USE OF AMPHIBIANS AS ECOSYSTEM INDICATOR SPECIES

By

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This dissertation is dedicated to my parents, Chris and Sherrell Waddle, who have always supported me and encouraged me to do what I love, and to Amanda, the love of my life.

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Amphibians are generally considered suitable as indicator species in a variety of systems. Their biphasic life cycle and semi-permeable skin are two justifications often given for this use of amphibians. In this dissertation, the use of amphibians as indicator species in support of management and restoration in the Everglades of southern Florida was investigated. Methods for monitoring amphibians and specific uses of amphibians as indicator species were evaluated.

Techniques to reduce observer bias in visual encounter surveys, a common method of sampling amphibians for monitoring purposes, were tested. Both double observer and distance based methods were shown to have significant bias in enumerating a known population of artificial frogs. Toe-clipping, a standard method for individually marking frogs was also studied on two treefrog species in south Florida. Toe-clipping was found to have a slight negative effect on survival in one species, but not the other. These studies demonstrate the importance of carefully choosing and evaluating monitoring methods to appropriately address questions concerning amphibian populations.

The occupancy of four anuran species was estimated in relation to off-road vehicle (ORV) use in Big Cypress National Preserve to determine if amphibians are useful as indicators of this form of anthropogenic disturbance. Results confirmed that ORV use was a significant factor in

the site occupancy of the four species of ground-dwelling anurans studied. In another study, the survival and recruitment of Green Treefrogs were estimated in relation to hydrology and habitat to better understand how frogs might respond to hydrologic changes proposed under the Comprehensive Everglades Restoration Plan. Water depth and hydrologic season were both important factors in survival and recruitment, and population growth rates varied with seasons.

This research concludes that amphibians meet the criteria for ecosystem indicator species in south Florida. They are abundant, may be efficiently sampled, and have been demonstrated to respond in a predictable way to stresses to the system. Monitoring of amphibians is a useful tool for determining the success of ecosystem restoration and management in the Everglades of south Florida.

CHAPTER 1
INTRODUCTION

Ecological indicators can have many purposes, including being used to assess the condition of the environment or monitor trends in condition over time (Cairns et al. 1993, Dale and Beyeler 2001). Some species suitable for monitoring trends in condition over time may be useful as indicators of restoration success in ecosystems in which restoration activities are occurring. Amphibians are widely considered to be useful as indicator species (Welsh and Ollivier 1998, Sheridan and Olson 2003), but little direct evidence has been gathered that evaluates the usefulness of amphibians for this role. There are several reasons why amphibians may be excellent indicators, but there are also limitations to their use. In this chapter, I discuss the characteristics of good indicators and whether amphibians display these characteristics. In addition, I will outline important considerations for evaluating amphibians as indicators for any particular system. Finally, I will introduce my research in the Everglades of southern Florida and outline the rest of this dissertation.

Characteristics of Indicator Species

Dale and Beyeler (2001) discuss several general characteristics of useful indicator species. Indicators should be easily sampled, sensitive to stresses on the system, and respond to stress in a predictable manner. These responses should be anticipatory of an impending change in the whole system, and they should predict changes that can be averted by management. Indicators should provide information regarding changes to the whole system rather than a few habitats or locations, and have a known response to anthropogenic stresses and natural disturbances, and the response should have low variability (Dale and Beyeler 2001). Indicators for restoration success need to be predictable enough to determine whether they are responding to changes due to management actions or just natural fluctuations in the system.   Finally, indicator species should also be abundant or cost-effective to sample.

Using vertebrates as indicators of habitat quality requires special consideration (Landres et al. 1988). Using abundance of vertebrate species requires robust estimation techniques that explicitly deal with imperfect detection (MacKenzie et al. 2002, Williams et al. 2002). Also, the efficacy of the indicator species as an index for the abundance of other species must be determined. Using one or more species as indicators of habitat quality for other species is valid only after research validating this approach has been conducted (Landres et al. 1988). Managing for one indicator may ignore ecological processes not important to the indicator but vital to other species (Kushlan 1979).

Suitability of Amphibians as Indicator Species

Amphibian species or communities have been touted as useful indicators in many situations recently (Welsh and Ollivier 1998, Galatowitsch et al. 1999, Collins and Storfer 2003, Sheridan and Olson 2003, Hammer et al. 2004). Some studies use amphibians as indicators of environmental contamination or pollution (Hammer et al. 2004). Others attempt to use the species assemblage (Sheridan and Olson 2003) or the abundance of populations (Welsh and Ollivier 1998, Campbell et al. 2005) as indicators of ecosystem health or habitat quality.

Amphibians have several characteristics that make them useful as indicator species. They are often locally abundant (Rocha et al. 2001, Watanabe et al. 2005) and may be sampled with low-cost standard methods (Heyer et al. 1994, Pierce and Gutzwiller 2004). Because of their permeable skin and biphasic life cycle amphibians are likely sensitive to environmental stress (Vitt et al. 1990, Wake 1991, Blaustein 1994, Blaustein et al. 1994), but there is some debate about whether this sensitivity is consistent and predictable (Pechmann and Wilbur 1994). It is imperative that any study using amphibians as indicators of ecosystem stress demonstrates a direct causal link between the stress and its effect on the indicator species.

More research is also needed to determine if the response of amphibians to a particular stress is indicative of the management action taken. In some situations amphibians may serve as “canaries” (Blaustein 1994), but not necessarily in all cases (Pechmann and Wilbur 1994). The responsiveness of amphibians as indicator species will depend on the type of stress and the particular amphibians in the system.

It is likely that amphibians will be good indicators of changes to the whole ecosystem because they are sensitive to changes in the aquatic and terrestrial environments. The aquatic environment is required for reproduction in most species (Duellman and Trueb 1986) and the permeable skin of amphibians makes them sensitive to water quality and UV radiation in the egg and larval as well as adult life stages (Gerlanc and Kaufman 2005, Taylor et al. 2005). Many amphibian species spend much of their life in terrestrial environments for activities like feeding and dispersal. Amphibians should also respond to changes in the terrestrial environment that would affect water relations through their integument with behavioral responses (e.g., shifting activity periods or moving to different microhabitats) or less frequently with phenotypic responses (e.g., facultative lipid barrier adjustment; Lillywhite 2006).

Outline of the Dissertation

The Everglades ecosystem of southern Florida has been substantially altered over the last 100 years by loss to agriculture and urbanization (South Florida Water Management District [SFWMD] 1992, Ogden et al. 2005). Compartmentalization of the remaining system has impeded historic flow patterns and altered the temporal and spatial dynamics of hydrology in the Everglades (Davis et al. 1994). A large-scale restoration effort, the Comprehensive Everglades Restoration Plan (CERP), was devised to attempt to restore natural hydrologic regimes to the remaining Everglades (DeAngelis et al. 1998). Managers charged with decision making for CERP need species that can serve as indicators of ecosystem restoration success. A necessary condition before a species may be used as an indicator in a system is a model of how the species will respond to changes in the system (Kremen 1992, Dale and Beyeler 2001). Some species (e.g., wading birds; Crozier and Gawlik 2003) have been monitored for many decades; therefore data exist on pre-alteration conditions. Other species (e.g., periphyton; McCormick and Stevenson 1998) have been manipulated in experiments to better understand their expected response to changes that will be imposed during Everglades restoration.

My research for this dissertation focuses on using amphibians as indicator species in support of management of the >1,000,000 hectares under restoration in CERP. Although some higher trophic level species are monitored and modeled to evaluate restoration scenarios currently (DeAngelis et al. 1998), many of these species do not meet Dale and Beyeler's (2001) criteria for good indicator species. For instance, the Cape Sable Seaside Sparrow and the Florida Panther are rare species of conservation interest, but these species may not respond in a predictable way to changes to the system, and it is unproven that their responses will be anticipatory of effects on other components of the system.

There is also a need for indicator species that can be used to identify the effects of certain human activities other than CERP on these natural areas. The use of off-road vehicles (ORV) is an important management concern in Big Cypress National Preserve (BCNP) (NPS 2000). The extent to which ORVs impact wildlife in Big Cypress is of great interest to park managers. My objective was to research the efficacy of amphibians as indicator species in southern Florida to support information needs for both CERP and for the management of ORVs in BCNP.

Chapter 2 describes a study designed to evaluate bias when using the visual encounter survey, a standard sampling technique for reptiles and amphibians. Two estimation methods designed to account for incomplete detectability were applied to count data collected by observers on a known population of artificial frog models. This study underscores the need for accounting for incomplete detectability in amphibian monitoring programs and the potential for bias in count data. Accurate sampling techniques with reliable methods for determining the precision of estimates is critical when using amphibians as indicator species.

Chapter 3 describes the use of site occupancy estimation (MacKenzie et al. 2002) to model the effects of ORV use on the distribution of four anuran species in BCNP. Site occupancy modeling determined that the index of ORV use created for this study was an important factor in the occupancy of ground-dwelling frog species. Only one species was positively associated with the ORV index, while the other three were less likely to occupy sites with higher ORV use. A monitoring program designed to use these amphibians as indicators would be useful for evaluating the continuing impact of ORVs in Big Cypress.

Chapters 4 and 5 describe the use of hylid treefrogs as indicators of restoration success in the Everglades. Chapter 4 examines the effects of toe-clipping as a marking technique for individual treefrogs. Uniquely marking individuals is necessary for estimation of survival and movement rates, but the marking method must be validated. Chapter 5 describes a study to examine survival and recruitment rates of green treefrogs in relation to hydrology and habitat. This information is vital for building a model of how these potential indicator species will respond to the hydrologic changes of CERP.

Finally Chapter 6 discusses the overall usefulness of amphibians as ecosystem indicator species in southern Florida. I will make recommendations for monitoring and analysis techniques of amphibian populations that are appropriate at particular scales. I will summarize the extent to which amphibians are useful as indicator species in the Everglades ecosystem.

CHAPTER 2
SAMPLING METHODS FOR AMPHIBIAN MONITORING

Introduction

The visual encounter survey (VES) is widely used as a sampling method for reptiles and amphibians (Crump and Scott 1994, Doan 2003). In this method, one or more observers search a defined area for animals for a specified amount of time. Usually the number of individuals of a species counted is standardized by time or area searched (i.e., effort) to determine the relative abundance of the species. Relative abundance among sites may only be compared under the restrictive assumptions of an index to actual abundance. The primary assumptions are that individuals of a species have a constant probability of detection across time and space (e.g., different seasons or habitats) and that different observers all have the same probability of detecting species of interest (Crump and Scott 1994, Williams et al. 2002). These assumptions may be violated with improper study design or by uncontrollable factors such as weather. Some authors have demonstrated that the assumptions underlying the use of VES data as a measure of relative abundance of amphibians and reptiles are unlikely to hold in actual sampling (Henke 1998, Rodda et al. 2005).

The major obstacle to using this index approach is heterogeneity in detection probability (p) of individuals of a given species and among different observers (Pollock and Kendall 1987, Williams et al. 2002). It is possible that p may change in relation to sampling conditions, individual behavior, or across habitat types. Further, different observers may be more or less adept at finding a species and may therefore record different proportions of individuals (i.e., perception bias; Marsh and Sinclair 1989). Sampling methods based on distance sampling have been developed to deal with heterogeneity in p across space and time to produce robust estimates of density (Burnham et al. 1980, Buckland et al. 2001). Other methods involving multiple observers have been developed to account for observer bias (Cook and Jacobson 1979, Pollock and Kendall 1987, Marsh and Sinclair 1989, Nichols et al. 2000), and recent advances in distance sampling of line transects have combined information from multiple observers to improve density estimates where detection at the line is not always perfect (Buckland et al. 2004).

I evaluated the use of double observer and distance sampling approaches using a population of artificial frogs with known abundance. This technique lacks the realism of actual frogs, but provides a better evaluation of the potential bias associated with distance sampling and double observer sampling separately and together. The objective of this study was to evaluate sampling approaches that incorporate estimates of detection probability over line transects sampled similarly to the standard VES. I hypothesized that both methods would yield similar results and that the 95% confidence intervals of the estimates from both methods would include the true abundance of frogs. Strengths and weaknesses of the sampling methods will be discussed.

Methods

Sampling Experiment

To test the efficacy of the double observer and distance methods, a pair of 50-m transects in 2 habitats (4 transects total) were established in Big Cypress National Preserve, Collier County, Florida, USA, on 14 June 2005. Transects were arranged as 2 parallel lines spaced 30 m apart. Each transect was in a continuous tract of either prairie or pineland habitat. Prairie consists of short hydroperiod wetlands that lack an overstory and woody vegetation in general. Prairies are dominated by sedges, usually up to 1 m in height (Duever et al. 1986). Pinelands are forested habitats that form on slightly higher elevation sites in BCNP dominated by Slash Pine (*Pinus elliottii*). Pinelands tend to have a dense understory of woody plants, especially Wax Myrtle (*Myrica cerifica*) as well as grasses and sedges (Duever et al. 1986). The centerline of each transect was clearly marked with string attached to polyvinyl chloride (PVC) poles every 10 m. The string on the centerline was stretched and tied to insure that it remained taut during the entire sampling experiment.

Artificial frogs consisted of small (50 mm total length) plastic frog models (Daytona Vending, www.freightcloseouts.com). The artificial frogs were painted with flat black spray paint on the underside and glossy green spray paint on the upper surface to conceal the bright color of the plastic and to reasonably represent the appearance of the Green Treefrog (*Hyla cinerea)*, an abundant hylid in the region (Meshaka et al. 2000). Frog models, 50 per transect, were located randomly within 2 m of either side of each line. The maximum vertical height of frog placement was selected as a random number between 0 and 150 cm, and actual height was the highest point on which the frog could be securely fastened in an upright position but not greater than the maximum. Artificial frogs were attached to vegetation using a single loop of clear monofilament fishing line. All frogs were recovered after the experiment and determined to be in the same location as their original placement.

The sampling scheme was based on a combination of the dependent double-observer approach of Cook and Jacobson (1979) and the distance sampling approach of Buckland et al. (2001). To sample transects, volunteers were organized into teams of 2 observers. Observers were told to designate one member of the group as the primary observer and another as the secondary observer for the first transect, and then to switch roles for the second transect. First, the primary observer was instructed to walk along the transect and indicate all frogs observed. Next, the secondary observer was told to record the side of and perpendicular distance from the transect centerline to each frog detected by the primary observer. Finally, the secondary observer was instructed to search for frogs not observed by the primary observer (i.e., after the primary observer passed their location). The secondary observer then recorded their perpendicular distance and noted that they were missed by the primary observer. The teams of observers worked at night using headlamps in similar conditions to a standard VES survey. Seven teams sampled the prairie habitat and 6 teams sampled the pineland habitat. All of the observers were trained biologists, but none had searched for artificial frogs prior to this experiment. None of the observers were involved in placing the artificial frogs on transects.

Double Observer Analysis

The double observer data were analyzed using the model of Cook and Jacobson (1979). This model is based on data collected in which 2 individuals alternate roles as the primary and secondary observer. Three models of detection probability (p) were analyzed in program SURVIV (White 1992): individual detection probabilities for each observer ($p_{\text{obs*hab}}$), a single detection probability for each habitat, respectively (p_{hab}), and a constant detection probability among observers and habitats ($p_{..}$). Model selection was conducted using Burnham and Anderson’s (1998) information-theoretic approach based on the quasi-likelihood Akaike’s Information Criterion adjusted for small sample sizes (QAIC$_c$).

Estimates of $\hat{p}_i$ were obtained for individual observers using the methods of Cook and Jacobson (1979) as implemented by Nichols et al. (2000) in Program SURVIV (White 1992) using the equations:

$$\hat{p}_1 = \frac{x_{11}x_{22} - x_{12}x_{21}}{x_{11}x_{22} + x_{22}x_{21}} \qquad \text{and} \qquad \hat{p}_2 = \frac{x_{11}x_{22} - x_{12}x_{21}}{x_{11}x_{22} + x_{11}x_{12}}$$

where x_{11} is the number of individuals detected by observer 1 in the role of primary observer, x_{22} is the number detected by observer 2 as primary, and x_{12} and x_{21} are the number of individuals observed by observer 1 as the secondary and observer 2 as the secondary, respectively. The overall estimated $\hat{p}$ of each team was determined following the methods of Nichols et al. (2000) using the equation:

$$\hat{p} = 1 - \frac{x_{12}x_{21}}{x_{22}x_{11}},$$

and the estimate of the total abundance ($\hat{N}$) of frogs from each sample was produced using the equation:

$$\hat{N} = \frac{x..}{\hat{p}}$$

where *x*.. is the sum of the counts of both observers. The estimated variance for this estimate is given by Nichols et al. (2000):

$$\hat{\mathrm{var}}(\hat{N}) = \frac{(x..)^2\ \hat{\mathrm{var}}(\hat{p})}{\hat{p}^4} + \frac{(x..)(1-\hat{p})}{\hat{p}^2}.$$

Distance Analysis

The perpendicular distance data were analyzed in Program DISTANCE (Thomas et al. 2003) to estimate the density and abundance of artificial frogs. Density was estimated independently for each team. To increase precision of the estimate, the detection function was produced from distances pooled across teams but within each habitat stratum. Observers were told to only look for frogs within 2 m of the transect centerline, and all frogs were placed within 2 m of the centerline. Therefore, the data were truncated to 2 m in the field. Truncation at 1 m and at 1.5 m was also explored using data filters in DISTANCE.

Results

The randomly chosen locations of the artificial frogs were evenly distributed around the transect center line (Figure 2-1). The 7 teams in the prairie habitat found 41-68 of the 100 frogs, and the 6 teams in the pine habitat found 18-43 of the 100 frogs present along both transects

(Table 2-1). Team 5 in the prairie habitat and Team 10 in the pine habitat had an observer who did not find any frogs in the role of secondary observer. Using location information noted by observers it is believed that a total of 94 of the possible 100 artificial frogs in prairie habitat and 67 of the 100 artificial frogs in pineland habitat were observed by at least one team.

Actual detection rates calculated within 30 cm, within 50 cm, beyond 50 cm, and overall varied by team and were not consistently higher closer to the transect centerline (Table 2-2). Several teams saw fewer frogs near the centerline than further away, most notably teams 2, 4, and 6 in the prairie habitat (Figure 2-2) and teams 9 and 10 in the pineland habitat (Figure 2-3).

Double Observer

Model selection in Program SURVIV indicated that model p_{obs} (with individual observer detection probabilities) was better than habitat level or constant detection probability models as model p_{obs} received all of the QAIC$_c$ weight (Table 2-3). Individual detection probabilities varied widely among observers ranging from 0.40 -1.0 in prairie habitat and from 0.01 – 1.0 in pineland habitat (Table 2-4).

Estimates of total frog abundance along transects in both habitats were lower than the actual abundance of 100 per habitat (Table 2-5). Abundance estimates ranged from 43–70 on prairie transects and from 20-49 on pineland transects.

Distance Analysis

Model selection in Program DISTANCE favored models with habitat-specific detection functions. Models with no post hoc truncation were suitable for the analysis as data were truncated in the field, and additional truncation did not improve the models. The hazard-rate key function with cosine adjustment was chosen as the best model for the detection function (AIC weight = 0.73; Table 2-6). The second best model used the global detection rate with the hazard rate key function (delta AIC= 1.99, AIC weight= 0.27). Models based on sample (team) level detection functions did not improve the fit of the model and received no AIC weight (Table 2-6). The stratum-level detection functions for the prairie and pineland habitat transects have a flat shoulder to about 175 and 160 cm, respectively, from the centerline (Figure 2-4)

Abundance estimates based on habitat stratum-level detection functions for each individual team ranged from 46-76 in the prairie and 22-51 in the pineland habitats (Table 2-7). These abundance estimates from distance analysis were similar to those from the double observer analysis, but precision was much lower for the distance method (Figure 2-5).

Discussion

Despite the use of data collection protocols and analytical techniques designed to account for heterogeneity in detection probabilities, there was a large amount of bias in estimates of artificial frog abundance in the 2 habitats. The true abundance of 100 frogs was not within the 95% confidence intervals of any of the abundance estimates from either the double observer method (Table 2-5) or the distance method (Table 2-7) in either habitat. Additionally, counts and estimates varied widely among teams, even though the transects sampled, frog placements, and environmental conditions were identical. Furthermore, habitat differences between prairie and pineland led to large differences in estimates of abundance and detection rates of artificial frogs.

