Finding Wood Stork Habitat and Conserving the Right Features

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Executive Summary

Wood Storks are federally and state-listed as Endangered in the southeastern United States. Since they are also wetland-dependent they are often an important consideration in permitting, and thus become key in development and management issues. Yet the information available for identifying and prioritizing stork colonies and feeding habitat is dated, and limited in type. Many colony sites have not been used for many years, and for some, the surrounding landscape may have changed to the point that it no longer can support nesting. For those that exist, we have no way to prioritize the sites or the supporting habitat for conservation and management – they are rated only on the presence or absence of nesting storks. In this project, we first painstakingly updated the existing database of stork colony records in the southeastern Unite State, increasing the number of usable records by over 200%, and importantly, clarified the distinction between colonies that were not surveyed and those that were surveyed but were inactive in any year. We also compared the attributes of colonies that have lasted many years with those that winked out after only a few years as a way to identify high priority colony characteristics. Using a 41-year record of colonies, we examined vegetation, physiographic, land use, and hydrologic characteristics both of the colony sites themselves, and the surrounding landscape in an occupancy analysis framework.

We identified 330 colonies with 3,312 confirmed observations (i.e., active and inactive records) from 1970-2010 in the southeastern United States, including 236, 59, 34, and 1 in Florida, Georgia, South Carolina, and North Carolina, respectively. Among them, 194 colonies had consecutive observations that could be incorporated into an occupancy analysis. Most of the colonies had relatively short survival histories and only a handful of colonies survived more than 20 years. The large numbers of short-lived colonies indicated that stork colony abandonment and novel colony initiation seems to be typical of the species.

We initially developed a set of potential explanatory variables that might be related to occupancy. These were developed both from an understanding of the nesting and feeding ecology of the species and from explicit hypotheses about how storks might react to specific kinds of land use change like human encroachment and conversion of wetland forests to open wetlands. These potential variables were constrained by existing data to a large degree. The variables we developed included characteristics of colony sites (i.e., nesting tree type and change in condition, six levels of human activity, and three levels of the degree to which colony islands

were isolated from the mainland), hydrology (precipitation 12 months before and 5 months after nest initiation), and change in land use in the landscape surrounding the colony (% change in forested wetland, non-forested wetland, agriculture, grassland, developed area, upland forest, and lake/open water within 12.5- and 25-km buffers). We used available GIS layers from two sources that spanned appreciable portions of our study area and time period, the Coastal Change Analysis Program (CCAP) and the Florida Land Use and Cover Classification System (FLUCCS). We created three response variables: longevity score, mean colony size and median colony size. For land use change, however, we were only able to use FLUCCS layers from 1999, 2000, 2004, and 2007 due to the lack of either resolution or consistency with classification in other datasets or time periods.

We used several kinds of statistical comparisons to identify possible relationships between colony/land use measures and our three response variables. The purpose of this screening level analysis was to better refine a candidate set of variables for occupancy analysis. We found that nesting tree type, disturbance variables, and island variables were related to longevity score, mean colony size, and median colony size in different degrees. Longevity score was higher for colonies with shrubs than for those with only trees. Generally, longevity score, mean colony size, and median colony size were also higher when colonies are more isolated from land. Colony longevity was positively related to human activity at several scales, but size of colony was only weakly related to nearby human activity. Precipitation 5 months after nest initiation was positively related to mean and median colony size. The percent increase in non-forested wetlands within the 12.5-km buffer was positively related to longevity but none of the land use categories in 25-km buffer were related to longevity score. The percent change in grassland was positively related to mean and median colony size in both 12.5-km and 25-km buffers.

For final analyses, we modeled occupancy of stork colonies expressed as a function of local extinction and colonization probabilities and we used these models to explore a series of general hypotheses about time-specific occupancy and underlying extinction and colonization probabilities in relation to site and landscape characteristics. The variables we used were those previously identified as significant through ANOVA, and included colony site variables (i.e., nesting tree type, nesting tree condition change, human activity nearby, island isolation), precipitation (i.e., 12 months before, 36 months before, and 5 months after nest initiation), longevity, colony size, a colony proximity variable, and land use change variables (% land use change of forested wetland, non-forested wetland, agriculture, grassland, developed area, and upland forest within the 12.5-km buffer). Because GIS data were limited in space and time (Florida only, 1999-2007), we conducted separate occupancy analyses. The first analysis (SE models) included all usable colonies (208) in the southeastern United States from 1970-2010 with all variables except land use change variables (i.e., colony site variables, precipitation, colony history, and colony connectivity). The second analysis (FL models) included 73 colonies in Florida from 1999-2007 with all variables including land use change. We built 84 and 112 *a priori* models to describe occupancy using 10 and 16 variables for SE and FL models, respectively. We ranked models using corrected Akaike's Information Criterion (AIC_c).

For SE runs, the global model that included all variables was the highest ranked model describing stork colony occupancy. Colonies with less connection to the mainland had a lower extinction rate than colonies on the land, and greater human presence was associated with higher recolonization rates. Colonies with larger numbers of pairs nesting were less likely to go extinct than smaller colonies. Longevity did not influence the extinction rate but longer lived colonies (15 – 20 yr old) were more likely than small ones to recolonize after temporary abandonment. Colonies receiving higher precipitation during the 12 months preceding nesting had lower extinction rates, and were more likely to recolonize. Colonies with another, larger stork colony nearby were less likely to recolonize than breeding locations without a large colony nearby.

For FL models, island isolation, human activity nearby, colony size, and longevity were the most important variables describing occupancy, followed by precipitation 36 months before nest initiation. Similar to SE models, colonies with less connection had a smaller chance of extinction, and those with human activities nearby had lower extinction rates. Colonies with wetter conditions 36 months before nest initiation had a lower colonization rate compared to colonies with dryer conditions.

Finally, to understand whether storks prefer certain types of land use when they select colony locations, we calculated percent cover of seven land use categories (i.e., forested wetland, non-forested wetland, agriculture, grassland, developed area, upland forest, and lake/open water) within the 25-km buffer of the colony at the time the colony was probably formed, and compared observed (colonies initiated in year 1998-2000 and 2003-2005) vs. expected (random point in 2004 GIS layers) colonies. Overall, land use categories within the buffers differed between those surrounding known colonies and those around random points. More specifically, storks preferred 25-km buffers that contained less grassland and upland forest, and more developed area and lake/open water than the available landscape.

In summary, Wood Stork colony extinction rates were lower for colonies on islands, larger colonies, longer lived colonies, colonies with shrubs as opposed to trees only, and colonies with some form of human habitation or activity in the 500m surrounding the colony. Therefore, we recommend that management and conservation priority should be given to colonies that are large, have been in existence for more than 10 years, and are located on islands rather than mainland shorelines. Management actions that can enhance the isolation of colonies from the mainland apparently are very effective, since colonies on true islands are less likely to go extinct and are much more likely to be colonized than those that have partial or complete connection with the mainland. We did not attempt to tally the number or type of available islands in any parts of the stork range and therefore cannot comment on whether island habitat is limiting for this species. We suggest that such a study would be inexpensive and could potentially yield a definitive answer that could have important management implications.

Colony nesting trees should include a mix of tall trees and shrubs. Within Florida, storks seemed to prefer landscapes with less grassland and upland forest, though these relationships were somewhat contradictory across analyses. Landscapes that have relatively more human activity were associated with greater colony longevity, lower extinction rates, and higher colonization rates. The interpretation of the latter finding is unclear. At minimum, it suggests that storks do not seem to be particularly vulnerable to the effects of human land use in the vicinity of the colony, and their nesting may be compatible with a number of different kinds of nonintrusive human uses in the vicinity of colonies. However, we only considered evidence of human structures and other activity visible from satellite images in this study and did not measure other forms of human disturbance directly. The finding of a positive relationship between stork colony resilience and human land use nearby may also simply be the result of humans and storks preferring many of the same landscape features.

Due to the limited availability of GIS data, our analyses were not able to examine the effect of land use on stork persistence definitively. Apparent habitat preferences based on land use categories indicated relatively weak relationships, leaving open the possibility that the land use categories as defined do not represent the characteristics that storks use in choosing nesting areas. For these reasons, we suggest that further work is needed prior to using land use as a means to define where and when storks should nest. While several excellent studies exist of micro and meso-scale foraging habitat preference in south Florida and Georgia, we suggest that detailed studies are needed to better outline the role of land use in colony site location. Our study was limited because it required long time series over very large landscapes for analysis. Studies at a smaller scale may be more revealing.

Our attempts to infer the importance of local hydrology were similarly blunted because hydrological information was only sparsely available over the entire range of the storks, leaving us with a relatively low quality data set. While understanding hydrological relationships with nesting was not a focus of this study, we believe that there is value in attempting to understand these relationships in part because human hydrological manipulations are increasing, and because surface water dynamics may be profoundly affected by future trends in global climate change. We therefore also recommend examination of hydrological relationships, targeted to specific geographic areas. South Florida seems to be well researched and understood in this regard. Studies of hydrological relationships in central Florida and the Atlantic Coastal Plain should be a high priority to enhance management and conservation of this species.

Introduction

The breeding population of Wood Storks (*Mycteria americana*) are federally listed as Endangered in the southeastern United States, largely as a result of the widespread loss and continued failure of nesting in south Florida, and generally declining population size (USFWS, 1996). This large-bodied wetland specialist feeds only in shallow water, and needs dense concentrations of food to enable efficient use of its tactile and non-visual foraging strategy (Kahl, 1964). Dense concentrations of prey (usually fish) occur ephemerally where antecedent and current water conditions allow both the growth of a robust fish population, and concentration/entrapment of those prey (Gawlik, 2002). These conditions are temporary, and not always widespread. Thus storks often need large expanses of dynamic, uncontrolled wetlands to find and exploit prey concentrations, especially during the breeding season when energetic requirements increase dramatically (Kahl, 1964). Access to high quality foraging must occur for over 110 days in order to complete a nesting cycle (Kahl, 1964), and interruptions before, after, and during this time can result in abandonment of nests and even entire breeding colonies, often leaving live young to starve. In addition, foraging conditions during the first month after young fledge can have a large effect on survival of fledged, juvenile birds, to the extent that the trajectory of the population may be affected (Borkhataria, 2009). Foraging habitat is therefore a critical resource for reproduction in this species, and foraging habitat quality is probably directly linked to population trajectory through effects on several life stages.

Foraging habitat has been described for storks in some detail. However this information is usually specific only to one area or habitat type such as the Everglades of south Florida (Kahl, 1964; Kushlan, 1986; Ogden, 1994; Herring & Gawlik, 2011) or Georgia (Coulter & Bryan, 1993; Bryan et al., 2002). Further, these assessments have usually been made at fine spatial scales, and there has been little work examining the role of landscape components in relation to location and success of colonies (But see Cox, 1991; Borkhataria, 2009).

In addition to foraging habitat, storks are known to have specific requirements for nesting colonies (Coulter & Bryan, 1995). In general, storks need a central location that is geographically handy to a wide variety of potential foraging sites, since it is probably difficult for a nesting stork to predict where and when food will be available during the highly unpredictable spring weather weeks and months after nesting is initiated. Storks are colonial nesters, and nesting sites must be large enough to accommodate some critical mass of pairs in order to be viable, though the effect of size of colony is not known. Nesting trees species and tree characteristics can be variable (Rodgers et al., 1996), however, they must also be of a size to support the large, bulky nests and the weight of stork adults and several young. Storks do not have well developed nest defense, and their nests are highly vulnerable to mammalian predators (e.g., raccoon, *Procyon lotor*) that can climb trees (Coulter & Bryan, 1995). One of the main evolved defenses of storks and other Ciconiiform birds is a strong preference to nest in trees that are in standing water, or are located on islands; this strategy ensures that mammalian predators must swim to colonies, and so be vulnerable to crocodilian predators that often congregate under wading bird colonies. Extent of colony habitat, protection from predators, and tree type are likely to be important factors leading to suitability for breeding colonies.

Stork colonies may also be influenced by human activities. On the one hand, colonies have been found to initiate and persist near residential areas, such as densely populated cities in central Florida. However, an understanding of disturbance effects for this species is weak. One problem for determining thresholds is that there may be a lag between disturbance and its effects. Bouton et al. (2005) found Wood Storks in Brazil did not abandon nesting in direct response to close approach of ecotour operators in boats and on foot (< 10 m), but areas of the colony that were disturbed regularly showed a much higher probability of abandonment than undisturbed areas when weather-related stressors occurred weeks later. This suggests that disturbed storks may be predisposed towards abandoning nests even if they do not do so at the time of the disturbance. Rodgers and Schwikert (2002) found that non-nesting Storks flushed at relatively long distances compared with other waterbirds, a finding in keeping with the large body size of storks. It is also possible that disturbance on foraging sites can affect stork nesting and foraging behavior, though little work has been devoted to understanding disturbance at this scale. Frederick (unpublished) noted that both nearby road construction work (cf 100 m) and dynamite blasting (cf 400 m distant) had little effect on ongoing stork nesting. It is unclear, however, what these effects might have if they occurred at the time storks were attempting to initiate nesting.

Thus there is evidence that both colony site characteristics and foraging habitat are important to the success and persistence of nesting in this species, though the relative contributions of these somewhat geographically separate attributes are not known. Since reproductive success is affected by both, these attributes are likely to have direct or indirect effects on the trajectory of the population. Recognition of the importance of habitat has been recognized in the updated version of the federal Recovery Plan for storks (USFWS, 1996), which emphasizes protection of habitat (Recovery tasks and action 1.0), development of a habitat prioritization scheme (task 1.2), management guidelines for private and public land (task1.3.3), enhancement of nesting habitat (task 2.2) and acquisition of land for foraging and breeding (task 1.4).

Although it is possible to identify and protect colony sites themselves, there are several barriers to achieving the broader habitat related goals of the Recovery Plan, particularly those addressing the habitat matrix in which breeding storks feed. First, how much habitat is enough? Although nesting substrate and foraging microhabitat features have been described (Coulter & Bryan, 1993; USFWS, 1996), it is not clear how much habitat is required to maintain a colony of given size. A colony size/habitat size relationship has been established for several other waders and seems very plausible for storks. In addition, a trend towards smaller stork colonies during the past two decades (Brooks & Dean, 2008) suggests that an understanding of the colony size/area relationship would be very important to managing this species.

