 1993) have the potential to influence amphibian species richness and composition within wetland communities.

Wetland canopy cover and fish presence have been shown to negatively affect amphibian diversity and abundance in other regions (Hecnar and M'Closkey 1997a, Porej and Hetherington 2005, Skelly et al. 1999, Werner and Glennemeier 1999). Canopy cover can have a profound effect on the wetland environment by creating biologically relevant differences in temperature, water chemistry, and productivity (Battle and Golladay 2001, Werner and Glennemeier 1999). Similarly, fish predation can influence amphibian community composition through direct extirpation of amphibian species (Baber 2001, Hamer et al. 2002, Hecnar and M'Closkey 1997a, Kurzava and Morin 1998, Porej and Hetherington 2005), indirect mortality through costs associated with anti-predator behaviors (Semlitsch 1987), reversing competitive outcomes between species through selective predation (Walls et al. 2002, Werner and McPeek 1994), and adult avoidance of breeding sites with predators (Binckley and Resetarits 2002, Resetarits and Wilbur 1989). Differences in the ability of individual species to persist with fish have been attributed to differences in the existence and effectiveness of anti-predator defenses. Species that are large, unpalatable, or exhibit predator avoidance behaviors tend to be less susceptible to fish predation and are more commonly found in wetlands with fish (Kats et al. 1988, Semlitsch and Gibbons 1988, Hecnar and M'Closkey 1997a). However, few studies have examined the effects of fish or canopy cover on amphibian communities in southeastern isolated wetlands.

Isolated wetlands in southwestern Georgia consist of limesink depressional wetlands formed by the subsidence of underlying limestone deposits (Sutter and Kral 1994). Wetlands in the region are highly variable in size, hydrology, water chemistry, and dominant vegetation (Kirkman et al. 2000). Kirkman et al. (2000) identified three primary wetland types in southwestern Georgia based on soil and vegetation characteristics. These wetland types vary widely in canopy cover, which in conjunction with soil characteristics, cause subsequent differences in dissolved oxygen levels, water chemistry and temperature, understory vegetation, hydroperiod, and invertebrate abundance and diversity (Kirkman et al. 2000, Battle and Golladay 2001).

The long-term persistence of fish in isolated wetlands is prevented by the temporary hydroperiods of these water bodies. However, periods of heavy rain result in over-land sheet flow that can connect isolated wetlands both with each other and with permanent wetlands, streams, and ditches that serve as sources for fish colonization (Freeman and Freeman 1992). Common fish colonists include pirate perch (*Aphredoderus sayanus*), eastern mosquitofish (*Gambusia holbrooki*), and several centrarchid (Family Centrarchidae) and ictalurid (Family Ictaluridae) species (Freeman and Freeman 1992; A. Liner, personal observation).

We examined the relationships between wetland- and landscape-scale factors and amphibian community composition in a relatively undisturbed longleaf pine-dominated landscape. In particular, we documented the distributions of individual amphibian species in naturally occurring wetlands of different types and with or without fish. Our ultimate objective was to provide a baseline understanding of how these factors influence amphibian distributions to guide future amphibian monitoring and wetland mitigation and restoration efforts in the region.

METHODS

Study Area

This study was conducted on Ichauway (31° 13' 16.88" N and 84° 28' 37.81" W), an 11,800 ha private reserve that serves as the outdoor laboratory of the Joseph W. Jones Ecological Research Center. The property is located in Baker County, Georgia, within the Gulf Coastal Plain and the Dougherty Plain physiographic province (Figure 2.1). The site is primarily composed of 70-90-year-old, second-growth longleaf pine forest interspersed with 98 shallow limesink wetlands ranging from 0.2 - 76.5 ha. Kirkman et al. (2000) characterized wetlands in the region into three basic types based on vegetation and soil characteristics. Grass-sedge marshes are characterized by coarse sandy soils, an open overstory, and an understory dominated by dense panic grasses (*Panicum* spp.) and cutgrass (*Leersia hexandra*). Cypress savannas exhibit finer textured sandy soil underlain by a layer of clay, a relatively open pond cypress (*Taxodium ascendens*) overstory, and an understory of panic grasses and broomsedge (*Andropogon virginicus*). Cypress/gum swamps have thick organic soils and a dense overstory comprised of pond cypress and swamp tupelo (*Nyssa biflora*) with virtually no understory or midstory vegetation (Battle and Golladay 2001, Kirkman et al. 2000). Wetlands within the site vary considerably in hydroperiod, which is dependent upon annual rainfall patterns, as well as morphological characteristics of individual wetlands (Battle and Golladay 2001). Amphibian breeding activity within the wetlands occurs year-round, but involves different species at different times of the year.

Field Methods

Twenty-nine wetlands on the property were selected for study based on the availability of long-term hydroperiod data. These sites included 10 marshes, 7 cypress savannas, 11 cypress/gum swamps, and 1 wetland of mixed marsh/cypress savanna habitat. Amphibian sampling at wetlands was conducted in summer (June 23 - August 20, 2004), winter (December 17, 2004 - February 9, 2005), and spring (March 15 - May 21, 2005). A combination of five sampling methods was used at all wetlands. Dipnet surveys were conducted using a square-frame dip net (36 x 38 cm, 5 mm mesh) and consisted of a single visit to a study wetland per sampling period. The number of 1 m sweeps was scaled according to wetland perimeter as follows: small wetlands (0-500 m) 50 sweeps, medium wetlands (500-1500 m) 100 sweeps, and large wetlands (>1500 m) 200 sweeps. Sweeps were distributed equally around the wetland perimeter and among all shallow (< 0.5 m) microhabitats. Anuran call surveys were conducted using automated recording devices (frogloggers), as described in Dodd (2003). Frogloggers were placed at the wetland edge and programmed to record 1 minute per hour between 2000 and 0700 hours for three consecutive nights during each sampling period. Commercial crayfish traps (Johnson and Barichivich 2004) and funnel traps were set in wetlands for 6 consecutive nights and checked every 2 days during each sampling period. Crayfish traps were constructed of plastic-coated 2.5 cm hexagonal mesh with a plastic-coated rectangular wire mesh (2.5 x 1.25 cm) lid and neck. Five crayfish traps were distributed evenly around the wetland perimeter at a depth of ca. 20 cm. Funnel traps were double-ended and were constructed from aluminum window screen (as described in Heyer et al. 1994) and contained a styrofoam float that kept the funnels submerged just below the surface. To avoid a bias in the timing of trapping, wetlands were randomly sorted into trapping weeks within a sampling period. Funnel traps were placed every 50 m parallel to the bank at a water depth of ca. 0.25 m. The number of funnel traps was scaled to wetland size; between 2 and 30 funnel traps were used in each wetland.

Amphibians captured in aquatic traps and dipnet surveys were identified and counted in the field and released. Representative amphibian larvae that could not be identified in the field were raised in the lab to metamorphosis or euthanized with chloretone solution, preserved in 10% buffered formalin, and identified from appropriate keys (Altig 1970, Altig et al. 1998). Larvae of the spring peeper (*Pseudacris crucifer*), southern chorus frog, (*Pseudacris nigrita*), and upland chorus frog (*Pseudacris feriarum*) are similar in appearance and there are currently no adequate keys to distinguish between these species. Therefore, only data from locations from which larvae of these species were successfully reared and identified or adults were observed are reported. Fish incidentally caught in traps or during dipnet surveys were identified to the lowest taxonomic classification possible in the field, and representatives of each taxon were euthanized with MS 222 and preserved in 10% formalin.

Polyvinylchloride (PVC) pipes were used to detect adult hylid frogs (Moulton et al. 1996). One-meter segments of open-ended opaque, schedule 40 white PVC pipe (5 cm inside diameter) were inserted upright into the ground at 50 m intervals around the perimeter of each wetland. Pipes were deployed approximately 1 month before the first sampling period to give frogs time to colonize them and were left in the same location for the duration of the study. Pipes were checked at the beginning and end of each sampling period, and occupant frogs were identified to the species level and counted. Because the pipes serve as a diurnal refuge for frogs (Heyer et al. 1994), frogs were released back into the pipes after all animals in a pipe were recorded.

Water depths were measured to the nearest 0.01 m at staff gauges positioned in the deepest point of each wetland. Short-term (study period) and long-term (5 years preceding the study period) hydroperiod scores for each wetland were derived by calculating the percentage of days with water to the number of days measured. PH was measured at each wetland concurrent with aquatic trapping using a hand-held Hanna Instruments HI9812 pH-EC-TDS meter (Hanna Instruments, Woonsocket, Rhode Island, USA).

GIS Methods

Land cover and road data digitized from 2002 aerial photos (scale: 1:12,000) were obtained from the Joseph W. Jones Ecological Research Center and updated to include all land management manipulations conducted previous to the study using ArcGIS version 9.1 (ESRI, Redlands, California, USA). Additional land cover beyond the Ichauway boundary was digitized from 2002 aerial photos. To determine the characteristics of the landscape surrounding each study wetland, buffers were created at 3 distances from the edge of each wetland: 200 m, 500 m, and 1000 m. These distances were chosen to incorporate known mean and maximum terrestrial movements of southeastern amphibians (Dodd 1996; Semlitsch 1981, 1983, 1998). Within each buffer, the percentage of open habitat, which included all agricultural areas and non-forested terrestrial areas, was calculated. The total density of paved roads was also determined by summing the total length of roads within each wetland buffer. Wetland densities were determined by counting the total number of wetlands within each buffer.

Data Analysis

Principal Components Analysis (PCA) was used to examine relationships among habitat variables at the 29 wetland sites. The number of axes retained for interpretation was determined by the broken stick criterion (McCune and Grace 2002). Habitat variables were square root (wetland density 1 km), inversely (distance to nearest road), arcsine (% open habitat at all buffer sizes, short-term hydroperiod scores, paved road density 1 km, wetland density 500 m), or log (Area) transformed prior to analysis to meet the assumption of multivariate normality. For some variables (wetland density 200 m, paved road density 200 m and 500 m) it was not possible to meet assumptions of normality. These variables were removed from the analysis.

Detrended Correspondence Analysis (DCA) was used to determine if patterns existed in the species composition of amphibians present at wetlands. DCA is an unconstrained eigenvector ordination technique that corrects for the distortions common in most other ordination techniques and is effective for presence/absence data (Hill and Gauch 1980). DCA uses a chi-square distance metric to maximize the correspondence between species and sample scores (McCune and Grace 2002). Both PCA and DCA were conducted using PC-ORD for Windows Version 4.01 (MjM Software Design, Gleneden Beach, Oregon, USA). All other analyses were performed in SAS Version 8.2 (SAS Institute, Cary, North Carolina, USA).

Differences in anuran and salamander species richness among wetland types and wetlands varying in fish presence were examined using a one-way Analysis of Variance. When significant differences existed among groups, posthoc Tukey's HSD was used to identify individual group differences. We compared the frequency of occurrence of each species among wetland types and among wetlands with and without fish using Fisher's exact tests.

RESULTS

A total of 17,748 captures of 25 amphibian species was recorded over the study period. Larvae or metamorphs were detected for 21 of the 25 species. Larvae were not observed for the two-toed amphiuma (*Amphiuma means*), dwarf siren (*Pseudobranchus striatus*), pig frog (*Rana grylio*), and greater siren (*Siren lacertina*). Mean species richness across all wetlands was 12.7 ± 2.7 species (range 7-18). The pine woods treefrog (*Hyla femoralis*), southern leopard frog (*Rana sphenocephala*), and squirrel treefrog (*Hyla squirella*) were found in all 29 wetlands. The eastern narrow-mouthed toad (*Gastrophryne carolinensis*), green treefrog (*Hyla cinerea*), ornate chorus frog (*Pseudacris ornata*), southern chorus frog, and southern cricket frog (*Acris gryllus*) were commonly observed in 22, 27, 22, 26, and 25 wetlands, respectively. Rarely encountered species included the gopher frog (*Rana capito*), which was observed in only 1 wetland, and the dwarf salamander (*Eurycea quadridigitata*), which was observed in only 3 wetlands. The federally threatened flatwoods salamander (*Ambystoma cingulatum*) and Georgia protected striped newt (*Notophthalmus perstriatus*), though previously recorded in some study sites (L. Smith, unpublished data; J. Jensen, pers. comm.), were not observed in this study.

A total of 12 fish species were captured in 10 of the 29 wetlands (Table 2.2). Large predatory species, including catfish and centrarchids, were found in 6 of the 10 wetlands. These wetlands were primarily cypress/gum swamps, although 2 cypress savannas also supported large predatory fish. Large predatory fish were not found in any of the marshes studied. Two cypress savannas, one marsh, and one cypress/gum swamp had populations of eastern mosquitofish as the sole fish species.

Habitat Characterization

Habitat characteristics varied among wetland types (Table 2.1). In general, cypress savannas were smaller, shallower, shorter in hydroperiod, and supported fewer predatory amphibian species than marshes and cypress/gum swamps. Cypress savannas also tended to be closer to paved roads and to have greater densities of surrounding isolated wetlands and paved roads. Marshes were characterized by intermediate hydroperiods, intermediate numbers of predatory amphibians, and intermediate densities of surrounding wetlands. On average, marshes were surrounded by larger areas of open habitat than the other wetland types, although the percentage of open habitat surrounding most marshes was still relatively small (< 30 %). Cypress/gum swamps displayed the longest hydroperiods and largest number of predatory amphibians and tended to be more isolated from other wetlands than either cypress savannas or marshes.

The PCA identified several relationships between habitat variables and wetland types. The first two axes of the PCA explained 61% of the variation in the habitat data (Figure 2.2). Additional axes were not retained for interpretation based on the broken-stick criterion. Axis 1 represents a gradient from shallow, small wetlands of short hydroperiod that are in close proximity to other wetlands and roads to large, deep, wetlands of longer hydroperiod that are far from paved roads and isolated from other wetlands. Short-term hydroperiod ($r^{2} = 0.62$), area ($r^{2} = 0.48$), long-term hydroperiod ($r^{2} = 0.43$), predatory amphibians ($r^{2} = 0.36$), average pH ($r^{2} = 0.19$), and maximum depth ($r^{2} = 0.50$), were positively correlated with the first axis, while paved road density at the 1 km buffer distance ($r^{2} = 0.62$), the proximity to the nearest paved road (the inverse of the distance to nearest paved road) ($r^{2} = 0.60$), and wetland density at the 500 m ($r^{2} = 0.54$) and 1 km ($r^{2} = 0.64$) buffer distances were negatively correlated with the first axis. Axis 2 was positively correlated ($r^{2} > 0.70$) with the percentage of open habitat surrounding wetlands at all buffer distances and therefore represents a gradient from wetlands surrounded by forests to wetlands surrounded by open habitats.

All but one of the cypress/gum swamps and most marshes were positively associated with axis 1, whereas all cypress savannas were negatively associated with axis 1 (Figure 2.2). Associations between wetland types and axis 2 were less clear, however marshes were more commonly surrounded by open habitat and cypress/gum swamps were more often surrounded by forest. Cypress savannas appeared to be relatively evenly distributed along axis 2.

Effects of Wetland Type and Fish Presence on Amphibian Communities

Species Richness Differences. Wetland type appeared to influence salamander species richness ($F_{2,25} = 4.36$, $p = 0.02$, $n = 28$) but had no effect on anuran species richness ($F_{2,25} = 0.61$, $p = 0.55$, $n = 28$). A Tukey's HSD test revealed that cypress/gum swamps had significantly more (1.7 ± 1.45 species, 95% confidence interval) salamander species than cypress savannas (Figure 2.3). There was no effect of predatory fish on either anuran ($F_{2,26} = 2.31$, $p = 0.12$, $n = 29$) or salamander species richness ($F_{2,26} = 0.79$, $p = 0.47$, $n = 29$) (Figure 2.4).

Species Composition. Axes 1 and 2 of the DCA explained 53.5% of the variation in amphibian species composition among wetland sites (Figure 2.5). Additional axes did not significantly contribute to the percentage of variance explained and were not considered. The DCA revealed a strong association between amphibian communities and wetland type. Axis 1 separated cypress/gum swamps from all other wetland types. Cypress/gum swamps were negatively associated with axis 1, whereas marshes and cypress savannas were positively associated with axis 1. Cypress savannas and marshes displayed similar community structure, although marshes were generally more positively associated with axis 1 than cypress savannas. Fish presence did not appear to strongly influence species composition, although 2 cypress/gum swamps with large predatory fish were more positively associated with axis 2 than cypress/gum swamps without fish (Figure 2.6).