Some apparent bias in both sampling methods may be explained by unobservable frogs. Only 67 of the artificial frogs were observed by any team in the pineland and only 94 were observed in the prairie. If we consider frogs not observed by any observer as “unobservable,” than we would only expect estimates to be similar to the number of observable frogs. However, only the abundance estimate of team 7 in prairie habitat and team 12 in pineland habitat using the distance sampling method included the “observable” number of frogs in the 95% confidence interval.

These results support concerns that the use of counts from VES sampling unadjusted for detection probability is inappropriate (Crump and Scott 1994, Schmidt 2003). Even under identical conditions in this survey, different observer teams produced dissimilar counts. Some of the difference in counts among teams may be attributable to observer skill, although no observer had previous experience searching for the artificial frogs used in this experiment. Failure to account for observer bias (Pollock and Kendall 1987) in VES samples could lead to gross errors as was demonstrated in this study. This is especially important to studies seeking to identify long-term trends in amphibian populations using data collected over many seasons by different observers.

Although the dependent double-observer approach of Cook and Jacobson (1979) is designed to estimate individual detection probabilities and therefore eliminate some of the bias associated with observers, there are limitations to this approach. Nichols et al. (2000) hypothesize that detection probability estimates may be biased high using this approach, which would lead to abundance estimates that are biased low. This study provides empirical evidence that detection probability estimates are indeed biased high under the assumptions of the Cook and Jacobson (1979) model. If both observers are not evenly matched in skill, the detection estimate of the better observer will be biased high. If the poorer observer does not find any objects missed by the better observer in the role of the primary observer, estimated detection could reach 100%. Likewise, if both observers are poor and detect few missed objects as secondary observers, detection estimates for the team will be biased high. It seems likely that some examples of both of the above scenarios took place in this study (Table 2-4).

Distance analysis is considered useful for estimating density and abundance of objects, especially when detection rates decline with distance from the observer (Buckland et al. 2001).

In this study, however, there was little noticeable decline in detection rates at distances up to 2 m from the transect centerline (Table 2-2). Detection rates were estimated to be as high as 1.0 out to more than 1.5 m from the centerline (Figure 2-4), leading to estimates of abundance that were biased low as with the double observer method.

Rigorous testing for bias in animal sampling protocols is not always performed, but can be informative. Anderson et al. (2001) found that modifications to desert tortoise line transect sampling protocols were necessary after testing the technique with artificial tortoises. Nichols et al. (1986) found evidence of inter-observer variation in searches for white-winged dove nests marked by individual observers and recommended future estimation of observer-specific detection rates. Rodda et al. (2005) evaluated relative abundance estimates based on visual searches against absolute abundance estimates based on removal techniques and found poor correspondence between the two. They concluded that visual searches alone were only suitable for 1 of the 6 reptile species they surveyed.

This study provides evidence that observer differences in detection rates are very important and even sampling methods designed to be robust to these differences may be inadequate to describe the absolute abundance of animals. Clearly, we have an advantage in this study of knowing the true abundance of objects. Such information is not available in actual animal populations. However, we cannot assume that the artificial frogs in this study were perfect surrogates for actual frogs. The fact that they are immobile probably decreased their detectability, as many observers find frogs by detecting their movements. Also, many observers key detection on eyeshines not present in the surrogates. Therefore, we cannot use this study to calibrate the amount of bias in VES sampling, but it does help illustrate an important problem.

Researchers gathering VES data should be aware that there is potential for great bias in abundance estimates using this method.

Table 2-1. Number of artificial frogs (out of a possible 100) observed by each team in prairie and pineland habitats in BCNP. x_{11} is the count of objects detected by observer 1 when observer 1 was the primary observer, x_{22} is the count of objects by observer 2 when observer 2 was primary, and x_{12} and x_{21} are the counts of observers 1 and 2 in the roles of secondary observer, respectively.

Habitat	Team	x11	x22	x12	x21	Total
Prairie	Team 1	28	14	8	6	56
	Team 2	25	16	9	1	51
	Team 3	21	15	3	4	43
	Team 4	20	22	1	12	55
	Team 5	22	13	8	0	43
	Team 6	13	13	4	11	41
	Team 7	24	32	10	2	68
Pineland	Team 8	9	1	5	4	19
	Team 9	9	4	1	4	18
	Team 10	11	10	0	4	25
	Team 11	17	7	6	2	32
	Team 12	19	10	12	2	43
	Team 13	11	7	3	3	24

Table 2-2. Actual detection rates of a known population of artificial frogs within 30 cm, within 50 cm, beyond 50 cm, and overall for teams searching in prairie and pineland habitat of BCNP.

Habitat	Team	p <30 cm	p <50 cm	p >50 cm	Overall
Prairie	Team 1	0.611	0.600	0.547	0.56
	Team 2	0.500	0.520	0.507	0.51
	Team 3	0.333	0.360	0.453	0.43
	Team 4	0.389	0.560	0.547	0.55
	Team 5	0.500	0.600	0.373	0.43
	Team 6	0.444	0.360	0.427	0.41
	Team 7	0.444	0.720	0.667	0.68
Pineland	Team 8	0.357	0.269	0.162	0.19
	Team 9	0.071	0.077	0.216	0.18
	Team 10	0.143	0.269	0.243	0.25
	Team 11	0.500	0.385	0.297	0.32
	Team 12	0.643	0.577	0.378	0.43
	Team 13	0.429	0.385	0.189	0.24

Table 2-3. Model selection for the three double-observer models analyzed in Program SURVIV with the model log-likelihood, number of parameters (K), quasi-likelihood Akaike's information criterion adjusted for small sample sizes (QAIC$_c$), difference between each QAIC$_c$ and the minimum QAIC$_c$ (Delta QAIC$_c$) and the QAIC$_c$ weight.

Model	Log Likelihood	K	QAICc	Delta QAICc	QAICc Weight
$p_{obs*hab}$	-35.32	26	125.507	0	1.0000
P_{hab}	-75.76	2	153.074	27.567	0.0000
$p_.$	-74.53	1	153.524	28.017	0.0000

Table 2-4. Estimates from program SURVIV of individual detection probabilities ($\hat{p}_i$) of artificial frogs for each observer in prairie and pineland habitat with standard error (S.E.) and 95% confidence intervals (C.I.) taken from the double observer method..

Habitat	Observer	$\hat{p}_i$	S.E.	Lower 95% C.I.	Upper 95% C.I.
Prairie	1	0.7230	0.1119	0.5036	0.9424
	2	0.5590	0.1293	0.3055	0.8125
	3	0.9389	0.0601	0.8211	1.0567
	4	0.6251	0.1010	0.4271	0.8231
	5	0.8082	0.0902	0.6313	0.9850
	6	0.8017	0.1060	0.5940	1.0094
	7	0.6079	0.0912	0.4292	0.7866
	8	0.9304	0.0687	0.7957	1.0651
	9	1.0000	0.0002	0.9996	1.0004
	10	0.6197	0.1059	0.4120	0.8273
	11	0.4019	0.1554	0.0974	0.7064
	12	0.5667	0.2062	0.1625	0.9709
	13	0.8977	0.0696	0.7614	1.0341
	14	0.7415	0.0728	0.5988	0.8842
Pineland	15	0.0123	0.8123	-1.5798	1.6044
	16	0.0044	0.2948	-0.5735	0.5823
	17	0.6156	0.1814	0.2601	0.9712
	18	0.7122	0.2635	0.1958	1.2286
	19	0.7330	0.1142	0.5092	0.9569
	20	1.0000	0.0001	0.9999	1.0001
	21	0.8046	0.1400	0.5302	1.0789
	22	0.4845	0.1598	0.1714	0.7977
	23	0.7912	0.1488	0.4996	1.0829
	24	0.3979	0.1248	0.1533	0.6425
	25	0.6931	0.1694	0.3612	1.0251
	26	0.6168	0.1923	0.2400	0.9936

Table 2-5. Abundance estimates ($\hat{N}$) of artificial treefrogs for each team in prairie and pineland habitat with standard error (S.E.) and upper and lower 95% confidence intervals (C. I.) based on Chaos's estimator (Nichols et al. 2000) taken from the double observer data..

				Chao 95% C.I.	
Habitat	Team	$\hat{N}$	S.E. $\hat{N}$	Lower.	Upper
Prairie	Team 1	62.3	3.01	58.59	71.34
	Team 2	56.7	2.85	53.29	65.39
	Team 3	47.8	2.57	44.82	55.86
	Team 4	61.2	2.98	57.53	70.15
	Team 5	47.8	2.57	44.82	55.86
	Team 6	45.6	2.50	42.71	53.47
	Team 7	75.7	3.40	71.33	85.59
Pineland	Team 8	21.1	1.62	19.57	26.99
	Team 9	20.0	1.57	18.53	25.78
	Team 10	27.8	1.88	25.85	34.27
	Team 11	35.6	2.16	33.21	42.69
	Team 12	47.8	2.57	44.82	55.86
	Team 13	26.7	1.84	24.81	33.06

Table 2-6. Model selection for detection functions in Program DISTANCE showing number of parameters (K), Akaike's Information Criterion (AIC), the difference between each AIC and the minimum (Delta AIC), and the AIC Weight of each model. Detection was modeled at the sample, stratum, or global level with the hazard rate key function or the half normal key function.

Model Name	K	AIC	Delta AIC	AIC Weight
Stratum detection; Hazard Rate Key	4	5374.38	0	0.7300
Global detection, Hazard Rate Key	2	5376.37	1.99	0.2697
Global detection, Half-normal Key	5	5390.49	16.10	0.0002
Stratum detection; Half-normal Key	6	5404.70	30.32	0.0000
Sample detection; Hazard Rate Key	26	5413.01	38.63	0.0000
Sample detection; Half-normal Key	13	5436.28	61.90	0.0000

Table 2-7. Abundance ($\hat{N}$) estimates of artificial frogs by team for transects in the prairie and pineland habitats with coefficient of variation (CV) and 95% confidence interval (CI) from the distance sampling approach.

Habitat	Team	$\hat{N}$	CV	Lower 95% C.I.	Upper 95% C.I.
Prairie	Team 1	49	15.16	37	66
	Team 2	57	14.09	43	75
	Team 3	48	15.33	36	65
	Team 4	62	13.58	47	81
	Team 5	48	15.33	36	65
	Team 6	46	15.70	34	63
	Team 7	76	12.23	60	97
Pineland	Team 8	23	23.08	14	36
	Team 9	22	23.70	14	34
	Team 10	30	20.16	20	44
	Team 11	38	17.85	27	54
	Team 12	51	15.45	38	70
	Team 13	29	20.56	19	43

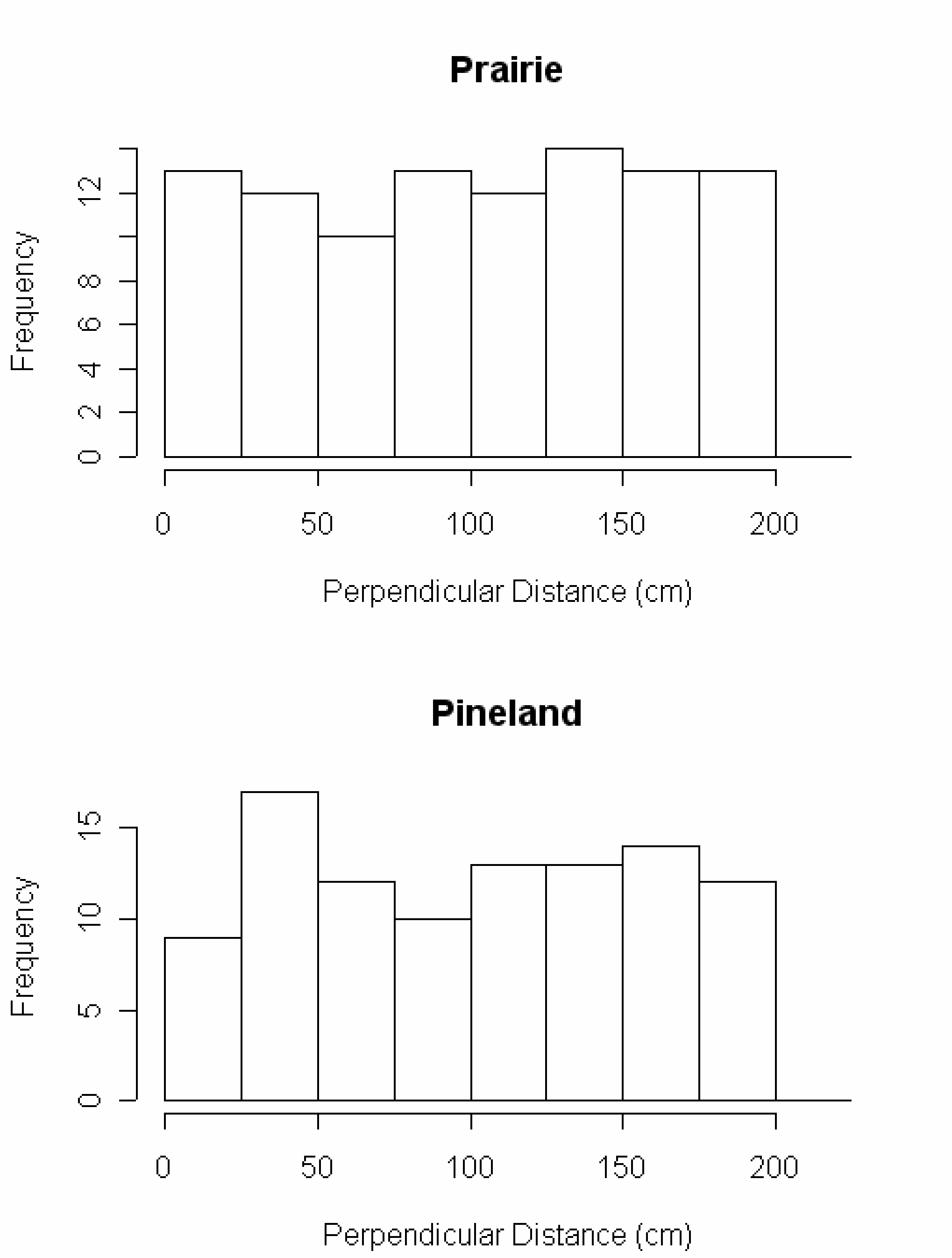


Figure 2-1. Histograms of the frequency of perpendicular distances in cm of actual artificial frog placements along the 2 transect lines in the prairie and pineland habitat.

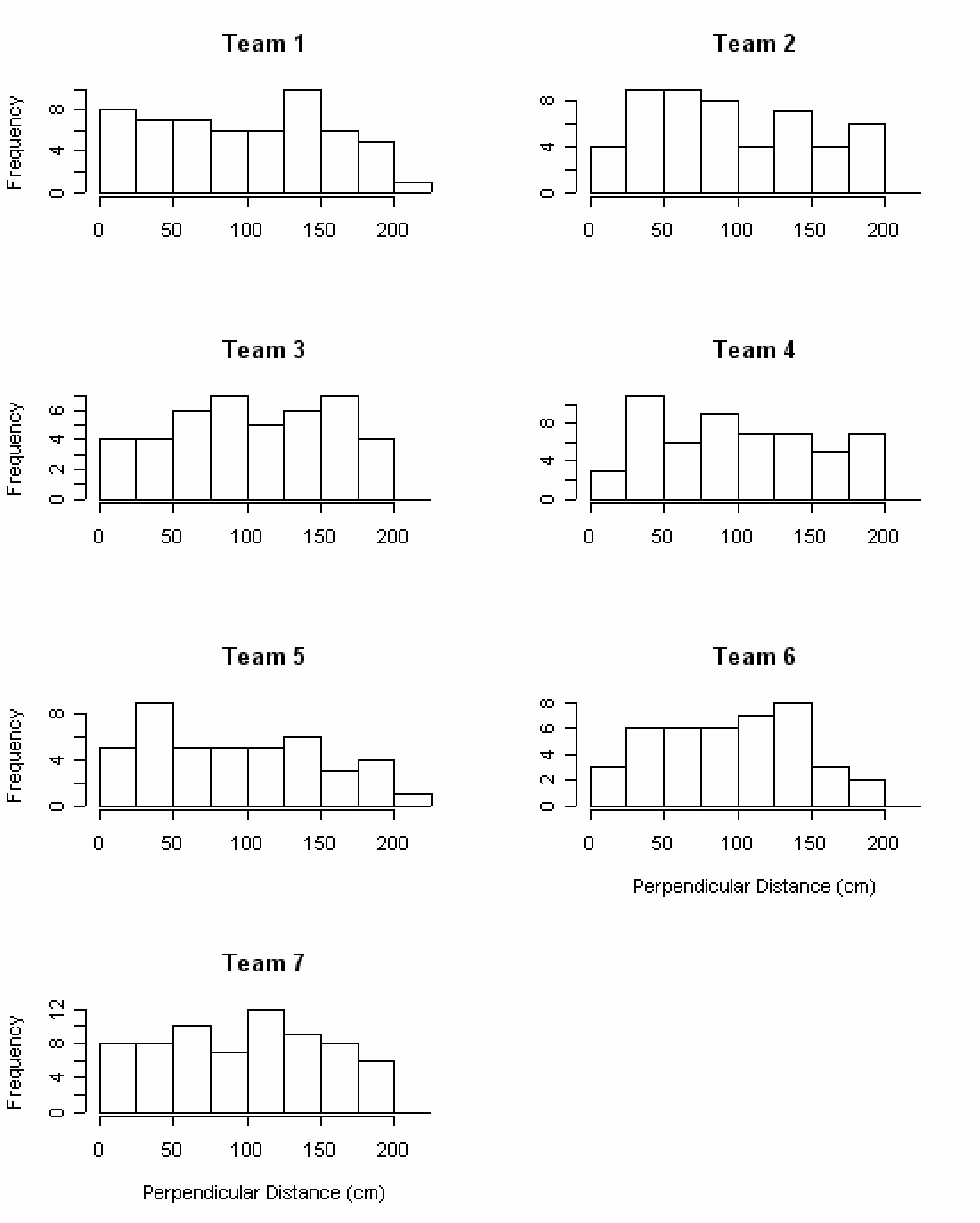


Figure 2-2. Histograms of the frequency of detections of artificial frogs by each team at perpendicular distances in cm along the 2 transect lines in the prairie habitat at BCNP.

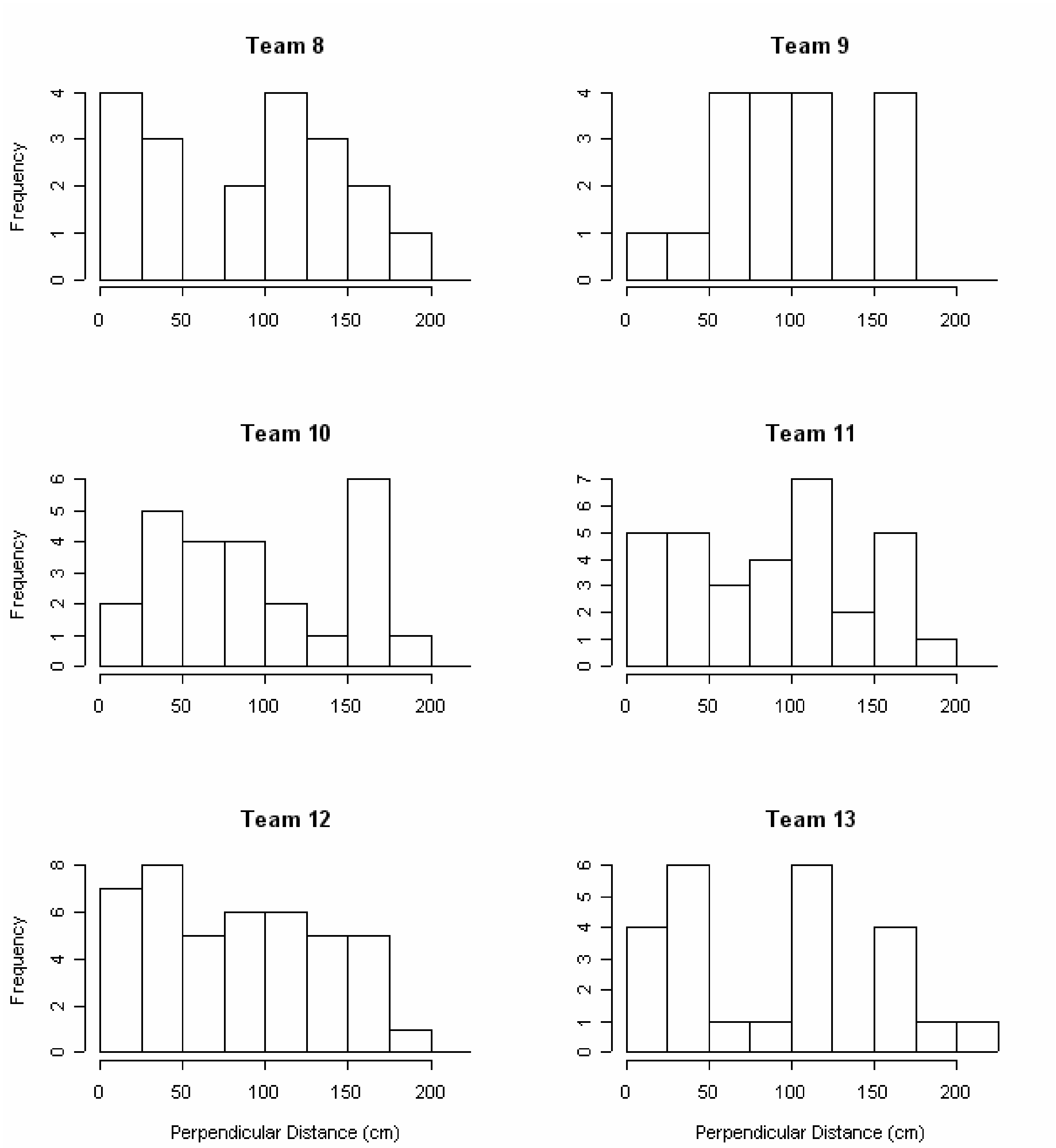


Figure 2-3. Histograms of the frequency of detections of artificial frogs by each team at perpendicular distances in cm along the 2 transect lines in the pineland habitat of BCNP.