Second**,** it is currently impossible to predict the persistence of colonies, and the possibility of a relationship between persistence and habitat quality makes this question important for conservation and management. Although storks are more philopatric to breeding sites than other Ciconiiform birds (Frederick & Ogden, 1997), there is enormous variation in the duration of colony site occupancy – some colonies last for decades while others wink out after two years (Frederick & Meyer, 2008). While it seems clear that some degree of colony site extinction and colonization are natural processes, it is unclear whether the current rates of colony turnover are typical of the species. Further, there has been a major shift in the distribution of nesting within the range. During the past 30 yr, a significant portion of the breeding population has moved north from Florida into Georgia and the Carolinas (Brooks & Dean, 2008), following abandonment of the former stronghold in wetlands of south Florida. While long range regional movements of individuals are typical of the species (Borkhataria, 2009), this large change in the distribution of nesting suggests a regional change in habitat quality, and is important to understand in order to effectively restore the species. Although storks abandoned south Florida during and following a period of intense hydrological degradation (Ogden, 1994), the cues for abandonment in south Florida have never been examined in the context of more general nesting needs and abandonment cues for the species.

Based on what we know about colony site and feeding site characteristics and nesting requirements, it seems very likely that colony site abandonment (permanent cessation of nesting rather than nest failure within the nesting season) and colonization must be based on habitat quality. An understanding of the relationship between persistence and habitat quality would therefore be a very powerful tool in conserving and restoring this species to a non-endangered status. Prioritization of colonies for management, land acquisition, mitigation and permitting is currently based solely on current size and immediate past history, and on the historical locations of colonies. Colony protection therefore is not currently proactive and may in many cases be misguided. For example, we may be maintaining many inactive colony sites as high conservation priorities, yet the surrounding landscape or colony site may have changed to the point that it no longer can support nesting. This problem was recognized explicitly in the Recovery Plan, calling for the development of a tool to allow prioritization of habitat.

A proactive conservation strategy also would include recognition of the need for enough unoccupied but protected habitat to support the formation of future, novel colonies. Detailed knowledge of habitat needs for stable, persistent colonies could presumably also enable identification of future colony sites. Land acquisition to protect habitat for future foraging and breeding is recognized as an important task in the Recovery Plan (Task 1.4). Yet there are no tools currently available to predict where new colonies are likely to form. Such a toolset would allow an assessment of potential stork breeding habitat in a way that could efficiently guide managers of currently conserved lands as well as prioritization for future land preservation.

The overarching goal of this project has been to understand and predict the quality and quantity of essential habitat for breeding Wood Storks. The very high variability in colony persistence can perhaps be exploited to investigate breeding habitat needs. Our research plan has been to examine a long-term dataset of stork colonies in the southeastern United States in order to discover any links between longevity (persistence) with specific attributes both of colony sites, and their surrounding landscapes.

Objectives

1. Using an existing database of known stork colonies, quantify associated characteristics such as nesting tree type and condition change, potential for disturbance, hydrological history, colony size, and surrounding land use.
2. Compare colony persistence in relation to habitat features and history.
3. Use results of this analysis to identify high quality habitat.
4. Make recommendations, reports, and GIS-based products widely available to public land managers and to county, regional, and state planning agencies. Thus, promote a range-wide conservation strategy that will ensure sufficient breeding and foraging habitat to support a stable population that exceeds federal recovery goals for delisting.

Methods

1. Preparation of a breeding Wood Stork dataset

1.1 Analysis of original Wood Stork dataset

We began coalescing information on stork nesting over the last 40 years with a dataset from the U.S. Fish and Wildlife Service, circa 2007 (USFWS). The raw data on location and size of stork colonies in the southeastern United States came from combined annual statewide surveys from Florida, Georgia, and South Carolina. These surveys were done using different protocols and data recording standards in different decades and locations, and have been performed by at least 30 biologists in aggregate. There are also a handful of recent observations that had not made it into the dataset yet from North Carolina, a recent expansion of breeding range. In addition to upgrading this database with higher quality information and filling in holes, we also applied uniform standards for inclusion or rejection of data based on the likelihood that the colony was positively identified as active or inactive in any year, with a goal of identifying records that could be used in occupancy analysis.

There were a total of 246 colony locations in the original "uncorrected" dataset, with 1,194 total observations (Table 1). The majority of colonies (71%) and observations (66%) were in Florida, which is not surprising given that Florida occupies much of the breeding range of the species. Georgia had 18% of the colonies and 24% of the observations, with a higher number of observations per colony than the two other states. It is not clear whether this is because Georgia surveys concentrated on more stable colonies despite the existence of novel colonies forming through time, or because new colonies simply were not found. South Carolina accounted for 11% of colonies and 10% of total observations.

1.2 Correcting and updating the Wood Stork colony dataset

We validated and screened each colony report in the original dataset. We checked all the available documentation including scientific literature, project final reports, within-agency summaries, government documents or original field notes to confirm these observations. We also interviewed the majority of the biologists who had conducted stork surveys for the past 30 years to obtain detailed colony information and to discover any special events that may have happened within or around individual colonies, such as water condition, management actions, habitat change, disturbance, or severe weather. We also acquired field notes and photos from biologists where available to search for miscellaneous observations that were not reported.

Colony records must be scored as either "alive" = active or "dead" = inactive in any year in order to be used in occupancy analysis. The original dataset provided some information about individual colony history. However, the majority of the observations were reports of colonies with actively breeding Storks. It was not clear if a year-colony combination without any notation indicated the colony was visited and not active or was simply not visited. Since this distinction is crucial for occupancy analysis, we verified the survey and notation protocol of each biologist and focused on determining whether colonies that were visited but not active were actually noted as such. All the year-colony combinations in our dataset were classified as active, inactive, or not checked/unknown. We then classified the status of each colony into 5 categories – "high quality", "low quality", "redundant", "empty", and "only1". "High quality" colonies were defined as those with at least two active observations, and these observations occurred in consecutive years or were linked by a confirmed inactive observation(s). "Low quality" colonies had at least two active observations but these observations did not occur in consecutive years or were not connected with confirmed inactive observations. The difference between high and low quality was that high quality colonies had complete occupancy information for an identifiable, contiguous period while low quality colonies may have had intermittent information. It may be feasible to use low quality colonies in occupancy analysis but certain assumptions have to be made, thereby reducing the quality of the information. "Redundant" colonies were those in which the same colony was named differently in two different years or by two different biologists. In these cases, other identifying information such as position or proximity indicated the two colony names should be collapsed. A colony was scored as "Empty" if it was visited, and did not show a count of nests for any year (only zeroes or blanks). Colonies were scored as "only1" if it had only one active count. Single counts are not useful in occupancy analysis.

For the purpose of occupancy analysis, we considered colonies with "high quality" and "low quality" status as usable colonies and colonies with "redundant", "empty", and "only1"adesignations as unusable colonies. The final dataset after screening is submitted with this report as a file in Microsoft Excel 2007 format. See Appendix 1 for detail explanations and legends of the dataset.

1.3 Characteristics of the updated Wood Stork dataset

After checking the dataset against all available supporting information and documentation we found a total of 330 colony locations (Table 2). There were 236, 59, 34, and 1 colony locations in Florida, Georgia, South Carolina, and North Carolina, respectively, which had not been included for various reasons in the uncorrected dataset, but which we discovered with checking. The majority of the resulting colonies were located in Florida (72%) and the allocations of colonies in the three states were similar to those in the original (unchecked) USFWS dataset. Because we were able to assign status to many of the originally blank or ambiguous year-colony cells, there were now 3,312 usable observations in the final dataset, which was a nearly 200% increase compared to the original dataset. The average number of observations per colony for all three states increased from 4.9 to 10. Georgia and South Carolina had a higher number of observations per colony than Florida. Only one colony in North Carolina became active in recent years, with 6 observations.

The locations of colonies in the final dataset are shown in Figure 1. The colony locations in the final dataset are spread widely across the southeastern coastal plain states and seem representative of the species' known range. Colony locations in Georgia and South Carolina are more concentrated along the coast than those in Florida, in keeping with the distribution of wetlands in those states.

Of the total of 330 colonies, 194 (59%) were considered usable for occupancy analysis (Table 3). Florida had the most usable colonies (127) but the lowest usable percentage (54%) among all states. The low percentage of usable colonies in Florida may be due to the larger number of new colonies and lack of consistent survey effort during the longer history of surveys in Florida. Georgia and South Carolina had 44 and 22 usable colonies and the usable percentages were 75% and 65% of the total colonies (Table 3). North Carolina only had one colony and it was considered usable.

Among the 136 unusable colonies, 49 were redundant entries, and 15 did not show a count of nests for any year. There were 72 colonies with only one active count. Without additional information of colonies with “empty” or “only1” status, these entries were not usable for occupancy analysis.

Of the 194 usable colonies, 171 were high quality and 23 were low quality. Figure 2 shows the geographical distribution of usable colony locations. These usable colony locations occurred across a wide geographic area, suggesting that we could encompass a wide variety of habitats and potential occupancy effects in our analysis.

The preceding information suggested that the dataset was robust for occupancy analysis. A conservative estimate was that there were at least 194 usable colonies spread across a wide geographic area from four decades. This allows room for both time and geographic groupings as possible variables. Finally, the distribution of observations also suggested that there was a good mix of both long-lived (or at least long-observed) colonies and those that were short-lived.

2. Screening environmental variables

We screened a set of potential explanatory variables to identify candidates that might be related to occupancy, including characteristics of colony sites, hydrology, and landscape surrounding the colony. These were developed both from an understanding of the nesting and feeding ecology of the species, and from explicit hypotheses about how storks might react to specific kinds of land use change like human encroachment and conversion of wetland forests to open wetlands. We also believed that size characteristics, proximity of other colonies and other social factors might be related to occupancy and persistence. These potential variables were also constrained by existing data to a large degree. For example, though hydrological dynamics are known to be very important to stork breeding dynamics, we could find no consistent hydrological measures that could be used across the breeding range, and so resorted to local rainfall as a proxy.

We then proceeded to analysis in a two-step process. First, we screened potential variables using an analysis of variance (ANOVA) to identify variables that might be important to stork reproduction, as well as to reduce the number of variables to be included in the final occupancy model. Secondly, we used the variables identified in the screening process in an occupancy analysis, attempting to predict colony persistence and colony size. Occupancy analysis is often used to generate predictions about variables affecting spatial use of habitat – in our case we were particularly interested in the ability of occupancy analysis to generate predictions about extinction and colonization of stork colonies.

While many colony site variables (e.g., size, % cover, tree species, and connectivity with mainland) generally change slowly through time, landscape and hydrological variables are usually more variable over time. Land use information turned out to be the limiting factor, as we discovered reliable and consistent data were available in only a handful of years. Moreover, the years with available colony records did not necessarily have matching land use layers, or vice versa. Therefore, we used the years with available GIS layers as a base to create response variables and conduct screening analyses across all other environmental variables. During occupancy analysis, we used the entire colony dataset to examine variables other than land use, and the shorter period of records in which land use information was available to include all variables.

We chose land cover layers from two GIS sources based on coverage and availability of years. First, we obtained land cover layers from the Coastal Change Analysis Program (CCAP), which provides the coastal expression of the National Land Cover Database (NLCD). The CCAP layer is a raster-based layer from Landsat TM satellite images with 30 m resolution. This layer covered all of our study area across four states including Florida, Georgia, and South and North Carolina. Three sets of CCAP layers were available: 1996, 2001, and 2006.

We also obtained information from the Florida Land Use Cover and Classification System (FLUCCS), from the Florida Water Management Districts (WMD). The FLUCCS layer is a vector-based layer from aerial photos with 1-3 m resolution depending on years. As the name suggested, this layer only covers the state of Florida. Two to six sets of FLUCCS layers (from 1973-2007) were available depending on WMD.

We created three colony response variables (longevity score, mean colony size, and median colony size). To qualify as a useful interval of both colony information and land use information, the interval needed to have at least half of the years with confirmed (active or inactive) colony information, with no periods of unknown information for 3 or more consecutive years. For the colonies with more than two matching land use layers, we used multiple smaller intervals rather than a long interval to capture the change through time. For example, when GIS layers were available in 1996, 2001, and 2006, we used two intervals, 1996-2001 and 2001-2006, instead of one longer interval 1996-2006. We also calculated longevity score, mean colony size, and median colony size separately for colony intervals that were available for GIS layers of both FLUCCS and CCAP. There were 140 intervals from 92 colonies for FLUCCS and 200 intervals from 144 colonies for CCAP.

To calculate longevity, we first assigned years within any interval for any colony with confirmed active and inactive information as 1 and 0, respectively, and assigned years with unknown colony status (usually years of no reports sandwiched between years of confirmed 0 or 1) a value of 0.5. The longevity score of each interval was defined as the sum of values from each year divided by the total numbers of years in that interval. To evaluate how environmental variables influenced colony size, we also calculated mean and median colony size for each interval by colony.

2.1 Screening of colony site variables

Existing information about colony site characteristics was sporadic and incomplete. To expand this database, we conducted aerial surveys of inactive and active colony sites from May to August, 2010 in Florida, Georgia, South Carolina, and North Carolina using a Cessna 172 or helicopter. We circled each stork colony at 500-1000 feet and recorded nesting tree type and location, water condition, vegetation condition, and potential sources of human disturbance around the colony. We also took digital pictures of each colony. We surveyed 109, 46, 23, and 1 colonies in Florida, Georgia, South Carolina, and North Carolina, respectively. We also used images from Google Earth to obtain information from earlier dates (e.g., 1980s).

Using this information, we created 11 categorical variables describing colony site characteristics: nesting tree type (NTT), nesting tree condition change (NTCC), three island isolation variables (ISLA1, ISLA2, ISLA3), and six disturbance variables (DIST05, DIST1, DIST2, DIST3, DIST4, DIST5) (Table 4). Nesting tree type was defined as tree only, or shrubs dominant. Nesting tree condition change was defined as change due to logging, acute weather (hurricane or major storm effect), or effects of accumulation of guano or no change using a combination of Google Earth, GIS layers, and colony surveys. We defined five degrees of accessibility of colonies to terrestrial predators, 1) ISO: colony on isolated island, 2) W1: colony in a wetland where < 1/3 circumference of nesting trees are connected with land through secondary vegetation/floating mat, 3) W2: colony in a wetland where >1/3 and < 2/3 circumference of nesting trees are connected with land through secondary vegetation/floating mat, 4) W3: colony in a wetland where >2/3 circumference of nesting trees are connected with land through secondary vegetation/floating mat, and 5) LA: colony on mainland apparently not separated by water. We then created three variables ISLA1, ISLA2, and ISLA3, based combinations of these five conditions to represent different resolutions on isolation (Table 4). We recorded whether or not there are potential human disturbance sources within 50 m, 100 m, 200 m, 300 m, 400 m, and 500 m and created six categorical disturbance variables as DIST05, DIST1, DIST2, DIST3, DIST4, DIST5, respectively.