Gopher frogs, southern toads (*Bufo terrestris*), tiger salamanders (*Ambystoma tigrinum*), southern cricket frogs, ornate chorus frogs, barking treefrogs (*Hyla gratiosa*), northern dwarf sirens, and eastern narrow-mouthed toads were positively associated with axis 1, which explained 47.5 % of the variation in the wetland species composition data (Figure 2.7). Eastern newts (*Notophthalmus viridescens*), pig frogs, mole salamander (*Ambystoma talpoideum*) paedomorphic and terrestrial adults, little grass frogs (*Pseudacris ocularis*), upland chorus frogs, eastern spadefoots (*Scaphiopus holbrookii*), Cope's gray treefrogs (*Hyla chrysoscelis*), dwarf salamanders, two-toed amphiumas, bullfrogs (*Rana catesbeiana*), spring peepers, and greater sirens were negatively associated with axis 1. Several species displayed associations with axis 2, which explained 6.0 % of the variation in the data. However, this axis did not appear to have any relationship with fish presence or wetland type.

Frequency of Occurrence of Species. The distributions of amphibian observations among wetlands types and wetlands differing in fish presence are shown in Table 2.3. Six species displayed significant associations with wetland type (Table 2.4). Two-toed amphiumas and mole salamander paedomorphs were positively associated with cypress/gum swamps and negatively associated with marshes and cypress savannas. Cope's gray treefrog was also positively associated with cypress/gum swamps but was found less frequently than expected in marshes. Barking treefrogs, ornate chorus frogs, and tiger salamanders were negatively associated with cypress/gum swamps and positively associated with marshes. Barking treefrogs were also positively associated with cypress savannas.

Three species displayed significant associations with fish presence (Table 2.4). The southern cricket frog, barking treefrog, and ornate chorus frog all were positively associated with fish-free wetlands and negatively associated with wetlands with large predators. Although not statistically significant, several other species appeared to exhibit a response to fish presence. Mole salamanders, tiger salamanders, southern toads, and northern dwarf sirens were rarely observed in wetlands with fish, and spring peepers, gopher frogs, and pig frogs were never observed in wetlands with fish (Table 2.3). The two-toed amphiuma and upland chorus frog were only rarely observed in wetlands with mosquitofish, whereas the dwarf salamander, eastern newt, eastern spadefoot, and greater siren were never found in wetlands with mosquitofish (Table 2.3).

DISCUSSION

Influence of Wetland Type

Individual species were both positively and negatively associated with different wetland types. Cypress/gum wetlands maintained a less diverse but distinct amphibian assemblage from marshes and cypress savannas. The observed differences between the cypress/gum swamp amphibian community and that of the other wetland types may be related to a number of factors. In southwest Georgia, cypress/gum swamps display a dense canopy cover in comparison to the sparse canopy of cypress savannas and the open canopy of marshes. Battle and Golladay (2001) observed that cypress/gum swamps in the region displayed lower average water temperatures and minimal algal growth due to solar insulation from the dense canopy cover. Detrital inputs from the dense overstory also result in lower dissolved oxygen levels and higher levels of tannins than marshes and cypress savannas. Low dissolved oxygen levels in turn, result in low abundance and diversity of aquatic macroinvertebrates in cypress/gum swamps.

Several studies have documented correlations between canopy cover and amphibian distributions. The majority of amphibian species in Michigan wetlands exhibited nonrandom distributions with respect to forest canopy cover (Skelly et al. 1999). Later experiments demonstrated that food was a limiting factor in the growth and survivorship of certain larval anuran species in Michigan’s closed canopy wetlands (Werner and Glennemeier 1999). Ultimately, this food limitation may be the result of decreased algal growth due to decreased light levels within closed canopy wetlands. Recently, Halverson et al. (2003) found that the density and growth of spring peeper tadpoles were directly proportional to the amount of solar radiation reaching the surface of ephemeral wetlands in Connecticut, whereas the density and growth of wood frogs were not.

Decreased light levels within closed-canopy wetlands also result in decreased water and air temperatures (Battle and Golladay 2001, Skelly et al. 2002). Battle and Golladay (2001) noted that water temperatures in cypress/gum wetlands were on average 2.7 ˚C lower than marshes and 2.1 ˚C lower than cypress savannas. Developmental rates of larvae are strongly tied to temperature and food availability (Alvarez and Nicieza 2002, Newman 1998, Smith-Gill and Berven 1979). Laboratory studies have demonstrated that temperature decreases of only 5 ˚C resulted in large increases in the length of the larval period and increases in size at metamorphosis for various amphibian species (Alvarez and Nicieza 2002, Smith-Gill and Berven 1979). Therefore, amphibian larvae in cypress/gum wetlands should develop more slowly and metamorphose at a larger size and later date than conspecifics in marshes or cypress-savannas due to the relatively lower temperatures. While this may at first seem advantageous given the well-documented link between size at metamorphosis and increased terrestrial survival (Altwegg and Reyer 2003, Beck and Congdon 1999), a prolonged larval period may expose larvae to increased risks of predation from the large suite of amphibian predators associated with this wetland type. Furthermore, food availability and quality has been shown to increase size at metamorphosis but not the timing of metamorphosis (Alvares and Nicieza 2002, Beck 1997, Doughty and Roberts 2003). In cypress/gum swamps, the combination of cooler temperatures and less abundant food resources may result in both a longer larval period and a smaller size at metamorphosis, compromising the survival of larvae in the aquatic environment and metamorphs in the terrestrial environment.

High tannin concentrations in cypress/gum swamps may also serve as a limiting factor for the breeding of certain species. Survival and growth of American toads (*Bufo americanus*) is significantly lower in the presence of purple loosestrife (*Lythrum salicaria*) extracts, which contain high levels of tannins (Maerz et al. 2005). Tannins from tree bark have been shown to cause damage to the epithelium of carp (*Cyprinus carpio)* gills and may exclude larvae that are obligate gill breathers, such as the southern toad, from cypress/gum swamps through a similar mechanism (Duellman and Trueb 1994, Maerz et al. 2005, Temmink et al. 1989). The presence of tannins also can lower the pH of wetlands, which can be a limiting factor for the reproduction of certain species (Portnoy 1990, Warner 1994). In laboratory tests, tiger salamander embryo survival decreased rapidly below pH 4.5 (Whiteman et al. 1995), a value greater than the average pH of cypress savanna (4.1) and cypress/gum swamps (4.4) in this study. Similarly, in a survey of temporary wetlands in northern Florida, southern toads, eastern narrowmouth toads, barking treefrogs, and squirrel treefrogs were never found in wetlands with a pH less than 4.4 (Warner 1994).

The low dissolved oxygen in cypress/gum swamps also may play a role in limiting use by certain species. Most isolated wetland amphibians respond to extremely low oxygen concentrations by switching to aerial respiration, a process that entails swimming to the surface to gulp air (Duellman and Trueb 1994). Wassersug and Seibert (1975) noted that three species of amphibians increased aerial respiration rates exponentially at dissolved oxygen levels below 4 ppm. In a previous study, the mean dissolved oxygen level in cypress/gum swamps on our study site was below this critical level (2.7 ppm), whereas that of cypress savannas (4.4 ppm) and marshes (5.0 ppm) was above the critical level (Battle and Golladay 2001). However, larval toads do not develop lungs until just before metamorphosis and cannot take advantage of aerial respiration and thus may be excluded from hypoxic wetlands (Duellman and Trueb 1994). Furthermore, frequent swimming to the surface for air involves an energetic cost, reduces foraging time, and exposes larvae to greater predation risk, particularly from movement oriented predators (Feder 1984). Hypoxic conditions can also decrease the development rates and the stage of development at hatching of amphibian embryos (Mills and Barnhart 1999).

The relatively long hydroperiod of cypress/gum swamps also results in the presence of a large suite of predatory amphibians including: bullfrogs, two-toed amphiumas, greater sirens, eastern newts, and larval and paedomorphic mole salamanders. A large body of evidence has documented the importance of predatory amphibians in structuring larval anuran communities (Hecnar and M'Closkey 1997b; Kurzava and Morin 1998; Morin 1981, 1983; Wilbur 1987, among others). In particular, the ability of eastern newts to exclude competitively superior species that exhibit high activity rates (southern toads, spadefoot toads) is well known (Morin 1981, 1983; Wilbur 1987). Eastern newts are also efficient egg predators that can eliminate species that lay eggs in strands or clumps (Wilbur 1997). Adult bullfrogs are generalist predators which prey on adult and larval amphibians (Hecnar and M'Closkey 1997b, McAlpine and Dilworth 1989).

Little is known about the impacts of the two-toed amphiuma, greater siren, or mole salamander on larval anuran assemblages, but there is limited evidence to suggest that they may play an important role in shaping wetland tadpole composition. The two-toed amphiuma is a large and formidable predator of a wide variety of vertebrates including adult and larval salamanders and frogs (Petranka 1998). Similarly, the lesser siren (*Siren intermedia*) is a generalist predator that preys nonselectively on salamander and anuran larvae (Fauth and Resetarits 1991). Thus, it is likely that the closely related greater siren is also a generalist that structures the amphibian community by nonselectively removing larval amphibians. Although the impacts of mole salamanders on larval amphibian communities are undocumented, salamanders of the genus *Ambystoma* are, in general, voracious predators capable of eliminating whole tadpole assemblages (Morin 1983, 1995). Given the widespread occurrence and abundant nature of paedomorphic and larval mole salamanders in fishless cypress/gum swamps (A. Liner, personal observation), it is possible that they play a key role in determining the larval anuran assemblage of this wetland type. Foraging strategies of this large suite of predators may interact to result in the reduced larval anuran community we observed in cypress/gum swamps. Calling males or ovipositing females may also avoid cypress/gum swamps due to the high numbers of predators, a behavior which has been documented in Cope's gray treefrog (Resetarits and Wilbur 1989).

Influence of Fish Presence

In our study, wetlands with fish (Table 2.2) had a reduced amphibian assemblage in which several species were consistently excluded. Other studies also have documented the exclusion of various amphibian species in wetlands inhabited by large predatory fish (Hecnar and M'Closkey 1997a, Porej and Hetherington 2005, Semlitsch 1988, Snodgrass et al. 2000b, among others). However, overall we did not observe a significant reduction in species richness in association with fish presence, which has been the general trend observed in other studies (Baber 2001, Hecnar and M'Closkey 1997a, Knutson et al. 2004, Porej and Hetherington 2005, Snodgrass et al. 2000b). Several explanations may exist for this difference. First, a large number of landscape and wetland habitat variables are known to influence amphibian species richness (Hecnar and M'Closkey 1998, Herrmann et al. 2005, Houlahan and Findlay 2003). The negative effects of fish predation may have been masked by other factors that positively influenced species richness. Secondly, other studies have documented that the densities of some amphibian species gradually decline in wetlands where they co-occur with fish, suggesting the gradual elimination of these species through predation (Baber 2001). Given our seasonal sampling regime, we were unable to detect changes in larval distributions over the course of a season. Thus, our results may merely reflect a snapshot in time rather than the final endpoint of predation. Lastly, only a small number of the wetlands we surveyed were colonized by predatory fish, and the majority of ponds with large predatory fish in this study were of the same wetland type, cypress/gum wetlands. It is possible that the wetlands we sampled with predatory fish were not representative of those in the region.

Our finding that barking treefrogs occur significantly less often in ponds with centrarchids or catfish is consistent with field and laboratory studies, which suggest that this species lacks defensive and behavioral adaptations to fish predation (Baber 2001, Snodgrass et al. 2000b). In addition, laboratory studies have found that barking treefrogs are more palatable to bluegills (*Lepomis machrochirus*) than green treefrogs (Blouin 1990), a species known to persist in wetlands with fish (Baber 2001, Gunzberger and Travis 2004). Furthermore, Kats et al. (1988) observed that spring peepers, upland chorus frogs, and southern cricket frogs were palatable to green sunfish (*Lepomis cyanellus*) and did not display any avoidance behaviors when exposed to water conditioned by green sunfish. All of these species were less common in wetlands with fish in our study. However, other studies have noted the coexistence of southern cricket frogs with predatory fish (Baber 2001, Snodgrass et al. 2000b). Ornate chorus frogs on the Savannah River Site in South Carolina preferred wetlands of medium hydroperiod, which dried too frequently to be colonized by fish (Snodgrass et al. 2000b). The absence of this species in longer hydroperiod wetlands lacking fish may reflect a preference for intermediate hydroperiods rather than an impact of fish presence.

Mole salamanders (Family Ambystomatidae) generally were not detected in wetlands with fish in this study. Only six mole salamanders were found in wetlands containing large predatory fish during this year-long study, whereas hundreds were found in fishless wetlands. Similarly, only one tiger salamander was found in a wetland with fish. Several studies have documented the vulnerability of ambystomatid salamanders to fish predation. The presence of bluegill significantly reduced survival and body size of mole salamanders in outdoor mesocosms (Semlitsch 1987), and mole salamander eggs and larvae were palatable and readily eaten by bluegill in laboratory trials (Semlitsch 1988). Our data are further supported by other surveys that have noted the absence of mole and tiger salamanders in the presence of fish (Porej and Hetherington 2005, Semlitsch 1988, Snodgrass et al. 2000b).

In contrast, bullfrogs and southern leopard frogs were common in wetlands with large predatory fish. These results are consistent with other studies (Kurzava and Morin 1998, Porej and Hetherington 2005, Richardson 2002, Werner and McPeek 1994). Field surveys in Michigan documented a positive association between bullfrogs and predatory fish (Werner and McPeek 1994). In experimental mesocosms, bluegill sunfish eliminated a ranid competitor and invertebrate and salamander predators, allowing bullfrogs to dominate (Werner and McPeek 1994). Several studies have suggested that larval bullfrogs are unpalatable to fish or are not preferred prey (Kats et al. 1988, Werner and McPeek 1994, Woodward 1983), whereas the eggs of southern leopard frogs are unpalatable to bluegill sunfish (Werschkul and Christensen 1977).

Bullfrog larvae also have been shown to reduce activity levels in response to the presence of predators or chemical predator cues (Anholt et al. 2000, Eklöv 2000, but see Woodward 1983). However, this strategy is only used by small tadpoles (Eklöv 2000). Both bullfrogs and southern leopard frogs displayed higher absolute burst swim speeds in response to a simulated predator attack than 12 other anuran species (Richardson 2002).

The prevalence of pine woods treefrogs and squirrel treefrogs in wetlands with large predatory fish in this study was unusual. Pine woods treefrogs were only rarely encountered in wetlands colonized by fish on the Savannah River Site (Snodgrass et al. 2000b), and neither species persisted with fish in central Florida wetlands (Baber 2001). Furthermore, Binckley and Resetarits (2002) demonstrated that female squirrel treefrogs avoided ovipositing in experimental ponds with banded sunfish. However, the majority of pine woods and squirrel treefrog captures in this study were of adults within PVC pipes. This suggests that the adults we observed are either animals that bred in other wetlands or were individuals derived from breeding years in which the wetland was fishless.

Despite their small size, eastern mosquitofish appeared to exclude many of the same species as large predatory fish, although these results were not statistically significant due to the small number (n = 4) of wetlands colonized exclusively by this species. Previous studies have found mosquitofish to be voracious and efficient predators (both in their native range and in areas where they have been introduced) capable of extirpating amphibians from wetlands (Baber 2001, Baber and Babbitt 2003, Hamer et al. 2002). Moreover, mosquitofish use repeated attacks to subdue and consume their prey allowing them to consume larger tadpoles than other gape-limited fishes (Baber 2001). In addition to being efficient predators, mosquitofish are also effective dispersers, making them more prevalent in the landscape than other species. Our results suggest that the eastern mosquitofish may play an important role in shaping amphibian distributions in isolated wetlands in southwest Georgia.

Conservation Implications

Amphibian populations in isolated wetlands are inherently variable in time and space. Therefore, we caution that a single year of study cannot provide definitive answers to the driving mechanisms of amphibian community dynamics, but merely suggest hypotheses which must be later tested against long-term data. However, our results suggest that cypress/gum wetlands provide habitat for a different suite of species than marshes and cypress savannas. In addition, we observed that wetlands with fish displayed a reduced larval amphibian community. Thus, we recommend that future wetland monitoring and restoration efforts in the region should take both wetland type and fish presence into account when conducting amphibian surveys.

Our study also emphasizes the importance of wetland diversity in supporting amphibian diversity. Southwest Georgia wetlands exist as a patchwork of wetlands of different types that support different amphibian species. Individual wetlands also exhibit a high degree of spatial and temporal variation in hydroperiod, water chemistry, and invertebrate and plant diversity (Battle and Golladay 2001, Kirkman et al. 2000), which in turn promotes regional amphibian diversity. Future amphibian and wetland conservation efforts in this area must recognize the importance of this mosaic of wetland variation on amphibian diversity if they are to succeed. Protecting only individual wetlands and small surrounding buffer zones will not preserve the integrity of the local amphibian community.

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Figure 2.1. Location of Ichauway study area in southwest Georgia (31° 13' 16.88" N and 84° 28' 37.81" W) used in an investigation of the influence of wetland and upland habitat variables on amphibian distributions from June 2004 to May 2005.