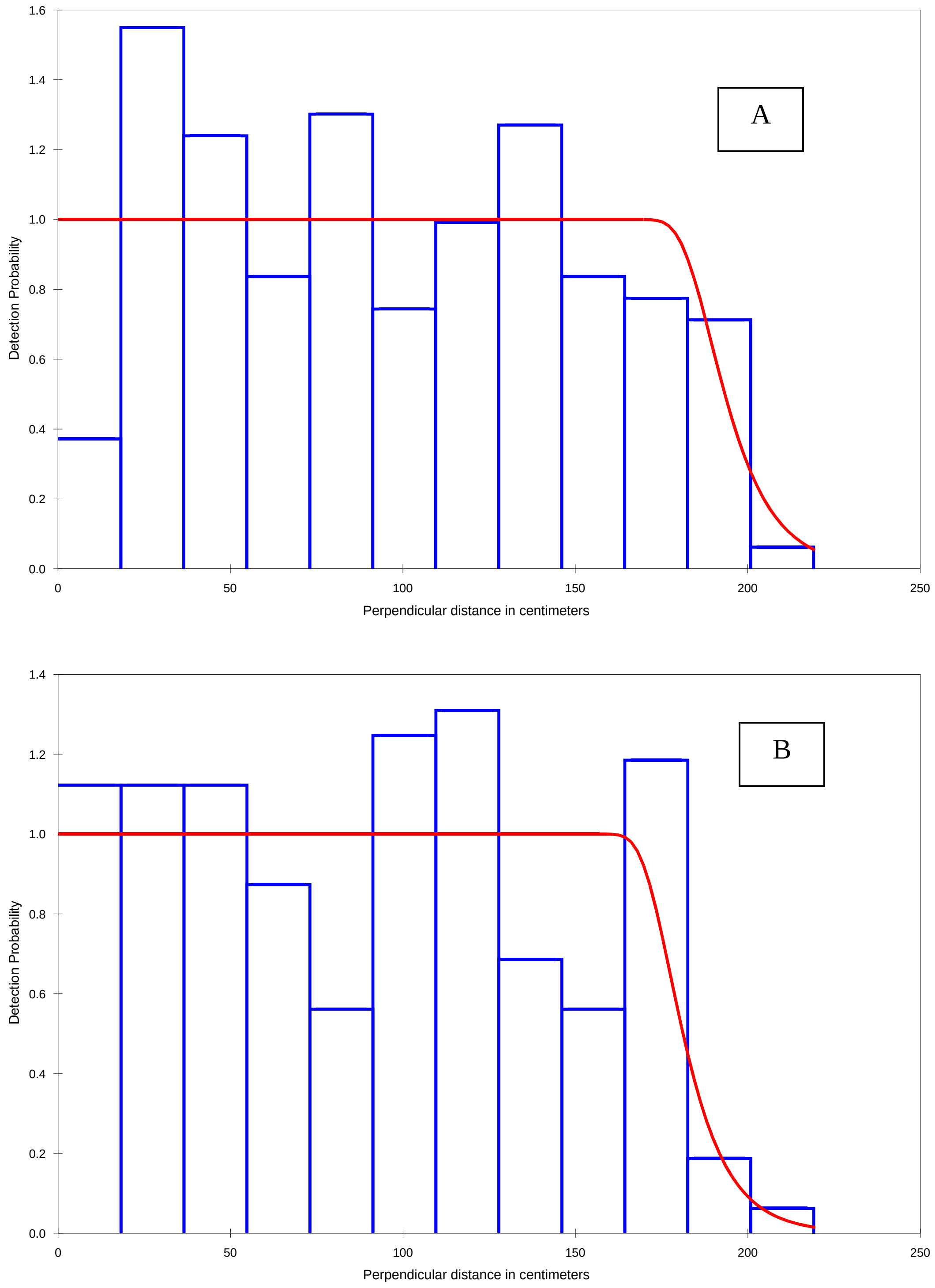


Figure 2-4. Histograms of the frequency of detections of artificial frogs at perpendicular distances in cm along the 2 transect lines for all teams in the prairie habitat (A) and the pineland habitat (B) with the best model of the detection function (red lines) from Program DISTANCE superimposed.

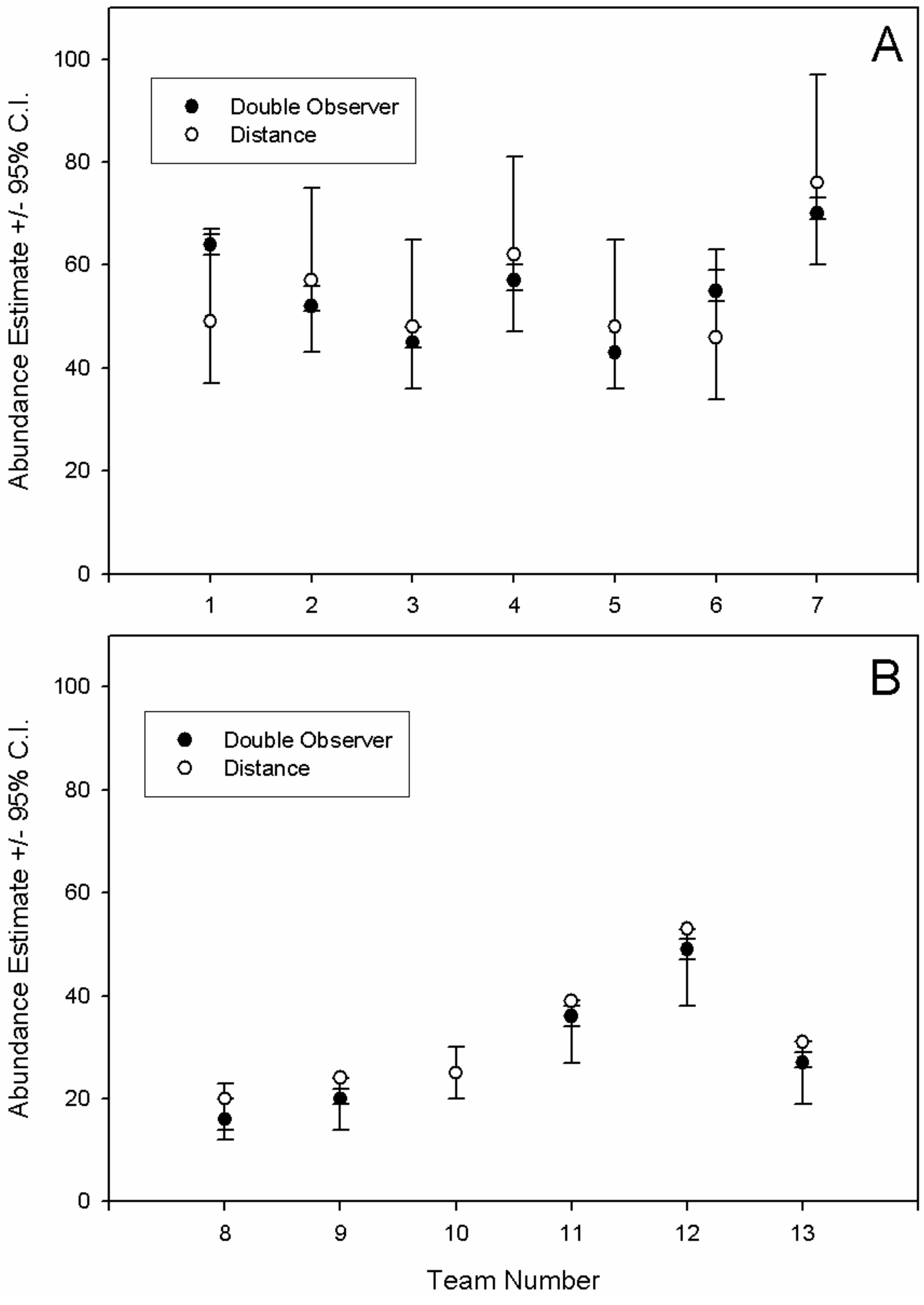


Figure 2-5. Abundance estimates with standard error for each team from prairie (A) and pineland habitat (B) using the double observer and distance methods. True abundance was 100 in both habitats.

CHAPTER 3
USING SITE OCCUPANCY MODELING TO DETERMINE THE EFFECT OF OFF-ROAD VEHICLE USE ON GROUND-DWELLING ANURANS

Introduction

Off-road vehicles (ORV) can impact wildlife species directly by causing physical harm (Steiner and Leatherman 1981) or indirectly by altering behavior or disturbing habitats (Brattstrom and Bondello 1995, Guyer et al. 1996). ORVs create noise which may be disruptive to wildlife, or the presence of large moving vehicles may be disturbing. In addition, ORVs may create trails and damage to the vegetation in areas that receive heavy use. One of the major management concerns of Big Cypress National Preserve (BCNP) in southern Florida, USA is the regulation of ORV use (NPS 2000, Duever 2005) where mapped ORV trails total over 47,900 km in length (Welch et al. 1999). Janis and Clark (2002) found evidence that ORV use altered the behavior of the endangered Florida panther in Big Cypress, and Duever et al. (1981) demonstrated that ORVs alter vegetation composition and hydrology at impacted sites (Figure 3-1). It is unclear how other species of wildlife, especially amphibians, are affected by ORV use in BCNP.

Determining the impacts of ORVs on local populations may be possible through mark-recapture sampling or some other technique that provides estimates of abundance. However, at larger spatial scales (i.e. across landscapes) it becomes increasingly futile to attempt to estimate the abundance or density of amphibians. It is difficult to enumerate such large populations, and population sizes may fluctuate with season and environmental conditions (Green 2003). A relatively new method, site occupancy or proportion area occupied, allows collection of simple presence/absence data across the entire landscape to make inference regarding species status. The site occupancy rate of species across a landscape is more meaningful at large scales since a larger proportion of the area can be sampled than in traditional mark-recapture. Also unlike simple counts and estimates of relative density (catch per unit effort), occupancy accounts for detection or non-detection of the species after repeated samplings of many sites (MacKenzie et al. 2002). Covariates (e.g. habitat type, ORV use) may be used to improve estimates of occupancy probabilities (MacKenzie et al. 2002), and model selection may also be used to make inferences about the effects of covariates (MacKenzie et al. 2005, Schmidt and Pellet 2005).

Ground dwelling anurans are one group of amphibians that may be especially affected by ORV use. These species often occur far from permanent water, and most breed in small, fish-free ponds (Duellman and Trueb 1986). They tend to have a low dispersal capability (Blaustein et al. 1994, Alford and Richards 1999), so they are likely to spend most of their life within the same small area. For these reasons I expect these species to be especially affected by ORV use in Big Cypress. ORV use may alter microhabitats at sites by decreasing vegetation or increasing drainage. These alterations may make some sites less suitable for ground dwelling anurans.

The objective of this study was to determine if ORV use was an important factor influencing the site occupancy of four ground-dwelling anuran species in BCNP: Oak Toad (*Bufo quercicus*), Southern Toad (*Bufo terrestris*), Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis*), and Greenhouse Frog (*Eleutherodactylus planirostris*). Detection data of amphibians from a random sample of sites in BCNP were modeled with site covariates including an index of ORV use created from geographic information system (GIS) data of ORV trails using the site occupancy method of MacKenzie et al. (2002). I hypothesized that occupancy of these four ground-dwelling anuran species would be negatively associated with ORV use.

Methods

Study Area

Big Cypress National Preserve is a 295,000 ha natural area managed by the National Park Service in Collier and Monroe Counties of southwestern Florida, USA. BCNP is bordered on the south and east by Everglades National Park and Water Conservation Area 3A (managed by the South Florida Water Management District). Cape Romano/10,000 Islands National Wildlife Refuge and Florida Panther National Wildlife Refuge, as well as Fakahatchee Strand State Preserve lie on the western boundary of Big Cypress. Because of its large size and geographic location, Big Cypress is not heavily influenced by habitat loss due to development like many other areas in Florida. However, Big Cypress has been used by recreational ORV users since before its establishment in 1974 (NPS 2000). Current regulations limit use to no more than 2000 registered ORVs per year, but lasting signs of 47,900 km of old and current ORV trails are apparent throughout the preserve (Duever et al. 1987, Welch et al. 1999, NPS 2000).

Sampling

Random sites were chosen throughout Big Cypress using the animal movement analysis extension of Hooge and Eichenlaub (1997) in ArcView 3.2 (Environmental Systems Research Institute, Inc., www.esri.com). A sample of these random points accessible by foot or ORV was chosen for amphibian sampling (Figure 3-2). These sites represented 5 different habitat types: cypress strand, cypress prairie, prairie, hammock, and pineland, based on the vegetation classification scheme of Madden et al. (1999). The number of sampling occasions per site was variable. Some were sampled on a monthly basis from February 2002 to March 2003 to provide a time series of detection data from sites. Other sites were sampled just twice during the entire project to increase the geographic coverage of the sampling. This approach was intended to balance the effort between repeated sampling and additional sites.

Sampling for amphibians consisted of standard visual encounter survey (VES) techniques (Crump and Scott 1994). All VES samples were initiated at least 30 minutes after sunset, and each survey was conducted by at least two experienced observers using 6-volt spotlights with halogen bulbs. VES samples were time and area constrained such that the area within a 20-m radius of the randomly chosen point (1,256 m2) was searched for 1 person-hr. All areas of each plot were visually scanned, but judgment of the observers was used to determine which areas within the plot received the most emphasis. The goal was to find as many individual amphibians as possible. All possible amphibian locations were searched, including trees and other vegetation as well as bare ground and leaf litter. Each amphibian observed was captured (if possible) and identified to species. A 10-minute vocalization survey was conducted during each VES sample. All species of frogs and toads heard vocalizing were noted. All anurans that could be heard were included, even if it was possible or likely that they were calling from a location outside of the 20-m radius plot.

In addition to the biological data, environmental data were collected in the field during each survey. Air temperature and relative humidity were measured using a digital thermohygrometer. The date and time of the sample and whether the plot was inundated with water at the time of the sample also were recorded. Sampled sites were assigned an ORV use index based on the sum of ORV trails within a 500-m radius circle around the sampling point by using the ORV trail GIS dataset developed by Welch et al. (1999). The Welch et al. (1999) map includes all trails visible from aerial photos, even ones still visible in areas that had been closed to ORVs for as much as 2 decades prior to the photographs. Eight of the 70 sites sampled in this study fell in areas designated as “high use” by Welch et al. (1999), and trails were not mapped in these high use areas because of the high density of trails. The ORV index for sites located in high use areas was set equal to the highest value from sites for which trail data were available. In addition to the ORV index, a hydrologic index was created based on number of months inundated for each site using a habitat and hydrologic model developed by Duever et al. (1986).

Data Analysis

Site occupancy rates and detection probabilities were modeled in program PRESENCE (MacKenzie et al. 2002, MacKenzie et al. 2006) using the single season model. This method assumes that sites are closed to changes in occupancy within the study, and that detection of a species at a site is independent of detections at other sites. This method also assumes that species are not falsely detected, but species may or may not be detected when present. This method was deemed appropriate for these focal anuran species due to their difficulty to detect and low dispersal.

Site-specific covariables, those that directly affect the estimate of occupancy (ψ) were habitat type, hydrologic index and ORV use index. Values for the indices were standardized so that the means fell between 1 and 0, a necessary condition when using the logit link function (MacKenzie et al. 2006). Sampling occasion covariates that could affect detection probability (p) were air temperature, relative humidity, presence of standing water, and season of the year. For each species, we considered 80 models that were combinations of the covariates thought to be biologically meaningful (Table 3-1). The best model was chosen as the one with the lowest value for Akaike's information criterion (AIC), or the most parsimonious model (model with the best fit for the fewest parameters; Burnham and Anderson 1998). The effect of ORV use on species occupancy was determined using model selection to determine the AIC weight of all models including the ORV use covariate and by examining the beta estimates for the ORV use index in the models including that covariate.

Results

A total of 469 sampling visits to 70 sites were made from February 2002 to March 2003. The highest number of study sites (31) was in prairie habitat. Between 7 and 12 sites in each of the other habitats were visited (Table 3-2). The four focal anuran species were detected between

13 and 117 times, and naïve occupancy rates (proportion of sites at which a detection occurred) varied from 17 to 52% (Table 3-3).

The best model (model with lowest AIC value; Burnham and Anderson 1998) for each of the four species included the ORV index as a site covariate (Tables 3-4 – 3-7). When AIC weights of models including specific site covariates were summed, the ORV index covariate had the most weight for southern toads, greenhouse frogs, and eastern narrow-mouthed toads (Table 3-8). Only oak toads had less weight on models including the ORV index than other covariates.

Beta parameters for the ORV index in the best models were negative for all species except southern toads (Table 3-9). Numerical convergence could not be reached to estimate standard error (S.E.) for the ORV index beta parameter for oak toads, but S.E. estimates were obtained for the other species. The 95% confidence intervals of the beta parameter estimates for the ORV index covariate overlapped 0 for all species but greenhouse frogs.

Discussion

The results of this study indicate that the ORV index and, thus, ORV-use is a strong predictor of whether a site will be occupied by these four species of anurans. Each of these species had the ORV index covariate in the best models for occupancy, and the sum of the model AIC weights was highest for those models including the ORV index except for oak toads. This indicates that for some species, occupancy of a site may depend more on ORV use than on hydrology or habitat.

Three of the four species of anurans had beta values for ORV index that were negative, indicating negative associations with ORV use (Table 3-9). It was predicted that these small, ground-dwelling anurans would be negatively influenced by the use of ORVs due to ground level disturbance of vegetation and altered hydrology. One species, however, the Southern Toad, was positively associated with ORV use. Although this is counter to the original prediction, morphology and reproductive strategy of this species might explain the difference in response to ORV use. Southern Toads are larger than the other species, and their tadpoles require up to twice as long (2 months compared to 1 month) to develop as Oak Toads or Eastern Narrow-mouthed Toads (Ashton and Ashton 1988). ORVs can alter the vegetation and hydropattern of areas resulting in a loss of vegetation and increased ponding in ruts and artificial depressions (Duever et al. 1981). Southern Toads may take advantage of the increased temporal and spatial extent of standing water for breeding purposes.

For all of the species other than oak toads, habitat was not as important in prediction of site occupancy as the ORV index (Table 3-8). This may be in part due to the fact that these 4 anurans are habitat generalists in south Florida and are not closely associated with any particular habitat type (Duellman and Schwartz 1958, Meshaka et al. 2000, Rice et al. 2004). Habitat was a covariate in the best models for both American Toad (*Bufo americanus*) and Spring Peeper (*Pseudacris crucifer*) in a the study of MacKenzie et al. (2002) in Maryland wetlands, but habitat was not as important as the previous years count in the study of Schmidt and Pellet (2005) of Tree Frog (*Hyla arborea*) and Natterjack Toad (*Bufo calamita*) in Europe. Landscapes in Big Cypress are very heterogeneous; thus different habitat types are often in close proximity to one another (McPherson 1974, Duever et al. 1986) and frogs might easily transition from one habitat to another. Thus, it is more difficult to determine differences in habitat-level occupancy at the scale of this study.