We conducted a series of Analyses of Variance (ANOVA) to examine the relationship between colony site variables and longevity score, mean colony size, and median colony size. Colony site variables were explanatory variables while longevity score, mean colony size, and median colony size were response variables. We used $\alpha = 0.05$ to indicate significance for all analyses. We used Tukey-Kramer's Honestly Significant Differences (HSD) test to compare means among different groups of each colony variable. We performed the analyses for the intervals that matched up with availability of land use data in the FLUCCS and CCAP GIS layers separately.

2.2 Screening of hydrological variables

To evaluate the influence of local hydrology on colony persistence and colony size, we collected stage data for emergent wetlands, lakes, and rivers from the U.S. Geological Survey and Florida WMDs. However, only 35 colonies had water gauge information within 10 km of the colony during the past 40 years, and most of the colonies did not have continuous hydrological data over the periods when they were active. Therefore, we concluded that hydrological data currently available did not provide sufficient information to allow meaningful inference for occupancy analyses.

Precipitation information may sometimes serve as a useful proxy for the surface water levels, particularly in shallow wetland systems. Precipitation data can provide coarse yet consistent information for an extended geographic area, which was of particular interest in this study. We obtained monthly precipitation data from 23 weather stations across the southeastern United States from the National Climatic Data Center from 1959 to 2009. The distance between precipitation stations and colonies ranged from 2 to 80 km with an average of 33 km. We created two indices representing total precipitation occurring 12 months before nest initiation (setting the stage for prey populations, Preci I) and total precipitation occurring 5 months after nest initiation (determining drying patterns and availability of food to storks, Preci III) for each nesting season, respectively. We defined timing of nest initiation for four general regions: south Florida (December), central Florida (January), north Florida (February), and South and North

Carolina (March). We used 26º 55’ N (Lake Okeechobee) and 29 º 20’ N as boundaries to separate north-center Florida and center-south Florida, respectively.

We calculated an index for each month using the following formula:

$$(Preci_{i.j} - Mean_i)/(Max_i - Min_i)$$

where $Preci_{i,j}$ is the total precipitation for month i in year j; $Mean_i$ is the historical mean for month i for that station; Max_i and Min_i stand for maximum and minimum monthly precipitation for month i for that station. More simply put, it was the ratio of the departure from the mean to the range for the area. For each breeding season, we summed the index for 12 months before and 5 months after the proscribed nest initiation month according to geographical location. We conducted simple linear regressions between precipitation indices and longevity score, mean colony size and median colony size. We also conducted analyses separately for the intervals that matched up with availability of land use data in the FLUCCS and CCAP GIS layers.

2.3 Screening of landscape variables

Storks have exceptional abilities to forage at long distances from breeding colonies by using low energy consumption soaring flight (Kahl, 1964). Therefore, stork colonies may well be affected by characteristics of a rather large potential foraging area, and it was initially unclear how large we should make the buffer area surrounding each colony. We reviewed studies in Georgia and Florida on stork feeding flight characteristics during the breeding season to derive a reasonable buffer distance for analyses. Though there was considerable geographic and temporal variation in foraging distances, mean flight distances ranged from 5-12 km from colonies. Because flight distances at any colony also generally have high variation due to availability of thermals and suitable foraging habitat (Bryan & Coulter, 1987), we also obtained distances of 85% (roughly, the mean number of the feeding locations plus one standard deviation) of feeding locations in each study, which was less than 10 km in central Florida (K. Meyer, personal communication) and less than 25 km in south Florida (Bryan & Coulter, 1987; Bryan et al., 1995; Gaines et al., 1998; J. Lauritsen and K. Meyer, personal communications).

We therefore chose 12.5 and 25 km as the buffer distances in this study. As a visual example of the size of these areas, we plotted 25-km buffers from each of the 266 known colonies in the southeastern United States, including “high quality”, “low quality”, and “only1” status (Figure 3).

There were 22 and more than 100 land use and land cover categories in CCAP and FLUCCS layers, respectively. For the purpose of this study, we combined land use and land cover into 7 major categories: forested wetland (FW), non-forested wetland (NFW), agriculture (AG), grassland (GR), developed area (DE), upland forest (UF), and lake/open water (LA).

However, after carefully examining all available GIS layers from both CCAP and FLUCCS, we decided to use only FLUCCS layers from a restricted period (1999, 2000, 2004, and 2007). This decision was primarily because of poor resolution and discrepancies in categories over time. The resolution of CCAP layers (30m) was generally not fine enough to capture the land use and land cover change between years, especially in the immediate area around the colony. Some FLUCCS datasets from some WMDs had layers from earlier dates but this was not consistent across areas. More importantly, the land use classifications often were not consistent across years, especially the categories FW, UF, and GR. Categories were consistent for FLUCCS layers from 1999, 2000, 2004, and 2007, and these were the only ones we used in the screening and final occupancy analyses.

We calculated the total area of each land use category within both 12.5- and 25-km buffers from the center of each colony using ArcGIS. We then calculated percent change in each land use category between each interval for 12- and 25-km buffers of FLUCCS layers. An example of land use changes over time is shown for a single colony in Figure 4.

To examine the potential explanatory value of landscape variables, we used stepwise multiple regression, with percent change in land use categories as explanatory variables, and longevity score, mean colony size, and median colony size as response variables. We conducted analyses in both 12.5- and 25-km buffers. There were 88 and 87 colony intervals with GIS information for the 12.5- and 25-km buffers, respectively.

3. Occupancy analyses

We modeled occupancy of stork colonies expressed as a function of local extinction and colonization probabilities. We used these models to explore a series of general hypotheses about time-specific occupancy and the underlying extinction and colonization probabilities. The relationship between occupancy (Ψ), local extinction (ε), and colonization (γ) can be described as follows:

$$\Psi_{t+1} = \Psi_t(1-\varepsilon_t) + (1-\Psi_t)\gamma_t$$

where Ψ_{t+1} is the probability that any given colony is occupied in year $t + 1$; ε_t is the probability that an occupied colony in year t is unoccupied by storks in year $t + 1$; γ_t is the probability that an unoccupied colony in year t is occupied by storks in year $t + 1$. Therefore, a colony occupied in year $t + 1$ is composed of two elements 1) the colonies occupied in year t where storks do not go extinct in year $t + 1$, and 2) the colonies that were unoccupied in year t but where storks colonized in year $t + 1$. A first-order Markov process was used in this model to incorporate the dynamic changes in occupancy. In other words, the probability that a colony is occupied in year $t + 1$ depends on the occupancy in year t.

We were ultimately more interested in dynamics of extinction and colonization rather than the occupancy of given colony in a given year, and in this sense occupancy models were simply a handy way to explore the correlates of extinction and colonization. We hypothesized that year-specific local extinction and colonization were associated with environmental factors (i.e., colony, hydrological, and landscape variables). In addition, we also hypothesized that colony history by itself may be a strong predictor of future occupancy – birds almost certainly have memories and therefore may come back to successful colonies more than unsuccessful ones, all other variables being equal. This effect might be powerful enough to swamp effects of other variables. Finally we also believed that there may be dynamics among closely spaced colonies that may influence future occupancy. Some particularly large colonies may outgrow their space, and therefore be more likely than small colonies to spawn or be associated with new colonies nearby. Conversely, storks nesting in small, unsuccessful colonies may be drawn in future years to nearby large successful colonies. We therefore hypothesized that distance between colonies and the size of nearby colony may have an influence on future occupancy.

During the screening process, we used high and low status colonies that also had matching GIS data in the analyses. For occupancy analyses, we included all the colonies that had at least two consecutive confirmed records (either active or inactive) to utilize as much as information as possible about colony history. A total of 208 colonies were selected for the occupancy analyses.

3.1 Definition and treatment of variables used in occupancy analysis.

We incorporated most of the variables used in screening analyses, and added several new variables in our analyses.

Nesting tree type (NTT) – this was defined based on primary cover in the colony, and fell into two categories: "trees only" (1) and "shrubs dominant" (0).

Nesting tree condition change (NTCC) – colonies either had noticeable change in nesting tree condition (=1, using a combination of Google Earth, GIS layers, and colony surveys) or no change (0).

Island isolation (ISLA) – we modified the categories of ISLA2 (Table 4, ISO, W12, and W3L) into a single score (1, 2, or 3) representing increasing accessibility of colonies to terrestrial predators, based on the degree to which the colony was isolated (island) or connected to the mainland.

Disturbance (DIST) – we scored each colony into one of 6 categories: source of human activity (house, industrial building or other structure within 100 m (5), activity between 100-200 m (4), activity between 200-300 m (3), activity between 300-400 m (2), activity between 400-500 m (1), no activity at greater than 500 m (0).

Precipitation (P1, P2& P3) – we calculated indices P1, P2, and P3 based on precipitation index 12 months before nest initiation, 36 months before nest initiation, and 5 months after nest initiation, respectively. Total precipitation in each period was referenced to longer term patterns by subtracting the long term mean, and dividing by the standard deviation of that mean, expressed below:

$$(Preci_{12.j} - Mean_{12})/Std_{12}$$

$$(Preci_{36.j} - Mean_{36})/Std_{36}$$

$$(Preci_{5.j} - Mean_{5})/Std_{5}$$

where $Preci_{12,j}$, $Preci_{36,j}$, and $Preci_{5,j}$, are the total precipitation for 12 months before nest initiation, 36 months before nest initiation, and 5 months after nest initiation in year j, respectively; $Mean_{12}$, $Mean_{36}$, and $Mean_{5}$ are the historical mean for the same 12 months, 36 months, and 5 months period for that station, respectively; Std_{12}, Std_{36}, Std_{5},stand for standard deviation of 12 months, 36 months, and 5 months period for that station, respectively.

Landscape variables – we included six land use change categories (% change of FW, NFW, GR, AG, DE, UF between intervals) at the 12.5-km buffer from 1999-2007 in the occupancy analyses. Because the length of interval of available GIS information was often different from colony to colony, we standardized % change of land use of each category by dividing the total % change in the interval by the total years during each interval. For each year in the occupancy dataset within any interval, we input this averaged % change value. We tested correlations between landscape variables and avoided using highly correlated variables in the occupancy models.

Longevity (LONG) – to explore whether history of colony activity influenced its chances for future extinction or recolonization, we defined numbers of years since the first active record as longevity. If the colony had fewer than 4 consecutive years of confirmed inactive or unknown status between active records, we considered the colony to have a continuous history. However, if a colony did not have an active record for 5 or more consecutive years in a row, the longevity record was broken, and we treated the next active year as year 1 in a new colony history interval.

Colony size (CS) – to evaluate whether colony size in year *i* was associated with extinction in year *i* + 1, we used the mean of the numbers of nesting pairs reported by field biologists. In some instances, colonies were noted only as "active" with no colony size information. In all cases, we calculated the mean colony size over all active years.

Influence of nearby colonies (IFM) – to incorporate the influence of nearby colony size and distance to the nearest colony on colony occupancy, we modeled extinction and colonization as a negative exponential dispersal kernel (Moilanen & Nieminen, 2002) similar to Hanski's Incidence Function Models (IFM; Hanski, 1994) and modified to account for the nearest colony instead of all neighboring colonies. The time-dependent covariate can be expressed as:

$$S_i = \exp\left(-\alpha d_{ij}\right) A_j$$

where S_i is the influence of nearby colonies on colony *i*; α is a scaling parameter where $1/\alpha$ is defined as average movement distance for the species. In our analyses, we used 25 km for breeding storks; d_{ij} is the distance from colony *i* to the nearest colony *j*. A_j is the colony size in number of pairs of the nearest colony *j*.

3.2 Occupancy modeling

We conducted our analyses using single-species, multiple-season occupancy models in program MARK 6.0 (White & Burnham, 1999). There are two scales of time frame in this model, a larger scale that has surveys conducted in multiple seasons on the same site and a smaller scale that has multiple surveys within a season. We treated year as the season variable in this model. As a concept similar to the robust design, the model incorporates multiple surveys within a single season to account for imperfect detection. In most of our data, there was only one observation during any breeding season. However, because biologists only visited colonies with known coordinates and because we were not attempting to estimate detection, we assumed a 100% detection probability and fixed that parameter to 1 in the model.

Because GIS data were so limited in space and time (Florida only, 1999-2007), this severely constrained the portion of the data set for which we could incorporate land use change information. For this reason, we conducted separate occupancy analyses for land use change plus colony site characteristics, and for all variables other than landscape variables. The first analysis (hereafter SE models) included all 208 colonies in the southeastern United States from 1970-2010 with all variables except landscape variables (i.e., colony site variables, colony history, precipitation, and colony influence). The second analysis (hereafter FL models) incorporated all the above variables, but added landscape variables. Only 73 colonies in Florida were available to work with from 1999-2007.

For the SE models, we built 84 *a priori* models to describe occupancy using combinations of 10 variables. We first included single-variable models for each explanatory variable, all colony variables only, precipitation only, and colony history only. We then expanded the model set by adding combinations of variables based on biological knowledge from the literature and field observations. We also included global models that incorporated all variables (9 variables total as P1 and P2 were never in the model together). For FL models, we constructed 112 *a priori* models to describe occupancy using combinations of 16 variables. We used the same approach to build the model set which included single-variable models, combination models, and global models. We used all variables to examine probability of local extinction and colonization except colony size, which was used to model only probability of local extinction, not colonization.

We ranked models using corrected Akaike's Information Criterion (AIC_c) (Burnham & Anderson, 2002), which balances model fit with parsimony. The model with the lowest AIC_c value in a given set of models indicated the best model supported by the data. We considered models with $\Delta AIC_c < 2$ as best fit models for occupancy (Burnham & Anderson, 2002). We present a 95% confidence set of models that best describe occupancy. We also used the concept of multimodel inference and used Akaike's weighted values (w_i) to calculate relative importance of variables in each model set (Burnham & Anderson, 2002). To further explore the relationship between explanatory variables and occupancy and provide management recommendations, we also plotted the relationship between explanatory variables that appeared in the models with $\Delta AIC_c < 2$ that also had significant effect sizes and occupancy parameters (i.e., local extinction and colonization).

4. Colony habitat selection

We conducted a separate analysis to further understand whether storks prefer certain types of land use when they select colony locations (observed vs. expected). We first selected colonies that were established between 1998-2000 and 2003-2005 in Florida. We chose these two 3-year periods because we had GIS layers for 1999 and 2004 and there were enough colonies that started in these periods. We calculated percent cover of each of seven land use categories (FW, NFW, AG, GR, DE, UF, LA) within the 25-km buffer of the colony center as observed data. Secondly, we randomly selected 50 points within the boundary of the state of Florida and created 25-km buffers for each point based on the 2004 GIS layer. We then calculated % cover of each land use category of 50 random points as expected data. We compared observed vs. expected data using a Multivariate Analysis of Variance (MANOVA) because the % land use categories were not independent. Wilks' lambda (λ) was used as the test criterion with α level of 0.05. Following a significant overall MANOVA, separate ANOVAs were used to determine the differences in individual land use categories between observed and expected data.