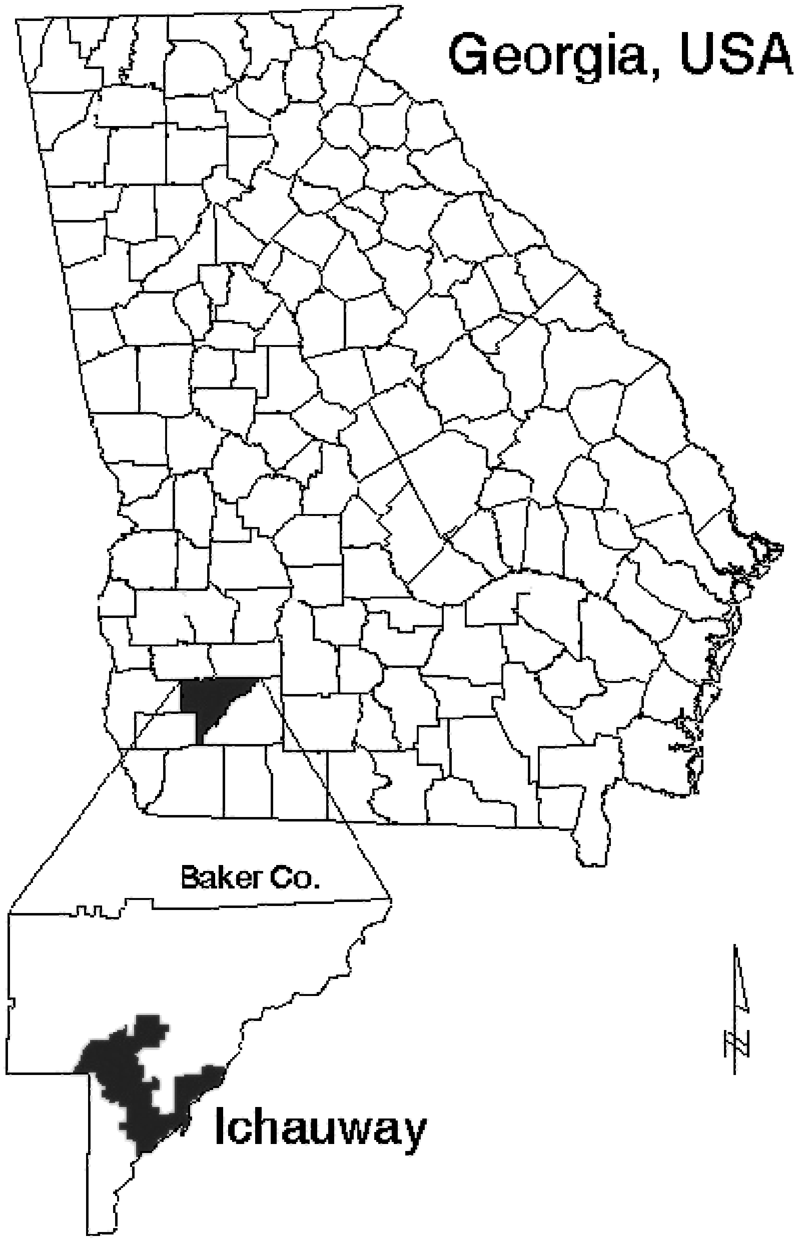

Georgia, USA
Baker Co.
Ichauway
N

Figure 2.2. Principal components analysis of habitat variables measured in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005. Points represent individual wetlands categorized by symbols representing different wetland types. Vectors indicate habitat variables.

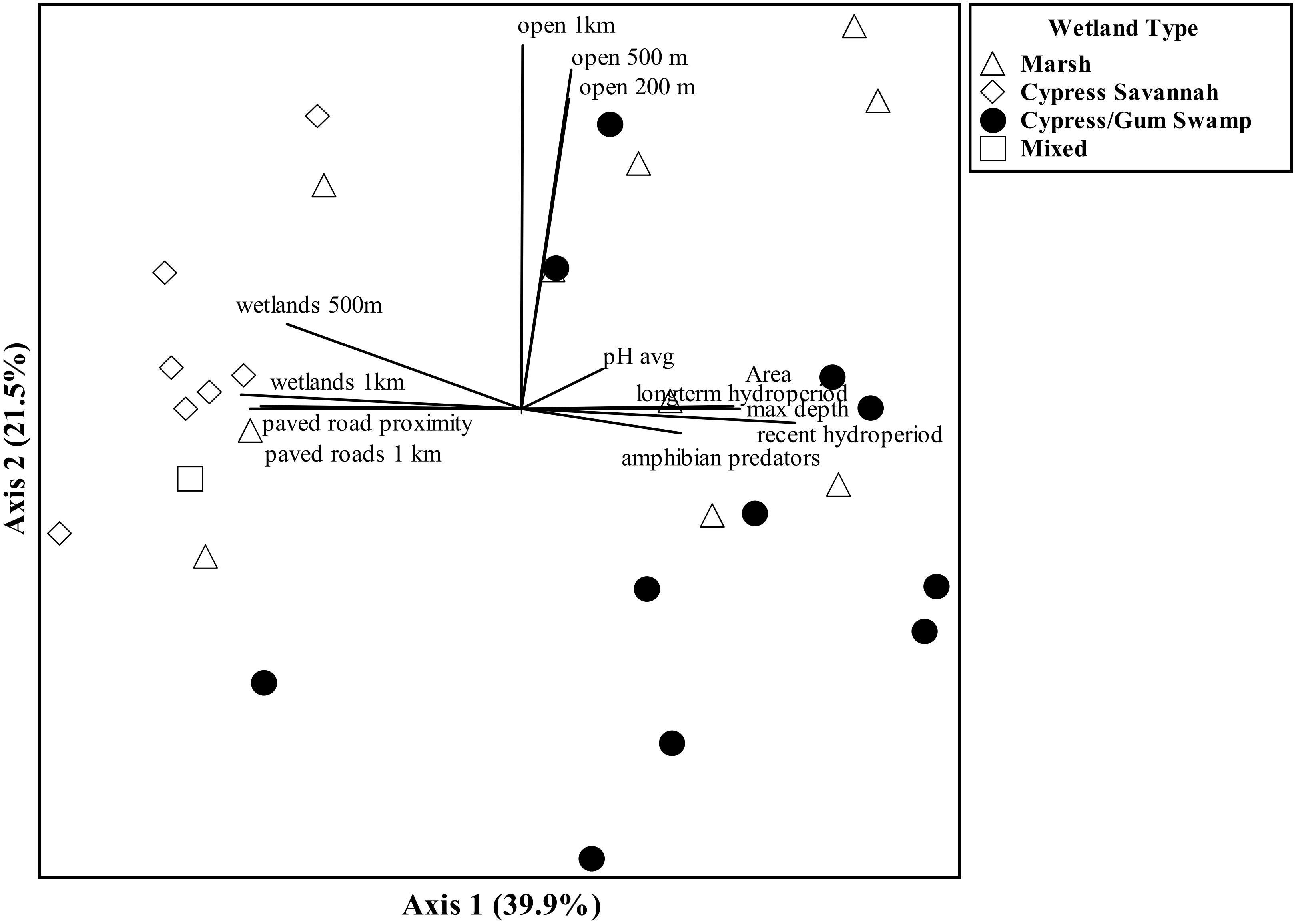
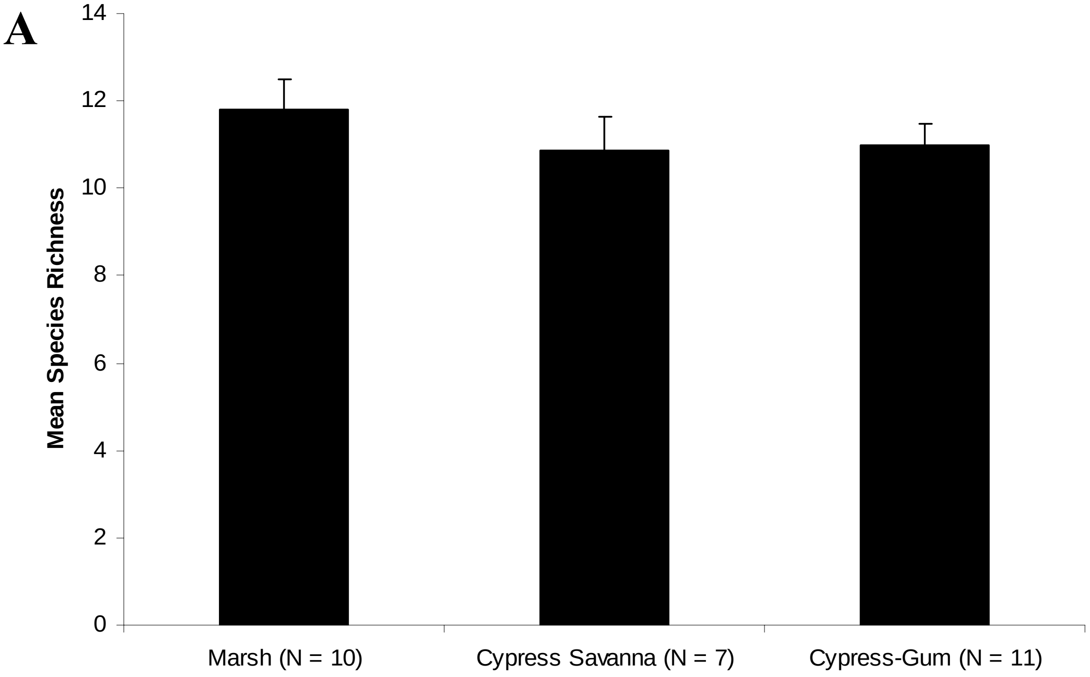

open 1km
open 500 m
open 200 m
wetlands 500m
wetlands 1km
paved road proximity
paved roads 1 km
pH avg
Area
longterm hydroperiod
max depth
recent hydroperiod
amphibian predators
Axis 1 (39.9%)
Axis 2 (21.5%)
Wetland Type
△ Marsh
◇ Cypress Savannah
● Cypress/Gum Swamp
□ Mixed

Figure 2.3. Comparison of mean (±SE) species richness of a) anurans and b) salamanders captured in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005 among three wetland types.


A
Mean Species Richness
14
12
10
8
6
4
2
0
Marsh (N = 10)
Cypress Savanna (N = 7)
Cypress-Gum (N = 11)

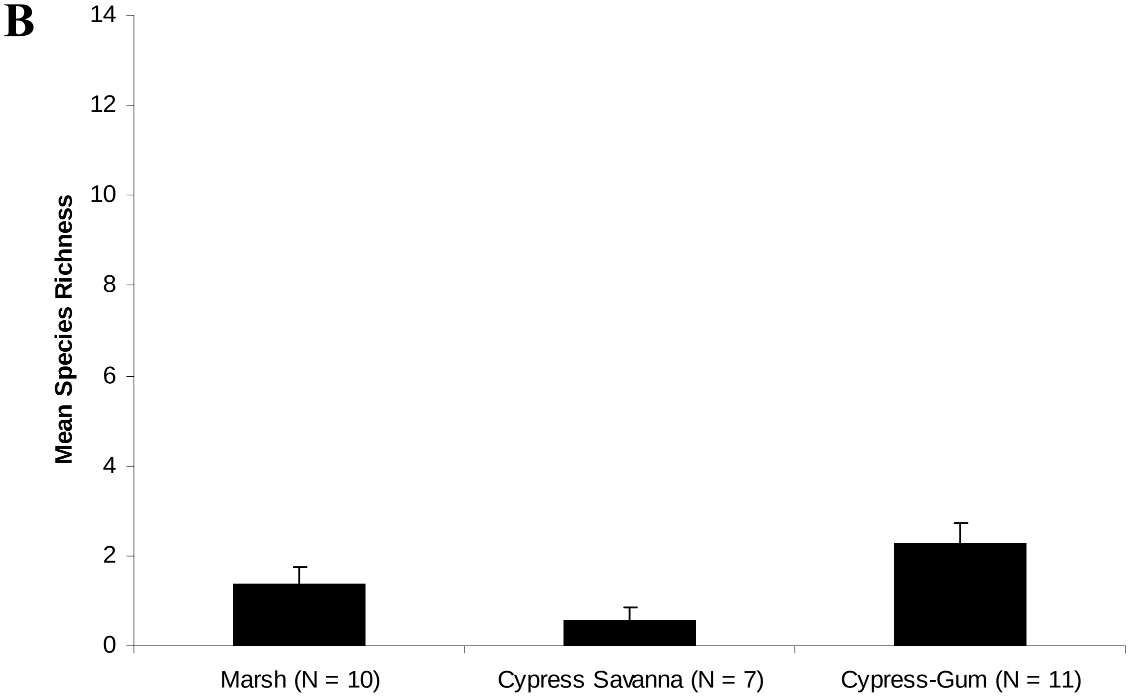
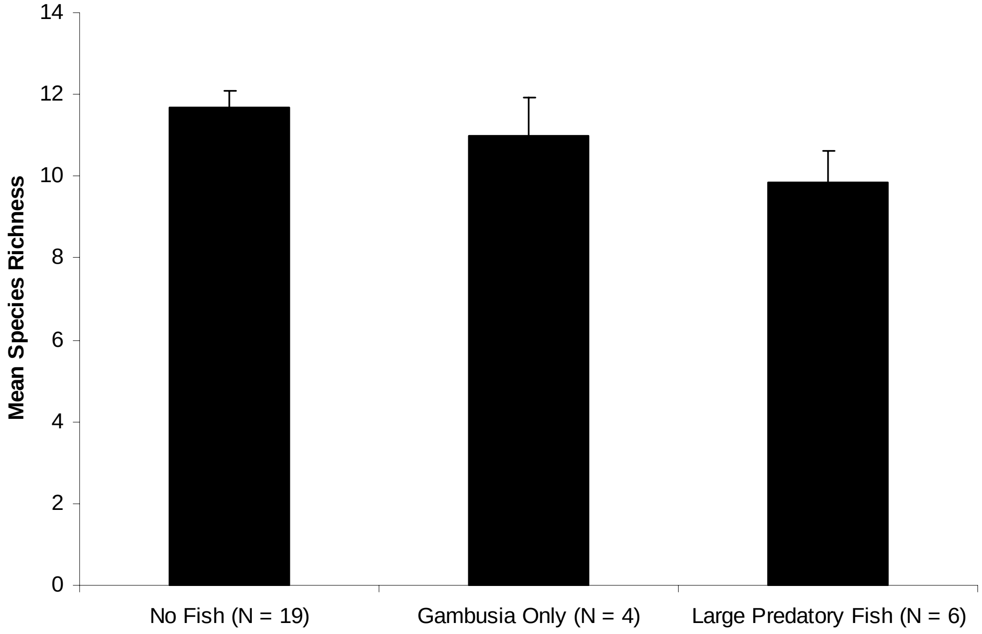

B
Mean Species Richness
14
12
10
8
6
4
2
0
Marsh (N = 10)
Cypress Savanna (N = 7)
Cypress-Gum (N = 11)

Figure 2.4. Comparison of mean (±SE) species richness of a) anurans and b) salamanders captured in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005 among wetlands with different suites of fish species.