The hydrologic index used in this study generally had higher AIC weights in model sets than habitat, but lower than the ORV index. Oak Toad was the one exception to this pattern, for which the hydrologic index had the most AIC weight in the model set. The hydrologic index was based on the number of months each site would typically be inundated with water in a year.

Although this hydroperiod is highly correlated with habitat type (Duever et al. 1986), there are some examples of sites being wetter or drier than others with the same habitat type. It is possible that the occupancy was more sensitive to the hydrological index than habitat, but this index will change between years as local rainfall varies (DeAngelis et al. 1998). Habitats are much more fixed and tend to be primarily a result of microtopography (Duever et al. 1986).

Amphibians are often used as indicator species (Vitt et al. 1990, Welsh and Ollivier 1998, Galatowitsch et al. 1999, Sheridan and Olson 2003). This study illustrates how amphibians may be indicators of the effects of ORV use in Big Cypress. The ORV trail data provided by Welch et al. (1999) shows all trails and does not differentiate between old, persistent trails and currently used ones. Duever et al. (1987) demonstrated that old trails may take many decades to recover. Some of the sites sampled in this study are in areas that have been closed to ORV use for more than 10 years, although they still retain many visible ruts and other physical evidence of ORV use. It is important to remember that this study only considers evidence of ORV use in the form of the index used, and does not examine the temporal component of when ORV use occurred. Consequently, this study found evidence of an impact of ORV use on amphibian species occupancy but did not address recovery of previously impacted areas.

Due to the observational nature of this study, it is not possible to determine the mechanisms by which ORV use influences amphibian occupancy. However, this study should help stimulate more research on the topic. Resource management staff at Big Cypress concerned with reducing impacts of ORV use in the preserve should be aware that there is evidence that ORV use influences the site occupancy of amphibians. These amphibian species may be indicators of ecosystem impacts not previously shown. A monitoring program designed using the same techniques of this study could be used to track changes over time. Stratifying sampling by historic and current ORV use areas could also help determine how long the impacts of ORV use can be detected in amphibian occupancy. Colonization and extinction of sites with varying levels of ORV use could also be monitored over time using the open model approach of MacKenzie et al. (2003).

Table 3-1. Combinations of the 3 site covariates and 4 sampling covariates that were used in the occupancy analysis for each species. Each set of site covariates was modeled along with each set of sampling covariates for a total of 80 unique models for each species.

Site Covariates	Sampling Covariates
Constant	Constant
Habitat	Season
Hydrologic Index	Temperature
ORV Index	Temperature, Humidity
Habitat, ORV Index	Temperature, Humidity, Water
Habitat, Hydrologic Index	Temperature, Humidity, Water, Season
ORV, Hydrologic Index	Temperature, Water
Habitat, ORV, Hydrologic Index	Temperature, Water, Season
	Water
	Water, Season

Table 3-2. Number of sampling sites and total number of site visits by habitat.

Habitat	Number of Sites	Number of Visits
Cypress Strand	11	89
Cypress Prairie	9	78
Prairie	31	122
Hammock	7	72
Pineland	12	108
Total	70	469

Table 3-3. Number of detections by species, and proportion of sites at which a detection occurred (naive occupancy) during amphibian surveys across all habitat types.

Species	No. Detections	Naive Occupancy
Oak Toad	17	21.43%
Southern Toad	26	28.57%
Greenhouse Frog	117	52.86%
Eastern Narrow-mouthed Toad	13	17.14%

Table 3-4. Model selection results for the oak toad (Bufo quercicus), including Akaike's Information Criterion (AIC) and the delta AIC and AIC weight (Burnham and Anderson 1998) for all models with any AIC weight.

Model	AIC	delta AIC	AIC weight
psi(Hab,ORV,Hydro), p(Temp,Humid,Water,Season)	117.92	0.00	0.2946
psi(Hab,ORV,Hydro), p(Temp,Water,Season)	118.01	0.09	0.2817
psi(Hab,Hydro),p(Temp,Humid,Water,Season)	119.92	2.00	0.1084
psi(Hab,Hydro),p(Temp,Water,Season)	119.98	2.06	0.1052
psi(Hab,ORV,Hydro),p(Water,Season)	121.54	3.62	0.0482
psi(Hydro),p(Temp,Humid,Water,Season)	122.17	4.25	0.0352
psi(Hydro),p(Temp,Water,Season)	122.24	4.32	0.0340
psi(Hab,ORV,Hydro),p(Season)	122.96	5.04	0.0237
psi(Hab,Hydro),p(Water,Season)	123.58	5.66	0.0174
psi(Hydro,ORV),p(Temp,Humid,Water,Season)	123.91	5.99	0.0147
psi(Hydro,ORV),p(Temp,Water,Season)	123.98	6.06	0.0142
psi(Hab,Hydro),p(Season)	124.76	6.84	0.0096
psi(Hydro),p(Water,Season)	125.43	7.51	0.0069
psi(Hydro,ORV),p(Water,Season)	127.29	9.37	0.0027
psi(Hydro,ORV),p(Season)	127.82	9.90	0.0021
psi(Hydro),p(Season)	132.56	14.64	0.0002

Table 3-5. Model selection results for the southern toad (*Bufo terrestris*), including Akaike's Information Criterion (AIC) and the delta AIC and AIC weight (Burnham and Anderson 1998) for all models with any AIC weight.

Model	AIC	Delta AIC	AIC Weight
psi(Hab,ORV),p(Season)	194.32	0.00	0.1109
psi(.),p(season)	194.50	0.18	0.1014
psi(ORV),p(Season)	194.99	0.67	0.0793
psi(.),p(Water,Season)	195.14	0.82	0.0736
psi(Hab,ORV),p(Water,Season)	195.85	1.53	0.0516
psi(.),p(Temp,Humid,Water,Season)	195.86	1.54	0.0514
psi(.),p(Temp,Water,Season)	196.09	1.77	0.0458
psi(Hydro),p(Season)	196.21	1.89	0.0431
psi(Hydro),p(Water,Season)	196.38	2.06	0.0396
psi(ORV),p(Temp,Humid,Water,Season)	196.48	2.16	0.0377
psi(ORV),p(Temp,Water,Season)	196.68	2.36	0.0341
psi(Hab,ORV),p(Temp,Humid,Water,Season)	196.77	2.45	0.0326
psi(Hydro),p(Temp,Humid,Water,Season)	197.16	2.84	0.0268
psi(Hydro),p(Temp,Water,Season)	197.27	2.95	0.0254
psi(Hydro,ORV),p(Season)	197.28	2.96	0.0252
psi(Hydro,ORV),p(Water,Season)	197.33	3.01	0.0246
psi(Hydro,ORV),p(Temp,Humid,Water,Season)	198.07	3.75	0.017
psi(Hydro,ORV),p(Temp,Water,Season)	198.17	3.85	0.0162
psi(.),p(Temp,Water)	198.78	4.46	0.0119
psi(Hab,ORV),p(Temp,Water,Season)	198.78	4.46	0.0119
psi(.),p(Water)	198.99	4.67	0.0107
psi(ORV),p(Temp,Water)	199.45	5.13	0.0085
psi(ORV),p(Water)	199.51	5.19	0.0083
psi(.),p(Temp,Humid,Water)	199.56	5.24	0.0081
psi(Hydro),p(Temp,Water)	199.68	5.36	0.0076
psi(Hab),p(Season)	199.75	5.43	0.0073
psi(Hab,ORV),p(Water)	199.96	5.64	0.0066
psi(Hydro),p(Water)	200.02	5.70	0.0064
psi(Hab,ORV),p(Temp,Water)	200.08	5.76	0.0062
psi(ORV),p(Temp,Humid,Water)	200.32	6.00	0.0055
psi(Hab),p(Water,Season)	200.36	6.04	0.0054
psi(Hab,Hydro),p(Season)	200.43	6.11	0.0052
psi(Hydro),p(Temp,Humid,Water)	200.56	6.24	0.0049
psi(Hab,Hydro),p(Water,Season)	200.57	6.25	0.0049
psi(Hydro,ORV),p(Temp,Water)	200.76	6.44	0.0044
psi(Hab),p(Temp,Water,Season)	201.06	6.74	0.0038
psi(Hab),p(Temp,Humid,Water,Season)	201.09	6.77	0.0038
psi(Hydro,ORV),p(Water)	201.14	6.82	0.0037
psi(Hab,Hydro),p(Temp,Water,Season)	201.24	6.92	0.0035
psi(Hab,Hydro),p(Temp,Humid,Water,Season)	201.27	6.95	0.0034
psi(Hydro,ORV),p(Temp,Humid,Water)	201.67	7.35	0.0028

Table 3-5 (Continued).

Model	AIC	Delta AIC	AIC Weight
psi(Hydro,ORV),p(.)	202.13	7.81	0.0022
psi(Hab,ORV,Hydro),p(Season)	202.49	8.17	0.0019
psi(Hab,ORV,Hydro),p(Water,Season)	202.62	8.30	0.0017
psi(Hab,ORV),p(Temp,Humid,Water)	202.74	8.42	0.0016
psi(Hab,ORV,Hydro),p(Temp,Water,Season)	203.23	8.91	0.0013
psi(Hab,ORV,Hydro),p(Temp,humid,Water,Season)	203.27	8.95	0.0013
psi(Hab,Hydro),p(Temp,Water)	204.37	10.05	0.0007
psi(Hab),p(Temp,Water)	204.38	10.06	0.0007
psi(Hydro,ORV),p(Temp,Humid)	204.48	10.16	0.0007
psi(Hab),p(Water)	204.87	10.55	0.0006
psi(ORV),p(.)	204.93	10.61	0.0006
psi(.),p(.)	204.94	10.62	0.0005
psi(Hab,ORV,Hydro),p(.)	205.08	10.76	0.0005
psi(Hab,Hydro),p(Water)	205.11	10.79	0.0005

Table 3-6. Model selection results for the greenhouse frog (*Eleutherodactylus planirostris*), including Akaike's Information Criterion (AIC) and the delta AIC and AIC weight (Burnham and Anderson 1998) for all models with any AIC weight.

Model	AIC	Delta AIC	AIC Weight
psi(Hydro,ORV),p(Temp,Humid,Water,Saeson)	409.4	0	0.5162
psi(Hydro,ORV),p(Temp,Water,Season)	411.01	1.61	0.2308
psi(Hab,ORV,Hydro),p(Temp,Humid,Water,Season)	413.43	4.03	0.0688
psi(ORV),p(Temp,Humid,Water,Season)	414.09	4.69	0.0495
psi(Hydro,ORV),p(Water,Season)	414.57	5.17	0.0389
psi(Hab,ORV,Hydro),p(Temp,Water,Season)	415.02	5.62	0.0311
psi(ORV),p(Temp,Water,Season)	415.89	6.49	0.0201
psi(.),p(Temp,Humid,Water,Season)	417.42	8.02	0.0094
psi(Hab,Hydro),p(Temp,Humid,Water,Season)	418.25	8.85	0.0062
psi(Hab,ORV,Hydro),p(Water,Season)	418.51	9.11	0.0054
psi(ORV),p(Water,Season)	418.96	9.56	0.0043
psi(.),p(Temp,Water,Season)	419.14	9.74	0.004
psi(Hab,ORV),p(Temp,Humid,Water,Season)	419.36	9.96	0.0035
psi(Hydro),p(Temp,Water,Season)	419.45	10.05	0.0034
psi(Hab,Hydro),p(Temp,Water,Season)	420.07	10.67	0.0025
psi(Hab),p(Temp,Humid,Water,Season)	421.13	11.73	0.0015
psi(Hab,ORV),p(Temp,Water,Season)	421.28	11.88	0.0014
psi(.),p(Water,Season)	422.41	13.01	0.0008
psi(Hab),p(Temp,Water,Season)	423.08	13.68	0.0006
psi(Hydro),p(Water,Season)	423.14	13.74	0.0005
psi(Hab,Hydro),p(Water,Season)	423.97	14.57	0.0004
psi(Hydro,ORV),p(Season)	424.02	14.62	0.0003
psi(Hab,ORV),p(Water,Season)	424.67	15.27	0.0002
psi(Hab),p(Water,Season)	426.55	17.15	0.0001
psi(Hab,ORV,Hydro),p(Season)	427.21	17.81	0.0001

Table 3-7. Model selection results for the eastern narrow-mouthed toad (*Gastrophryne carolinensis*), including Akaike's Information Criterion (AIC) and the delta AIC and AIC weight (Burnham and Anderson 1998) for all models with any AIC weight.

Model	AIC	Delta AIC	AIC Weight
psi(Hydro,ORV),p(Season)	113.97	0.00	0.3182
psi(Hydro,ORV),p(Water,Season)	115.96	1.99	0.1177
psi(ORV),p(Season)	117.04	3.07	0.0686
psi(Hydro,ORV),p(Temp,Water,Season)	117.49	3.52	0.0548
psi(Hydro,ORV),p(Water)	117.65	3.68	0.0505
psi(Hab,Hydro),p(Season)	118.15	4.18	0.0394
psi(.),p(Season)	118.43	4.46	0.0342
psi(ORV),p(Temp,Water,Season)	119.00	5.03	0.0257
psi(ORV),p(Water,Season)	119.03	5.06	0.0254
psi(Hydro,ORV),p(Temp,Humid,Water,Season)	119.48	5.51	0.0202
psi(Hydro,ORV),p(Temp,Water)	119.52	5.55	0.0198
psi(Hab,ORV,Hydro),p(Season)	119.56	5.59	0.0194
psi(Hydro,ORV),p(.)	119.73	5.76	0.0179
psi(Hydro,ORV),p(Temp)	120.31	6.34	0.0134
psi(.),p(Water,Season)	120.41	6.44	0.0127
psi(Hydro),p(Season)	120.43	6.46	0.0126
psi(Hydro,ORV),p(Temp,Humid,Water)	120.82	6.85	0.0104
psi(Hab,Hydro),p(Water,Season)	121.21	7.24	0.0085
psi(Hab),p(Season)	121.38	7.41	0.0078
psi(ORV),p(Water)	121.45	7.48	0.0076
psi(Hab,ORV,Hydro),p(Water,Season)	121.54	7.57	0.0072
psi(ORV),p(.)	121.68	7.71	0.0067
psi(.),p(Temp,Water,Season)	121.77	7.80	0.0064
psi(Hab,ORV,Hydro),p(Temp,Water,Season)	121.94	7.97	0.0059
psi(Hydro,ORV),p(Temp,Humid)	122.03	8.06	0.0057
psi(Hydro),p(Water,Season)	122.41	8.44	0.0047
psi(ORV),p(Temp,Humid,Water,Season)	122.47	8.50	0.0045
psi(ORV),p(Temp,Water)	122.77	8.80	0.0039
psi(Hab,Hydro),p(Temp,Water,Season)	122.82	8.85	0.0038
psi(.),p(.)	122.86	8.89	0.0037
psi(.),p(Water)	122.94	8.97	0.0036
psi(Hab,ORV),p(Season)	123.08	9.11	0.0033
psi(ORV),p(Temp)	123.21	9.24	0.0031
psi(Hab,Hydro),p(.)	123.30	9.33	0.0030
psi(Hab),p(Water,Season)	123.34	9.37	0.0029
psi(Hab,Hydro),p(Water)	123.34	9.37	0.0029
psi(Hab,Hydro),p(Temp,Water)	123.42	9.45	0.0028
psi(.),p(Temp,Humid,Water,Season)	123.77	9.80	0.0024
psi(Hydro),p(Temp,Water,Season)	123.77	9.80	0.0024
psi(Hab,Hydro),p(Temp,Humid,Water,Season)	123.78	9.81	0.0024

Table 3-7 (Continued).

Model	AIC	Delta AIC	AIC Weight
psi(Hab,ORV,Hydro),p(Temp,Humid,Water,Season)	123.99	10.02	0.0021
psi(Hab,ORV,Hydro),p(Water)	124.05	10.08	0.0021
psi(.),p(Temp,Water)	124.14	10.17	0.0020
psi(Hab,Hydro),p(Temp,Humid,Water)	124.30	10.33	0.0018
psi(.),p(Temp)	124.31	10.34	0.0018
psi(Hab,ORV,Hydro),p(Temp,Water)	124.50	10.53	0.0016
psi(Hab,ORV,Hydro),p(Temp)	124.55	10.58	0.0016
psi(Hab),p(Temp,Water,Season)	124.65	10.68	0.0015
psi(ORV),p(Temp,Humid,Water)	124.66	10.69	0.0015
psi(Hydro),p(.)	124.86	10.89	0.0014
psi(ORV),p(Temp,Humid)	124.92	10.95	0.0013
psi(Hydro),p(Water)	124.94	10.97	0.0013
psi(Hab,ORV),p(Water,Season)	125.08	11.11	0.0012
psi(Hab,Hydro),p(Temp)	125.12	11.15	0.0012
psi(Hab,ORV,Hydro),p(Temp,Humid,Water)	125.43	11.46	0.0010
psi(Hab),p(.)	125.77	11.80	0.0009
psi(Hydro),p(Temp,Humid,Water,Season)	125.77	11.80	0.0009
psi(.),p(Temp,Humid)	126.03	12.06	0.0008
psi(.),p(Temp,Humid,Water)	126.04	12.07	0.0008
psi(Hydro),p(Temp,Water)	126.14	12.17	0.0007
psi(Hab),p(Water)	126.17	12.20	0.0007
psi(Hydro),p(Temp)	126.31	12.34	0.0007
psi(Hab,ORV),p(Temp,Water,Season)	126.39	12.42	0.0006
psi(Hab),p(Temp,Humid,Water,Season)	126.65	12.68	0.0006
psi(Hab,Hydro),p(Temp,Humid)	127.00	13.03	0.0005

Table 3-8. Sums of Akaike's Information Criterion (AIC) weights for all models including the ORV index, habitat type, or hydrologic index covariates for each of the four focal anuran species.