Results

1. Wood Stork colony dataset

Figure 5 shows the distribution of colonies observed and active for different numbers of years. This distribution indicates there were relatively few long-lived colonies (> 10 years) and only three that were observed for longer than 35 years (Corkscrew, East River and Cuthbert Lake, all in south Florida). The very large number of colonies existing for only a single year may be a partial result of sampling bias – many of these were noted in a single year but simply not visited the next. However, the very large number of these argues that there may be some biological reality contributing to this pattern as well – colonies that persist for long periods usually are noted by multiple sources and as a result are sampled repeatedly. Otherwise, the distribution suggests a biological rather than sampling process at work. This suggests that sampling of colonies by survey methodology has indeed been representative, at least of longevity.

The emerging picture suggests that during the period of record, storks often tried to establish new colonies, many of which failed after a single year. While there may be some long-lived colonies, the vast majority last less than 20 years. While the frequency of short- and long-lived colonies typical of pre-European settlement cannot be known, stork colony abandonment and novel colony initiation seems to be typical of the species, a characteristic that has not been emphasized until recently in the literature (Frederick & Meyer, 2008).

2. Environmental variables

2.1 Screening of colony site variables

The results of how individual colony variables are related to longevity score, mean colony size, median colony size are presented in Table 5, 6, and 7, respectively. Although most of the variables were not significant for mean and median colony size, ISLA2 was significantly related to both measures. The results for the FLUCCS GIS layer were generally similar to those for CCAP.

Longevity score was higher for colonies with shrubs than for those with only trees (Table 5). Nesting tree condition change did not appear to explain significant amounts of variation in longevity score, mean colony size, or median colony size. Longevity score varied with all island isolation variables. Generally, longevity score, mean colony size, and median colony size were higher when colonies were more isolated from land, suggesting that this variable was a good candidate for explaining variation in colony size and persistence.

Longevity score varied with all human activity variables except DIST1 and colonies with human activity had a higher longevity score compared to colonies with low human activity or activity at greater distances. Median colony size was not related to any of the human activity variables. Mean colony size showed a relationship only with the closest human activity (DIST1), and colonies without human activity were larger than those with human activity. The results suggested that colony longevity may be related positively to human activity nearby at several scales, but that size of colony was only weakly related to human activity. It is important to keep in mind that these results did not include all explanatory variables together at once and were for screening purposes only. They may also be misleading, since inclusion of all variables may be much more powerful for discerning net, biologically meaningful effects.

Although colony site variables showed mixed results in explaining longevity score, mean colony size, and mean colony size, the results suggested that all variables could be important in influencing stork colony. Thus we were unable to exclude any of the colony site variables. Therefore, we incorporated all colony site characteristics but modified island isolation variables and disturbance variables in occupancy analysis (see below).

2.2 Screening of hydrological variables

Preci-I and Preci-III were not related to longevity score (Table 9). Preci-I was not related to mean and median colony size while Preci-III was positively related to mean and median colony size. Although the amount of variation explained by Preci-III was not high, the screening results suggested that precipitation variables could be important in influencing stork colonies. Therefore, we included precipitation variables in the occupancy analyses.

2.3 Screening of landscape variables

The percent change in non-forested wetlands in the 12.5-km buffer was positively related to longevity score while none of the land use categories in 25-km buffer were related to longevity score (Table 8). The percent change in grassland was an important predictor with positive influence for mean and median colony size in both 12.5-km and 25-km buffers, suggesting stork colony sizes respond to grassland of 12.5- and 25-km buffers in a similar way.

Although only non-forested wetlands and grassland appeared as important predictors, these preliminary, screening level results suggested that that some land use change variables may be important in predicting stork colony longevity and size. Therefore, we retained all land use categories in the occupancy analyses. However, we did not include lake/open water because there was some discrepancy between the subcategories of bay/estuary and ocean in some years. Since we had excluded ocean entirely from the analysis, this seemed like a temporally unstable bias, which we did not wish to retain. Because we saw only very weak effects of variables at the 25 km buffer distance, we only included 12.5 -km buffer variables to reduce the number of variables in the occupancy models.

3. Occupancy modeling

For SE models (those that did not include landscape variables), we found two top models with differences in Akaike's weights of less than two. The global model that included all variables (NTT, NTCC, ISLA, DIST, CS, LONG, P1, P3, IFM) showed the highest Akaike's weight (0.73, Table 10). The next best model included ISLA, DIST, CS, LONG, P1, P3, and IFM, and had a $\Delta AIC_c < 2$, suggesting it showed strong support. The combined Akaike's weight for these two top models was 1. Because the top model is a global model that retained all the variables, most of the variables except P2 had high relative importance (Table 12). Colonies with nesting trees > 3 m had a higher rate of extinction than those with nesting trees < 3 m (Figure 6). Colonies with less connection to the mainland had a lower extinction rate than colonies on the land (Figure 7), indicating that island colonies were much more likely to persist than those attached in any degree to the mainland. Human activity near the colony tended not to influence extinction but greater or closer activity indices were associated with higher colonization rates (Figure 8). Colonies with larger numbers of pairs nesting were less likely to go extinct than smaller colonies (Figure 9). Longevity did not influence extinction rate but was positively related to colonization, or more accurately, recolonization of the colony after temporary abandonment. Colonies existing for more than 15 years had a high recolonization rate (Figure 10). Precipitation during the 12 months preceding nesting had a negative relationship with local extinction and was positively related to colonization (Fig.11). Colonies with a large colony nearby were no more or less likely to go extinct, but were less likely to colonize than breeding locations without a large colony nearby.

Keep in mind that the SE models (above) did not include landscape variables. For FL models (those including landscape variables but having a small number of years in the dataset), the model including ISLA, DIST, CS, LONG, P2, P3, and IFM was the best model (Table 11) describing occupancy (Akaike's weight = 0.54). Models 2-5 (Table 11) also showed some support and though the ΔAIC_c values were > 2, the differences in AIC weight among these models did not exceed 6. Overall, ISLA, DIST, CS, and LONG were the most important variables describing occupancy with relative importance values > 0.9 followed by P2, P3, and IFM (Table 12). NTT, NTCC, and P1 also appeared in the 95% confidence set of models, but these models had low weights. The highest ranked model that included effects of any landscape variables on occupancy received essentially 0 weight, implying little or no explanatory power. In the FL models, ISLA had a negative relationship with probability of extinction, suggesting that colonies with less connection had smaller chance of extinction than the colonies with more connection to the mainland, similar to the SE models (Figure 12). Human activity had a negative relationship with probability of extinction (similar to the SE models), but did not influence colonization (Figure 13). Similar to SE models, colony longevity had a positive relationship with colonization (Figure 14). P2 was negatively related to colonization (Figure 15), suggesting colonies with wetter conditions 36 months before nest initiation had a lower colonization rate compared to colonies with dryer conditions.

4. Colony habitat selection

Overall land use categories differed in the buffers surrounding known colonies and random points (Wilks' $\lambda = 7.70$, $P < 0.001$). An ANOVA showed that known colonies and random points differed in % cover of grassland, area of development, upland forest, and lake/open water (Table 13). The results suggested that the storks prefer habitat within a 25-km buffer that contains less grassland and upland forest, and more developed area and lake/open water compared to the available landscape.

Discussion

Comparison between SE and FL models

Because of the severe limitation of GIS data availability in space and time, we were forced to conduct two occupancy analyses using data from different geographical regions and temporal scales. The SE models included all available colonies in the southeastern US from 1970-2010 and are probably the most robust models because of sample size and length of record used. The FL models utilized only colonies in Florida from 1999-2007, but included landscape variables. The landscape variables did not emerge as being important in the FL model. Although the best fit models in the two analyses were not the same, the variables retained as having strong explanatory power in both model sets were very similar and for the most part had the same relationships with extinction and colonization parameters. Since the SE models used a much larger data set from a longer period, there is some argument that the SE analysis should be given more weight when considering the non-landscape variables. As below, we do not believe that the FL models were a definitive test of the prediction that changes in land use affect colony occupancy, extinction or colonization.

Colony site variables

Among the four colony variables, human activity and island isolation were consistently important in predicting occupancy, while nesting tree type or condition had a less consistent effect. Nesting tree condition change appeared in the best fit models for SE models, but the effect size was not large. The degree to which islands were connected to the mainland was quite important and consistently negatively related to colony occupancy in both SE and FL models. Colonies with greater connection to the mainland were more likely to go extinct. We presume that this effect is largely due to the action of nest predation. Previous studies and observations are consistent in predicting that without the protection of water, mammalian predators are much more likely to gain access to stork colonies and cause abandonment (Rodgers, 1987; Coulter & Bryan, 1995). In any case, our analysis shows that for whatever reason, true islands that are well separated from the mainland are much less likely to go extinct and much more likely to be colonized than those that have partial or complete connection. This rather strong finding can be used with confidence as a criterion for prioritizing the quality of nesting sites. In this light, it could be very important to conduct an analysis of islands at a landscape and regional scale. Are islands a limiting resource for stork nesting?

Colonies with a higher degree of human activity, or closer human activity to the colony, were less likely to become extinct and were more likely to be colonized compared to colonies with lower degrees of disturbance. When thinking about this result, it is important to recall that we used any kind of human structure or activity within various distances of a colony as indicative of disturbance – we did not measure disturbance per se and many levels and types of direct disturbance could be represented by this gross measure. Further, close proximity was defined as human disturbance within categories of 100 – 500 meters. The result could easily have been generated by having human disturbance in all cases that was well beyond typical recommended setback distances from colonies. Therefore this result does not necessarily indicate that setback distances should be changed.

On its face, the result suggests that storks are not particularly vulnerable to the effects of human disturbance and their nesting may be compatible with a number of different kinds of nonintrusive human land uses in the vicinity of colonies. Frederick (unpublished) found no effects of construction dynamiting within 0.4 km of an actively nesting stork colony in the Everglades. Similarly, the same colony has persisted despite the existence of a major road (US 41), and two different bouts of intensive road building and habitat disturbance along its immediate borders. Thus established colonies may be relatively robust to disturbance along its edges.

Depending on the type, intensity, and frequency of human disturbance, storks may have different responses to disturbance. For example, the effects of chronic disturbance (e.g., ecotourism, permanent development nearby) may cause quite a different effect from short-term disturbance events. Disturbances may also operate at different scales. While storks may tolerate the disturbance at a distance from colony, disturbance events that happened within the colonies such as logging can have direct effects by removing the nesting trees.

Since some kinds of human disturbance can evidently predispose storks to later abandon nesting, it seems clear that stressors may be cumulative, implying there may be a long lag time between chronic local disturbance and longevity of the colony. For example, storks did not abandon south Florida colonies until at least a decade of poor reproduction had occurred (Ogden, 1994). Lagged effects of habitat suitability may in fact be a characteristic of reproduction by this species and may make it difficult to discern cause and effect. Moreover, while established colonies may be somewhat resistant to local disturbance, it is unclear whether human activity is an important factor in the location of new colony sites.

The relationship between disturbance and low extinction that we have reported may also be an artifact. Both humans and storks may settle near similar resources, creating an apparent association between disturbances and nesting suitability. In central Florida, a high density of lakes and watercourses seems to be preferred by both species, and the same is true in coastal regions. Both may avoid areas of poor productivity – the density of both stork colonies and humans are very low both in planted pine forests and the vast, oligotrophic wetlands of south Florida. It is also possible that proximity of human activities guarantees some level of ecological disturbance that is beneficial for stork foraging (e.g., presence of open habitat, ditches, and watercourses). It is also possible that human activities may in some way decrease the density of potential nest predators, or at least keep nest predators occupied with human generated food sources. Perhaps the only unambiguous recommendation here is that storks do not seem to be particularly vulnerable to human activity in the vicinity of the colony, and human activities in the 100 – 500 meter distance from colonies do not seem to be strongly negatively influencing colonization rates.

Thus there are two basic interpretations of this result – one being that storks are not strongly affected by human activities and may be positively affected, the other that storks are negatively affected but seem willing on balance to nest near humans because humans are occupying the best stork habitat. Since human presence seems to be a statistically important and consistent variable in stork geographic nesting patterns, it seems important to resolve these two different explanations in order to better manage human disturbance and understand the drivers behind stork nesting patterns. We suggest studies should be undertaken to look for mechanisms of possible positive effects, and to further test the hypothesis that storks and humans prefer the same landscape features.

Hydrological variables

Previous studies have shown that stork breeding success and productivity were associated with hydrological conditions, since particular sequences of hydrology may be required to produce access to high concentrations of prey and make them available through the concentrating action of falling surface water (Kushlan & Frohring, 1986; Ogden et al., 1987; Coulter & Bryan, 1995). In the SE models, colonies with wetter conditions 12 months before nest initiation had higher occupancy probability. Bryan and Robinette (2008) found that pre-breeding season rainfall had a moderate positive relationship with breeding success for the colonies in coastal Georgia, but not the colonies inland. This relationship may due to a positive effect on prey population expansion and subsequent availability during the breeding season.

In FL models from 1999-2007, precipitation 36 months before nest initiation had a negative relationship with probability of colonization. This may or may not be inconsistent with the SE model results, since the time periods over which rainfall was measured were different. The relationship between rainfall and colony attractiveness may be highly dynamic and even colony- or region- specific. Additionally, the effect of precipitation 36 months before, 12 months before, and 5 months on stork colonies may not be independent. The wetland type and recharge rate, habitat availability, foraging pattern and behavior further complicate the relationship. For example, the influence of precipitation on coastal stork colonies may be less prominent than inland colonies because coastal colonies always have tidal habitats to forage in (Bryan & Robinette, 2008). At minimum, we feel it was very important to include precipitation variables in the models to control for their local effect when estimating the effect of other more management-specific variables like colony site characteristics. We suggest that the effects of local precipitation and hydrology can probably only be accurately understood using water level information in local wetlands. There are currently so few gauges in wetlands that this kind of analysis is impossible on the scale of the breeding range of storks. Focused studies are badly needed for understanding these relationships outside of south Florida, especially since altered precipitation patterns are likely to occur as a result of global change.

Colony longevity, size, and dynamics with nearby colonies

Longevity was a strong positive factor influencing colonization in both SE and FL models, showing that independent of other variables, the longer the colony has been established, the less likely it will go extinct and the more likely it will be re-colonized following temporary abandonment. It is unclear what attributes of longevity make older colonies more attractive. It is possible that storks have a better chance of re-locating previous mates at the beginning of the nesting season at the more stable colonies, or that longer lived colonies provide storks with the opportunity to enhance breeding success through social dominance or knowledge of local food sources. Longer lived colonies may also simply tend to have more successful reproduction, and that premium on lifetime reproductive success may make storks return more reliably to these high productivity sites. In any case, our results indicate that older colonies are inherently stable, and therefore more valuable to stork individuals and populations than younger ones. Older colonies should therefore receive the highest conservation and management priority.