A


Mean Species Richness
14
12
10
8
6
4
2
0
No Fish (N = 19)
Gambusia Only (N = 4)
Large Predatory Fish (N = 6)

B

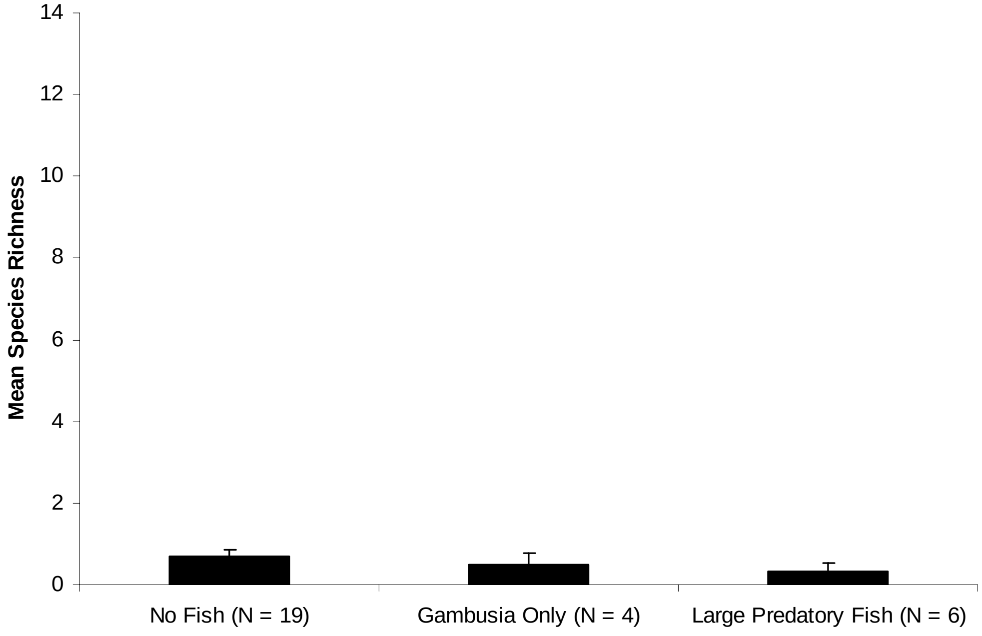
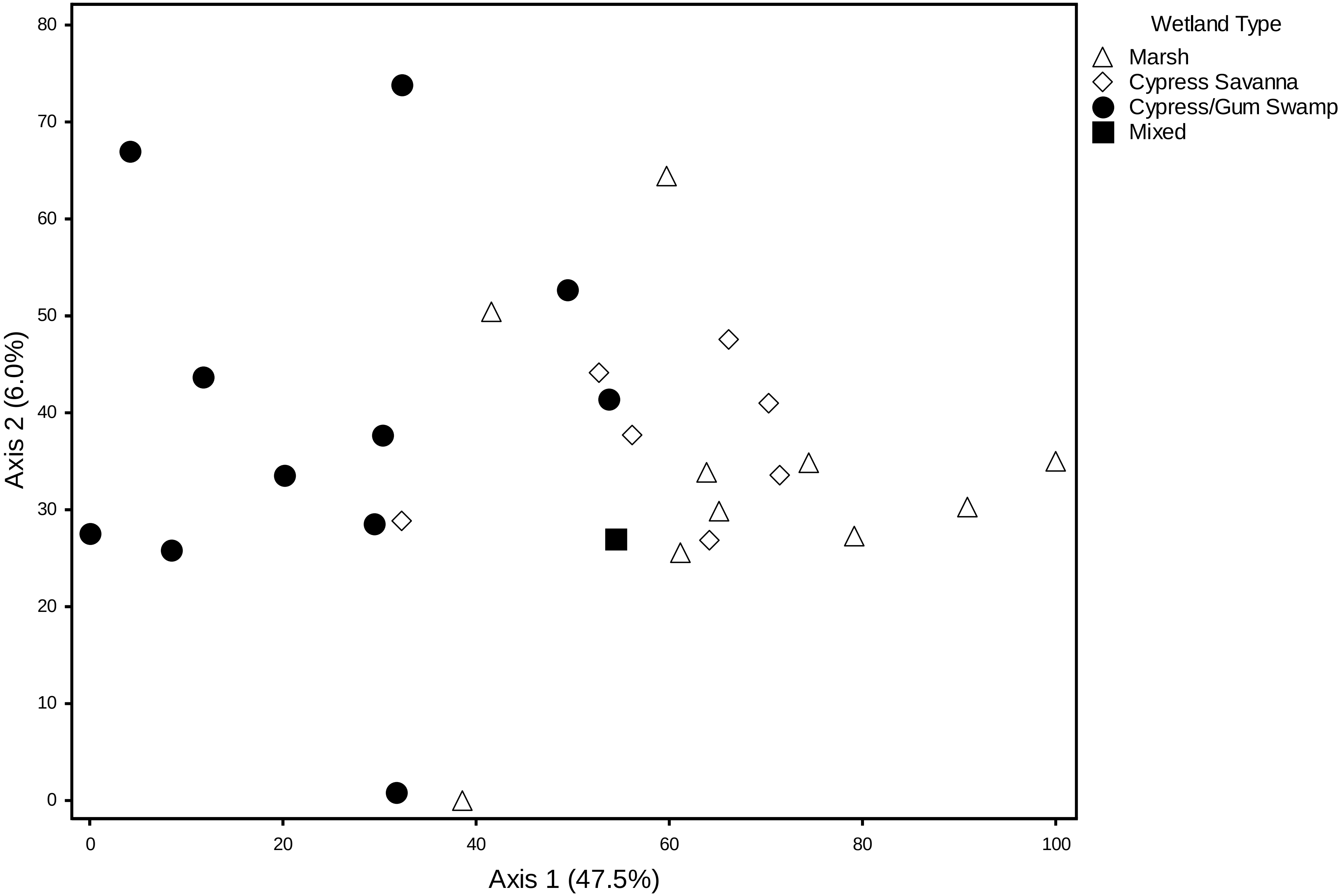
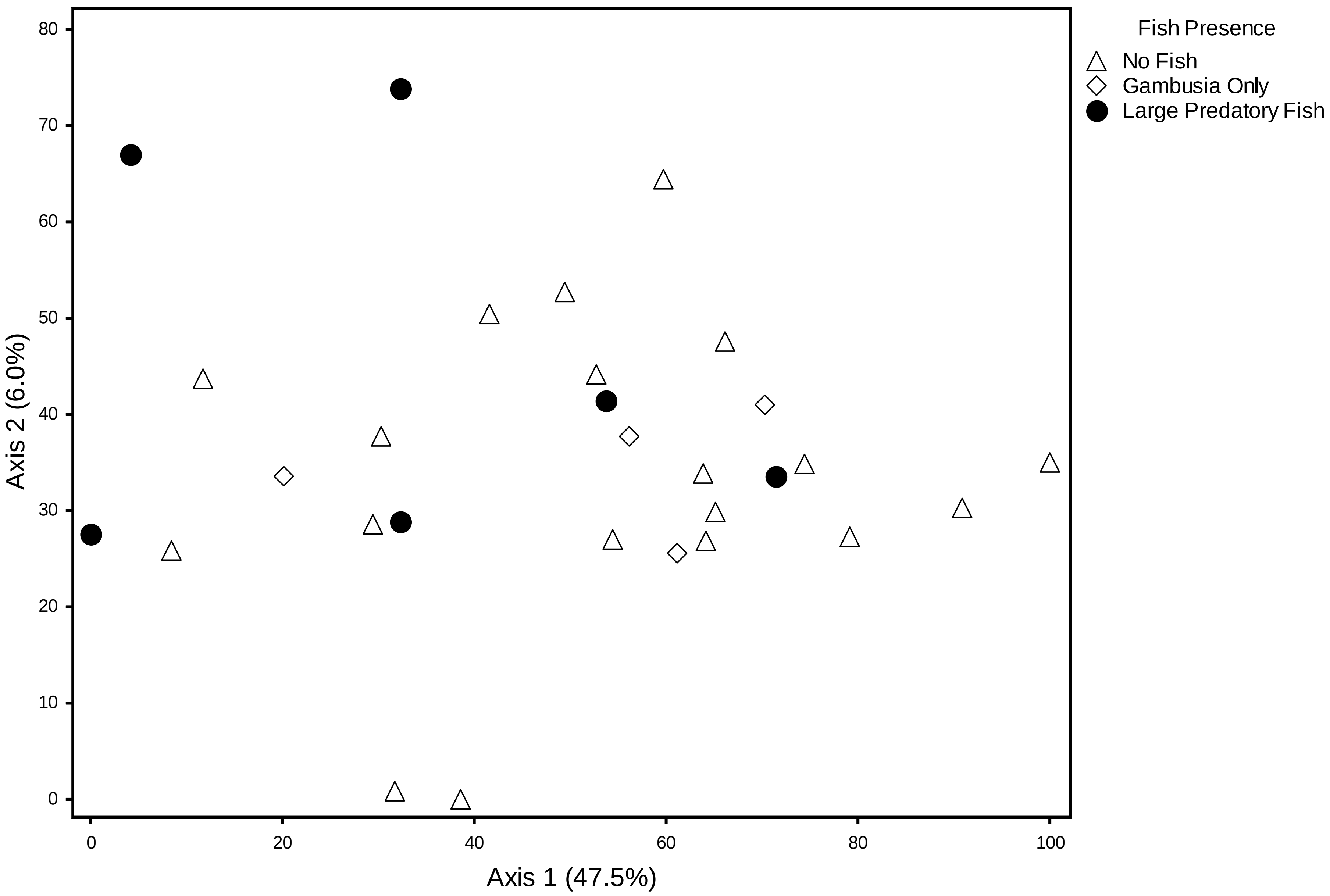

Mean Species Richness
14
12
10
8
6
4
2
0
No Fish (N = 19)
Gambusia Only (N = 4)
Large Predatory Fish (N = 6)

Figure 2.5. Detrended Correspondence Analysis of amphibian species composition observed in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005 versus wetland type. Points represent individual wetlands categorized according to wetland type.



Wetland Type
△ Marsh
◇ Cypress Savanna
● Cypress/Gum Swamp
■ Mixed
Axis 2 (6.0%)
Axis 1 (47.5%)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100

Figure 2.6. Detrended Correspondence Analysis of amphibian species composition observed in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005 versus fish presence. Points represent individual wetlands categorized according to fish presence.



Fish Presence
△ No Fish
◇ Gambusia Only
● Large Predatory Fish
Axis 2 (6.0%)
80
70
60
50
40
30
20
10
0
0
20
40
60
80
100
Axis 1 (47.5%)

Figure 2.7. Detrended Correspondence Analysis of amphibian species composition observed in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005. Points represent individual species (ACGRY = *Acris gryllus*, AMMEA = *Amphiuma means*, AMTAL - GA = *Ambystoma talpoideum* gilled adult, AMTAL - TA = *Ambystoma talpoideum* terrestrial adult, AMTIG = *Ambystoma tigrinum*, BUTER = *Bufo terrestris*, EUQUA = *Eurycea quadridigitata*, GACAR = *Gastrophryne carolinensis*, HYCHR = *Hyla chrysoscelis*, HYCIN = *Hyla cinerea*, HYFEM = *Hyla femoralis*, HYGRA = *Hyla gratiosa*, HYSQU = *Hyla squirella*, NOVIR = *Notophthalmus viridescens*, PSCRU = *Pseudacris crucifer*, PSFER = *Pseudacris feriarum*, PSNIG = *Pseudacris nigrita*, PSOCU = *Pseudacris ocularis*, PSORN = *Pseudacris ornata*, PSSTR = *Pseudobranchus striatus*, RACAT = *Rana catesbeiana*, RACAP = *Rana capito*, RAGRY = *Rana grylio*, RASPH = *Rana sphenocephala*, SCHOL = *Scaphiopus holbrookii*, SILAC = *Siren lacertina*).

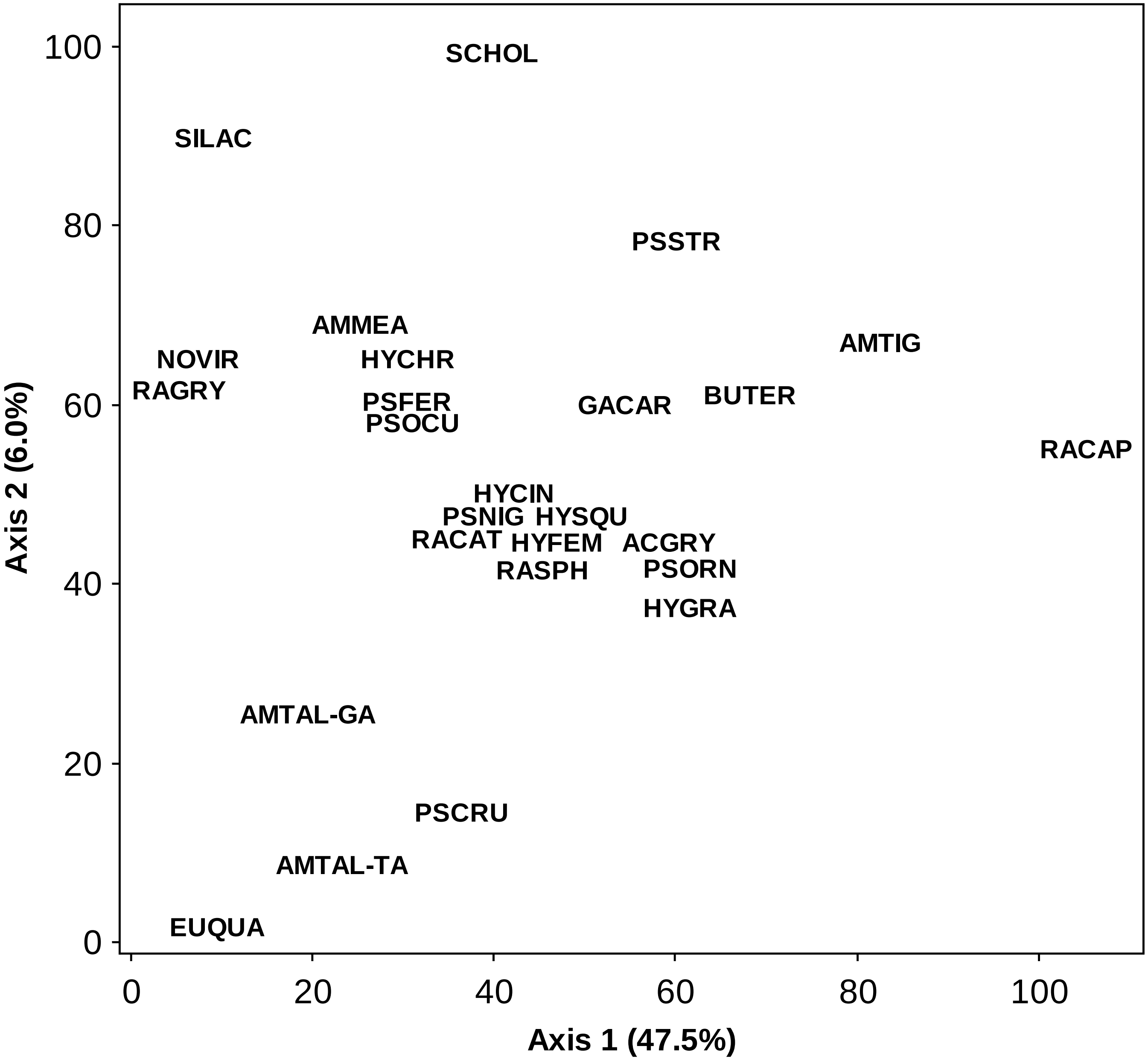

SCHOL
SILAC
PSSTR
AMMEA
AMTIG
NOVIR
HYCHR
RAGRY
PSFER
PSOCU
GACAR
BUTER
RACAP
HYCIN
PSNIG
HYSQU
RACAT
HYFEM
ACGRY
RASPH
PSORN
HYGRA
AMTAL-GA
PSCRU
AMTAL-TA
EUQUA
0
20
40
60
80
100
0
20
40
60
80
100
Axis 1 (47.5%)
Axis 2 (6.0%)

Table 2.1. Habitat characteristics of 29 isolated wetlands in southwestern Georgia measured from June 2004 to May 2005 by wetland type. Values displayed are mean (range) of variables. One wetland of mixed habitat type not shown.

Habitat Variables	Marsh (N = 10)	Cypress Savannah (N = 7)	Cypress/Gum Swamp (N = 11)
Wetland Characteristics			
Area (ha)	5.92 (0.89 – 19.56)	2.70 (0.35 – 10.32)	5.24 (0.71 – 12.18)
Maximum Depth (m)	1.20 (0.55 – 1.92)	0.76 (0.63 – 0.89)	1.10 (0.62 – 1.84)
Recent Hydroperiod (% Days)	66.2 (30.8 – 84.6)	39.6 (19.2 – 65.4)	91.6 (53.8 – 100)
Longterm Hydroperiod (% Days)	52.7 (30.8 – 68.9)	35.5 (16.8 – 46.4)	62.2 (48.3 – 78.4)
Average pH (S.U.)	4.5 (3.9 – 5.0)	4.1 (3.7 – 4.5)	4.4 (3.4 – 5.2)
No. Predatory Amphibians	1.8 (0 – 3)	0.9 (0 - 2)	3 (0 – 5)
Landscape Characteristics			
Open Habitat 200 m (%)	23.4 (0.5 – 58.4)	10.9 (1.6 – 33.1)	11.0 (1.0 – 33.1)
Open Habitat 500 m (%)	25.2 (6.4 – 58.6)	16.5 (5.5 – 35.1)	16.9 (1.6 – 39.6)
Open Habitat 1 km (%)	26.9 (9.7 – 43.6)	25.9 (13.5 – 37.0)	18.7 (6.7 – 41.0)
Wetland Density 200 m	1.9 (0 – 5)	1.7 (0 – 4)	0.5 (0 – 3)
Wetland Density 500 m	4.3 (1 – 9)	7 (5 – 10)	1.6 (0 – 5)
Wetland Density 1 km	10.4 (2 – 19)	17.4 (15 – 21)	7.3 (2 – 14)
Paved Road Density 200 m (km)	0.16 (0 – 0.41)	0.42 (0 – 0.97)	0.12 (0 – 0.61)
Paved Road Density 500 m (km)	0.54 (0 – 1.13)	1.44 (1.01 – 2.80)	0.64 (0 – 2.33)
Paved Road Density 1 km (km)	1.50 (0 – 5.08)	3.66 (2.05 – 5.54)	1.85 (0 – 5.47)
Distance to Nearest Road (km)	0.79 (0 – 2.10)	0.09 (0 – 0.20)	0.70 (0 – 3.07)

Table 2.2. Fish species recorded in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005.