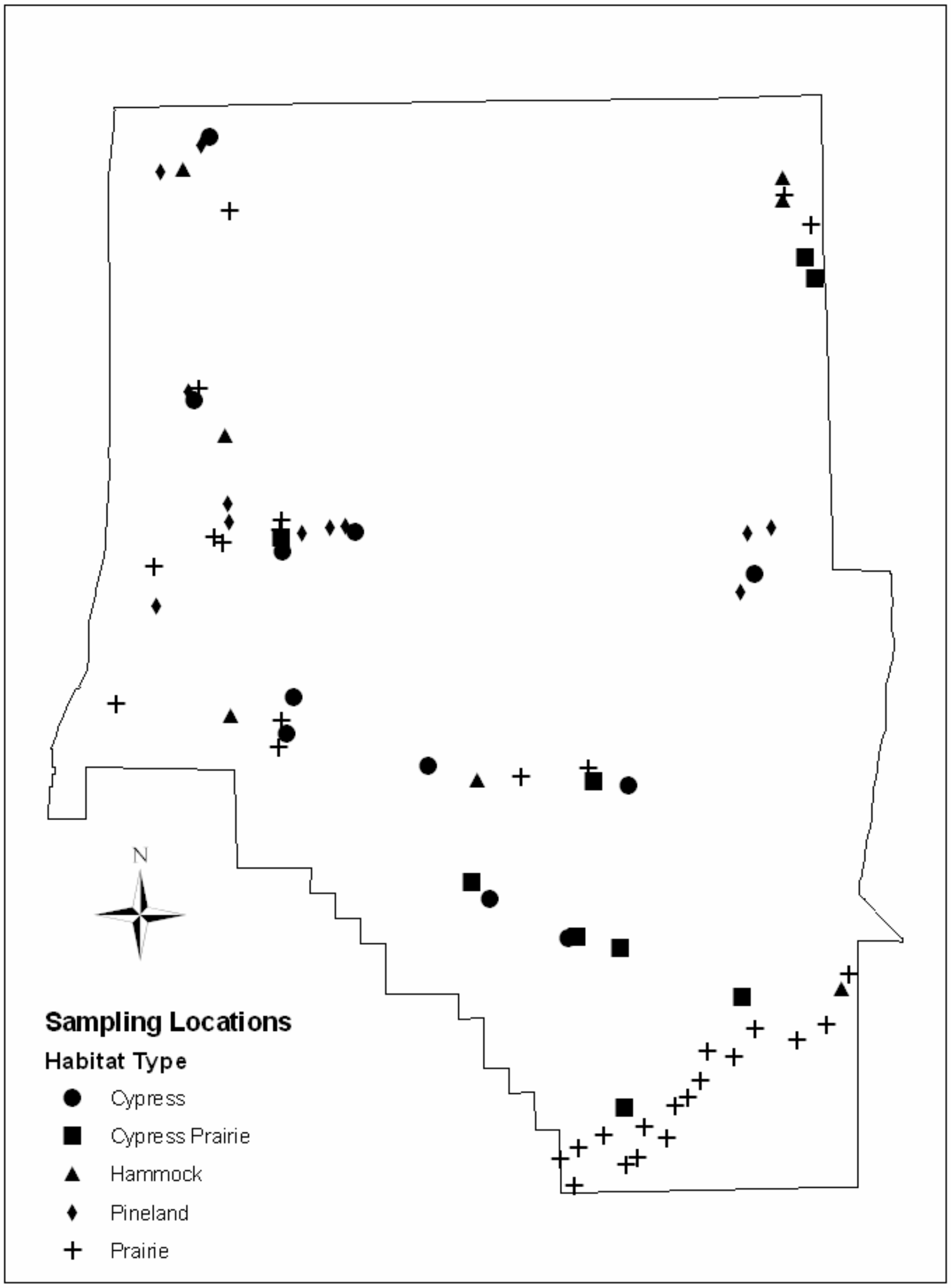
Species	ORV Index	Habitat	Hydrologic Index
Oak Toad	0.6819	0.8888	0.9988
Southern Toad	0.4989	0.2679	0.2755
Greenhouse Frog	0.9706	0.1218	0.7992
Eastern Narrow-mouthed Toad	0.8050	0.1267	0.7605

Table 3-9. Beta estimates, standard errors (S.E.), and lower and upper 95% confidence intervals (C.I.) for the ORV use index covariate from the best model for each of the four focal anuran species. NA indicates that numerical convergence could not be reached and no estimate of the S.E. is available.

Species	Beta estimate	S.E.	Lower 95% C.I.	Upper 95% C.I.
Oak Toad	-580.9251	NA	-	-
Southern Toad	21.2321	24.0724	-25.9498	68.4140
Greenhouse Frog	-3.9188	1.6130	-7.0803	-0.7573
Eastern Narrow-mouthed Toad	-5.5601	6.1949	-17.7021	6.5819

Figure 3-1. An aerial photograph depicting off-road vehicle damage in marl prairie habitat in Big Cypress National Preserve.

Figure 3-2. Map of amphibian occupancy sampling locations within BCNP during 2002-2003 (n=70).



CHAPTER 4
THE EFFECT OF TOE-CLIPPING ON TWO SPECIES OF TREEFROGS

Introduction

Accurately assessing the status and trends of amphibian populations is an important part of amphibian conservation and management, especially where amphibian species are threatened with extinction or are of special interest to managers (Alford and Richards 1999, Stuart et al. 2004). Many studies rely on counts of amphibians to provide information on populations, but count data not adjusted for detection cannot be used to monitor amphibian population status (Schmidt 2003). Further, estimates of vital rates, such as survival probability, are crucial for addressing the causes of declines and managing populations (Biek et al. 2002). One important method for obtaining estimates of abundance and survival involves recapturing uniquely marked individuals (Jolly 1965, Seber 1965).

Many marking methods have been developed for amphibians (Donnelly et al. 1994). To be suitable for use in estimation of survival rates, a marking technique must be permanent, not adversely affect the marked animal, and not affect the probability of capture on subsequent samples (Williams et al. 2002). Few marking methods meet these assumptions when applied to small anurans (<30 mm). Tagging methods such as passive integrated transponder (PIT) microchips (Ireland et al. 2003) may be suitable for larger anurans, but are not useful for species with small body size. Tattooing (Kaplan 1959), freeze branding (Daugherty 1976), and fluorescent dye (Nauwelaerts et al. 2000) techniques are cumbersome for field use and may not be permanent. Toe-clipping, the systematic removal of toes in unique combinations, is a low-cost, efficient method of permanently marking anurans (Donnelly et al. 1994, Luddecke and Amezquita 1999), but recent analysis suggests that toe-clipping may decrease survival of some species of anurans (Parris and McCarthy 2001, McCarthy and Parris 2004) and some consider the practice unethical or scientifically unsound (May 2004).

McCarthy and Parris (2004) observed a negative relationship between the return rate (defined as the probability of survival times the probability of capture) of several species of anurans and the number of toes removed during marking. The models of McCarthy and Parris (2004) assume a constant probability of capture, and thus they conclude that survival rates are lower for frogs with more toes removed. However, it is known that capture and survival probabilities often vary with time due to environmental factors not related to the marking method (Williams et al. 2002). Mark recapture analytical techniques make it possible to use the information gained from uniquely marked animals to directly estimate survival and capture separately and determine whether there is an effect of toe removal on survival or capture rates.

I applied capture-mark-recapture techniques to estimate survival and capture probabilities of green treefrogs (*Hyla cinerea*) and squirrel treefrogs (*H. squirella*) in southern Florida, USA. My objective was to determine if increasing the number of toes removed for marking had a negative effect on survival or capture probability of these treefrog species. I hypothesized that toe-clipping would have no effect on survival or capture probability in either species. I used Cormack-Jolly-Seber open population mark-recapture models to estimate apparent survival and capture probability (Lebreton et al. 1992), and information theoretic methods based on Akaike's Information Criterion (AIC) for model selection (Burnham and Anderson 1998).

Methods

Study Site

I established six long-term research sites in Big Cypress National Preserve, Collier County, FL, USA in April 2004. Each site consisted of 100-170 5.1-cm polyvinyl chloride (PVC) pipe refugia (Boughton et al. 2000) erected from the ground in groups of 7 by 7 grids of 49 pipes with

5 m spacing and other pipes (6-9) located between grids to monitor movement between habitats. The total number of refugia at all sites was 840.

Sites were located in pineland and cypress strand habitats, as well as adjacent marsh and prairie habitats (Duever 2005). Pinelands are upland habitats dominated by slash pine (*Pinus elliottii*). Cypress strands are seasonally flooded forested wetlands with dominated by bald cypress (*Taxodium distichum*). Marsh habitats are long-hydroperiod forb-dominated wetlands, and prairie habitats are short-hydroperiod sedge-dominated wetlands. Both marsh and prairie lack a woody overstory (Duever et al. 1986). Captures from all habitats were combined in this analysis to examine the effect of toe-clipping as preliminary analysis indicated that survival and capture rate parameters were primarily homogeneous across habitats during the sampling period.

Capture Recapture

Refugia were checked once monthly during the period from 15 November 2004 to 30 June 2005. Frogs captured in or on the refugia were placed in clear plastic bags for measurement. Individual frogs were identified to species, measured snout-to-urostyle length (SUL) in mm, and examined for toe clip marks. Unmarked green treefrogs greater than 24 mm SUL and unmarked squirrel treefrogs greater than 17 mm SUL were assigned a new clip number, unique to the site, which required the removal of two, three, or four toes. It was difficult to mark and read marks on smaller individuals, so they were not marked. The numbering system followed that of Donnelly (1989) with the modifications that no more than one toe per foot was removed, and the proximal toe on each forelimb was never removed. Toes were removed with stainless steel scissors sterilized in alcohol. Recaptured frogs were examined for signs of toe regeneration, and when necessary, toes were re-clipped.

Survival Analysis

I used the Cormack-Jolly-Seber mark-recapture model (Lebreton et al. 1992) as implemented in program MARK (White and Burnham 1999) to perform survival analysis for both species. Individuals of both species were divided into three groups for analysis: those with two, three, and four toes removed. A series of 23 models representing different hypotheses about the effects of time and group on apparent survival (ϕ) and capture probability (p) were fit for both species (Table 4-1). Models including the effect of toe clipping were constructed so as to force the effect to be monotonic (i.e. removing 4 toes had twice the effect of removing 3 toes when compared to 2 toes).

Goodness of fit of the model structure was assessed by estimating the variance inflation factor $\hat{c}$ using the parametric bootstrap method implemented in program MARK (White and Burnham 1999) on the most general model in the model set, $\phi_{t*clip}\, p_{t*clip}$. Model selection was conducted using the information-theoretic approach of Burnham and Anderson (1998) with the Quasi-likelihood Akaike's Information Criterion adjusted for over dispersion of data and small sample sizes ($QAIC_c$).

Results

During the sampling period I captured, marked, and released a total of 1296 individual green treefrogs and 658 individual squirrel treefrogs, of which 712 and 408 respectively were subsequently recaptured. Return rates for frogs with 2, 3, and 4 toes removed declined monotonically from 60.92% to 51.25% among Green Treefrogs and from 70.00% to 60.19% among Squirrel Treefrogs (Table 4-2). At least 6 individuals of each species/toe-clip group were captured and released during each of the first seven capture occasions (Figure 4-1).

The parametric bootstrap of the most general Cormack-Jolly-Seber model chosen for Green Treefrogs produced an estimate of $\hat{c}$ = 1.656, indicating mild lack of fit of the data to the model. Two models, $\phi_{t+clip}\, p_t$ and $\phi_{t+clip}\, p_{t+clip}$, had a delta $QAIC_c$ of less than 2, and therefore had strong support (Table 4-3). Both of these models include the toe clip effect on survival, and one includes a toe clip effect on capture. Models that included a toe-clip group effect on survival had 85.14% of the QAICc weight among the set of candidate models, and models that included toe-clip group effect on capture probability had 34.16% of the model weight.

The estimated beta for the toe-clip effect on survival in green treefrogs from the best model was -0.3963 (S.E. =0.1377; Table 4-4). There was a mean absolute decrease in survival of 5.02 % and 11.16% for frogs with 3 and 4 toes removed, respectively, compared to frogs with just 2 toes removed (Figure 4-2). The estimated beta for the toe-clip effect on capture probability in green treefrogs was 0.1731 (S.E. =0.1270), but the 95% confidence interval included 0 (Table 4-4).

For Squirrel Treefrogs, the estimate of $\hat{c}$ from the parametric bootstrap was 1.848. Four models had delta $QAIC_c$ values less than 2 (Table 4-5). Two of the top 4 models included the toe-clip effect on survival and 2 included the toe-clip effect on capture. Models that included the toe-clip effect on survival for squirrel treefrogs received 36.09% of the $QAIC_c$ weight, and models that included the toe-clip effect on capture probability accounted for 47.29% of the total weight.

The estimated beta for the toe-clip effect on survival in Squirrel Treefrogs from the best model that included it was 0.0231 (S.E. =0.1379), which is a slightly positive effect of toe clipping, but the 95% confidence interval includes 0 (Table 4-4). The estimate of beta for the toe-clip effect of capture on Squirrel Treefrogs from the best model that included it was -0.1815 (S.E. =0.1139), but the 95% confidence interval for this parameter also includes 0 (Table 4-4).

Discussion

I found strong evidence of a negative effect of toe removal on Green Treefrog survival, but only very limited evidence of an effect of toe-clipping on Green Treefrog capture probability. On average, frogs with 3 and 4 toes removed had 5% and 11% lower survival probabilities respectively than Green Treefrogs with 2 toes removed. An effect of toe-clipping on capture in Green Treefrogs is not supported due to low AIC weights for models with a toe-clip effect on capture probability (Table 4-3) and a 95% confidence interval for the toe-clip effect beta that includes 0 (Table 4-4).

There was also little evidence of an effect of toe-clipping on survival or capture probability of Squirrel Treefrogs. This was due to low AIC weights for models that include toe-clip effects (Table3-5) and beta values that had 95% confidence intervals that included 0 (Table3-4). Average values for survival were equivalent regardless of the number of toes removed in Squirrel Treefrogs. Thus, only one species, the Green Treefrog, was found to show a negative response to toe-clipping.

McCarthy and Parris (2004) reported an estimated 4-11% reduction in the return rate of frogs for each toe removed. The best models in McCarthy and Parris’s (2004) analysis allow the change in return rate to vary linearly with the number of toes removed. This model appears to fit my results for Green Treefrog survival well, where there was 5-6% decrease in survival per toe removed. However Squirrel Treefrogs did not show the same pattern. Although there did appear to be a decline in the return rate of Squirrel Treefrogs (Table 4-2), there was no reduction in survival due to removing more toes (Figure 4-2).

My results differ from those of McCarthy and Parris (2004) in the magnitude and generality of the effect that was detected. Although return rates of both species in this study did decrease monotonically with the number of toes removed (Table 4-1), the estimated effect on survival was less than that expected from the results of McCarthy and Parris (2004). One reason for this difference is the inclusion of estimates of capture probability in my analysis. Rather than assuming constant capture probability, I directly estimated it. Using return rates alone without accounting for heterogeneity in capture probability could lead to misinterpreting a reduction in encounter rates as a reduction in survival. In addition, both capture probability and apparent survival were allowed to vary with time in this study. Most of the best models for both species include time dependence for both survival and capture probability.

It is apparent that all species of frogs do not show the same response to toe-clipping. Some species appear to be especially susceptible to infections or loss of mobility due to toe removal (Golay and Durrer 1994, Lemckert 1996). Even the two species at the same site in this study showed a difference in the effect of toe-clipping on survival. Mark-recapture analysis provides a robust method for estimating the effect of toe clipping on survival and capture probability. It is preferable to using the return rate because it does not assume a constant capture probability across time or toe clip treatment. Using mark-recapture modeling to estimate survival and capture probabilities and using information-theoretic model selection to look for effects of the marking method should provide a useful technique for testing the efficacy of toe-clipping for other amphibian species.

Table 4-1. List of 23 models analyzed in Program MARK for captures of both Green Treefrogs and Squirrel Treefrogs in Big Cypress National Preserve during 2004-2005. Explanation defines each model in terms of the effects of time (t) and toe-removal group (clip), on apparent survival (ϕ) and capture probability (p).

Model	Explanation
$\phi_{.} p_{.}$	Survival and capture probability constant throughout study
$\phi_{t} p_{.}$	Survival varies with time; capture constant
$\phi_{.} p_{t}$	Survival constant; capture varies with time
$\phi_{t} p_{t}$	Both survival and capture vary with time
$\phi_{clip} p_{.}$	Survival is different among toe removal groups; capture constant
$\phi . p_{clip}$	Survival constant; capture is different among toe removal groups
$\phi_{clip} p_{clip}$	Survival and capture are both different among toe removal groups
$\phi_{clip} p_{t}$	Survival is group-dependent; capture varies with time
$\phi_{t} p_{clip}$	Survival varies with time; capture is group-dependent
$\phi_{t*clip} p .$	Survival is a function of time, group, and their interaction; capture constant
$\phi . p_{t*clip.}$	Survival constant; capture is a function of time, group, and their interaction
$\phi_{t*clip} p_{t}$	Survival is interactive effect of time and group; capture varies with time
$\phi_{t} p_{t*clip}$	Survival varies with time; capture is interactive effect of time and group
$\phi_{clip} p_{t*clip}$	Survival varies with toe group; capture is interactive effect of time and group
$\phi_{t*clip} p_{clip}$	Survival is interactive effect of time and group; capture varies with toe group
$\phi_{t*clip} p_{t*clip}$	Survival and capture are both an interactive effect of time and group
$\phi_{t+clip} p .$	Survival is additive effect of time and group; capture constant
$\phi . p_{t+clip}$	Survival constant; capture is additive effect of time and group
$\phi_{t+clip} p_{t}$	Survival is additive effect of time and group; capture varies with time
$\phi_{t} p_{t+clip}$	Survival varies with time; capture is additive effect of time and group
$\phi_{clip} p_{t+clip}$	Survival varies with toe group; capture is additive effect of time and group
$\phi_{t+clip} p_{clip}$	Survival is additive effect of time and group; capture varies with toe group
$\phi_{t+clip} p_{t+clip}$	Survival and capture are both the additive effect of time and group

Table 4-2. The number of green treefrogs and squirrel treefrogs marked by removing 2, 3, or 4 toes in Big Cypress National Preserve, Collier County, FL, Nov. 2004-June 2005, the number of individuals recaptured, and the return rate (proportion of marked individuals recaptured at least once).

Species	Treatment	No. Marked	No. Recaptured	Return Rate
Green Treefrog	2 toes	87	53	60.92%
	3 toes	848	474	55.90%
	4 toes	361	185	51.25%
Squirrel Treefrog	2 toes	80	56	70.00%
	3 toes	470	287	61.06%
	4 toes	108	65	60.19%

Table 4-3 Model selection table for Cormack-Jolly-Seber open population mark-recapture model of Green Treefrogs, including Quasi-likelihood Akaike’s Information Criterion for small sample sizes (QAIC$_c$), model weights based on QAIC$_c$, the number of parameters n each model, and the model deviance. Model structure includes the effects of time (t), and toe-clip group (clip) on apparent survival (ϕ) and capture probability (p).

Model	QAICc	Delta QAICc	QAICc Weights	Num. Par	QDeviance
$\phi_{t+clip}\, p_{t}$	2944.1863	0.0000	0.5182	16	2911.9877
$\phi_{t+clip}\, p_{t+clip}$	2945.0711	0.8848	0.3329	17	2910.8476
$\phi_{t}\, p_{t}$	2946.8039	2.6176	0.1400	13	2920.6711
$\phi_{t}\, p_{t+clip}$	2952.4145	8.2282	0.0085	16	2920.2161
$\phi_{t*clip}\, p_{t}$	2958.9709	14.7846	0.0003	27	2904.4171
$\phi_{t}\, p_{t*clip}$	2962.4472	18.2609	0.0001	27	2907.8932
$\phi_{t*clip}\, p_{t*clip}$	2964.9310	20.7447	0.0000	36	2891.9520
$\phi_{clip}\, p_{t}$	2968.9725	24.7862	0.0000	9	2950.9070
$\phi_{t+clip}\, p_{clip}$	2972.6627	28.4764	0.0000	12	2948.5491
$\phi_{.}\, p_{t}$	2972.7609	28.5746	0.0000	8	2956.7085
$\phi_{t+clip}\, p\cdot$	2973.1139	28.9276	0.0000	11	2951.0178
$\phi_{clip}\, p_{t+clip}$	2974.8908	30.7045	0.0000	12	2950.7771
$\phi\cdot p_{t+clip}$	2976.2446	32.0583	0.0000	11	2954.1485
$\phi_{t}\, p_{.}$	2976.7255	32.5392	0.0000	8	2960.6730
$\phi_{t}\, p_{clip}$	2978.7064	34.5201	0.0000	9	2960.6409
$\phi\cdot p_{t*clip.}$	2985.5690	41.3827	0.0000	22	2941.1988
$\phi_{clip}\, p_{t*clip}$	2986.9087	42.7224	0.0000	24	2938.4695
$\phi_{t*clip}\, p_{clip}$	2987.4740	43.2877	0.0000	23	2941.0701
$\phi_{t*clip}\, p\cdot$	2987.6664	43.4801	0.0000	22	2943.2964
$\phi_{clip}\, p_{clip}$	3392.0314	447.8451	0.0000	4	3384.0168
$\phi_{clip}\, p_{.}$	3394.4325	450.2462	0.0000	3	3388.4238
$\phi_{.}\, p_{.}$	3404.7537	460.5674	0.0000	2	3400.7494
$\phi\cdot p_{clip}$	3406.7036	462.5173	0.0000	3	3400.6947

Table 4-4. Estimates, standard error (SE), and the 95% confidence interval of the beta values for the toe-clip effect on apparent survival (ϕ) and capture probability (p).

				95% Confidence Interval	
Species	Parameter	Beta	SE	Lower	Upper
Green Treefrog	ϕ	-0.3963	0.1078	-0.6075	-0.1851
	p	0.1731	0.1270	-0.0759	0.4221
Squirrel Treefrog	ϕ	0.0231	0.1379	-0.2472	0.2934
	p	-0.1815	0.1139	-0.4047	0.0417

Table 4-5. Model selection table for Cormack-Jolly-Seber open population mark-recapture model of Squirrel Treefrogs, including Quasi-likelihood Akaike’s Information Criterion for small sample sizes ($QAIC_c$), model weights based on $QAIC_c$, the number of parameters n each model, and the model deviance. Model structure includes the effects of time (t), and toe-clip group (clip) on apparent survival (ϕ) and capture probability (p).