There was also a negative relationship between colony size and local extinction, suggesting that larger colonies are more likely to persist, all other things being equal. This is not surprising, since many colonial nesting birds have size thresholds for successful nesting. Advantages to living in a large colony may include a dilution of predation, enhanced food finding, enhanced mate choice and mate finding. However, it is difficult to assign a threshold number to colony size since there is considerable variability in persistence across colony sizes. Additionally, colony size has become smaller in the U.S. through time (Brooks & Dean, 2008), so the effect of colony size and longevity may be confounded. It is therefore not clear if the recent trends toward smaller colonies, especially in northern range of the stork distribution, can be directly translated to a trend towards higher colony extinction probability. In any case, we feel confident that colony size can be used in a categorical way for prioritizing stork colonies. For example, it seems clear that colonies in the largest 20% of size categories should be in a much higher priority category than the lowest 20% of size categories.

There was a negative relationship between the colony proximity index (colony size and proximity) and colonization rate, indicating that colonies with a larger colony nearby were less likely to colonize compared to colonies without a large colony nearby. However, in this study we only incorporated characteristics (distance and size) of the closest colony. When there are multiple colonies nearby, the dynamics may be more complicated. The recommendations we can make here are somewhat weakly supported, in keeping with the magnitude of this effect. It does seem that larger colonies are likely to be more permanent, and in a case of choosing between two colonies close by, the larger should receive a higher priority since the smaller may have a lower chance of persistence.

Relative importance of landscape variables

It is initially striking that none of the landscape variables showed up as important in the FL occupancy models, since storks seem clearly respondent to type and quality of foraging habitat, especially during the breeding season. On its face, the lack of inclusion of landscape change variables in the occupancy models suggests that storks are generalist foragers that are resilient to changes in their foraging habitat, and may be able to use their long distance foraging abilities to compensate for changes in land use categories around them. However, it is important to remember that we found conflicting results about landscape variables in our different analyses (Table 14). At the approximate time of colony formation, colonies were less likely to be associated with grassland than random points, but our screening analysis suggested a positive influence of grassland on longevity. Change towards more non-forested wetlands was associated with longevity of colonies in the screening analyses, but non-forested wetlands were not identified as important in either occupancy analyses or habitat use studies. At minimum, it seems clear that we were not able to get a consistent message from our analyses with respect to land use preference or land use change.

It could also simply be that the degree of change that we were able to measure did not encompass what storks respond to. The GIS data we were able to use were only available from 1999-2007 in Florida, which may not reflect long term change well or at best only reflects a particular period in Florida's land use history. Indeed, the largest change in wetlands and human habitation near colonies probably happened much earlier in Florida's history. Further, we have no evidence that the composite land use categories that we were limited to using are those that storks may be responsive to. For these reasons, we consider the influence of land use on colony occupancy to be an open question not addressed well by this study. We therefore strongly suggest that no recommendations on land use change be incorporated into planning for storks as a result of this study.

Habitat selection

Our analysis of habitat selection suggested that colonies were initiated in association with landscapes with that had less grassland and upland forest, and more development and lake/open water. The avoidance of upland forest and grassland is not surprising given the preference of this species for wetland habitats, and even forested wetland habitats. This apparent avoidance may be used with some confidence in categorizing areas that storks do NOT prefer.

The apparent preference for areas with a higher percentage of developed areas seems similar to the results of the occupancy modeling, and the same explanations may apply. This may indicate that storks are relatively tolerant of developed areas around them, though the threshold for this is not clear. It may also be that storks and humans seek many of the same resources in a landscape. Although newly formed colonies were established in areas with a higher percentage of developed area during the 1990s, we cannot assume those colonies necessarily have high productivity and can last long. Long term monitoring is needed to determine whether these are ecological traps or fitness based preferences. Further study on a finer scale of colony habitat selection will provide more information on their habitat selection preference.

Recommendations

Based on our analysis, the following recommendations can be made with regard to management and conservation of Wood Storks.

1. Management and conservation priority should be accorded to long-lived colonies, particularly those in existence for over 10 years. Our analyses suggest that the effect of longevity increases rapidly through at least 10 years of age, with a weak inflection point after about 15 years, and leveling off after about 20 years. Those years do not have to be contiguous, but a pattern of regular use and recolonization should be evident for a colony to be high ranking in this category. In addition to long-lived colonies obviously having characteristics that are regularly suitable for nesting, longevity by itself appears to lend a greater tendency for storks to return to the colony in the future, all other things being equal. This effect was strong and consistent in our analyses, and probably constitutes an important biological process.
2. Large colonies should be accorded higher management and conservation status, since large colonies were more persistent than small ones, and were more likely to absorb nearby smaller colonies. Our studies do not suggest a hard threshold for size of persistent colonies, but there did appear to be a leveling off of the effect after 300 – 500 pairs.
3. Colonies on true islands that are separated from the mainland by a clearly perceptible body of water should rank highly as deserving of conservation and management attention. All analyses supported the idea that island were preferred and resulted in greater persistence. We recommend a targeted analysis to identify appropriate island habitat, particularly those in areas of higher stork colony density, to determine whether islands are a critical limiting resource for the stork population in the southeastern United States. To be appropriate habitat, islands would need to support large trees and shrubs, be within the mean plus or minus one standard deviation of the mean areal size of colonies, and not be regularly visited by humans.
4. We found a strong relationship between proximity of human structures and colony persistence. While this suggests that storks at minimum are not extremely sensitive to human disturbance, it does not suggest that current guidelines for disturbance near colonies should be changed. Our closest categories for human activity near colonies

100 meters) were no less than those currently recommended as approach distances. More importantly, we have two competing explanations for the apparent relationship - one suggests that storks might be benefitting from human proximity; the other suggests that storks are forced to nest near people because of a strong overlap in human and stork resource needs. In the latter scenario, storks could be negatively affected by human activities, but left without a choice for nesting sites because of resource needs. We also remind readers that the information on human proximity was gathered only recently, leaving open the possibility that humans have simply encroached on stork nesting habitat, rather than storks preferring to nest near humans. We recommend studies to further examine the mechanisms involved in this association.

5. Relationships between land use change and stork colony size, longevity, extinction and colonization were relatively weak in our analyses and our analysis of these relationships was likely to have been compromised by the very short time span of land use change information available. We suggest that readers do NOT use the results of this study to prioritize or manage stork colonies based on land use change characteristics.
6. We recommend further studies on the effects of local hydrology on colony suitability. This study was not able to address this question well because of limited hydrological data, but this question remains as an important one for management and conservation. While local hydrology is not usually controllable, understanding the nature of effects (especially for areas outside of south Florida) may allow the identification of areas that are prone to poor or good hydrology. This is of special importance since hydrological/rainfall relationships and hydrological/human use relationships are likely to be strongly influenced by global climate changes.

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Tables

Table 1. Characteristics of the uncorrected Wood Stork colonies dataset in the southeastern United States, 1970 – 2004, by state (circa 2007 from U.S. Fish Wildlife Service).

	Colonies	%	Observations*	%	Mean obs/colony
Florida	175	71	793	66	4.5
Georgia	45	18	281	24	6.2
South Carolina	26	11	120	10	4.6
Total	246		1,194		4.9

* One observation is constituted by evidence that a colony was or was not active in any year.

Table 2. Numbers and observations of Wood Stork colonies in the fully checked and updated dataset in the southeastern United States, 1970 – 2010, by state.

	Colonies	%	Observations*	%	Mean obs/colony
Florida	236	72	2089	63	8.9
Georgia	59	18	804	24	13.6
South Carolina	34	10	413	12	12.1
North Carolina	1	0.3	6	0.1	6.0
Total	330		3312		10.0

* One observation is constituted by evidence that a colony was or was not active in any year.

Table 3. Numbers of Wood Stork colonies considered usable and unusable for occupancy analysis in the southeastern United States, 1970-2010, by state.

	Usable Colonies		Not Usable Colonies		Total Colonies	
	Number	%	Number	%	Number	%
Florida	127	54	109	46	236	100
Georgia	44	75	15	25	59	100
South Carolina	22	65	12	35	34	100
North Carolina	1	100	0	0	1	100
Total	194	59	136	41	330	

Table 4. Description of Wood Stork colony site variables used in initial screening and categorization.

Variable Name	Code	Description of categories
Nesting tree type	NTT	Tree: tree > 3 m Shrub: shrub or tree < 3 m
Nesting tree condition change	NTCC	Y: nesting tree condition changed (i.e., logging, acute weather, or effects of accumulation of guano) N: nesting tree condition did not change
Island1	ISLA1	Y: colony on isolated island N: colony not on isolated island
Island2	ISLA2	ISO: colony on isolated island W12: colony in a wetland where < 2/3 circumference of nesting trees are connected with land through secondary vegetation/ floating mat W3L: colony in a wetland where > 2/3 circumference of nesting trees are connected with land through secondary vegetation/ floating mat or on mainland not separated by water
Island3	ISLA3	ISO: colony on isolated island W1: colony in a wetland where < 1/3 circumference of nesting trees are connected with land through secondary vegetation/ floating mat W2: colony in a wetland where >1/3 and < 2/3 circumference of nesting trees are connected with land through secondary vegetation/floating mat W3: colony in a wetland where >2/3 circumference of nesting trees are connected with land through secondary vegetation/floating mat LA: colony on mainland not separated by water
Disturbance within 50m	DIST05	Y: disturbance activities (i.e., logging, road, house, agriculture, recreational activities) within 50 m from the center of colony N: no disturbance activities within 50 m from the center of the colony
Disturbance within 100m	DIST1	Y: disturbance activities (i.e., logging, road, house, agriculture, recreational activities) within 100 m from the center of colony N: no disturbance activities within 100 m from the center of the colony
Disturbance within 200m	DIST2	Y: disturbance activities (i.e., logging, road, house, agriculture, recreational activities) within 200 m from the center of colony

		N: no disturbance activities within 200 m from the center of the colony
Disturbance within 300m	DIST3	Y: disturbance activities (i.e., logging, road, house, agriculture, recreational activities) within 300 m from the center of colony N: no disturbance activities within 300 m from the center of the colony
Disturbance within 400m	DIST4	Y: disturbance activities (i.e., logging, road, house, agriculture, recreational activities) within 400 m from the center of colony N: no disturbance activities within 400 m from the center of the colony
Disturbance within 500m	DIST5	Y: disturbance activities (i.e., logging, road, house, agriculture, recreational activities) within 500 m from the center of colony N: no disturbance activities within 500 m from the center of the colony

Table 5. Relationship of Wood Stork longevity score to colony site characteristics using Analysis of Variance for FLUCCS and CCAP layers. Direction of differences, mean values, and sample size are given for each characteristic by variable and layer. Letters under Mean and N columns refer to the initials of the categories of each variable.

Variable	Layers	F	P	MEAN	n
NTT[a]	FLUCCS	$F_{1,138} = 4.78$	0.030	T (0.56) < S (0.67) *	T (82), S (58)
	CCAP	$F_{1,199} = 4.06$	0.045	T (0.52) < S (0.63) *	T (157), S (43)
NTCC	FLUCCS	$F_{1,138} = 0.82$	0.366	Y (0.73) = N (0.60)	Y (5), N (135)
	CCAP	$F_{1,199} = 1.93$	0.166	Y (0.70) = N (0.54)	Y (8), N (192)
ISLA1	FLUCCS	$F_{1,138} = 4.50$	0.036	Y (0.67) > N (0.56) *	Y (63) , N (77)
	CCAP	$F_{1,199} = 2.73$	0.100	Y (0.61) = N (0.52)	Y (52), N (148)
ISLA2	FLUCCS	$F_{2,137} = 7.66$	< 0.001	ISO (0.74) > W12 (0.57) = W3L (0.53) *	ISO (46), W12 (29), W3L (65)
	CCAP	$F_{2,198} = 8.11$	< 0.001	ISO (0.71) > W12 (0.58) > W3L (0.47) *	ISO (33), W12 (57), W3L (110)
ISLA3	FLUCCS	$F_{4,135} = 4.17$	0.003	ISO (0.74) = W1 (0.71) = LA (0.59) = W2 (0.54) = W3 (0.53) *	ISO (46), W1 (4), LA (4), W2 (25), W3 (61)
	CCAP	$F_{4,196} = 4.09$	0.003	A > B, A = ISO (0.71) = W1 (0.71) = W2 (0.54) B = W2 (0.54) = W3 (0.48) = LA (0.47) *	ISO (33), W1 (7), W2 (48), W3 (106), LA (6)
DIST05	FLUCCS	$F_{1,138} = 6.49$	0.012	Y (0.82) > N (0.59) *	Y (11), N(129)
	CCAP	$F_{1,199} = 0.42$	0.517	Y (0.59) = N (0.54)	Y (15), N (185)
DIST1	FLUCCS	$F_{1,138} = 1.09$	0.298	Y (0.66) = N (0.60)	Y (25), N (115)
	CCAP	$F_{1,199} = 0.01$	0.937	Y (0.54) = N (0.54)	Y (35), N (165)
DIST2	FLUCCS	$F_{1,138} = 10.17$	0.002	Y (0.72) > N (0.55) *	Y (46), N (94)
	CCAP	$F_{1,199} = 1.42$	0.235	Y (0.58) = N (0.52)	Y (74), N (126)
DIST3	FLUCCS	$F_{1,138} = 12.95$	<0.001	Y (0.72) > N (0.54) *	Y (53), N (87)
	CCAP	$F_{1,199} = 4.78$	0.030	Y (0.59) > N (0.50) *	Y (94), N (106)
DIST4	FLUCCS	$F_{1,138} = 12.11$	<0.001	Y (0.69) > N (0.53) *	Y (67), N (73)
	CCAP	$F_{1,199} = 5.54$	0.020	Y (0.59) > N (0.48) *	Y (107), N (93)

DIST5	FLUCCS	$F_{1,138} = 14.5$	<0.001	Y (0.70) > N (0.52) *	Y (72), N (68)
	CCAP	$F_{1,199} = 7.21$	0.008	Y (0.60) > N (0.48) *	Y (110), N (90)

[a] See Table 4 for complete definition and description of variables.

Table 6. Relationship of Wood Stork mean colony size to colony site characteristics using Analysis of Variance for FLUCCS and CCAP layers. Direction of differences, mean values and sample size are given for each characteristic by variable and layer. Mean and N columns refer to the initials of the categories of each variable.