Common Name	Scientific Name	No. Wetlands Occupied
Black Bullhead Catfish	*Ameiurus melas*	2
Yellow Bullhead Catfish	*Ameiurus natalis*	1
Bowfin	*Amia calva*	1
Pirate Perch	*Aphredoderus sayanus*	3
Flier	*Centrarchus macropterus*	2
Banded Pygmy Sunfish	*Elassoma zonatum*	3
Mosquitofish	*Gambusia holbrooki*	8
Warmouth	*Lepomis gulosus*	5
Spotted Shiner	*Lepomis punctatus*	1
Greater Jumprock	*Moxostoma lachneri*	1
Golden Shiner	*Notemigonus crysoleucas*	1
Coastal Shiner	*Notropis petersoni*	2

Table 2.3. Distribution of amphibians detected in 29 isolated wetlands in southwestern Georgia from June 2004 to May 2005 by wetland type and fish presence. Blanks denote non-detection of a species. TA = terrestrial adult. GA = gilled adult.

	Wetland Types			Fish Presence		
	Marsh (N = 10)	Cypress Savanna (N = 7)	Cypress/Gum (N = 11)	Absent (N = 19)	*Gambusia* Only (N = 4)	Large Predators (N = 6)
Acris gryllus	10	6	8	18	4	3
Ambystoma talpoideum (GA)			6	5	1	1
Ambystoma talpoideumm (TA)	2		2	3		1
Ambystoma tigrinum	4	1		4	1	
Amphiuma means	2	1	8	6	1	4
Bufo terrestris	7	4	2	9	2	2
Eurycea quadridigitata	1		2	2		1
Gastrophryne carolinensis	10	5	7	15	2	5
Hyla chrysoscelis	2	4	9	8	3	4
Hyla cinerea	9	6	11	19	3	5
Hyla femoralis	10	7	11	19	4	6
Hyla gratiosa	10	6	4	17	3	1
Hyla squirella	10	7	11	19	4	6
Notopthalmus viridescens	1		4	3		2
Pseudacris crucifer	2		2	4		
Pseudacris feriarum	4	3	8	11	1	4
Pseudacris nigrita	9	6	10	17	4	5
Pseudacris ocularis	4	5	9	12	4	3
Pseudacris ornata	10	6	5	17	3	2
Pseudobranchus striatus	4	2	1	6		1
Rana capito	1			1		
Rana catesbeiana	8	4	10	13	3	6
Rana grylio			1	1		
Rana sphenocephala	10	7	11	19	4	6
Scaphiopus holbrookii	2		2	3		1
Siren lacertina			3	1		2

Table 2.4. Probabilities (p) of significant association from Fisher's exact tests (all df = 2) assessing amphibian species presence from June 2004 to May 2005 among southwest Georgia wetlands that vary by type and fish presence. A significant ($p < 0.05$) association suggests that the distribution of the species is not independent of the tested wetland variable. Positive (+) and negative (-) associations are indicated in parentheses (CSG = cypress/gum swamp, CS = cypress savanna, M = marsh, NF = no fish, LP = large predatory fish). One wetland of mixed habitat was not included in wetland type analysis. *Hyla femoralis* and *Rana sphenocephala* were found in every wetland and were not included. *Rana capito* and *Rana grylio* were found in only one wetland and were not included. GA = gilled adult, TA = terrestrial adult

Species	Wetland Type (N = 28)	Fish Presence (N = 29)
Acris gryllus	0.264	0.028 (+NF, -LP)
Ambystoma talpoideum - GA	0.003 (+CSG, -CS, -M)	0.413
Ambystoma talpoideum - TA	0.643	1.000
Ambystoma tigrinum	0.030 (+M, - CSG)	0.608
Amphiuma means	0.020 (+CSG, -CS, -M)	0.385
Bufo terrestris	0.172	0.870
Eurycea quadridigitata	0.765	1.000
Gastrophryne carolinensis	0.112	0.672
Hyla chrysoscelis	0.019 (+CSG, -M)	0.346
Hyla cinerea	0.505	0.111
Hyla gratiosa	0.002 (+M, +CS, -CSG)	0.003 (+NF, -LP)
Notopthalmus viridescens	0.172	0.478
Pseudacris crucifer	0.643	1.000
Pseudacris feriarum	0.281	0.553
Pseudacris nigrita	1.000	1.000
Pseudacris ocularis	0.161	0.311
Pseudacris ornata	0.010 (+M, -CSG)	0.018 (+NF, -LP)
Pseudobranchus striatus	0.298	0.560
Rana catesbeiana	0.271	0.367
Scaphiopus holbrookii	0.643	1.000
Siren lacertina	0.098	0.142

CHAPTER 3

A COMPARISON OF TECHNIQUES FOR SAMPLING AMPHIBIANS IN SOUTHEASTERN ISOLATED WETLANDS[2]

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[2] Liner, A.E., L.L. Smith, S.B. Castleberry, and J.W Gibbons. To be submitted to The Journal of Applied Herpetology.

ABSTRACT

We evaluated the effectiveness of five amphibian survey methods in nine hydrologically isolated wetlands in southwestern Georgia during the spring 2005 breeding season. Overall, aquatic funnel traps detected the most species (19) followed by automated frog call recorders (14), dipnet surveys (11), PVC pipe refugia (4), and crayfish traps (3). There was considerable overlap among the species detected by aquatic funnel traps, frogloggers, and dipnet surveys, although each of these methods yielded species not detected by other methods. Crayfish traps and PVC pipe refugia were redundant with aquatic funnel traps in terms of species detected. No individual method or combination of methods captured as many species as all five methods combined. Detection rates of individual methods varied among species, but each method displayed high detection rates for at least one species. The number of species detected with frogloggers showed a positive correlation with maximum daily air temperature, but no other method appeared to be affected by air temperature or the amount of rainfall on the day of the survey. We recommend that a combination of aquatic funnel traps and frogloggers be used in amphibian surveys in southeastern isolated wetlands when an assessment of species richness is the goal.

INTRODUCTION

Recent concerns about worldwide amphibian population declines have highlighted the need for gathering baseline and long-term information on amphibian populations. A recent assessment of the status of all known amphibian species found that at least 1,856 species (32.5%) are globally threatened, while insufficient data exists to assess the status of another 1,294 species (Stuart et al. 2004). Little is known about the current or historical status of amphibian populations in the southeastern United States (Dodd 1997, LaClaire 1997), although extensive habitat loss has occurred in this region in the past century (Dodd 1997, Hefner and Brown 1985, Noss 1989, Sutter and Kral 1994). Baseline information on amphibians in the region is needed to assist future monitoring and conservation efforts (LaClaire 1997).

A wide variety of survey methods exist for sampling amphibians in aquatic habitats (Heyer et al. 1994). However, recent studies have shown that these methods can vary widely in effectiveness for individual species and life stages, and that their effectiveness can vary depending upon environmental conditions and habitats sampled (Buench and Egeland 2002, Jung et al. 2002, Lauck 2004, Willson and Dorcas 2003). Few studies have assessed the effectiveness of standard sampling methods for southeastern amphibians (but see Mitchell et al. 1993, Willson and Dorcas 2003), and we know of no studies that have evaluated the effectiveness of amphibian survey methods in southeastern isolated wetlands. Understanding and accounting for the biases associated with survey methods is necessary for developing accurate estimates of amphibian population sizes and distributions.

In this paper, we evaluate the effectiveness of five accepted amphibian survey methods in hydrologically isolated wetlands within the southeastern coastal plain. Our objectives were to: 1) assess the relative effectiveness of PVC pipe refugia, dipnet surveys, automated frog call surveys, crayfish traps, and aquatic funnel traps for detecting the occurrence of amphibians, 2) evaluate the effects of environmental variables on the detection ability of survey methods on three spring-breeding species with different life history strategies, and 3) compare costs associated with each method.

METHODS

Study Area

This study was conducted on Ichauway, an 11,800 ha private reserve that serves as the outdoor laboratory of the Joseph W. Jones Ecological Research Center. The property is located in Baker County, Georgia within the Gulf Coastal Plain and the Dougherty Plain physiographic province (Figure 2.1). The site is primarily comprised of 70-90 year old longleaf pine (*Pinus palustris*) forest interspersed with 98 shallow limesink wetlands ranging in size from 0.2 - 76.5 ha. Kirkman et al. (2000) characterized wetlands in the region into three basic types based on vegetation and soil characteristics. Grass-sedge marshes have coarse sandy soils, an open overstory, and an understory dominated by dense panic grasses (*Panicum* spp.) and cutgrass (*Leersia hexandra*). Cypress savannas exhibit finer textured sandy soil underlain by a layer of clay, a relatively open (*Taxodium ascendens*) overstory, and an understory of panic grasses and broomsedge (*Andropogon virginicus*). Cypress/gum swamps have thick organic soils and a dense overstory of pond cypress and swamp tupelo (*Nyssa biflora*) with virtually no understory or midstory vegetation (Battle and Golladay, 2001; Kirkman et al., 2000). Wetland hydroperiod is highly variable and is dependent on annual rainfall patterns, as well as morphological characteristics of individual wetlands (Battle and Golladay, 2001). Amphibian breeding activity within the wetlands occurs year-round, but involves different species at different times of the year.

Field Methods

We intensively sampled nine isolated wetlands for amphibians to evaluate the efficacy of different sampling techniques. This research was part of a larger study of the effects of habitat variables on amphibian distributions in 29 isolated wetlands. The wetlands sampled included 3 marshes, 3 cypress savannas, and 3 cypress/gum swamps ranging in size from 0.5 – 6.6 ha that were representative of the isolated wetlands on the property. Sampling at all sites took place during spring 2005 (March 15 - May 21, 2005) using a combination of dipnetting, aquatic funnel traps, crayfish traps, PVC pipe refugia, and automated frog call recorders (frogloggers).

Dipnet surveys were conducted using a square-frame dip net (36 x 38 cm, 5 mm mesh) and consisted of three separate visits to each study wetland. During each visit 100 1-m sweeps were distributed equally around the wetland perimeter and among all shallow (< 0.5 m) microhabitats. Anuran call surveys were conducted using frogloggers, as described in Dodd (2003). Frogloggers were placed at the wetland edge and programmed to record 1 minute per hour between 2000 and 0700 hours for six consecutive nights. Commercial crayfish traps and funnel traps were set in wetlands for twelve consecutive nights and checked every two days. Crayfish traps were constructed of plastic-coated 2.5 cm hexagonal mesh with a plastic-coated rectangular wire mesh (2.5 x 1.25 cm) lid and neck (Johnson and Barichivich 2004). Five crayfish traps were distributed evenly around the wetland perimeter at a depth of ca. 20 cm. Funnel traps were double-ended and were constructed from aluminum window screen (as described in Heyer et al. 1994) and contained a styrofoam float that kept the funnels submerged just below the surface. Funnel traps were placed every 50 m along a transect parallel to the bank at a water depth of 0.25 m. The number of traps was scaled to wetland size. A minimum of 2 and a maximum of 30 funnel traps were used in each wetland.

Amphibians captured in aquatic traps and dipnet surveys were identified in the field and released. Representative amphibian larvae that could not be identified in the field were raised in the lab to metamorphosis or euthanized with chloretone solution, preserved in 10% buffered formalin, and identified from appropriate keys (Altig 1970, Altig et al. 1998). Larvae of the spring peeper (*Pseudacris crucifer*), southern chorus frog, (*Pseudacris nigrita*), and upland chorus frog (*Pseudacris feriarum*) are similar in appearance and there are currently no adequate keys to distinguish between these species. Therefore, only data from locations from which larvae of these species were successfully reared and identified or adults were observed are reported.

Polyvinylchloride (PVC) pipes were used to detect adult hylid frogs (Moulton et al. 1996). One-meter segments of open-ended opaque, schedule 40 white PVC pipe (5 cm inside diameter) were inserted upright into the ground at 50 m intervals around the perimeter of each wetland. Pipes were checked at the beginning and end of the study period, and occupant frogs were identified to the species level and counted. Because the pipes serve as a diurnal refuge for frogs (Heyer et al. 1994), frogs were released back into the pipes after all animals were recorded.

Data Analysis

We calculated the total number of amphibian species captured by each method during the entire study, as well as the total number of species shared among each combination of methods and unique to each method. The number of amphibian species detected with each method was also calculated by site, and the mean number of species captured by each method was compared using Kruskal-Wallace chi-square approximation. Significant differences among methods were identified using posthoc Wilcoxon rank sum tests with a Bonferroni adjustment to maintain an experiment-wide alpha level of 0.05. The temporal accumulation of species over the number of sampling events was calculated for each method at each site.

Detection rates were calculated for each species and method by dividing the number of times a species was captured by the number of sampling events at each site where the species was observed. Thus, our detection rates were a measure of the average daily success of a method to detect a species when it is present.

To assess how environmental factors may have influenced capture success for dipnetting, funnel traps, and frogloggers, we used an information-theoretic approach (Burnham and Anderson 2002) in combination with logistic regression (PROC GENMOD, SAS Version 9.1, Cary, NC, USA) to evaluate the influence of weather and time covariates on detection/nondetection data for three spring-breeding species, southern toads (*Bufo terrestris*), barking treefrogs (*Hyla gratiosa*), and southern leopard frogs (*Rana sphenocephala*). These species were chosen because they represent a range of life history strategies and were detected by all three methods. We developed 7 *a priori* models which were evaluated for each method and species. Variables included in the models were the maximum temperature on the day of a survey (MaxTemp), total rainfall on the day of the survey (Rain), and Julian Date (Julian) of the survey. The models used were (1) Global (variables included Julian date, Rain, and MaxTemp); (2) Null (no variables included); (3) Julian (variables included Julian Date); (4) Rain (variables included Rain); (5) MaxTemp (variables included MaxTemp); (6) Rain-MaxTemp (variables included Rain and MaxTemp); and (7) Julian-Rain (variables included Julian date and Rain). To evaluate the relative importance of each model on the detection/nondetection of each species, Akaike's Information Criterion (AIC_c) values were derived from logistic regression analysis and used to calculate the Akaike differences between models (Δ_i) and Akaike model weights (ω_i). Akaike differences represent the relative distances between each model and the best approximating model among the candidate set of models. Models with $\Delta_i = 0 - 2$ can be considered to have substantial empirical support, models with $\Delta_i = 4 - 7$ should be interpreted as having considerably less support, and models with $\Delta_i > 10$ can be considered to have essentially no empirical support (Burnham and Anderson 2002). Akaike weights range from 0 -1 and represent the weight of evidence that a model is the best approximating model in a candidate set of models, with larger values indicating larger weights of evidence (Burnham and Anderson 2002). We also used model averaging across all models to estimate parameters, 95 % confidence intervals, and odds ratios for each variable. Our approach to the interpretation of the results of AIC model selection varied from the traditional approach outlined in Burnham and Anderson (2002). Because our primary interest was in determining whether any covariate influenced the detection ability of a method, we focused on whether any model containing a covariate provided additional explanatory power over a null model. Thus, when the null model was selected as the best model or was strongly competing with the best selected model, we interpreted this as evidence that none of the competing models had any additional explanatory power and therefore none of the covariates within them had any influence on the detection ability of a method. Also, when the model averaged parameter estimates for the variables in the candidate set of models included zero in the 95% confidence intervals, we interpreted this as evidence that a covariate did not significantly influence the detection ability of the method being considered.

We evaluated the efficacy of the three methods, dipnetting, frogloggers, and funnel traps by assessing the relationship between the temporal variation in the number of species captured at a site and environmental and time covariates. To remove the influence of site differences on the number of species captured, the response variable in this analysis was a daily index for each site and method that was calculated by subtracting a baseline number (the lowest number of species captured at a site using a given method) from the number of species captured on a given day. For example, if dipnetting at a site resulted in 3 species on day 1, 4 species on day 2, and 6 species on day 3, the index value for each day respectively would be 0, 1, and 3. Thus this index represented the amount of change in the number of species detected at a site. For this analysis we used the same approach and models used to assess the influence covariates on individual species, except a poisson regression analysis (PROC GENMOD, SAS Version 9.1, Cary, NC, USA) was used to generate initial AIC_c values.

RESULTS

Species richness estimates

Twenty-three amphibian species were recorded in the nine study wetlands over the sampling period (Table 3.1). Overall, aquatic funnel traps yielded the most species (19) followed by frogloggers (14), dipnet surveys (11), PVC pipe refugia (4), and crayfish traps (3). Species overlap between capture methods is shown in Figure 3.1. All species captured by crayfish traps and PVC pipe refugia were also captured by funnel traps. In addition, all species observed in PVC pipe refugia were also detected with frogloggers (Table 3.1). Four species: tiger salamanders (*Ambystoma tigrinum*), dwarf salamanders (*Eurycea quadridigitata*), eastern newts (*Notophthalmus viridescens*), and northern dwarf siren (*Pseudobranchus striatus*) were captured only with funnel traps. Eastern spadefoots (*Scaphiopus holbrookii*) were only captured by dipnetting, and eastern narrow-mouthed toads (*Gastrophryne carolinensis*) were only detected by frogloggers. Pig frogs (*Rana grylio*) were not detected with any of the above techniques, but were heard calling incidentally at one site during the study.