Model	QAICc	Delta QAICc	QAICc Weights	Num. Par	QDeviance
$\phi_t\, p_{t+clip}$	1653.9976	0	0.2481	16	1621.6121
$\phi_t\, p_.$	1654.0015	0.0039	0.2476	10	1633.8462
$\phi_{t+clip}\, p_t$	1655.3701	1.3725	0.1249	16	1622.9846
$\phi_{t+clip}\, p_{t+clip}$	1655.7340	1.7364	0.1041	17	1621.2999
$\phi_{t+clip}\, p\cdot$	1656.0325	2.0349	0.0897	11	1633.8461
$\phi_t\, p_{clip}$	1656.3014	2.3038	0.0784	9	1638.1745
$\phi_t\, p_t$	1656.7953	2.7977	0.0613	14	1628.4980
$\phi_{t+clip}\, p_{clip}$	1657.6489	3.6513	0.0400	12	1633.4284
$\phi_.\, p_t$	1663.6425	9.6449	0.0020	8	1647.5410
$\phi\cdot p_{t+clip}$	1664.1035	10.1059	0.0016	11	1641.9171
$\phi_{clip}\, p_t$	1664.1404	10.1428	0.0016	9	1646.0135
$\phi_{clip}\, p_{t+clip}$	1666.0178	12.0202	0.0006	12	1641.7974
$\phi_t\, p_{t*clip}$	1668.7560	14.7584	0.0002	26	1615.7538
$\phi_{t*clip}\, p_t$	1670.3368	16.3392	0.0001	25	1619.4096
$\phi_{t*clip}\, p\cdot$	1672.2840	18.2864	0.0000	21	1629.6268
$\phi_{t*clip}\, p_{clip}$	1675.9932	21.9956	0.0000	23	1629.2069
$\phi\cdot p_{t*clip.}$	1678.5895	24.5919	0.0000	21	1635.9323
$\phi_{clip}\, p_{t*clip}$	1681.6591	27.6615	0.0000	23	1634.8728
$\phi_{t*clip}\, p_{t*clip}$	1684.2103	30.2127	0.0000	35	1612.4000
$\phi_{clip}\, p_.$	1716.5722	62.5746	0.0000	3	1710.5552
$\phi_.\, p_.$	1716.7540	62.7564	0.0000	2	1712.7456
$\phi\cdot p_{clip}$	1716.7772	62.7796	0.0000	3	1710.7604
$\phi_{clip}\, p_{clip}$	1717.8694	63.8718	0.0000	4	1709.8412

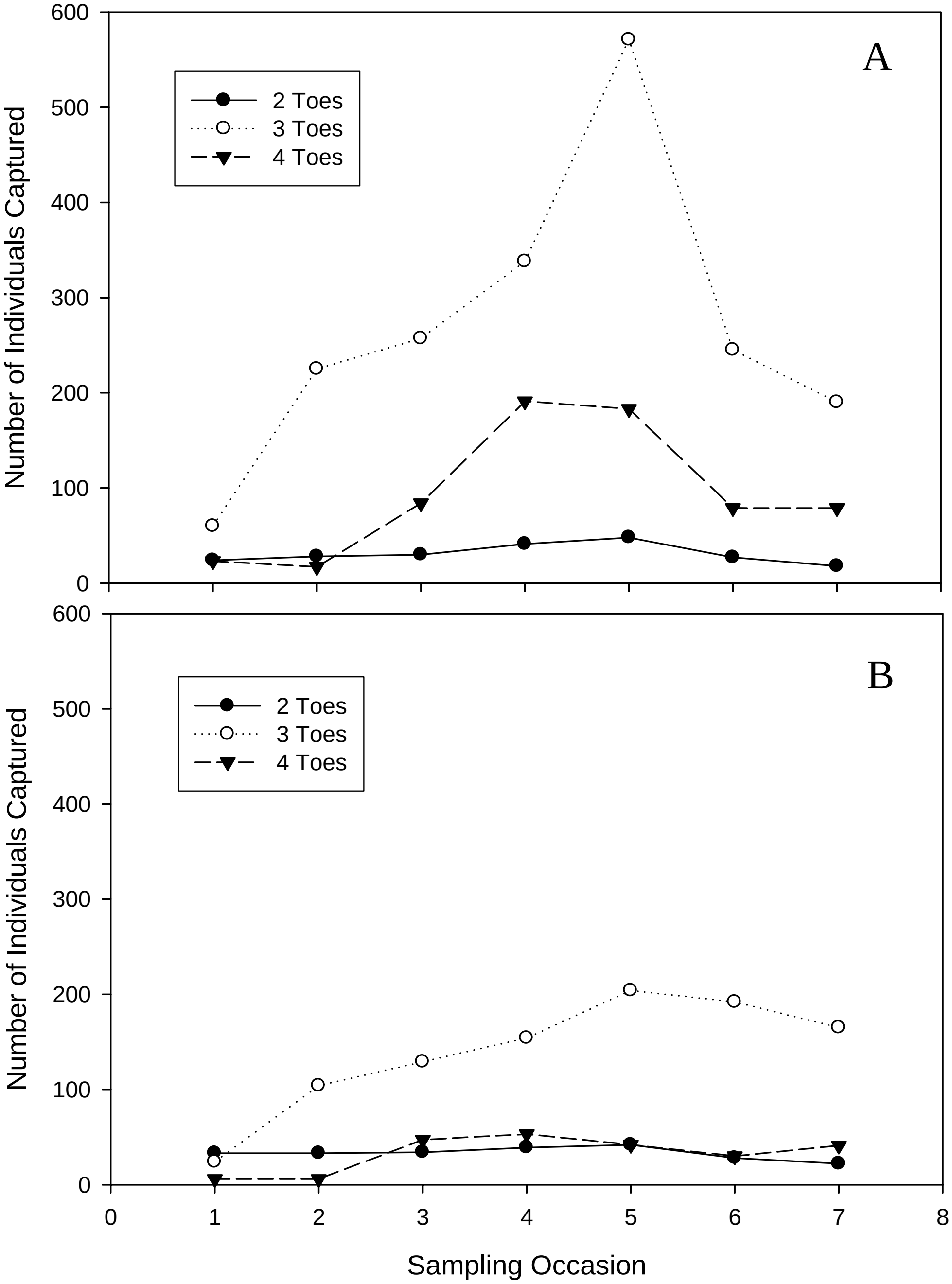


Figure 4-1. Numbers of individuals of green treefrogs (A) and squirrel treefrogs (B) captured and released in each of the three toe removal groups during the first 7 sampling occasions.

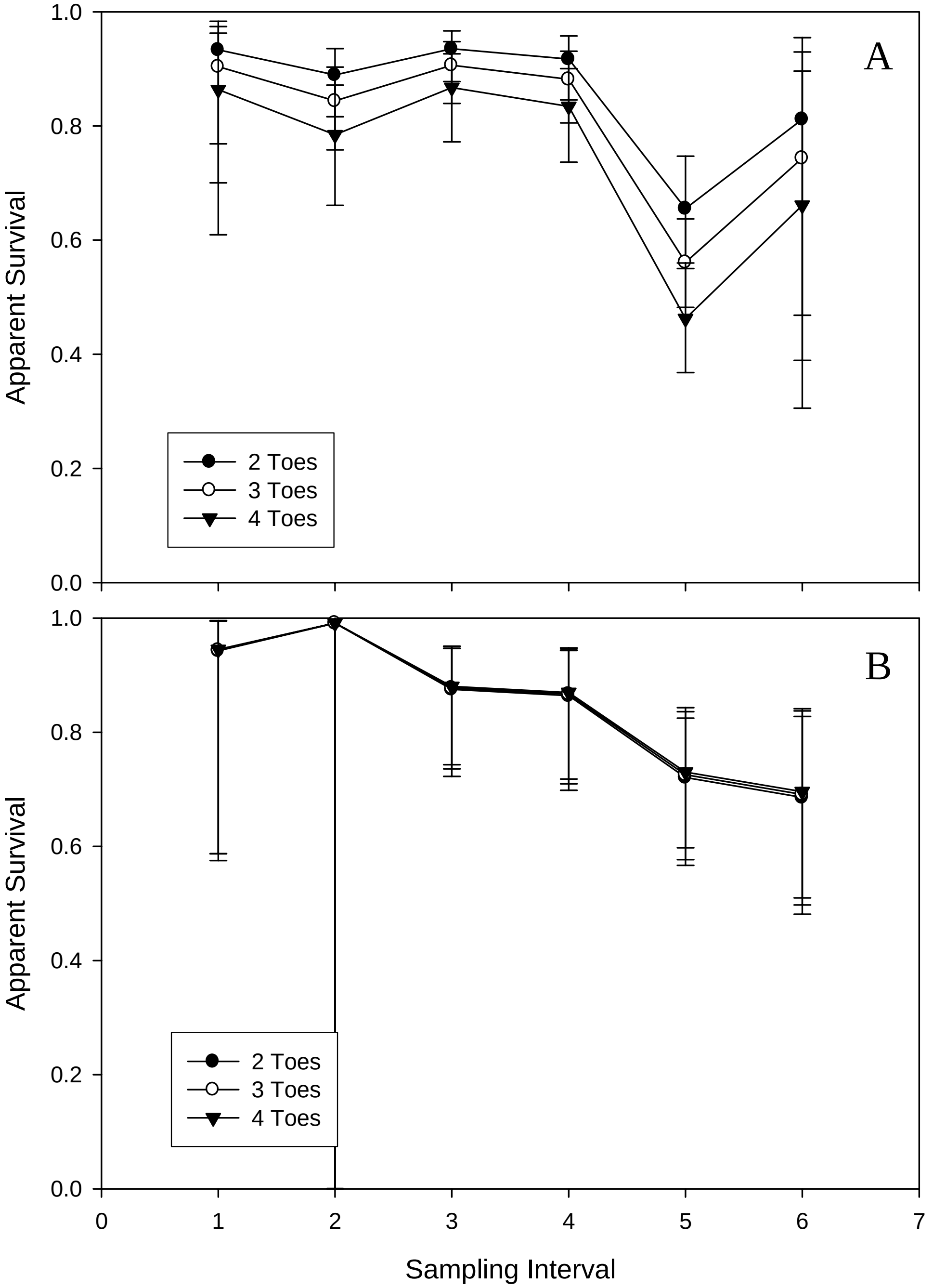


Figure 4-2. Apparent survival (ϕ) and 95% confidence interval of green treefrogs (A) and squirrel treefrogs (B) in each toe removal group category across the first 6 monthly sampling intervals. Estimates for squirrel treefrogs are averaged across models as no model had a majority of the QAICc weight (Burnham and Anderson 1998).

CHAPTER 5
INFLUENCE OF HYDROLOGY ON SURVIVAL AND RECRUITMENT OF GREEN TREEFROGS

The Everglades ecosystem of southern Florida has been substantially altered over the last 100 years by loss to agriculture and urbanization. Compartmentalization of the remaining Everglades into a network of artificially controlled impoundments has impeded historic flow patterns (Davis et al. 1994). A large-scale restoration effort, the Comprehensive Everglades Restoration Plan (CERP) was devised to attempt to restore natural hydrologic regimes to the remaining Everglades (DeAngelis et al. 1998). One measure of restoration success was defined as recovering ecological structure and function to the natural areas. Consequently, managers charged with decision-making for CERP need species that can serve as indicators of ecosystem restoration success.

Amphibians have been used in various locations as ecosystem indicator species (Welsh and Ollivier 1998, Galatowitsch et al. 1999, Sheridan and Olson 2003). Aspects of their natural history (e.g. aquatic larval phase, permeable skin, and low dispersal ability) make them potentially well-suited as indicator species in the Everglades as in other systems. However, there is no historical record of amphibian populations from before hydrologic alteration in the Everglades system to use for comparison to current and post-restoration populations. Likewise, it would be extremely difficult to experimentally manipulate environmental conditions at the scale necessary to gauge the response of amphibians to hydrologic restoration.

By monitoring amphibian populations and measuring how they respond to environmental changes at a local scale, it should be possible to make predictions about how amphibians will respond to Everglades restoration on a landscape scale. As the major goal of CERP is restoration of hydrology, it is important to know how amphibians will respond to changes in water depth and duration if amphibians are to be used as indicator species of restoration success. This response may be measured in population vital rates, and mark-recapture techniques allow the estimation of vital rates. Survival and recruitment rates can be estimated using open population mark-recapture analysis, and the population growth rate of populations can be derived from estimates of these two parameters (Pradel 1996).

The goal of this study is to determine effects of seasonal changes in hydrology on the population vital rates of Green Treefrogs (*Hyla cinerea*) in the Everglades ecosystem to provide information on how hydrologic restoration in the Everglades might impact frog populations. Modeling recruitment and survival with mark-recapture analysis will help build a model of how populations should respond to anthropogenic changes in hydrology. The contributions of survival and recruitment to population growth across seasons will be determined within closely connected habitats. The contributions may be important for determining critical time periods for reproduction at different water depths. I hypothesized that both survival and recruitment are dependent on water depth and hydrologic season as well as time. I also hypothesized that capture probability is dependent on season. The information gained in this study can later be used to build models predicting the response of frog populations to various scenarios of hydrologic restoration of CERP.

Methods

Three long-term study sites were established in Big Cypress National Preserve, Collier County, FL for this study. Each of these sites was placed at a location where 3 habitats, cypress strand, broad-leaf marsh, and short-hydroperiod prairie, were in close proximity. Habitats in the Everglades ecosystem are primarily different due to small topographical differences that create marked differences in hydrology (McPherson 1974, Duever et al. 1986). Broadleaf marshes have the longest hydroperiod, and never completely dried during this study (Figure 5-1). Marsh sites are comprised of tall (1-2 m) emergent forbs, especially Pickerelweed (*Pontedaria cordata*), and lack a woody overstory. Cypress strands are intermediate in hydrology (Figure 5-1), and are distinct from the other habitats because of their closed canopy of bald cypress (*Taxodium distichum*). Prairie, sometimes referred to as marl prairie or dry prairie, has the shortest hydroperiod (Figure 5-1). These sites are characterized by a sedge dominated flora usually up to 1 m in height (Duever et al. 1986).

A grid of 49 polyvinyl chloride (PVC) pipe refugia (Moulton et al. 1996, Boughton et al. 2000) was arranged within each habitat stratum at each site. Pipes were arranged 5 m apart in a 7 by 7 grid. Grids were located completely within a habitat stratum, but within 30 m of the adjacent grids in the other habitats. PVC pipes used in this study were 50 mm in diameter and 1 m long. Each pipe was placed vertically onto a wooden stake driven into the soil so the pipe could be easily lifted for inspection. All pipes in each grid were numbered for reference. Sites were sampled biweekly from April 2004 to November 2004 and once monthly from December 2004 to August 2005 (n=25). Water depth was measured at a fixed depth gauge in the center of each plot during each sampling occasion.

At each sample, all pipes were checked for frogs which were captured in sealable plastic bags. Frogs that escaped were noted and identified to species if possible. Captured frogs were identified to species and measured snout to urostyle (SUL). Green treefrogs less than 25 mm SUL were returned unmarked as frogs of this size were difficult to mark and read marks reliably. Previously unmarked frogs 25 mm SUL and larger were assigned a unique toe-clip combination (Donnelly et al. 1994) and marked by removing toes using stainless steel scissors sterilized in alcohol. Previously marked (recaptured) frogs were checked against a list of previously marked frogs to insure the clip was read correctly. The pipe number and grid location of each frog capture was noted, and frogs were released into the pipe opening immediately after necessary handling was completed.

Capture-recapture data were analyzed using the temporal symmetry approach of Pradel (1996) with the γ-parameterization (ϕ_t, p_t, γ_t; Williams et al. 2002) in Program MARK (White and Burnham 1999). The temporal symmetry approach uses reverse-time mark recapture analysis (Pollock et al. 1974, Pradel 1996) to estimate the seniority parameter, γ_i (i.e. the probability that an individual alive at time *i* was also alive at time *i* -1). Although the parameter of interest in this study is actually the population growth rate ($\hat{\lambda}_i$), the γ-parameterization of the Pradel (1996) model is known to perform better than alternative parameterizations including $\hat{\lambda}_i$, and $\hat{\lambda}_i$ may be derived from the estimates of the $\hat{\gamma}_i$ and $\hat{\phi}_i$ parameters (Williams et al. 2002). The temporal symmetry method uses assumptions similar to standard open-population Cormack-Jolly-Seber mark-recapture models (Lebreton et al. 1992). These assumptions include that no marks are lost or misread and that no non-random temporary emigration occurs. Every marked animal should have the same probability of capture in and survival to the next sampling period, and all individuals should have independent fates (Williams et al. 2002).

In the analysis, water depth was a covariate and captures were grouped by habitat and season. Mean water depth within each habitat across the 3 sites was standardized so that the mean fell between 0 and 1 as the logit link function was used in MARK analyses (Williams et al. 2002). Individual frogs were categorized as belonging to cypress, marsh, or prairie habitat groups. Although it was rare, some frogs were caught in one habitat and later moved to an adjacent habitat. Frogs that were captured in more than one habitat were assigned to the group with the most captures, or the last capture if caught an even number of times in two habitats. Sampling occasions were grouped into 5 “seasons” based on the annual pattern of rainfall (Table 5-1). These seasons were used in the models in place of full time dependence because they are more biologically meaningful than date alone.

There are three parameters estimated in this temporal symmetry model: survival (ϕ), capture probability (*p*), and the seniority parameter (γ). Models representing different combinations of the water depth covariate, habitat group, and season (time) structure were constructed that were *a priori* determined to be biologically meaningful. Model selection was conducted using the information-theoretic approach based on Akaike’s information criterion adjusted for small sizes ($\mathrm{AIC_c}$; (Burnham and Anderson 1998). $\hat{\lambda}_i$ during each sampling interval was derived in Program MARK using the equation given in Williams et al. (2002):

$$\hat{\lambda}_i = \hat{\phi}_i / \hat{\gamma}_{i+1}$$

Nichols et al. (2000) demonstrate the relationship between the γ parameter of the Pradel (1996) temporal symmetry modeling approach and relative contributions of survival and recruitment to the change in population growth. The contributions of survival and recruitment to $\hat{\lambda}_i$ are analogous in this case to $\hat{\gamma}_i$ and 1-$\hat{\gamma}_i$, respectively (Nichols et al. 2000).

Results

During the 17 months of sampling, a total of 1069 individual Green Treefrogs were marked and 1054 recaptures were recorded. There were 293 times that a frog escaped capture, and 173 frogs less than 25 mm SUL were released unmarked. Frog capture rates were higher in the dry season months, peaking in February and March 2005 (Figure 5-2), and frog captures were lowest during the peak of the wet seasons (August 2004 and June 2005). Sizes of captured frogs showed a seasonal pattern (Figure 5-3). Mean SUL was lowest in August 2004 after the onset of the wet season, with a similar dip in July 2005 after the beginning of the 2005 wet season. More frogs were captured in cypress and marsh habitats than in prairie, but habitat differences were only observed during the dry months (Figure 5-4).

Model selection results from the mark-recapture modeling indicated that the best model included the seasonal time structure, habitat group, and water-depth covariate for ϕ and γ, and only habitat and season for *p* (Table 5-2). No other models had any $\mathrm{AIC_c}$ weight (Burnham and Anderson 1998). The habitat and season-specific values for ϕ varied widely, but were generally around 0.80 (Figure 5-5). Estimates of γ also varied widely (Figure 5-6). Although season was included in the model for ϕ and γ, a seasonal trend in either was not apparent, but a pattern might be somewhat obscured by the water depth covariate. There does appear to be a strong seasonal trend in *p* (Figure 5-7). Capture rates were lowest at the sampling occasions corresponding to the wet seasons of 2004 and 2005 (Table 5-1). $\hat{\lambda}_i$ values across sampling intervals and habitats fluctuated from 0.22 to 2.02 (Figure 5-8). The contribution to $\hat{\lambda}_i$ from survival was almost always greater than the contribution of recruitment in each habitat (Table 5-3).