Variable	Layers	F	P	MEAN	n
NTT	FLUCCS	$F_{1,138} = 0.74$	0.392	T (105.14) = S (83.52)	T (82), S (58)
	CCAP	$F_{1,199} = 0.04$	0.836	T (68.54) = S (64.85)	T (157), S (43)
NTCC	FLUCCS	$F_{1,138} = 0.27$	0.609	Y (62.89) = N (97.42)	Y (5), N (135)
	CCAP	$F_{1,199} = 0.01$	0.911	Y (63.73) = N (67.91)	Y (8), N (192)
ISLA1	FLUCCS	$F_{1,138} = 0.33$	0.567	Y (88.31) = N (102.63)	Y (63), N (77)
	CCAP	$F_{1,199} = 0.05$	0.826	Y (70.47) = N (66.78)	Y (52), N (148)
ISLA2	FLUCCS	$F_{2,137} = 2.74$	0.068	W3L (115.84) = ISO (103.05) > W12 (41.23)	W3L (65), ISO (46), W12 (29)
	CCAP	$F_{2,198} = 0.70$	0.499	ISO (85.12) = W12 (70.24) = W3L (61.23) *	W3L (110), ISO (33), W12 (57)
ISLA3	FLUCCS	$F_{4,135} = 1.82$	0.128	W3 (120.12) = W1 (106.96) = ISO (103.05) = LA (50.60) = W2 (30.71)	W3 (61), W1 (4), ISO (46), LA (4), W2 (25)
	CCAP	$F_{4,196} = 0.52$	0.718	ISO (85.12) = W2 (70.98) = W3 (63.55) = W1 (62.30) = LA (26.69)	ISO (33), W2 (48), W3 (106), W1 (7), LA (6)
DIST05	FLUCCS	$F_{1,138} = 0.04$	0.845	Y (87.83) = N (96.90)	Y (11), N (129)
	CCAP	$F_{1,199} = 0.70$	0.404	Y (46.24) = N (69.49)	Y (15), N (185)
DIST1	FLUCCS	$F_{1,138} = 3.68$	0.057	Y (45.70) < N (107.16) *	Y (25), N (115)
	CCAP	$F_{1,199} = 3.56$	0.061	Y (37.96) < N (74.06) *	Y (35), N (165)
DIST2	FLUCCS	$F_{1,138} = 0.38$	0.541	Y (85.30) = N (101.51)	Y (46), N (94)
	CCAP	$F_{1,199} = 0.78$	0.380	Y (59.33) = N (72.68)	Y (74), N (126)
DIST3	FLUCCS	$F_{1,138} = 0.47$	0.493	Y (85.24) = N (102.85)	Y (53), N (87)
	CCAP	$F_{1,199} = 0.04$	0.846	Y (66.23) = N (69.09)	Y (94), N (106)
DIST4	FLUCCS	$F_{1,138} = 0.79$	0.377	Y (84.7) = N (106.72)	Y (67), N (73)
	CCAP	$F_{1,199} = 0.07$	0.795	Y (65.96) = N (69.79)	Y (107), N (93)

DIST5	FLUCCS	$F_{1,138} = 0.74$	0.390	Y (85.79) = N (107.19)	Y (72), N (68)
	CCAP	$F_{1,199} = 0.07$	0.792	Y (65.99) = N (69.88)	Y (110), N (90)

[a] See Table 4 for complete definition and description of variables.

Table 7. Relationship of Wood Stork median colony size to colony site characteristics using Analysis of Variance for FLUCCS and CCAP layers. Direction of differences, mean values and sample size are given for each characteristic by variable and layer. Mean and N columns refer to the initials of the categories of each variable.

Variable	Layers	F	P	MEAN	n
NTT	FLUCCS	$F_{1,138} = 0.28$	0.600	T (84.5) = S (72.35)	T (82), S (58)
	CCAP	$F_{1,199} = 0.13$	0.720	T (61.29) = S (55.38)	T (157), S (43)
NTCC	FLUCCS	$F_{1,138} = 0.17$	0.683	Y (55.30) = N (80.36)	Y (5), N (135)
	CCAP	$F_{1,199} = 0.00$	0.975	Y (61.06) = N (59.98)	Y (8), N (192)
ISLA1	FLUCCS	$F_{1,138} = 0.00$	0.996	Y (79.53) = N (79.42)	Y (63), N (77)
	CCAP	$F_{1,199} = 0.17$	0.677	Y (64.78) = N (58.35)	Y (52), N (148)
ISLA2	FLUCCS	$F_{2,137} = 2.43$	0.092	ISO (94.04) = W3L (90.72) > W12 (31.14) *	ISO (46), W3L (65), W12 (29)
	CCAP	$F_{2,198} = 0.99$	0.374	ISO (78.36) = W12 (63.75) = W3L (52.58)	ISO (33), W12 (57), W3L (110)
ISLA3	FLUCCS	$F_{4,135} = 1.49$	0.208	ISO (94.04) = W3 (93.73) = W1 (80.38) = LA (44.75) = W2 (23.26)	ISO (46), W3 (61), W1 (4), LA (4), W2 (25)
	CCAP	$F_{4,196} = 0.58$	0.674	ISO (78.36) = W2 (64.13) = W1 (58.86) = W3 (54.33) = LA (28.08)	ISO (33), W2 (48), W1 (7), W3 (106), LA (6)
DIST05	FLUCCS	$F_{1,138} = 0.03$	0.873	Y (85.73) = N (78.93)	Y (11), N (129)
	CCAP	$F_{1,199} = 0.27$	0.607	Y (47.80) = N (61.01)	Y (15), N (185)
DIST1	FLUCCS	$F_{1,138} = 1.98$	0.162	Y (45.40) = N (86.87)	Y (25), N (115)
	CCAP	$F_{1,199} = 2.57$	0.111	Y (36.66) = N (64.98)	Y (35), N (165)
DIST2	FLUCCS	$F_{1,138} = 0.61$	0.437	Y (66.80) = N (85.66)	Y (46), N (94)
	CCAP	$F_{1,199} = 1.36$	0.245	Y (49.76) = N (66.04)	Y (74), N (126)
DIST3	FLUCCS	$F_{1,138} = 0.65$	0.422	Y (67.75) = N (86.60)	Y (53), N (87)
	CCAP	$F_{1,199} = 0.19$	0.661	Y (56.87) = N (62.82)	Y (94), N (106)
DIST4	FLUCCS	$F_{1,138} = 1.05$	0.306	Y (67.31) = N (90.62)	Y (67), N (73)
	CCAP	$F_{1,199} = 0.44$	0.509	Y (55.85) = N (64.82)	Y (107), N (93)

DIST5	FLUCCS	$F_{1,138} = 1.14$	0.289	Y (67.73) = N (91.90)	Y (72), N (68)
	CCAP	$F_{1,199} = 0.40$	0.530	Y (56.17) = N (64.72)	Y (110), N (90)

[a] See Table 4 for complete definition and description of variables.

Table 8. Relationship between precipitation indices and longevity score, mean colony size, and median colony size. PRECI-I and PRECI-III correspond to precipitation indices 12 months before nest initiation and precipitation 5 months after nest initiation of Wood Storks colonies in the southeastern United States, respectively.

Response variable	Explanatory variable	Layers	P	R^2	n
Longevity score	PRECI-I	FLUCCS	0.329	0.01	140
		CCAP	0.638	0.00	200
	PRECI-III	FLUCCS	0.461	0.00	140
		CCAP	0.340	0.01	200
Mean colony size	PRECI-I	FLUCCS	0.170	0.01	140
		CCAP	0.084	0.02	200
	PRECI-III	FLUCCS	0.004 *	0.06	140
		CCAP	0.054	0.02	200
Median colony size	PRECI-I	FLUCCS	0.277	0.01	140
		CCAP	0.345	0.01	200
	PRECI-III	FLUCCS	0.014 *	0.04	140
		CCAP	0.089 *	0.02	200

Table 9. Summary of the relationship between Wood Stork colony longevity score, mean colony size, median colony size and percent change in land use using 12.5- and 25- km buffers of FLUCCS layers in Florida.

	12.5-km Buffer (n = 88)	25-km Buffer (n = 87)
Longevity Score	Non-forested Wetlands (+)	No relationships
Mean Colony Size	Grassland (+)	Grassland (+)
Median Colony Size	Grassland (+)	Grassland (+)

Table 10. “SE” Models predicting Wood Stork colony occupancy as a result of colony and site characteristics in the southeastern United States from 1970-2010 (n= 208 colonies).

Model	Variables in the model[a]	k[b]	AIC_c	ΔAIC_c	w_i
1	NTT+NTCC+ISLA+DIST+CS+LONG+P1+P3+IFM	21	2821.33	0.00	0.73
2	ISLA+DIST+CS+LONG+P1+P3+IFM	17	2823.29	1.96	0.27

[a] NTT = Nesting tree type, NTCC = Nesting tree condition change, ISLA = island, DIST = Disturbance, CS = Colony size, LONG = Colony longevity, P1 = Precipitation 12 months before nest initiation, P2 = Precipitation 36 months before nest initiation, P3 = Precipitation 5 months after nest initiation, and IFM = Colony Connectivity.

[b] number of parameters including the intercept

Table 11. “FL” Models predicting Wood Stork colony occupancy as a result of site and landscape characteristics in Florida from 1999-2007 (n= 73 colonies).

Model	Variables in the model[a]	k[b]	AIC_c	ΔAIC_c	w_i
1	ISLA+DIST+CS+LONG+P2+P3+IFM	17	511.50	0.00	0.54
2	ISLA+DIST+CS+LONG	11	513.92	2.42	0.16
3	NTT+NTCC+ISLA+DIST+CS+LONG+P2+P3	19	513.99	2.49	0.15
4	ISLA+DIST+LONG	10	515.39	3.88	0.08
5	ISLA+DIST+CS+LONG+P1+P3+IFM	17	517.46	5.95	0.03

[a] NTT = Nesting tree type, NTCC = Nesting tree condition change, ISLA = island, DIST = Disturbance, CS = Colony size, LONG = Colony longevity, P1 = Precipitation 12 months before nest initiation, P2 = Precipitation 36 months before nest initiation, P3 = Precipitation 5 months after nest initiation, IFM = Colony Connectivity, FW = % change of forested wetland, NFW = % change of non-forested wetland, GR = % change of grassland, AG = % change of agriculture, DE = % change of develop area, UF = % change of upland forest, and LA = % change of lake and open water.

[b] number of parameters including the intercept

Table 12. Relative importance of explanatory variables from models predicting occupancy for SE models (208 colonies in the southeastern United States from 1970-2010) and FL models (73 colonies in Florida from 1999-2007). Relative importance of each variable was calculated by adding Akaike's weighted values of models by which particular variable occurred in given model.

	Relative importance	
Explanatory variables	SE models	FL models
NTT	0.727	0.197
NTCC	0.727	0.184
ISLA	1.000	0.997
DIST	1.000	0.989
CS	1.000	0.919
LONG	1.000	0.999
P1	1.000	0.033
P2	0.000	0.714
P3	1.000	0.748
IFM	1.000	0.596
FW	N/A	0.000
NFW	N/A	0.000
GR	N/A	0.000
AG	N/A	0.000
DE	N/A	0.000
UF	N/A	0.000

[a] NTT = Nesting tree type, NTCC = Nesting tree condition change, ISLA = island, DIST = Disturbance, CS = Colony size, LONG = Colony longevity, P1 = Precipitation 12 months before nest initiation, P2 = Precipitation 36 months before nest initiation, P3 = Precipitation 5 months after nest initiation, IFM = Colony Connectivity, FW = % change of forested wetland, NFW = % change of non-forested wetland, GR = % change of grassland, AG = % change of agriculture, DE = % change of develop area, UF = % change of upland forest, and LA = % change of lake and open water.

Table 13. Comparison between percent land use cover of Wood Stork colonies established from 1999 - 2004 in Florida versus random points in Florida, using a 25 km buffer.

Land use	Expected (random; n = 50)		Observed (actual; n = 63)		
category[a]	Mean	SD	Mean	SD	P
FW	17.3%	15.0%	13.9%	12.4%	0.197
NFW	13.5%	11.1%	13.3%	15.0%	0.929
GR	13.5%	12.6%	7.8%	8.0%	0.004*
AG	13.3%	12.4%	13.6%	10.0%	0.877
UF	23.0%	19.2%	12.2%	8.3%	< 0.001*
DE	15.5%	16.9%	32.5%	16.0%	< 0.001*
LA	3.8%	3.7%	6.6%	5.5%	< 0.003*

[a] FW = Forested wetland, NFW = Non-forested wetland, GR = Grassland, AG = Agriculture, DE = Develop area, UF = Upland forest, and LA = Lake and open water.

Table 14. Summary comparison results among different analyses pertaining landscape variables. Please note that in screening and occupancy analysis, landscape variables were defined as percent change of land use categories between years. However, in nesting habitat preference analysis, landscape variables were defined as actual amount of land use categories surrounding the colony.

Type of analysis	12.5-km Buffer	25-km Buffer
Screening analysis†		
Longevity Score†	Non-forested Wetlands (+)	No relationships
Mean Colony Size†	Grassland (+)	Grassland (+)
Median Colony Size†	Grassland (+)	Grassland (+)
Occupancy Analysis†	No relationships	N/A
Nesting Habitat Preference*	N/A	Grassland (-) Upland Forest (-) Developed Area (+) Lake/Open water (+)

† landscape variables in these analyses were defined as percent change of land use categories between years.

* landscape variables in this analysis were defined as actual amount of land source categories surrounding the colony.