The median number of species detected varied among methods ($\chi^2 = 47.84$, $p < 0.0001$, $df = 9$, $n = 9$). Post-hoc Wilcoxon rank sum tests revealed that the median number of species detected by frogloggers, funnel traps, dipnetting, and PVC pipe refugia were not significantly different ($\alpha = 0.05$), but all of these methods detected significantly more species than crayfish traps (Figure 3.2). In addition, the median number of species detected by funnel traps and frogloggers was not different from the number of species detected by all five methods combined, whereas dipnetting detected significantly fewer species than all five methods combined. There was also no difference between the number of species detected by all five methods combined and the number of species detected by any combination of dipnetting, frogloggers, and funnel traps (the three most effective methods in terms of total species detected). However, there was an increasing trend in the median number of species detected as more methods were combined.

Temporal species accumulation rates were similar for frogloggers, dipnet surveys, funnel traps (Figure 3.3). Although the species accumulation curves for these three methods did not level off over the sampling period, the number of species captured during the initial sampling event was within 1 standard error of the last sampling event for each of these methods. In contrast, both PVC pipe refugia and crayfish traps had lower rates of species accumulation which leveled off after 1-2 sampling events.

Detection rates

Detection rates for individual methods varied widely among species (Table 3.2). Dipnet surveys displayed low detection rates for most salamander species, except mole salamanders (*Ambystoma talpoideum*). For anurans in general, most larval *Pseudacris* species were best detected by this method, whereas most *Hyla* were detected least often by this method. Small salamanders (e.g., *Eurycea quadridigitata* and *Notophthalmus viridescens*) were most often detected by funnel traps, however these traps rarely caught large salamanders such as two-toed amphiuma (*Amphiuma means*) and in general had low detection rates for anurans. Crayfish traps were the most effective means of capture for two-toed amphiuma, but were very ineffective for catching other species. The detection rates of PVC pipe refugia varied widely in treefrogs. In some cases, green treefrogs (*Hyla cinerea*) and squirrel treefrogs (*Hyla squirella*), they were the most effective method, but for some species, Cope's gray treefrogs (*Hyla chrysoscelis*) and barking treefrogs, they displayed the lowest detection rates of the suite of methods. The detection rates of frogloggers ranged widely across anuran species, although this method detected five species more often than other techniques.

Influence of environmental covariates on detection

The influence of environmental and time covariates on the daily number of amphibian species detected differed among dipnet surveys, frogloggers, and funnel traps (Table 3.4). The null model was selected as the best model (model with the lowest AIC_c) for the influence of covariates on dipnet survey capture success. In addition, the Rain and Julian Date models all displayed $\Delta_i < 2$, suggesting that they were also strongly competing models. However, when we used model averaging to estimate parameters, there were no variables that differed from zero based on 95% confidence intervals.

The model with the lowest AIC_c for froglogger surveys, the MaxTemp model, had considerable support with a $\omega_i = 0.6845$, suggesting that this model had a >68% chance of being the best approximating model. However, there was also some evidence for the Rain-MaxTemp model ($\omega_i = 0.2398$) and the Global model ($\omega_i = 0.0757$). When we used model averaging to estimate parameters, only maximum temperature differed from zero. The parameter estimate suggested a positive relationship between daily maximum temperature and the number of species recorded by frogloggers (Table 3.8).

The best selected model for funnel trap surveys, the global model, lacked strong support ($\omega_i = 0.3583$). Similar evidence also existed for the Julian Date model ($\omega_i = 0.3236$). Little evidence existed for models with environmental variables ($\omega_i < 0.15$) other than the global model. Parameter estimates from model averaging suggested that only the Julian date of a survey differed from zero and was slightly negatively associated with the number of species captured in funnel traps (Table 3.8).

The three species we tested showed different relationships between daily detection/nondetection and environmental covariates among the three methods. The null model was selected as the best model for dipnet surveys of barking treefrogs and southern leopard frogs. However, there was also some empirical support ($\omega_i > 0.10$) for the Julian Date, Rain, and MaxTemp models for both species. We were unable to assess the effects of environmental covariates on the detection of southern toads by dipnet surveys due to the small sample size of surveys in wetlands containing this species. When we used model averaging to estimate parameters, there were no variables that differed from zero for any species suggesting that none of the variables measured were associated with the capture success of dipnet surveys for any of the species tested.

The Julian model was selected as the best approximating model for the detection of southern toads by frogloggers. The null, global, and Julian-Rain models were also strongly competing models ($\Delta_i < 2$). However, parameter estimates based on model averaging revealed that no variables differed from zero, suggesting that none of the variables measured influenced the detection of southern toads by frogloggers. Conversely, strong evidence existed that the MaxTemp model ($\omega_i = 0.6307$) was the best approximating model of froglogger detection of barking treefrogs, although some evidence also existed for the Rain-MaxTemp model ($\omega_i = 0.2102$). Parameter estimates from model averaging for this species and this method found that only maximum temperature differed from zero and suggested a positive relationship between barking treefrog detection and maximum daily temperature (Table 3.9). The Julian date model also had the lowest AIC_c for the detection of southern leopard frogs by frogloggers. There was also evidence for the Julian-Rain model ($\omega_i = 0.2221$) and some support ($\Delta_i < 4$, $\omega_i > 0.05$) for the null, Rain, and global models. Parameter estimates based on model averaging for this species found that only the Julian date differed from zero and was slightly negatively associated with southern leopard frog detection by frogloggers (Table 3.10).

The null model was selected as the best model of southern toad detection by funnel traps. However, this model lacked strong support ($\omega_i = 0.2539$); and the Rain, Julian Date, Julian-Rain, and MaxTemp models were all $\Delta_i < 2$, and considered strongly competing . However, when we used model averaging to determine parameter estimates, no variables differed from zero suggesting no relationship between any of the variables measured and southern toad detection in funnel traps. In contrast, the Julian Date model was strongly supported as the best model for the detection barking treefrogs ($\omega_i = 0.6395$), although some evidence existed for the Julian-Rain and global models for this species ($\omega_i = 0.1996$ and 0.1609, respectively). The Julian Date model was also selected as the best model for southern leopard frogs, although the weight of evidence for the Julian-Rain model was similar ($\omega_i = 0.4272$ and $\omega_i = 0.3033$, respectively). However, parameter estimates from model averaging showed that no variables differed from zero for southern leopard frogs, whereas the Julian date was the only variable that differed from zero for barking treefrogs (Table 3.9). The parameter estimate and odds ratio suggested a positive relationship between the Julian date and the detection of barking treefrogs with funnel traps.

DISCUSSION

Southeastern isolated wetlands support a diverse amphibian fauna, and it is challenging to design a sampling regime to detect all species. In this study, while we found that no single method was effective for detecting all species, funnel trapping yielded 83% of all species and was the only method that was effective for most salamanders. However, both dipnet surveys and frogloggers were necessary to detect the remaining three species and often displayed higher detection rates for individual species than funnel traps.

Crayfish traps were generally redundant with other capture methods and caught relatively few amphibian species, however they were by far the most effective method for catching two-toed amphiumas. We also found these traps commonly captured greater siren (*Siren lacertina*) in a study we conducted on a larger set of isolated wetlands in the same study area (A. Liner, unpublished data). Other studies have documented the effectiveness of crayfish traps for catching *Siren* and *Amphiuma* (Johnson and Barichivich 2004, Sorenson 2004). Furthermore, Johnson and Barichivich (2004) used similar traps lined with 5mm Vexar^{TM} mesh, which allowed them to catch 14 species of amphibians in north Florida wetlands, including larval anurans. Their results suggest that lined crayfish traps may be equally as effective as funnel traps for sampling anurans and smaller salamanders. A study comparing the detection rates for larval and adult amphibian species of lined crayfish traps and funnel traps would be useful in determining their relative effectiveness.

PVC pipe refugia also proved to be a redundant method in our study, capturing the same species as funnel traps and frogloggers. However, this method had higher detection rates for green treefrogs, pinewoods treefrogs (*Hyla femoralis*), and squirrel treefrogs than any other method suggesting that this method may be useful for monitoring these species. However, it should be noted that pipe diameter, length, distance from ground, and surrounding habitat can affect the detection rates for treefrogs with this method (Boughton et al. 2000, Moulton et al. 1996, Zacharow et al. 2003). It is interesting to note that the pipe diameter used in this study (5 cm) displayed high capture success for green treefrogs, pinewoods treefrogs, and squirrel treefrogs, but was avoided by these same species in preference for smaller diameter pipes in other studies (Bartareau 2004, Moulton et al. 1996). In our study, we did not provide a range of pipe diameters for the frogs to choose among. Thus, this difference may reflect the response of treefrogs to a lack of suitable smaller diameter natural and artificial refugia in their environment. Therefore, we caution that detection rates of treefrogs in artificial refugia (such as PVC) may be influenced by availability of natural refugia in the surrounding habitat.

Few studies have compared the effectiveness of amphibian capture methods, particularly in the Southeast. A comparison of methods in North Carolina streams found that funnel traps yielded a higher diversity of amphibian species than dipnet surveys, although the range of life stages captured by the two techniques differed (Willson and Dorcas 2003). Dipnet surveys captured more amphibian species in the Okefenokee, St. Marks, Harris Neck, and Savannah National Wildlife Refuges than aquatic traps and frogloggers, although frogloggers detected more anuran species than any other method at three of the sites (Smith et al. 2006; Jennifer Staiger, U.S. Geological Survey Center for Aquatic Resource Studies, personal communication). However, detection rates of individual methods varied widely among species and sites. In Minnesota, dipnet surveys in forested seasonal ponds captured fewer species than call surveys or funnel traps (Buech and Egeland 2002). However, the detection rates of each method varied among species and years. In this study, as in ours, a combination of methods captured the most species and displayed the highest detectability for each species.

An important consideration in the design of amphibian surveys are the biases associated with each technique for the detection of particular life stages and taxonomic groups. Some of the differences that we noted in detection rates among methods reflect these biases. For instance, dipnet surveys and aquatic funnel traps are most effective at catching amphibian larvae, whereas they only occasionally capture adults (Heyer et al. 1994). On the other hand, frogloggers detect only adult male anurans. Thus, they cannot be used to detect caudates and must be deployed in wetlands during the breeding period of adults. In our study, we found that frogloggers displayed low detection rates for most *Pseudacris* species compared to dipnet surveys and funnel traps. This is probably because most *Pseudacris* species are primarily winter breeders in the South (Conant and Collins 1998), and therefore calling adults were probably no longer present during the spring sampling period. However, *Pseudacris* tadpoles were still present in the ponds when we began sampling. Differences between the detection rates of dipnet surveys and funnel traps for individual species may be related to the difference in the way the two methods trap animals. It is likely that adult and larval salamanders, which are powerful swimmers compared to anuran larvae, are more easily captured by funnel traps, which passively intersect their movements, than actively captured by sweeping with a net through wetland vegetation. Furthermore, dipnet surveys were conducted during the day and were therefore unable to detect nocturnal salamander species such as the two-toed amphiuma and greater siren. Funnel traps and crayfish traps, on the other hand, were left in the wetlands continuously and therefore able to capture both diurnal and nocturnal species. However, the large mesh size of the crayfish traps in this study undoubtedly limited their ability to catch only the largest salamander species, *Amphiuma means* and *Siren* species. PVC pipe refugia are appropriate only for climbing species, and thus can only effectively detect treefrogs.

Another important consideration in the design of amphibian surveys is the cost associated with each method. Dipnet surveys were the least costly of the methods used both in terms of money and time (Table 3.11), requiring no set-up time and the purchase of minimal materials (a dipnet). However, the method can be difficult to standardize and requires some degree of skill/training to identify larval amphibians. Funnel traps and PVC pipe refugia were both also relatively inexpensive per site, but were the most time intensive methods because they required considerable effort to install, although PVC pipes can be left in place indefinitely. In addition, we spent several hours (not included in the time estimate) to make traps from window screen, to avoid the higher costs of commercial minnow traps. Crayfish traps and frogloggers were among the most expensive methods, requiring the purchase of expensive commercial traps or equipment. It should be noted that although the time required to set a froglogger and listen to the recordings from one night at one wetland was relatively small, the time to listen to tapes increases exponentially with the number of sites sampled, nights deployed, and minutes per hour recorded. For example, ca. 180 hours were required to listen to tapes recorded during a larger study at 29 wetlands over 3 seasons. Our frogloggers also occasionally malfunctioned leaving gaps in the data. We were unable to assess the time needed to conduct crayfish traps surveys, because they were checked in conjunction with more numerous funnel traps at study sites.

We found that the number of species captured initially using each method did not vary significantly from the number of species accumulated after multiple sampling events. However, the species accumulation curve for frogloggers, funnel traps, and dipnet surveys did not level off in the number of sampling events (6 nights, 12 trap nights, and 3 dipnetting events respectively) used in this study. This pattern suggests that additional sampling events may be needed to detect rare species at our site.

Environmental variables did influence the detection success of frogloggers, but not the other methods used in this study. The number of species detected with frogloggers at a site was positively associated with daily maximum air temperature but displayed no association with the amount of rainfall on the day of the survey. However, of the three species examined, only the calling activity of barking treefrogs was influenced by air temperature. Other studies have related variation in frog calling activity to species specific preferences in barometric pressure, time of day, water temperature, wind speed, and rainfall (Oseen and Wassersug 2002, Paton et al. 2003). In Canada, summer breeding anurans called more frequently at high water temperature, whereas spring breeders were relatively unaffected by water temperature. The same study also noted that explosive breeders were far less responsive to environmental factors than prolonged breeders (Oseen and Wassersug 2002). The results of our individual species models appear to conflict with these results. Southern leopard frogs breed year-round in southern Georgia (Wright 1932), but calling activity did not appear to be influenced by either rainfall or air temperature. In contrast, the calling of barking treefrogs, a spring and early summer breeder (Conant and Collins 1998, Wright 1932), was strongly dependent on maximum temperature and detections increased markedly above a threshold of 23 ºC. However, it is likely that the more temperate climate and longer breeding season may influence calling activity in southern anurans differently than in their northern counterparts (Oseen and Wassersug 2002). For instance, a lack of sensitivity to rainfall and temperature may be part of the mechanism that enables southern leopard frogs to breed year-round and may explain their calling behavior. The increased calling activity of barking treefrogs above a particular temperature threshold may represent an adaptation to a warm weather breeding period. Also, we did not examine the effects of environmental covariates on calling intensity (individual calls versus a breeding chorus) in this study, but merely on the presence of calling by individual species. However, calling intensity may be more sensitive to environmental changes. Any effects of environmental covariates on calling intensity could have important implications for the detectability of species by frogloggers, particularly for species that have less audible calls.

The association between froglogger (breeding anurans) and funnel trap (primarily larval anurans) detection success and the survey date is probably a result of the relatively long period of time included in our study. The positive relationship between the detection of barking treefrogs in funnel traps and Julian date is most likely due to an increased presence of tadpoles of this late spring/early summer breeder in the late spring. Similarly, the slight negative relationship between the number of species captured by funnel traps and the Julian date may also be the result of tadpoles of certain species metamorphosing and leaving the ponds during the course of our study. For instance, many winter-breeding *Pseudacris* species bred during the late winter/early spring of our study due to later than usual winter rains. Many of the tadpoles of these species were therefore still in the wetlands when we started trapping in early April, but would have metamorphosed by the time we ended trapping in mid-May. We cannot explain the slight negative association between southern leopard frog detection by frogloggers and Julian date, because they are known to breed year-round in southern Georgia (Wright 1932). However, the small parameter estimate and log ratio for this variable suggest that there is not a strong relationship between detection of this species by frogloggers and the Julian date.

Overall, our results suggest that a combination of methods is necessary to detect the large number of species present in southeastern isolated wetlands. Based on this single-season study, we recommend that future amphibian surveys in southeastern isolated wetlands employ a minimum combination of funnel traps and frogloggers if an assessment of species richness is the goal. These methods detected the most species during our study and complement each other in their detection abilities for individual species. When feasible, dipnet surveys should also be included in amphibian sampling programs, as we observed this method to also be effective for detecting a large number of species. Crayfish traps should also be used in surveys where *Siren* spp. and *Amphiuma means* are target species. However, we caution that inter-annual and inter-season variation in the detectability of methods may exist and may affect the effectiveness of survey methods for particular species. Because the calling activity of some anurans appears to be influenced by air temperature, this covariate should be taken into account when using frogloggers. Future studies that quantify the affect of air temperature and other environmental variables on a wider range of southeastern anurans and on the calling intensity of those species would be useful in determining the optimum conditions for the detection of each species by frogloggers.