Discussion

The mark-recapture modeling results support the hypothesis that Green Treefrog survival and seniority varies with season and with water level, as well as among habitats. Capture probability also varied with season and habitat, but was not affected by water depth. Capture rates declined during the early wet seasons and capture probability was at minimum levels during the wet season. The mean size of individuals captured declined sharply during the wet seasons, presumably as young of the year individuals enter the population. Population growth rates were highest after the onset of the 2004 wet season and during December 2004 and January 2005 (Table 5-3). These two time periods also showed increased contributions to $\hat{\lambda}_i$ from recruitment (1-$\hat{\gamma}_i$).

Recruitment as it is modeled in this study includes animals that are enter the population from reproduction as well as immigrants into the population, and the models used can not differentiate the two (Nichols et al. 2000). Recruitment in this study may also include animals moving into the PVC pipe refugia for the first time, as the population studied is actually the population using the PVC pipes. The early wet season increase in recruitment was most likely a result of reproduction. This increase coincides directly with the large drop in mean SUL of captured frogs (Figure 5-3), and large choruses of calling males and Green Treefrogs in amplexus were observed at all of the sites at the onset of the wet season (personal observation). The increase in recruitment in December 2004 and January 2005 is likely the result of cold weather causing frogs to seek refuge in the PVC pipes. Increased capture rates in PVC refugia at times of cold weather have been observed elsewhere in Florida (Donnelly et al. 2001, Zacharow et al. 2003). Movements of frogs between habitats were very rare and only account for about

5% of all captures (unpublished data). It therefore seems unlikely that immigration into the study sites was a factor in recruitment rates.

One important assumption of the mark-recapture analysis used in this study is that there is no non-random temporary immigration. Immigration into the study sites does not appear to have occurred due to the very low movement rates between habitats. One potential violation of the temporary immigration assumption is the increased use of pipes during the colder samples. If the frogs captured and marked in these samples later emigrated back out of the pipe population it would affect estimates of survival. However, capture rates were actually higher in the months following the December and January increase in recruitment (Figure 5-2) when population growth was not increasing (Table 5-3). It appears from this pattern that once frogs moved into the PVC pipe population they remained in the population, therefore this would not be a case of temporary immigration.

Green Treefrog populations in BCNP fluctuate on a strongly annual cycle driven by the hydrologic cycle in the Everglades ecosystem. The majority of reproduction occurs at the onset of the wet season. The number of frogs in the population slowly declines until late in the dry season when few large, adult frogs remain to accomplish breeding at the onset of the next wet season. The mark-recapture modeling results from this study (Table 5-2) corroborate that survival and seniority rates are seasonal and related to water depth. The average monthly survival rate for green treefrogs across habitats and months is 81.0%, or only 8.0% annually. Few published survival rates of frogs exist for comparison, but these estimates appear to be low in comparison to estimates of survival of the Afro-Tropical Pig-Nosed Frog (Grafe et al. 2004) and the pig frog (Wood et al.1988).

The seasonal patterns observed in capture probability as well as recruitment into the population demonstrate the importance of long-term monitoring of sites. Studying the population during a single season could lead to incorrect conclusions about trends in the population. In addition, this study has demonstrated that differences in vital rates can exist between adjacent sites in different habitats. This suggests that population level changes may be occurring at a very small scale, and probably have a strong relationship to hydrology. Capture probability was not a function of water depth (Table 5-2), but there was a strongly seasonal pattern to capture probability (Figure 5-7) and to capture rates (Figure 5-2).

Although prairie habitat usually had the lowest rate of population growth (Figure 5-8) across sampling intervals, it almost always had the highest values for contribution to growth from recruitment (Table 5-3). This is noteworthy because prairie is the habitat with the shortest hydroperiod, meaning it is likely to be the most impacted by hydrologic restoration. Large areas of the eastern Everglades are comprised of a similar short-hydroperiod graminoid prairie, the rocky glades (Davis et al. 2005). If the spatial and temporal pattern of hydrology in the rocky glades area is altered during CERP restoration, an effect on Green Treefrog populations should be detected. For example, an extension of the annual period of inundation could increase Green Treefrog reproduction. Monitoring of Green Treefrog populations may provide an efficient means for indicating if the vital ecological processes associated with the seasonal pattern of inundation are functioning appropriately after hydrologic restoration. Prior to this study, this process was not well understood, and consequently, the proposed actions in CERP have not been evaluated with respect to effects on amphibian reproduction.

Table 5-1. Dates of each sample of the PVC pipe refugia and the season to which each sample was assigned for mark-recapture analysis.

Sample	Date	Season
1	4/23/04	Dry season 2004
2	5/7/04	Dry season 2004
3	5/19/04	Dry season 2004
4	6/5/04	Dry season 2004
5	6/18/04	Dry season 2004
6	6/30/04	Dry season 2004
7	7/15/04	Wet season 2004
8	7/29/04	Wet season 2004
9	8/10/04	Wet season 2004
10	8/27/04	Wet season 2004
11	9/9/04	Wet season 2004
12	9/23/04	Wet season 2004
13	10/13/04	Wet season 2004
14	10/21/04	Wet-dry transition
15	11/5/04	Wet-dry transition
16	11/22/04	Wet-dry transition
17	12/15/04	Wet-dry transition
18	1/6/05	Dry season 2005
19	2/3/05	Dry season 2005
20	3/7/05	Dry season 2005
21	4/15/05	Dry season 2005
22	5/18/05	Wet season 2005
23	6/15/05	Wet season 2005
24	7/22/05	Wet season 2005
25	8/17/05	Wet season 2005

Table 5-2. Model selection results for all models analyzed in Program MARK. Model describes the covariates and groups associated with ϕ (survival), *p* (capture probability), and γ (seniority parameter): s is the seasonal time structure (Table 5-1), h is the habitat grouping (different estimates among the habitats), and w is the water depth covariate. Akaike's information criterion adjusted for small sample sizes (AIC_c), Delta AIC_c (the difference between the AIC_c for a model and the AIC_c for the model with the lowest AIC_c), the AIC_c weight (Burnham and Anderson 1998), the number of parameters in each model and the model deviances are given.

Model	AIC_c	Delta AIC_c	AIC_c Weight	Num. Par	Deviance
ϕ(s+h+w), *p*(s+h), γ(s+h+w)	9496.89	0.00	1	39	1420.46
ϕ(s+h+w), *p*(s+h+w), γ(s+h+w)	9522.16	25.27	0	41	1441.57
ϕ(s+h+w), *p*(s), γ(s+h+w)	9613.15	116.26	0	32	1551.21
ϕ(s+h), *p*(s+h), γ(s+h+w)	9665.58	168.70	0	41	1585.00
ϕ(s+h), *p*(s+h+w), γ(s+h+w)	9665.98	169.09	0	42	1583.31
ϕ(s+h), *p*(s+h), γ(s+h)	9670.52	173.64	0	44	1583.69
ϕ(s+w), *p*(s+w), γ(s+w)	9700.29	203.40	0	18	1667.03
ϕ(h), *p*(s+h), γ(s+h+w)	9745.69	248.80	0	31	1685.80
ϕ(s+h), *p*(s+h), γ(h)	9750.95	254.06	0	32	1689.01
ϕ(h), *p*(s+h), γ(s+h)	9751.66	254.77	0	33	1687.65
ϕ(h+w), *p*(h+w), γ(h+w)	9877.47	380.58	0	12	1856.39
ϕ(h), *p*(s+h), γ(h)	9956.30	459.42	0	21	1916.93
ϕ(s), *p*(s), γ(s)	9988.10	491.21	0	15	1960.94
ϕ(s), *p*(s), γ(s+w)	9989.80	492.92	0	16	1960.61
ϕ(s+h), *p*(h), γ(h)	10191.78	694.89	0	20	2154.45
ϕ(w), *p*(w), γ(w)	10584.90	1088.01	0	3	2581.95
ϕ(h), *p*(h), γ(h)	11291.75	1794.86	0	9	3276.73
ϕ(.), *p*(.), γ(.)	11428.49	1931.60	0	3	3425.55

Table 5-3. Estimates of the population growth rate $\hat{\lambda}_i$, the contribution of survival to $\hat{\lambda}_i$ ($\hat{\gamma}_i$), and the contribution of recruitment to $\hat{\lambda}_i$ (1-$\hat{\gamma}_i$) and the standard error (S.E.) of each estimate for each sampling interval ending on the date given.

	Cypress			Marsh			Prairie		
Date	$\hat{\lambda}_i (S.E.[\hat{\lambda}_i])$	$\hat{\gamma}_i (S.E.[\hat{\gamma}_i])$	$1-\hat{\gamma}_i (S.E.[1-\hat{\gamma}_i])$	$\hat{\lambda}_i (S.E.[\hat{\lambda}_i])$	$\hat{\gamma}_i (S.E.[\hat{\gamma}_i])$	$1-\hat{\gamma}_i (S.E.[1-\hat{\gamma}_i])$	$\hat{\lambda}_i (S.E.[\hat{\lambda}_i])$	$\hat{\gamma}_i (S.E.[\hat{\gamma}_i])$	$1-\hat{\gamma}_i (S.E.[1-\hat{\gamma}_i])$
5/7/04	1.06 (0.056)	0.77(0.052)	0.23 (0.052)	1.07 (0.049)	0.90(0.044)	0.10 (0.044)	0.99 (0.084)	0.74(0.075)	0.26 (0.075)
5/19/04	1.06 (0.056)	0.77(0.052)	0.23 (0.052)	1.25 (0.096)	0.79(0.061)	0.21 (0.061)	1.02 (0.083)	0.73(0.076)	0.27 (0.076)
6/5/04	1.06 (0.056)	0.77(0.052)	0.23 (0.052)	1.25 (0.096)	0.79(0.061)	0.21 (0.061)	1.02 (0.083)	0.73(0.076)	0.27 (0.076)
6/18/04	0.89 (0.067)	0.79(0.050)	0.21 (0.050)	0.65 (0.134)	0.92(0.039)	0.08 (0.039)	1.02 (0.083)	0.73(0.076)	0.27 (0.076)
6/30/04	1.06 (0.056)	0.77(0.052)	0.23 (0.052)	1.24 (0.090)	0.80(0.058)	0.20 (0.058)	1.02 (0.083)	0.73(0.076)	0.27 (0.076)
7/15/04	1.06 (0.056)	0.77(0.052)	0.23 (0.052)	1.25 (0.096)	0.79(0.061)	0.21 (0.061)	1.02 (0.083)	0.73(0.076)	0.27 (0.076)
7/29/04	1.78 (0.205)	0.56(0.064)	0.44 (0.064)	1.55 (0.187)	0.64(0.077)	0.36 (0.077)	1.34 (0.135)	0.74(0.075)	0.26 (0.075)
8/10/04	1.39 (0.073)	0.66(0.040)	0.34 (0.040)	1.27 (0.071)	0.74(0.049)	0.26 (0.049)	1.72 (0.178)	0.54(0.076)	0.46 (0.076)
8/27/04	1.39 (0.073)	0.66(0.040)	0.34 (0.040)	0.86 (0.103)	0.78(0.044)	0.22 (0.044)	1.04 (0.139)	0.59(0.074)	0.41 (0.074)
9/9/04	0.76 (0.126)	0.71(0.046)	0.29 (0.046)	0.72 (0.116)	0.79(0.044)	0.21 (0.044)	0.94 (0.154)	0.59(0.074)	0.41 (0.074)
9/23/04	1.20 (0.070)	0.68(0.045)	0.32 (0.045)	1.20 (0.064)	0.75(0.047)	0.25 (0.047)	1.55 (0.119)	0.55(0.075)	0.45 (0.075)
10/13/04	1.35 (0.068)	0.66(0.046)	0.34 (0.046)	1.25 (0.067)	0.75(0.048)	0.25 (0.048)	1.69 (0.168)	0.53(0.076)	0.47 (0.076)
10/21/04	1.37 (0.070)	0.66(0.046)	0.34 (0.046)	1.24 (0.066)	0.75(0.048)	0.25 (0.048)	1.55 (0.119)	0.55(0.075)	0.45 (0.075)
11/5/04	0.64 (0.132)	0.75(0.049)	0.25 (0.049)	0.75 (0.226)	0.81(0.057)	0.19 (0.057)	0.64 (0.112)	0.74(0.053)	0.26 (0.053)
11/22/04	1.23 (0.077)	0.71(0.040)	0.29 (0.040)	1.17 (0.088)	0.78(0.055)	0.22 (0.055)	1.08 (0.069)	0.71(0.055)	0.29 (0.055)
12/15/04	1.48 (0.069)	0.66(0.032)	0.34 (0.032)	1.31 (0.091)	0.75(0.053)	0.25 (0.053)	1.19 (0.077)	0.70(0.056)	0.30 (0.056)
1/6/05	1.77 (0.119)	0.56(0.038)	0.44 (0.038)	1.68 (0.200)	0.59(0.070)	0.41 (0.070)	1.28 (0.090)	0.69(0.058)	0.31 (0.058)
2/3/05	0.86 (0.020)	0.87(0.017)	0.13 (0.017)	0.94 (0.100)	0.79(0.036)	0.21 (0.036)	1.01 (0.050)	0.67(0.040)	0.33 (0.040)
3/7/05	0.86 (0.020)	0.87(0.017)	0.13 (0.017)	1.44 (0.076)	0.69(0.036)	0.31 (0.036)	1.01 (0.050)	0.67(0.040)	0.33 (0.040)
4/15/05	0.86 (0.020)	0.87(0.017)	0.13 (0.017)	0.24 (0.028)	0.83(0.041)	0.17 (0.041)	1.01 (0.050)	0.67(0.040)	0.33 (0.040)
5/18/05	0.86 (0.020)	0.87(0.017)	0.13 (0.017)	1.47 (0.087)	0.67(0.040)	0.33 (0.040)	1.01 (0.050)	0.67(0.040)	0.33 (0.040)
6/15/05	1.00 (0.000)	1.00(0)	0 (0)	0.45 (0.142)	0.46(0.121)	0.54 (0.121)	2.02 (0.398)	0.40(0.088)	0.60 (0.088)
7/22/05	1.00 (0.000)	1.00(0)	0 (0)	0.70 (0.196)	0.44(0.120)	0.56 (0.120)	0.49 (0.114)	0.47(0.093)	0.53 (0.093)
8/17/05	1.00 (0.000)	1.00(0)	0 (0)	0.22 (0.086)	0.48(0.122)	0.52 (0.122)	0.49 (0.114)	0.47(0.093)	0.53 (0.093)

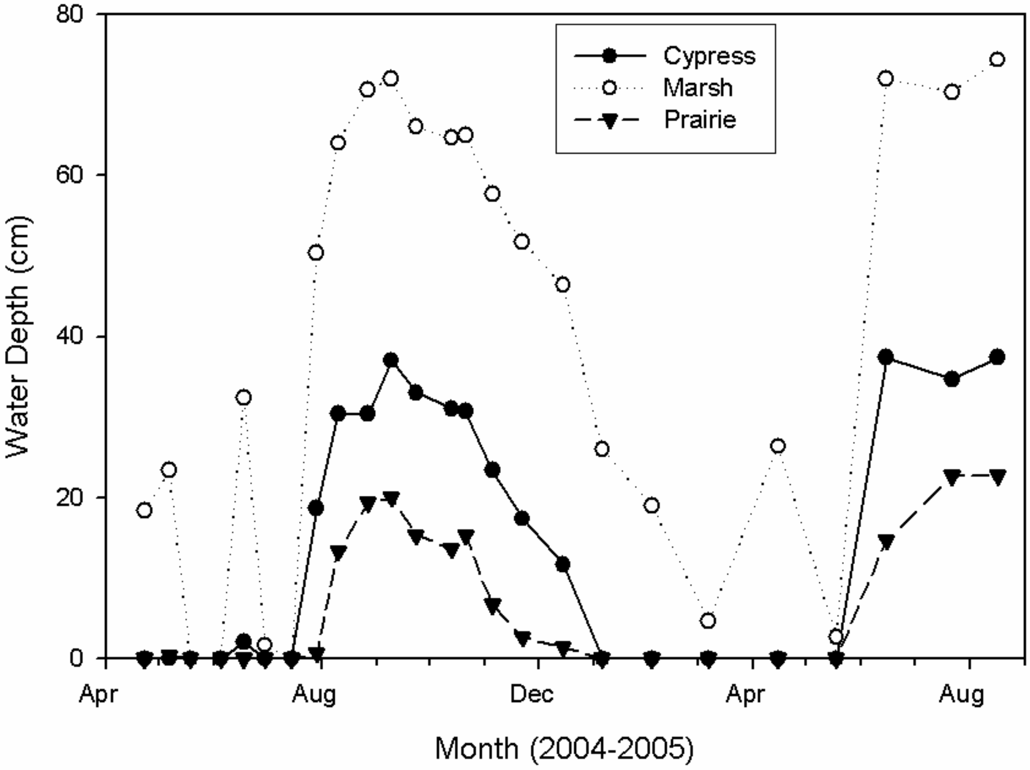


Figure 5-1. Mean water depth across the 3 sampling locations in BCNP in the cypress strand, broadleaf marsh, and prairie habitats from April 2004-August 2005.

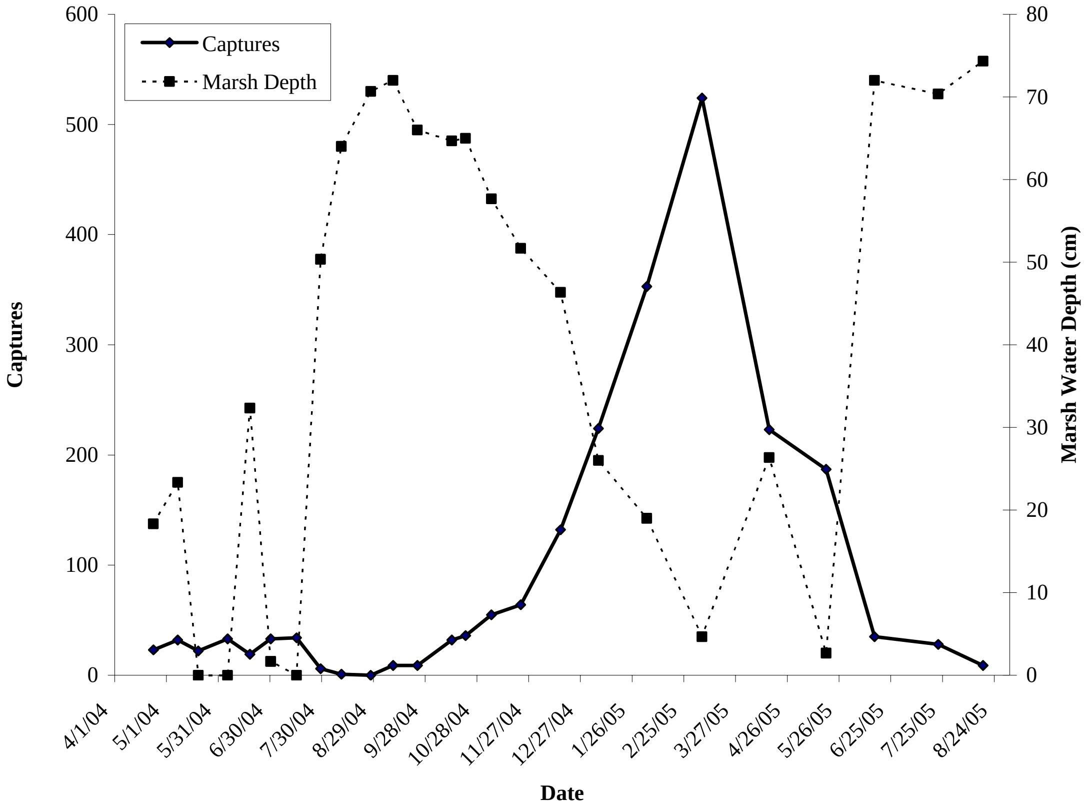


Figure 5-2. Number of captures of Green Treefrogs during each of the 25 samples from April 2004 to August 2005 (solid line) and mean water depth (in cm) of marsh plots (dotted line) across all 3 sites in BCNP.