Figures

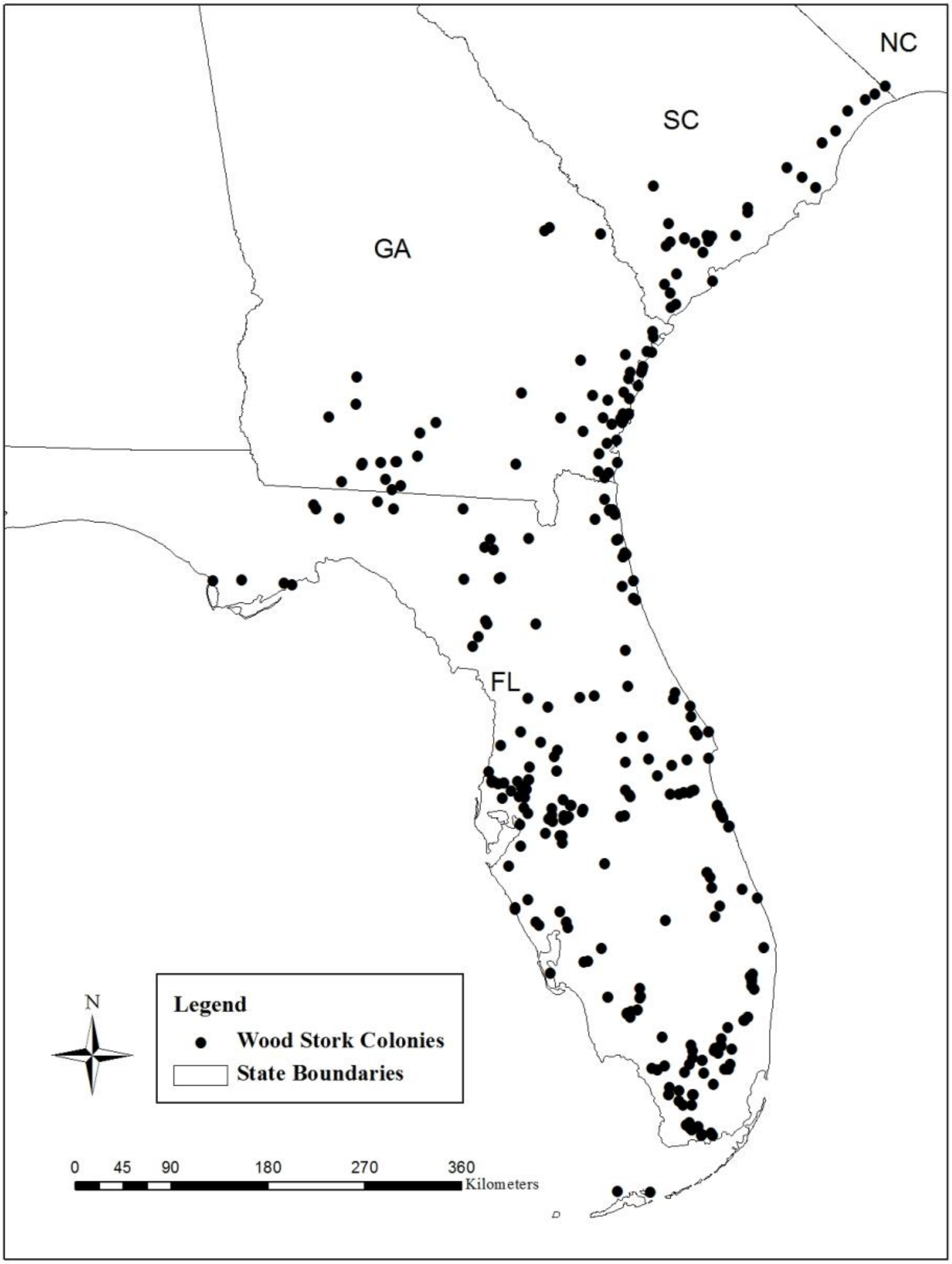

Figure 1. Wood Stork colony locations in the southeastern United States, 1970-2010.

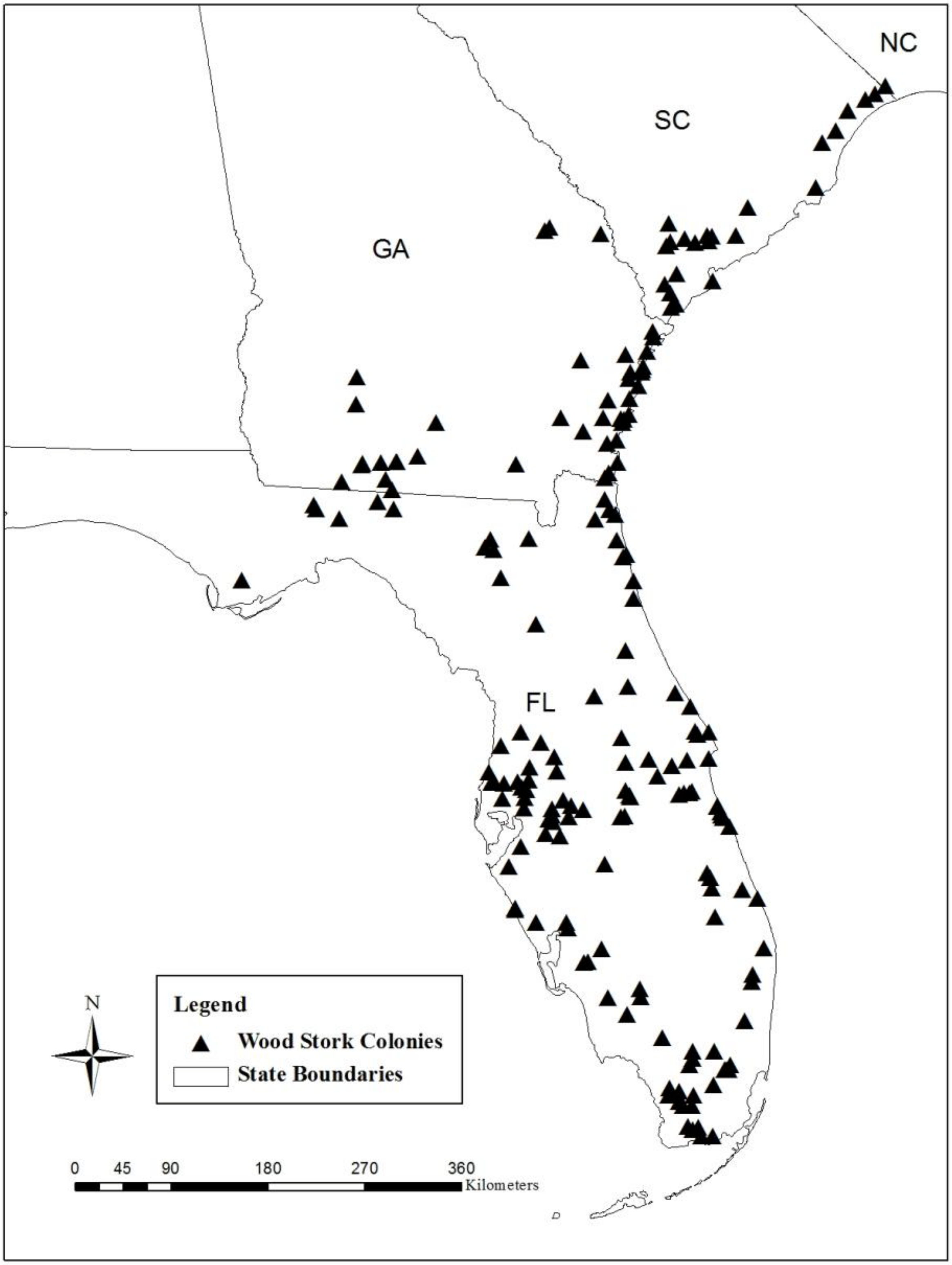

Figure 2. Wood Stork colonies locations with usable status (high and low quality) in the southeastern United States from 1970-2010.

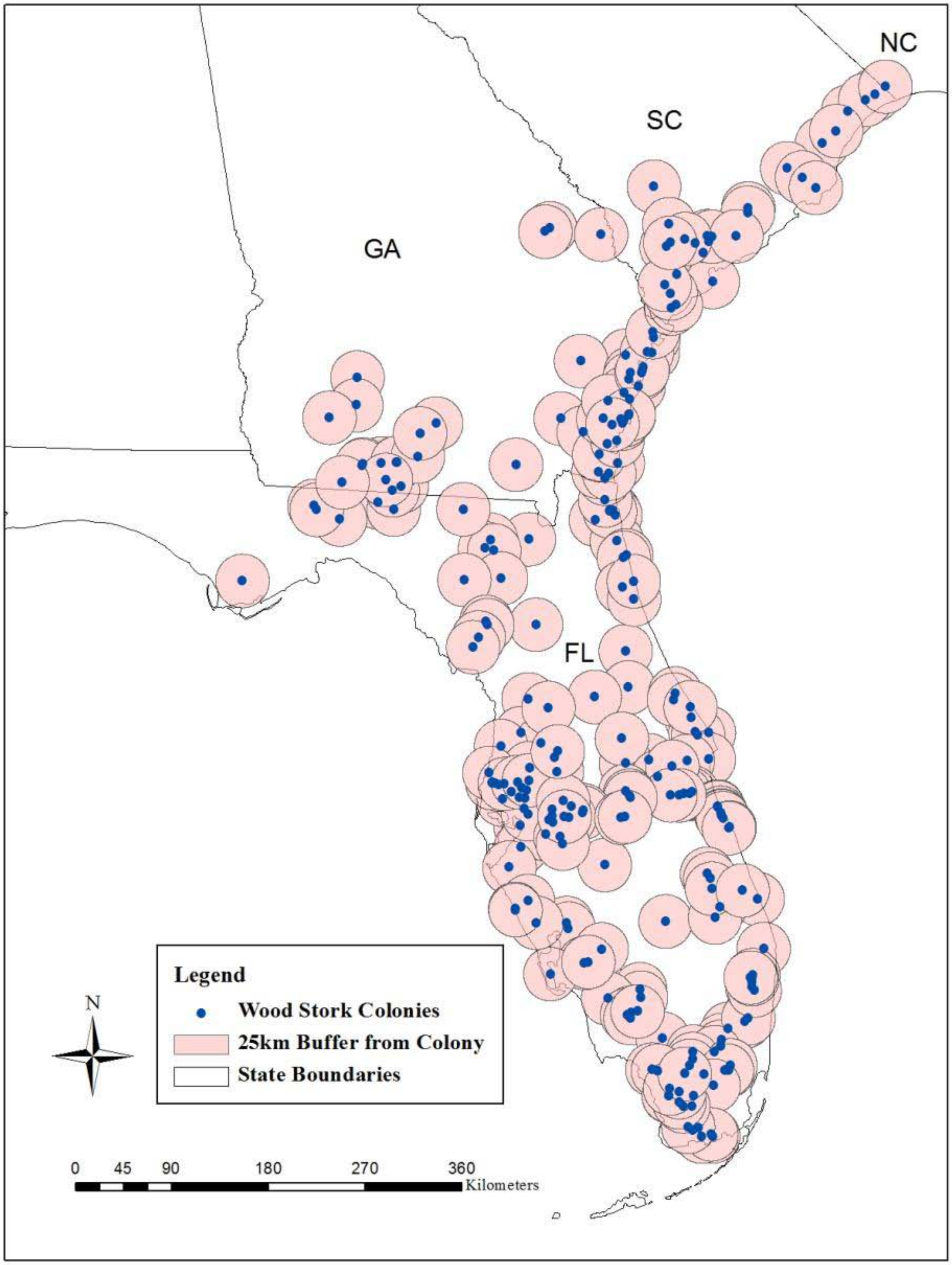

Figure 3. Known Wood Stork colonies and 25-km buffers in southeastern United States, from 1970-2010.

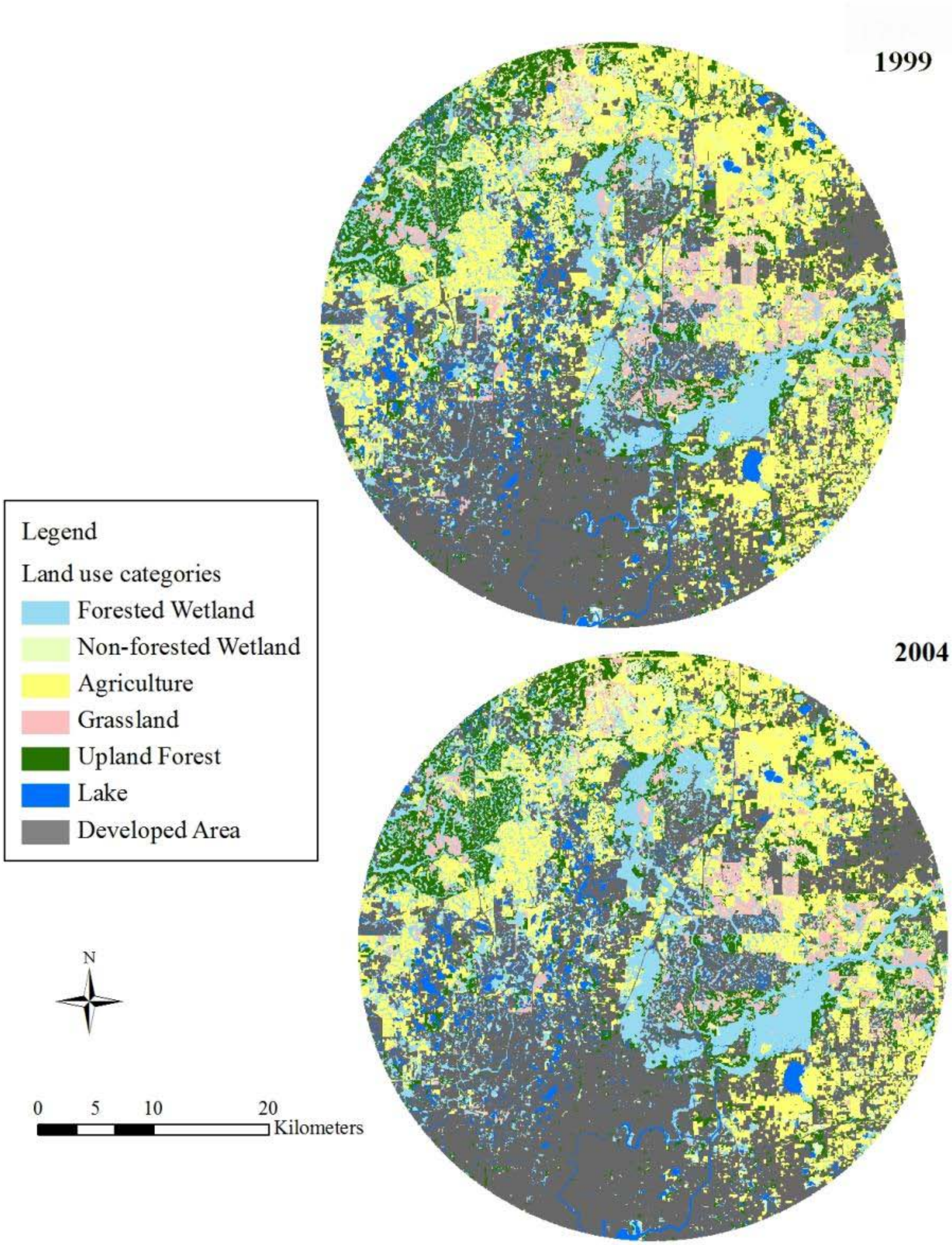

Figure 4. FLUCCS Land use and cover map of an example Wood Stork colony (Cypress Creek in Hillsborough County, Florida) within the 25-km buffer in 1999 and 2004.