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Figure 3.1. Total amphibian species detected using five different sampling techniques in nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Numbers indicate the total number of species detected by that method with the number of species exclusive to each method indicated parenthetically. Numbers in overlapping areas indicate shared species.

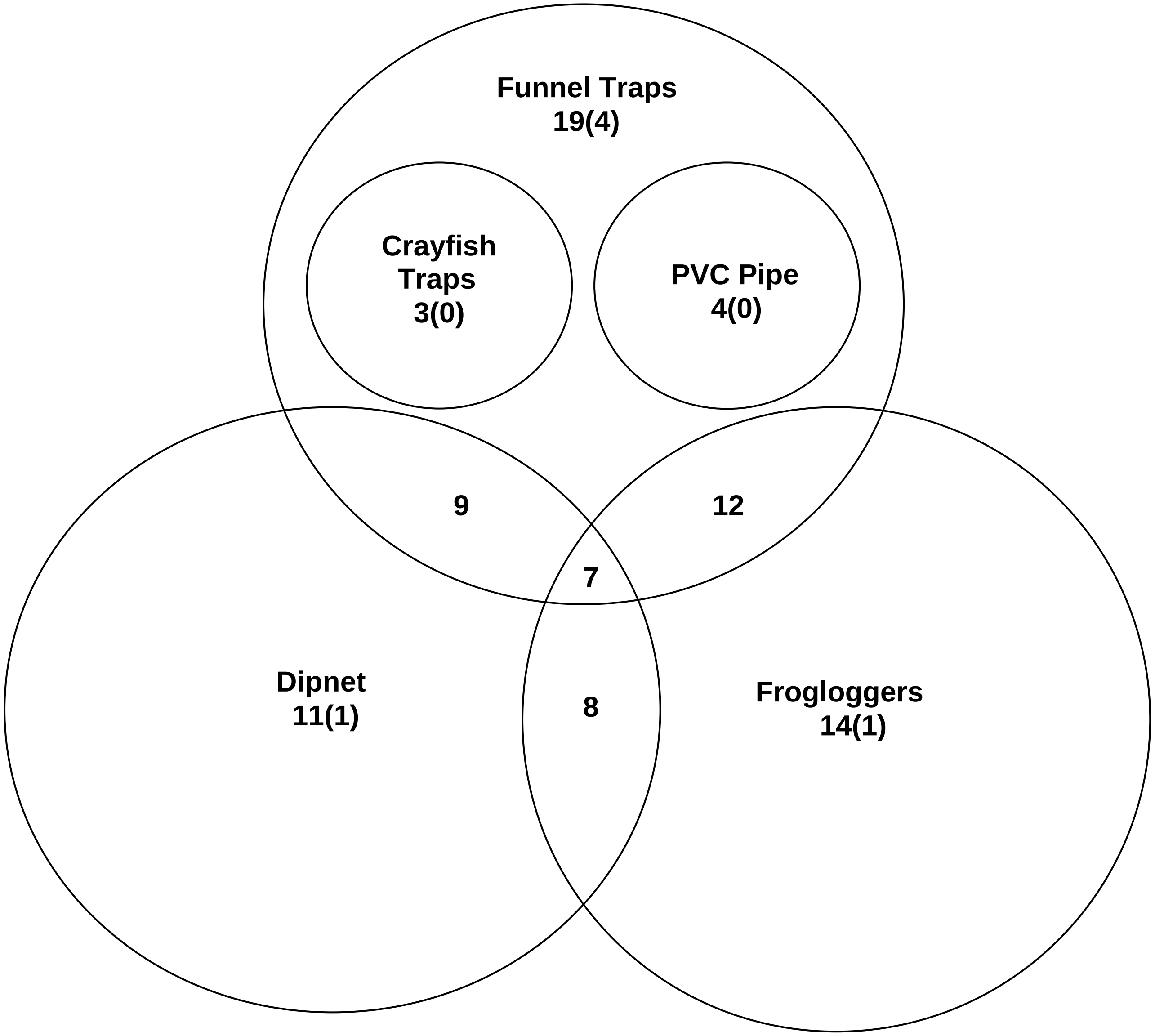
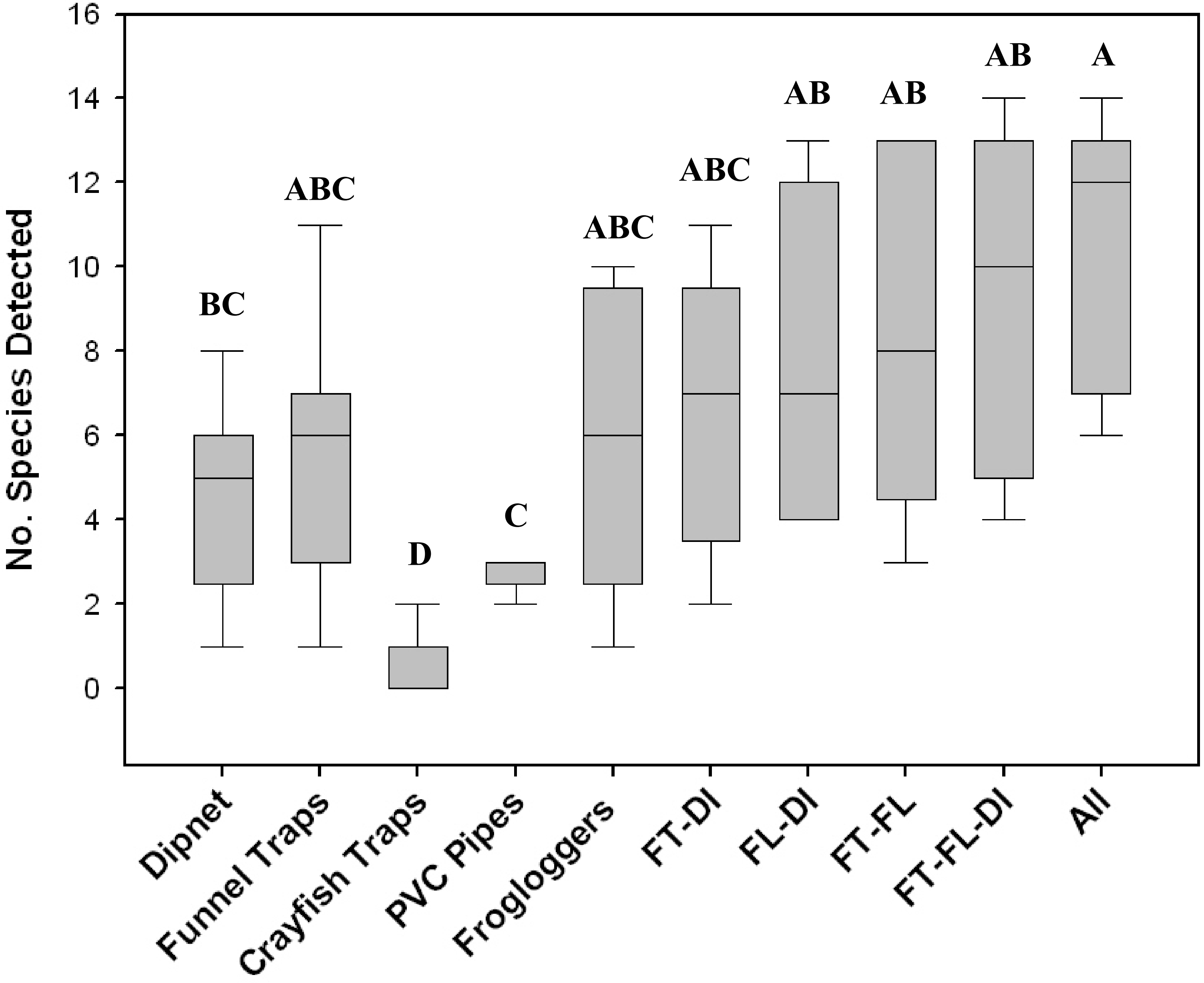
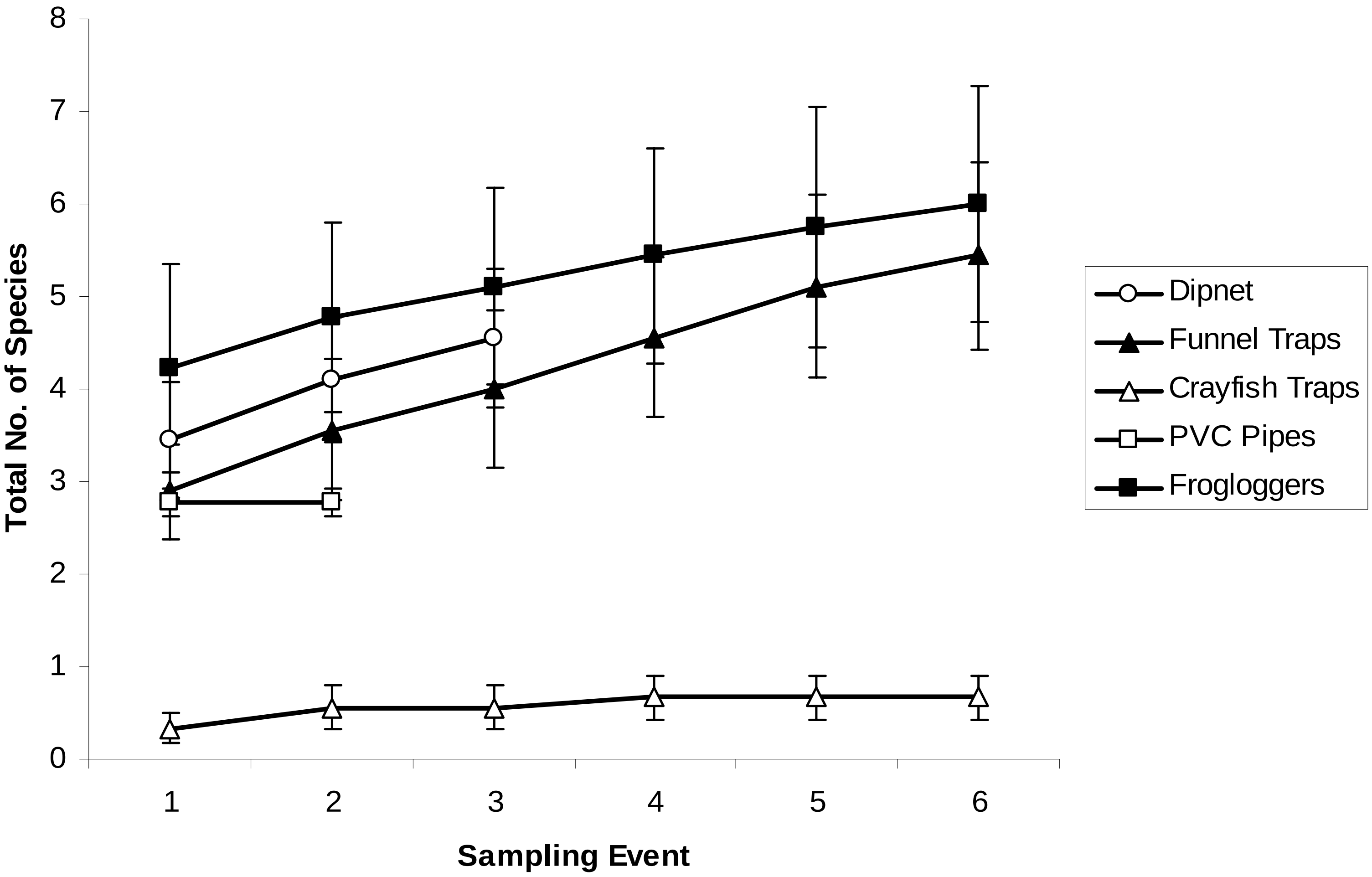

Funnel Traps
19(4)
Crayfish
Traps
3(0)
PVC Pipe
4(0)
9
12
7
Dipnet
11(1)
8
Frogloggers
14(1)

Figure 3.2. Box plots of the number of amphibian species detected with five different sampling methods and combinations of methods in 9 isolated wetlands from March 15 - May 21, 2005 in southwestern Georgia (median, 25th and 75th percentiles, maximum value, minimum value and outliers). Values with the same letter are not significantly different ($p \geq 0.001$) using Kruskal-Wallace and Wilcoxon rank-sum tests with a Bonferroni adjustment. FT-DI = funnel traps and dipnet surveys combined, FL-DI = frogloggers and dipnet surveys, FT-FL = funnel traps and frogloggers combined, FT-FL-DI = funnel traps, frogloggers, dipnet surveys combined, All = All 5 methods combined.



No. Species Detected
16
14
12
10
8
6
4
2
0
BC
ABC
D
C
ABC
ABC
AB
AB
AB
A
Dipnet
Funnel Traps
Crayfish Traps
PVC Pipes
Frogloggers
FT-DI
FL-DI
FT-FL
FT-FL-DI
All

Figure 3.3. Temporal accumulation of amphibian species (mean ± SE) with five different sampling methods used in nine isolated wetlands from March 15 - May 21, 2005 in southwestern Georgia.



8
7
6
5
4
3
2
1
0
Total No. of Species
1
2
3
4
5
6
Sampling Event
Dipnet
Funnel Traps
Crayfish Traps
PVC Pipes
Frogloggers

Table 3.1. Methods of capture for 23 amphibian species in nine isolated wetlands from March 15 - May 21, 2005 in southwestern Georgia. * = Species only incidentally observed.

Scientific Name	**Dipnet**	**Funnel traps**	**Crayfish traps**	**PVC pipe refugia**	**Frogloggers**
Anurans					
Acris gryllus		X			X
Bufo terrestris	X	X			X
Gastrophryne carolinensis					X
Hyla chrysoscelis		X			X
Hyla cinerea		X		X	X
Hyla femoralis	X	X		X	X
Hyla gratiosa	X	X		X	X
Hyla squirella		X		X	X
Pseudacris crucifer	X	X			
Pseudacris feriarum	X	X			X
Pseudacris nigrita	X	X			X
Pseudacris ocularis	X				X
Pseudacris ornata	X	X			X
Rana catesbeiana		X	X		X
*Rana grylio**					
Rana sphenocephala	X	X	X		X
Scaphiopus holbrookii	X				
Caudates					
Amphiuma means		X	X		
Ambystoma talpoideum	X	X			
Ambystoma tigrinum		X			
Eurycea quadridigitata		X			
Notophthalmus viridescens		X			
Pseudobranchus striatus		X			

Table 3.2. Detection rates ± (SD) for 23 amphibian species sampled using five different methods in nine isolated wetlands from March 15 - May 21, 2005 in southwestern Georgia.