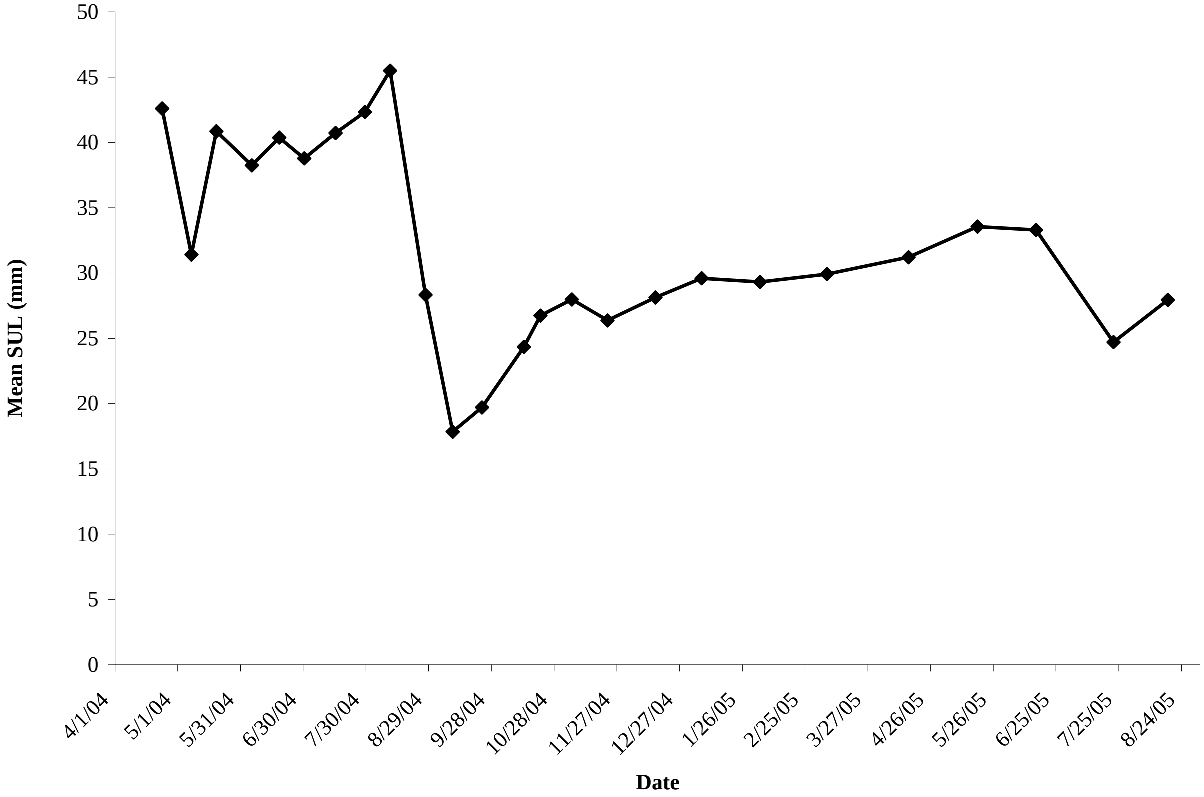


Figure 5-3. Mean snout-to-urostyle (SUL) in mm of Green Treefrogs captured in all habitats at the three sites at each sampling occasion in BCNP.

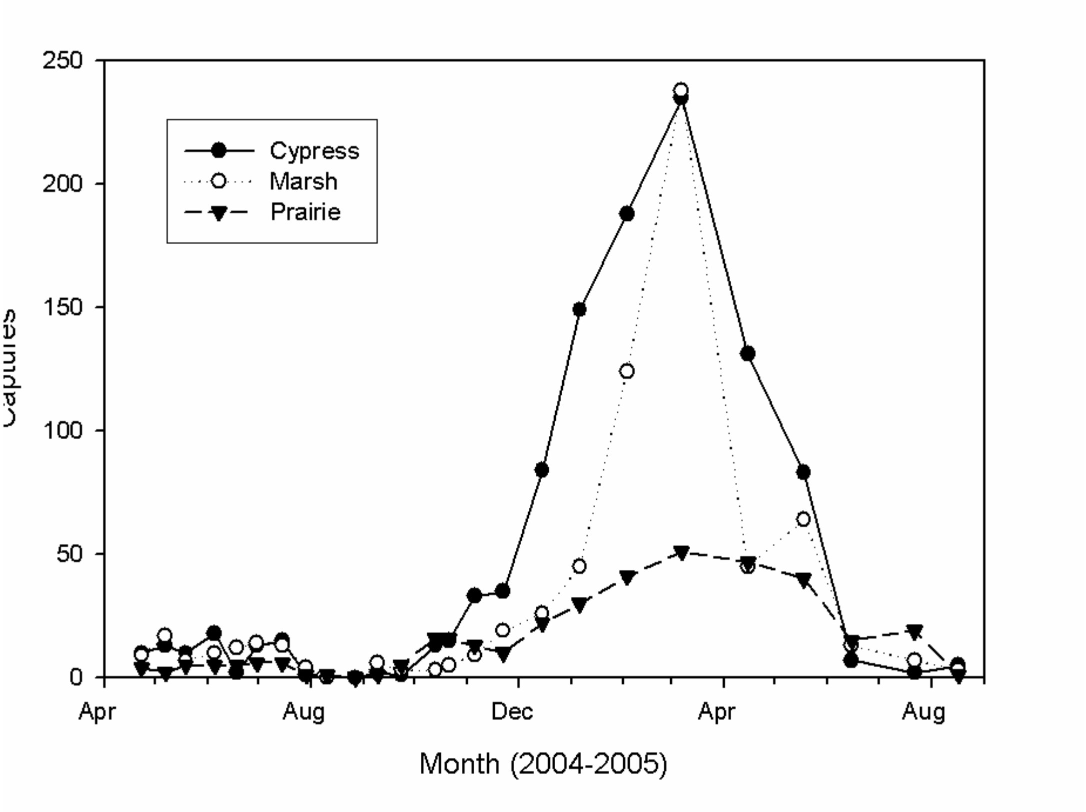


Figure 5-4. Number of captures by sample of Green Treefrogs in cypress, marsh, and prairie habitats at the three sites in BCNP.

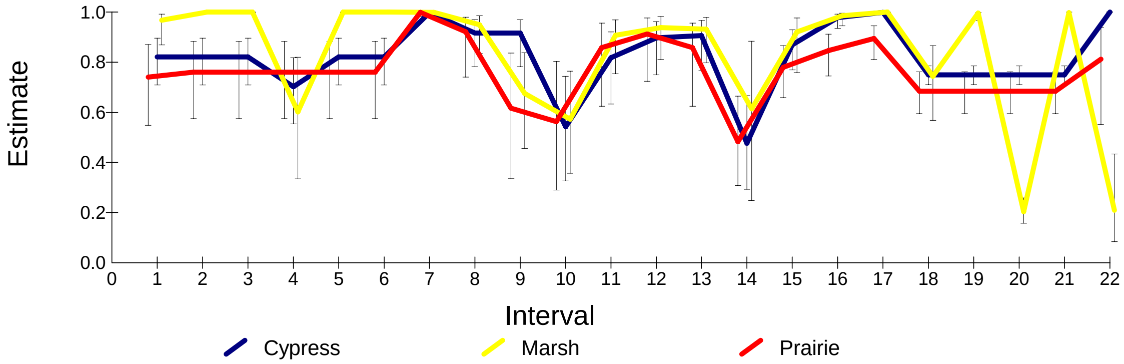


Figure 5-5. Estimates with 95% confidence intervals of apparent survival (ϕ) of Green Treefrogs for each sampling interval for cypress, marsh, and prairie habitat in BCNP.

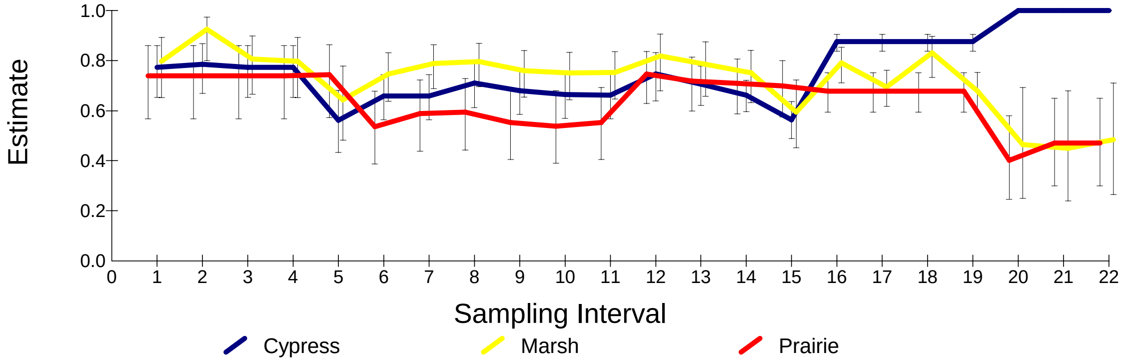


Figure 5-6. Estimates with 95% confidence intervals of seniority (γ) of Green Treefrogs for each sampling interval for cypress, marsh, and prairie habitat in BCNP.

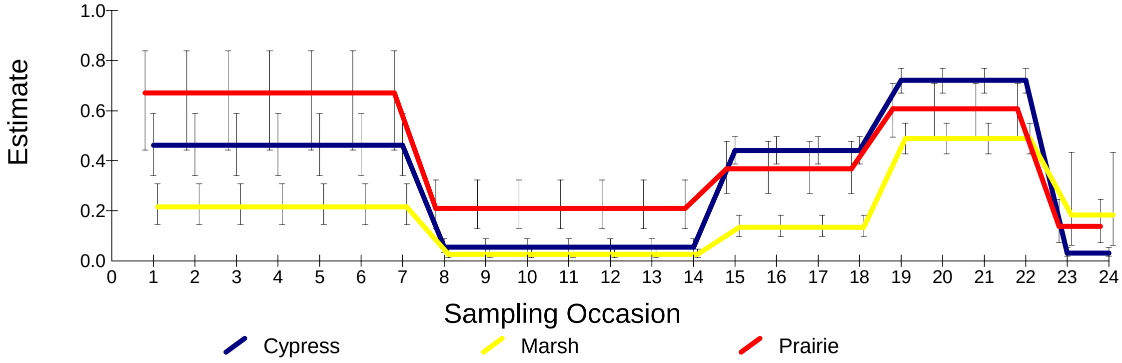


Figure 5-7. Estimates with 95% confidence intervals of capture probability (*p*) of Green Treefrogs at each sampling occasion for cypress, marsh, and prairie habitat in BCNP.

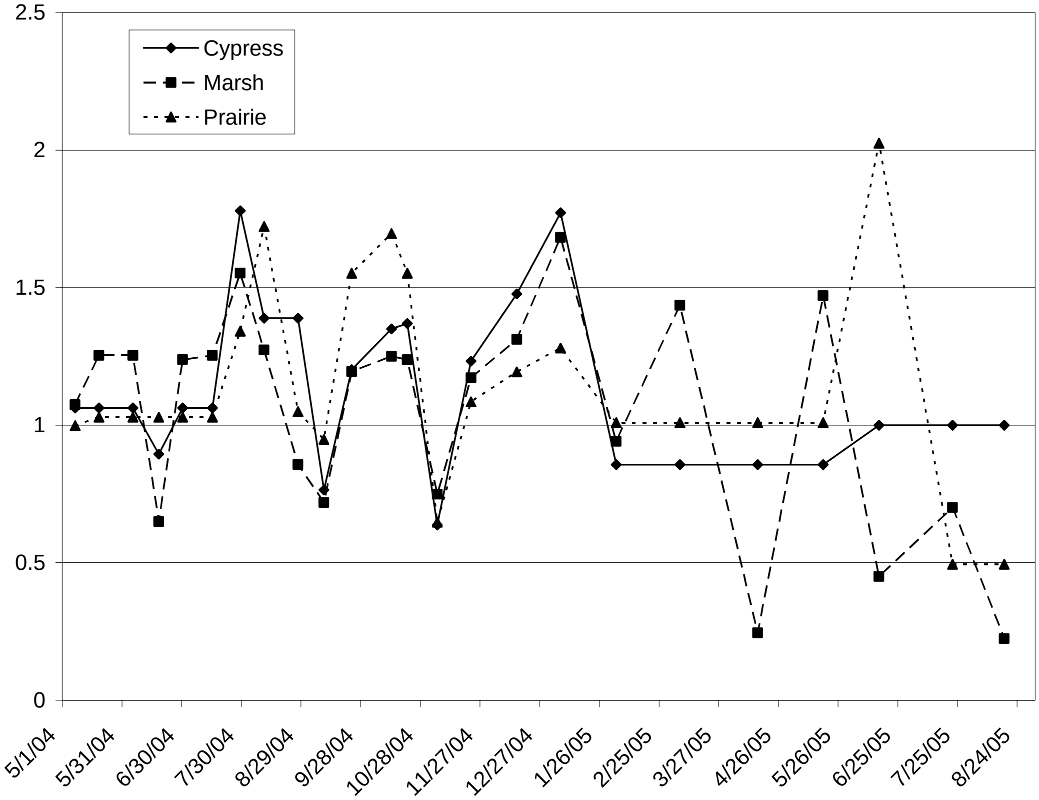


Figure 5-8. Derived estimates of population growth ($\hat{\lambda}_i$) of Green Treefrogs for each sampling interval for cypress, marsh, and prairie habitat in BCNP.

CHAPTER 6
CONCLUSION

Introduction

In the introductory chapter to this dissertation I outlined the characteristics of useful indicator species and described why amphibians should be suitable as ecosystem indicators. In this conclusion, I will address each of the major characteristics of indicator species and describe whether the results of this research support the use of amphibians as indicators in the Everglades ecosystem.

Characteristics of Indicators

Abundant and Efficient to Sample

In order to be useful as an indicator, a species must be abundant and/or cost-effective to sample. Amphibians in south Florida clearly meet this qualification. Sampling amphibians using visual encounter techniques, as in Chapter 3, was a very efficient way to sample several species at once with just 1 person hour per sample. This technique worked in a variety of habitats across a very large geographical area. Another sampling technique, PVC pipe refugia (Chapter 5), was also effective. This method involved more intensive work at fewer sites, but sample size was adequate to estimate population vital rates including survival and population growth. Collecting sufficient data to estimate these vital rates on many other species would require much more effort. Therefore, I conclude that amphibians are sufficiently abundant and easy to sample to be useful as indicators.

There were also caveats to amphibian sampling demonstrated in this dissertation. Results from a known population of artificial frogs illustrated severe bias in the sampling of amphibians using traditional methods, despite efforts to reduce observer bias (Chapter 2). For this reason, methods using counts of amphibians as an index should be investigated closely before they are adopted as part of a monitoring program. In Chapter 4, the Green Treefrog was shown to be negatively affected by a common and efficient marking method, toe-clipping. The effect was small and may be manageable for some studies, depending on the questions involved. The important lesson from these studies is that methods for sampling indicator species must be thoroughly evaluated before designing a monitoring program.

Sensitive to Stresses on the System

As previously mentioned, a species is only useful as an ecological indicator if it is sensitive to stresses to the ecosystem and responds to stress in a predictable manner. Chapter 3 demonstrated that four species of ground-dwelling anurans were sensitive to an index of off-road vehicle (ORV) use. Occupancy rates of three of the species had a negative relationship with ORV use, as was predicted. Occupancy of another species, the Southern Toad, showed a positive association with ORV use. Although this did not follow the prediction, there are morphological differences between Southern Toads and the other anurans that may explain the different response.

Green treefrog populations demonstrated sensitivity to an ecosystem process in Chapter 5. Water depth and season of year were included in the best model of survival and recruitment. A period of high population growth was shown to coincide with the onset of the wet season. This project was not manipulative, so we can only hypothesize how treefrogs would respond to various changes in the temporal and spatial pattern of hydrology. This could easily be investigated with additional monitoring at different sites. Further monitoring of anurans in relation to ORV use and treefrog populations in relation to hydrology will refine our knowledge of their response to these stressors and improve their use as indicator species.

Responses to Stress Should Be Anticipatory

To be useful to managers, indicator species should display a response to local changes that is anticipatory of an impending change to the whole system. These responses are most useful when they predict impacts that can be averted by management before the whole system is negatively impacted. Treefrog populations might serve as sentinels for the health of the Everglades ecosystem with regard to hydrologic restoration. Because of their annual cycle and short generation time (Chapter 5), we know treefrogs will respond faster to changes in the hydrology of a site than vegetation, for example. If monitoring of treefrogs shows that treefrogs are responding as would be expected (i.e., the treefrog population is changing to resemble other populations with the same hydrology), it is reasonable to assume that restoration is successful. In the case of ORV use in Big Cypress (Chapter 3), it is impossible to know if anuran occupancy responded anticipatorily to ORV use, as ORVs have been used for decades in that area.

Integrate a Response across the Whole System

Indicators are most useful when they can respond to changes in the whole system, rather than just in a few habitats or locations. Amphibians are clearly suitable for detecting changes to the whole Everglades system. They are found in all of the terrestrial and non-marine aquatic habitats in south Florida. Amphibians responded across many habitats to ORV use in Chapter 3. Many habitats in South Florida are defined by small differences in hydropattern resulting in very different vegetation communities. It is clear that treefrogs respond to both vegetation (habitat) and hydrology (Chapter 5).

Known Response to Anthropogenic Stresses and Natural Disturbances

In many situations it is important to be able to determine if a population of an indicator species is responding to anthropogenic changes (e.g., management actions) or natural disturbances. This would be especially useful in the Everglades ecosystem where rainfall can be extremely variable and hydrology at a site is a function of both natural phenomena (e.g., hurricanes) and water management. If a species is an indicator of hydrologic conditions, it might respond in a similar manner whether the change was a result of natural rainfall patterns or anthropogenic management actions. Two types of indicator species might be useful for differentiating the effects of natural and anthropogenic changes to the system: those that react very quickly and those that respond over decades or longer. Species that respond very quickly (6-12 months after a change to the system) can be monitored along with environmental variables to determine their response to specific management actions or natural events. Species that respond over very long time periods will integrate the effects of natural disturbances and should indicate the effects of management actions. Species that respond quickly will be most useful for adaptive management in Everglades restoration and species that respond over long periods will be indicative of restoration success.

Amphibians appear to be useful as indicators of both short and long-term effects. Green Treefrog populations will respond immediately to changes in the hydrologic cycle. If a wet season at a site is different because of a natural event or a management action, the treefrogs should respond immediately by increasing or decreasing reproduction. In the case of long-term anthropogenic changes, anurans were useful as indicators of ORV use, even years after use was suspended in some areas (Chapter 3). In this way, anurans were indicators of anthropogenic disturbance across a heterogeneous landscape subject to many natural disturbances.

Conclusion

This dissertation provides evidence that amphibians are suitable as ecosystem indicators in general, and specifically as indicators of restoration success in the Everglades ecosystem of southern Florida. As with any group of indicators, care should be used when choosing sampling methods and particular species to use as indicators. Continued monitoring and additional research are crucial in using amphibians as indicators of ecosystem restoration success in the Everglades.

Amphibian monitoring can benefit Everglades restoration if it is used wisely. I recommend sampling key amphibian species across the system. Hylid treefrogs are easily marked and studied using captures from PVC pipes. This type of monitoring occurs on a smaller spatial scale, but will provide information on the status and trends of local populations. A network of sites studied intensively and modeled appropriately would allow managers to track changes in populations in relation to management actions. At the landscape scale, site occupancy modeling can be used on all amphibian species to monitor the changes in occupancy (colonization and extinction) of sites throughout the Everglades region. Site occupancy should also be modeled with respect to management actions to determine the effects of such actions.

In addition to monitoring, an expanded research program can address questions about Everglades restoration efforts. One important question is the effect of restoration on the short hydroperiod wetland habitats of the eastern Everglades. How does the timing of inundation in these areas affect reproduction of amphibians? Is a reversal (inundation and then subsequent drying) event detrimental to frogs that may time breeding to coincide with the onset of inundation? These and other research questions can be addressed using amphibians as indicator species.

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BIOGRAPHICAL SKETCH

Hardin Waddle was born in Louisville, Kentucky, in 1972 and lived briefly in Overland Park, Kansas, before his family relocated to Anniston, Alabama, in 1980. Waddle received his high school diploma from the Donoho School in Anniston in 1991. He then attended Auburn University in Auburn, Alabama, where he received his Bachelor of Science degree in wildlife science in 1995. Waddle then worked as a research technician at Tall Timbers Research Station near Tallahassee, Florida, for two years. From 1997 to 2000 Waddle was enrolled at Florida International University in Miami, Florida, where he earned a Master of Science degree in biological sciences. In 2000 Waddle began working as a cooperator with the U.S. Geological Survey on amphibian and reptile projects in the National Parks of south Florida and the Caribbean. In 2002, Waddle enrolled in the University of Florida to pursue a Doctor of Philosophy degree in wildlife ecology and conservation.