Scientific Name	No. Sites Occupied	Dipnet	Funnel traps	Crayfish traps	PVC pipe refugia	Frogloggers
Acris gryllus	6	0.00 (0.00)	0.06 (0.09)	-	-	0.94 (0.14)
Amphiuma means	4	0.00 (0.00)	0.08 (0.10)	0.25 (0.22)	-	-
Ambystoma talpoideum	3	1.00 (0.00)	1.00 (0.00)	-	-	-
Ambystoma tigrinum	2	0.00 (0.00)	0.17 (0.00)	-	-	-
Bufo terrestris	5	0.67 (0.33)	0.37 (0.51)	-	-	0.13 (0.14)
Eurycea quadridigitata	1	0.00 (NA)	0.33 (NA)	-	-	-
Gastrophryne carolinensis	4	0.00 (0.00)	0.00 (0.00)	-	-	0.21 (0.08)
Hyla chrysoscelis	9	0.00 (0.00)	0.08 (0.12)	-	0.00 (0.00)	0.58 (0.35)
Hyla cinerea	2	0.00 (0.00)	0.02 (0.06)	-	0.78 (0.36)	0.15 (0.18)
Hyla femoralis	9	0.22 (0.29)	0.07 (0.17)	-	0.56 (0.39)	0.46 (0.40)
Hyla gratiosa	5	0.80 (0.45)	0.70 (0.41)	-	0.20 (0.45)	0.70 (0.27)
Hyla squirella	9	0.00 (0.00)	0.06 (0.12)	-	1.00 (0.00)	0.19 (0.21)
Notophthalmus viridescens	1	0.00 (NA)	0.67 (NA)	-	-	-
Pseudacris crucifer	1	0.33 (NA)	0.17 (NA)	-	-	0.00 (NA)
Pseudacris feriarum	2	0.33 (0.00)	0.17 (0.24)	-	-	0.08 (0.12)
Pseudacris nigrita	7	0.48 (0.26)	0.12 (0.13)	-	-	0.29 (0.49)
Pseudacris ocularis	1	0.33 (NA)	0.00 (NA)	-	-	1.00 (NA)
Pseudacris ornata	6	0.89 (0.27)	0.61 (0.40)	-	-	0.13 (0.31)
Pseudobranchus striatus	2	0.00 (0.00)	0.33 (0.00)	-	-	-
Rana catesbeiana	8	0.00 (0.00)	0.17 (0.24)	0.08 (0.18)	-	0.73 (0.40)
Rana sphenocephala	8	0.83 (0.36)	0.92 (0.24)	0.02 (0.06)	-	0.67 (0.47)
Scaphiopus holbrookii	1	0.33 (NA)	0.00 (NA)	-	-	0.00 (NA)

Table 3.3. Environmental covariates used to evaluate detection efficacy of dipnet (N = 27), froglogger (N = 52), and funnel trap (N=54) surveys for amphibians in nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Rain = rainfall day of survey, Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

	Dipnet Surveys	**Frogloggers**	**Funnel Traps**
Covariate	Mean, SD (Range)	Mean, SD (Range)	Mean, SD (Range)
Julian Date	112.3, 3.0 (109 - 116)	114.3, 11.6 (096 - 129)	115.8, 12.9 (092 - 134)
MaxTemp (˚C)	24.2, 3.5 (20.1 - 28.0)	24.4, 2.6 (18.2 – 28.7)	25.3, 3.3 (18.1 – 30.6)
Rain (mm)	6.6, 6.9 (0.0 – 15.0)	8.6, 21.8 (0.0 – 89.9)	5.2, 17.7 (0.0 – 89.9)

Table 3.4. Number of variables (k), AIC$_c$, distance from the lowest AIC$_c$ (Δ_i), and model weight (w_i) for poisson regression models comparing daily changes in the number of species detected by dipnetting, funnel traps, and frogloggers against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Only models with $\Delta_i \leq 10$ are presented. Rain = rainfall day of survey, Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	**Model**	**k**	**-2 logl**	**AIC$_c$**	Δ_i	w_i
Dipnetting	Null	1	45.0031	47.1631	0.00	0.4175
	Rain	2	44.6201	49.1201	1.96	0.1569
	Julian	2	44.6415	49.1415	1.98	0.1553
	MaxTemp	2	44.9378	49.4378	2.27	0.1339
	Rain-MaxTemp	3	44.2453	51.2888	4.13	0.0531
	Julian-Rain	3	44.5829	51.6264	4.46	0.0448
	Global	4	42.1128	51.9310	4.77	0.0385
Frogloggers	MaxTemp	2	60.0394	64.2843	0.00	0.6845
	Rain-MaxTemp	3	59.8820	66.3820	2.10	0.2398
	Global	4	59.8375	68.6886	4.40	0.0757
Funnel Traps	Global	4	94.5426	103.3589	0.00	0.3583
	Julian	2	99.3272	103.5625	0.20	0.3236
	Julian-Rain	3	99.0352	105.5152	2.16	0.1219
	Null	1	104.0084	106.0853	2.73	0.0917
	MaxTemp	2	102.8666	107.1019	3.74	0.0551
	Rain	2	104.0037	108.2390	4.88	0.0312
	Rain-Maxtemp	3	102.8531	109.3331	5.97	0.0181

Table 3.5. Number of variables (k), AIC_c, distance from the lowest AIC_c (Δ_i), and model weight (w_i) for logistic regression models comparing daily detection success of frogloggers and funnel traps for *Bufo terrestris* against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Dipnet models not included due to the small sample size of surveys in wetlands containing *Bufo terrestris*. Rain = rainfall day of survey, Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	**Model**	**k**	**-2 logl**	**AIC_c**	**Δ_i**	**w_i**
Frogloggers	Julian	2	19.0614	23.5414	0.00	0.3718
	Null	1	22.9665	25.1204	1.58	0.1688
	Global	4	15.4890	25.2282	1.69	0.1600
	Julian-Rain	3	18.2940	25.2940	1.75	0.1548
	MaxTemp	2	22.4048	26.8848	3.34	0.0699
	Rain	2	22.9153	27.3953	3.85	0.0541
	Rain-MaxTemp	3	22.3158	29.3158	5.77	0.0207
Funnel Traps	Null	1	39.4295	41.5723	0.00	0.2539
	Rain	2	37.4773	41.9217	0.35	0.2132
	Julian	2	37.6582	42.1026	0.53	0.1948
	Julian-Rain	3	36.1658	43.0889	1.52	0.1189
	MaxTemp	2	38.7445	43.1890	1.62	0.1131
	Rain-MaxTemp	3	37.1148	44.0379	2.47	0.0740
	Global	4	36.1081	45.7081	4.14	0.0321

Table 3.6. Number of variables (k), AIC_c, distance from the lowest AIC_c (Δ_i), and model weight (w_i) for logistic regression models comparing daily detection success of dipnet surveys, frogloggers, and funnel traps for *Hyla gratiosa* against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Only models with $\Delta_i \leq 10$ are presented. Rain = rainfall day of survey, Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	**Model**	**K**	**-2 logl**	**AIC_c**	**Δ_i**	**w_i**
Dipnet	Null	1	15.0121	17.3198	0.00	0.5170
	Julian	2	14.8962	19.8962	2.58	0.1426
	Rain	2	14.9190	19.9190	2.60	0.1410
	MaxTemp	2	14.9726	19.9726	2.65	0.1372
	Julian-Rain	3	14.8940	23.0758	5.76	0.0291
	Rain-MaxTemp	3	14.9188	23.1006	5.78	0.0287
	Global	4	14.8554	26.8554	9.54	0.0044
Frogloggers	MaxTemp	2	23.8956	28.3756	0.00	0.6307
	Rain-MaxTemp	3	23.5728	30.5728	2.20	0.2102
	Global	4	23.0517	32.7909	4.42	0.0694
	Null	1	31.4908	33.6446	5.27	0.0453
	Julian	2	30.5643	35.0443	6.67	0.0225
	Rain	2	31.3088	35.7888	7.41	0.0155
	Julian-Rain	3	30.5182	37.5182	9.14	0.0065
Funnel Traps	Julian	2	12.5301	16.9745	0.00	0.6395
	Julian-Rain	3	12.3806	19.3037	2.33	0.1996
	Global	4	10.1341	19.7341	2.76	0.1609

Table 3.7. Number of variables (k), AIC_c, distance from the lowest AIC_c (Δ_i), and model weight (w_i) for logistic regression models comparing daily detection success of dipnet surveys, frogloggers, and funnel traps for *Rana sphenocephala* against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Rain = rainfall day of survey, Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	**Model**	**K**	**-2 logl**	**AIC_c**	**Δ_i**	**w_i**
Dipnet	Null	1	21.6269	23.8088	0.00	0.3731
	Rain	2	20.5699	25.1413	1.33	0.1916
	Julian	2	20.9540	25.5254	1.72	0.1582
	MaxTemp	2	20.9849	25.5563	1.75	0.1557
	Rain-MaxTemp	3	20.4291	27.6291	3.82	0.0552
	Julian-Rain	3	20.5697	27.7697	3.96	0.0515
	Global	4	20.1880	30.2933	6.48	0.0146
Frogloggers	Julian	2	54.4399	58.7190	0.00	0.4523
	Julian-Rain	3	53.5697	60.1411	1.42	0.2221
	Null	1	59.4403	61.5312	2.81	0.1109
	Rain	2	57.8573	62.1363	3.42	0.0819
	Global	4	53.5160	62.4916	3.77	0.0686
	MaxTemp	2	59.4397	63.7188	5.00	0.0371
	Rain-MaxTemp	3	57.7791	64.3505	5.63	0.0271
Funnel Traps	Julian	2	21.1027	25.3693	0.00	0.4272
	Julian-Rain	3	19.5090	26.0544	0.69	0.3033
	Global	4	19.1251	28.0554	2.69	0.1115
	Null	1	27.5363	29.6232	4.25	0.0509
	Rain	2	25.9405	30.2071	4.84	0.0380
	Rain-MaxTemp	3	23.7320	30.2775	4.91	0.0367
	MaxTemp	2	26.2611	30.5278	5.16	0.0324

Table 3.8. Model-averaged parameter estimates and lower (LCI) and upper (UCI) 95% confidence intervals for variables used in poisson regression models comparing daily species detected by dipnetting, funnel traps, and frogloggers against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Only variables with parameter estimates that differ from zero included. No variables in the dipnet model have parameter estimates that differ from zero. Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	**Variable**	**Parameter Estimate**	**LCI**	**UCI**
Frogloggers				
	MaxTemp	0.370	0.242	0.497
Funnel Traps				
	Julian Date	-0.032	-0.059	-0.005

Table 3.9. Model-averaged parameter estimates, lower and upper 95% confidence intervals, and log-odds ratios for variables used in logistic regression models comparing daily *Hyla gratiosa* captures by dipnetting, funnel traps, and frogloggers against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Only variables with parameter estimates that differ from zero included. No variables in the dipnet model have parameter estimates that differ from zero. Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	Variable	Parameter Estimate	LCI	UCI	Odds Ratio
Frogloggers					
	MaxTemp	0.557	0.062	1.051	1.745
Funnel Traps					
	Intercept	-1615	-3090.58	-139.419	0.000
	Julian Date	0.316	0.028	0.604	1.372

Table 3.10. Model-averaged parameter estimates, lower and upper 95% confidence intervals, and log-odds ratios for variables used in logistic regression models comparing daily *Rana sphenocephala* captures by dipnetting, funnel traps, and frogloggers against environmental covariates for nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Only variables with parameter estimates that differ from zero included. No variables in the dipnet or funnel trap models have parameter estimates that differ from zero. Julian Date = Julian date of survey, MaxTemp = maximum temperature on day of survey.

Method	Variable	Parameter Estimate	LCI	UCI	Odds Ratio
Frogloggers					
	Julian Date	-0.065	-0.127	-0.002	0.938

Table 3.11. Average costs of materials and time involved for a single survey for amphibians using each of five techniques in nine isolated wetlands in southwestern Georgia from March 15 - May 21, 2005. Time is in person hours. Time cost for crayfish trap surveys not available.

Sampling Method	**Materials[a]**	**Cost (US$)[a]**	**Time spent (hr)**
Dipnet Survey	1 Dipnet	25	0.5
Crayfish Trap	5 Commercial Crayfish Traps	125	-
Froglogger	tape recorder, timers, wiring, tapes for 1 froglogger	340	0.5[b]
Funnel Traps	Aluminum window screen, staples, clips for 15 traps	38	1.5[c]
PVC Pipes	17 PVC pipes	28	3[d]

[a] Based on average of materials used in 9 isolated wetlands of intermediate size.

[b] Estimated time to listen to 24 hour period of tape recorded at 1 minute per hour intervals.

[c] Time includes 1 person hour estimated trap set time and a 0.5 person hour daily trap check time.

[d] Includes an estimated 2 person hours for pipe placement and 1 person hour for checking pipes.

CHAPTER 4

CONCLUSIONS

Seasonally flooded, hydrologically isolated wetlands are a habitat of primary importance for amphibian diversity in the southeastern Coastal Plain. In Georgia, these wetlands provide breeding and other critical habitat for 49% of the state's amphibian species (Conant and Collins 1998, Moler and Franz 1987, Petranka 1998). However, in Georgia and elsewhere in the United States, isolated wetlands are also a highly threatened habitat, receiving little legal protection and intense development pressure (Christie and Hausmann 2003, Sutter and Kral 1994, Tiner 2003). While conservation of these habitats is critical for maintaining regional amphibian diversity, relatively little is known about amphibian communities in these habitats. This is particularly true of the limesink wetlands of the Eastern Gulf Coastal Plain, which have received much less study than the Carolina Bays of the Atlantic Coastal Plain.

Isolated wetlands in southwestern Georgia can be categorized into three distinct types: marshes, cypress savannas, and cypress/gum swamps (Kirkman et al. 2000). Earlier studies have found that these wetland types differ in vegetation and soil characteristics, canopy cover, hydroperiod, dissolved oxygen content, water chemistry, water temperatures, and invertebrate abundance and diversity (Battle and Golladay 2001, Kirkman et al. 2000). These wetlands types displayed fundamental differences in size, recent and long-term hydroperiods, maximum water depth, isolation from other wetlands, and the number of predatory amphibians present. In this study I found a distinct difference between the amphibian species composition of cypress/gum swamps and that of marshes and cypress savannas. Two-toed amphiumas (*Amphiuma means*) and paedomorphic mole salamanders (*Ambystoma talpoideum*) were positively associated with cypress/gum swamps and negatively associated with marshes and cypress savannas. Cope's gray treefrog was also positively associated with cypress/gum swamps but was found less frequently than expected in marshes. Barking treefrogs (*Hyla gratiosa*), ornate chorus frogs (*Pseudacris ornata*), and tiger salamanders (*Ambystoma tigrinum*) were negatively associated with cypress/gum swamps and positively associated with marshes. Barking treefrogs were also positively associated with cypress savannas.

I hypothesize that the differences in amphibian composition among wetland types are primarily the result of differences in canopy cover, which in turn result in differences in water chemistry, solar insulation, and food availability. Cypress/gum wetlands display a dense canopy cover, low pH and dissolved oxygen, relatively low water temperatures, and decreased algal and invertebrate abundance (Battle and Golladay 2001, Kirkman et al. 2000), all of which have the potential to affect amphibian community composition. Cypress/gum wetlands also display longer hydroperiods relative to the other two types of wetlands, which I hypothesize results in a greater diversity of amphibian predators that either eliminate or deter the breeding of certain amphibian species.

Fish presence also had an influence on the distribution of amphibian species in this study. The southern cricket frog (*Acris gryllus*), barking treefrog, and ornate chorus frog all were found less frequently in wetlands with large predatory fish (centrarchid and ictalurid species) than in fish-free wetlands. Mole salamanders, tiger salamanders, southern toads (*Bufo terrestris*), and northern dwarf sirens (*Pseudobranchus striatus*) were rarely observed in wetlands with fish, and spring peepers (*Pseudacris crucifer*), gopher frogs (*Rana capito*), and pig frogs (*Rana grylio*) were never observed in wetlands with fish. However, these species were also fairly uncommon in fish-free wetlands. Eastern mosquitofish (*Gambusia holbrooki*) appeared to exclude many of the same species as large predatory fish, however we were unable to evaluate the impact of eastern mosquitofish due to the small number of wetlands colonized exclusively by this species.

Given the apparent influence of fish presence and wetland type on amphibian community composition, future amphibian monitoring and research programs in isolated wetlands in the region should consider these factors before drawing conclusions based solely on amphibian surveys. Fish presence in isolated wetlands is highly variable over space and time, depending on colonization during wet periods and extirpation during periodic wetland drying. If the presence of fish is not assessed, the results of amphibian surveys in wetlands colonized by fish could wrongly be interpreted as evidence of a population decline or a negative result of a wetland management decision. Similarly, the influence of wetland type must also be considered. In particular, wetland restoration and mitigation efforts should recognize the important influence of wetland type on amphibian species distributions. Restoring a wetland to a different type than the original or preservation of a wetland of one type as mitigation of for loss of a wetland of another type will result in a loss of wetland function in terms of supporting an equivalent amphibian community. This change in the amphibian composition can be in turn expected to echo throughout the food web of that wetland creating an altered wetland system from the original restoration or mitigation goals.

This research also highlights the importance of wetland diversity within a landscape. Isolated wetlands on Ichauway exist as a patchwork of wetlands of different types, sizes, and hydroperiod that vary in distances from other wetlands and in the presence of fish. All of these factors are known to influence amphibian distributions creating an intricate and dynamic mix of amphibian communities within the larger landscape. It is this wetland diversity that promotes amphibian diversity among the isolated wetlands on Ichauway. This study has shown that no single wetland contained all amphibian species present on site, but rather species distributions varied among wetlands with different combinations of habitat characteristics. These habitat variables undoubtedly change with time in individual wetlands through the processes of fish colonization, succession, and drought and flood. However, it is likely that the variation of wetlands in the landscape sustains regional amphibian diversity, even as individual wetlands become uninhabitable for particular species. Future wetland and amphibian efforts in the region must recognize the importance of this wetland diversity and the importance of interconnectedness of diverse wetland habitats if they are to succeed. Merely protecting individual wetlands and small adjacent terrestrial buffer zones will not suffice to protect the diversity of the regional amphibian fauna. Future wetland mitigation and restoration efforts must also recognize the importance of this wetland diversity in the region. Only restoring or protecting one type of wetland will have negative effects on the distributions of particular species.

This research suggests that future amphibian surveys in southwest Georgia isolated wetlands should use a combination of frogloggers, aquatic funnel traps, and dipnet surveys. These methods were effective for the largest number of species, captured species not captured by other methods, and complement each other in terms of their detection rates for individual species. Crayfish traps, though relatively expensive on a per trap basis, should also be used if the detection of large aquatic salamander species (*Amphiuma* or *Siren* species) is desired, as no other method was as effective for detecting these species. PVC pipe refugia, though highly effective for the capture of three species of treefrog (*Hyla* spp.), was the most time consuming method and is associated with a number of biases in terms of pipe placement and size. In addition, I hypothesize that the use of PVC pipe refugia by treefrogs is highly dependent on the availability of natural refugia in individual wetlands. For these reasons, I do not recommend this method be used in future surveys.

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