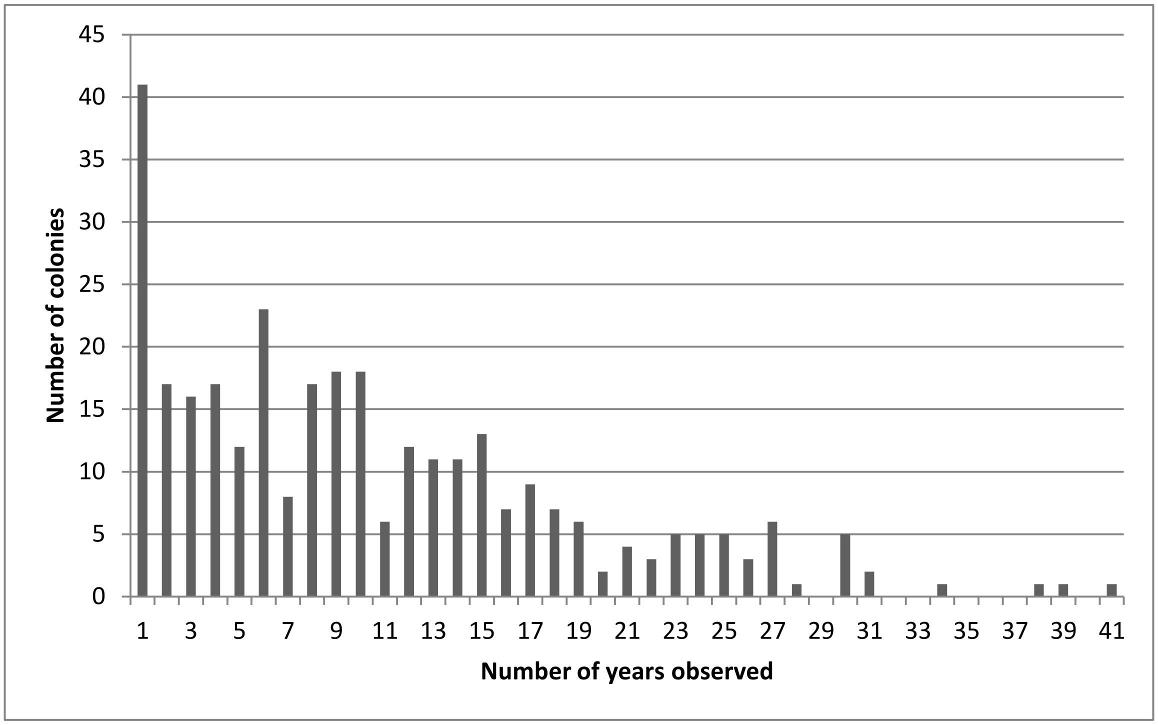

Figure 5. Numbers of Wood Stork colonies in the southeastern United States by number of years observed.

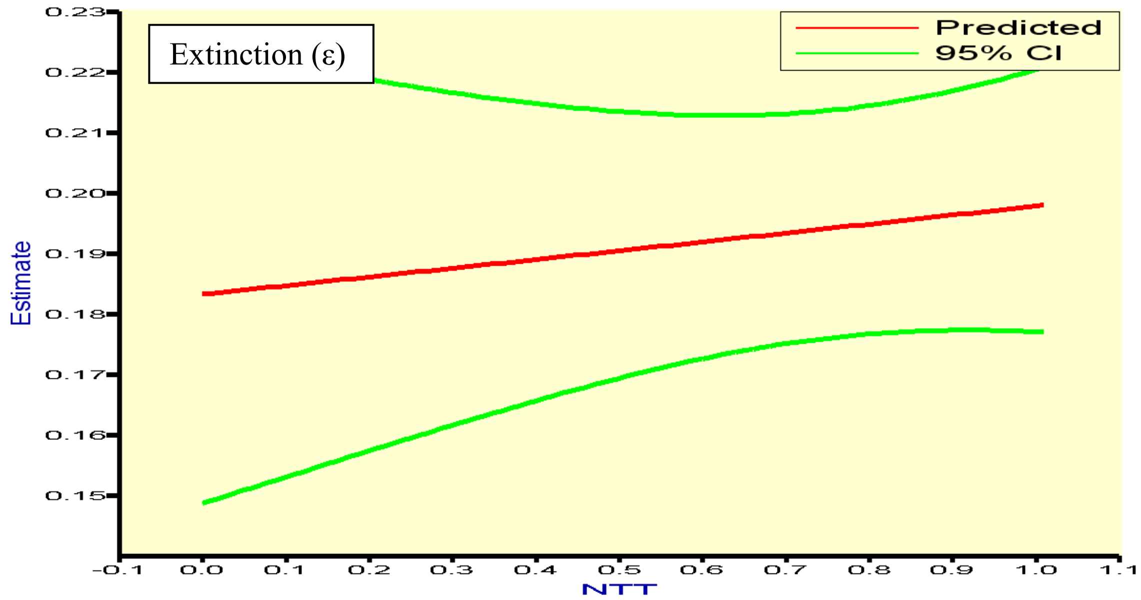

Figure 6.Univariate relationship between nesting tree type and Wood Stork colonies local extinction rate from 1970-2010 in the southeastern United States. Higher values of NTT indicate more trees than shrubs in the colony.

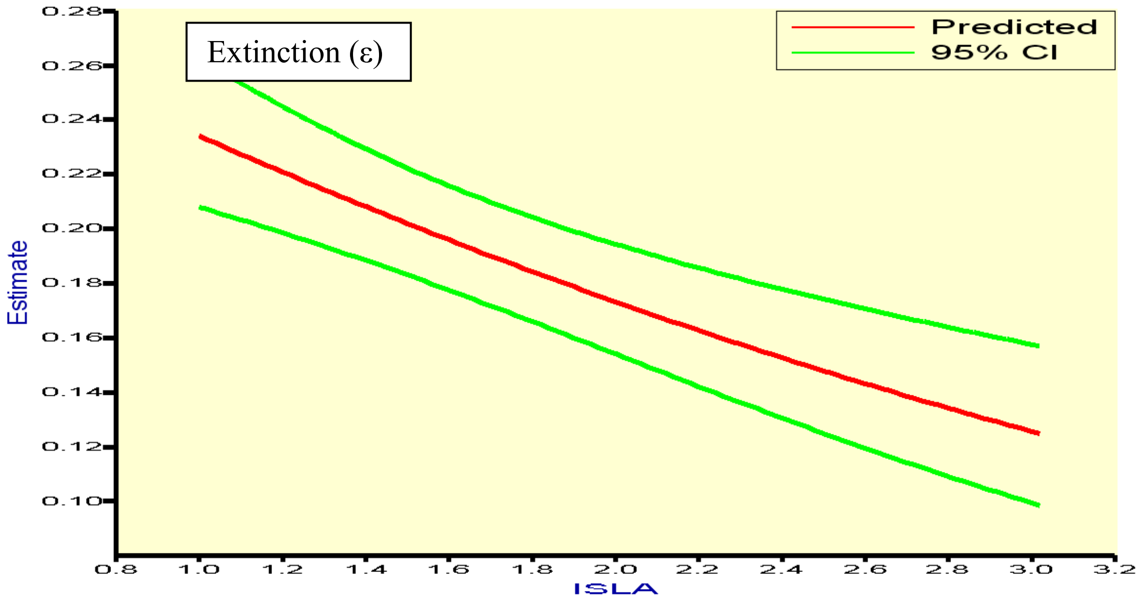

Figure 7. Relationship between degree of isolation of colony islands from mainland edge and Wood Stork colony local extinction rate from 1970-2010 in the southeastern United States. Higher values of ISLA indicate less connectivity with the mainland.

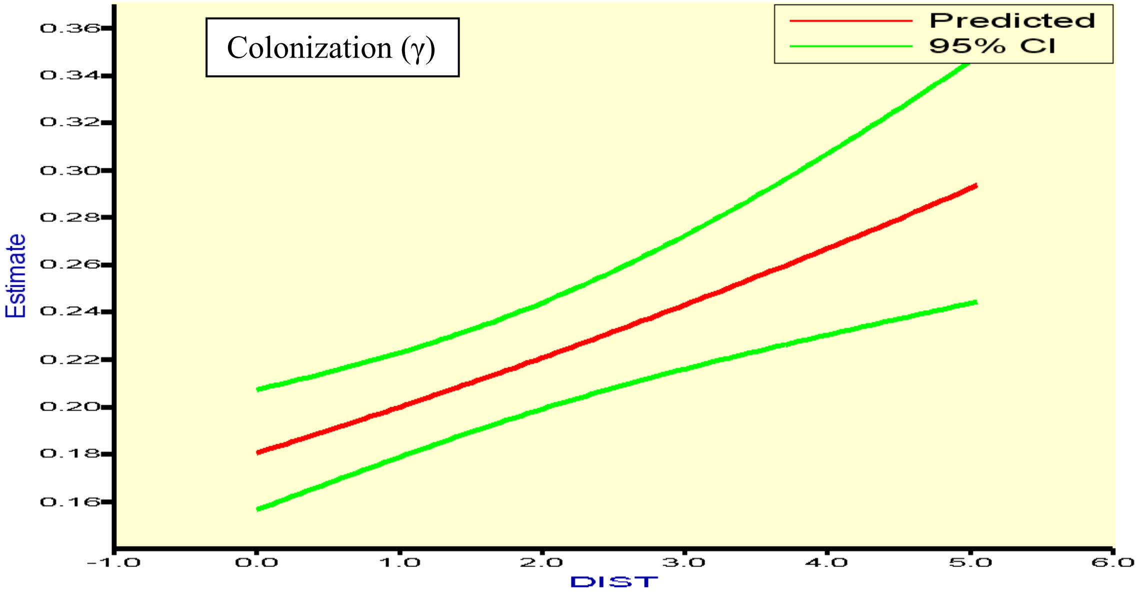

Figure 8. Relationship between disturbance close to Wood Stork colony and colony colonization rate from 1970-2010 in the southeastern United States. Higher values of disturbance indicate more human activity close to stork colonies.

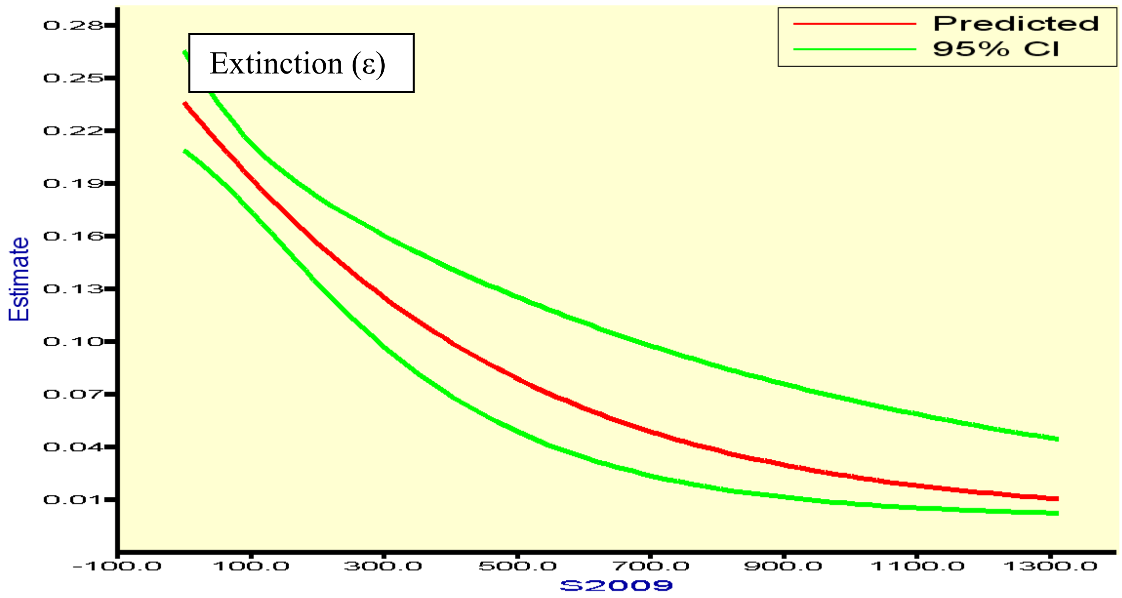

Figure 9. Relationship between Wood Stork colony size and stork colony local extinction rate from 1970-2010 in the southeastern United States.

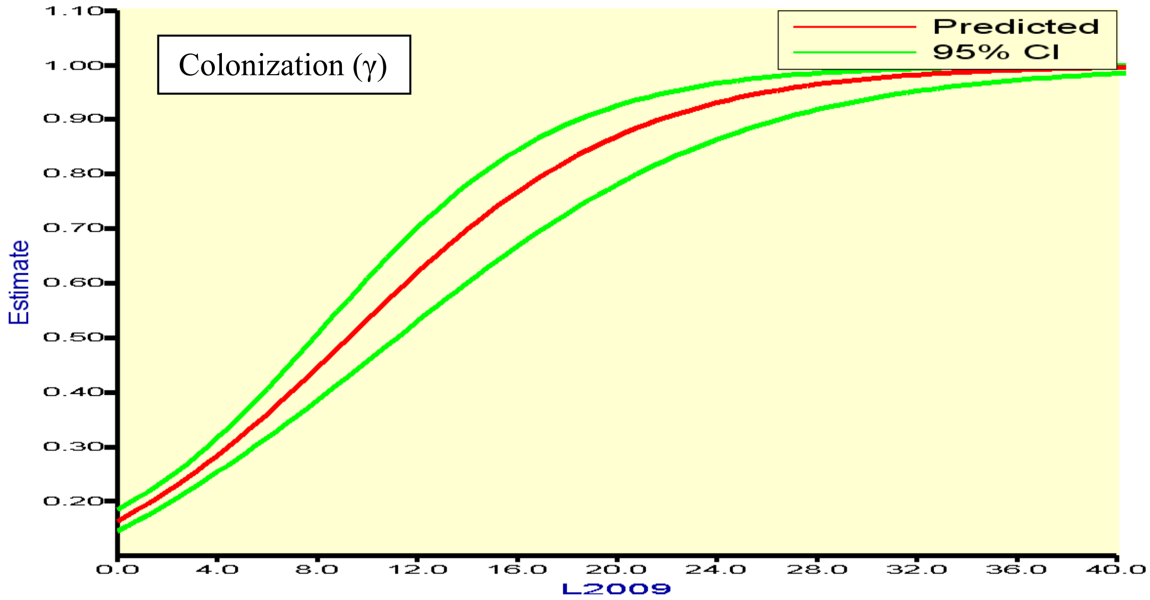

Figure 10. Relationship between Wood Stork colony longevity and stork colony recolonization rate from 1970-2010 in the southeastern United States.

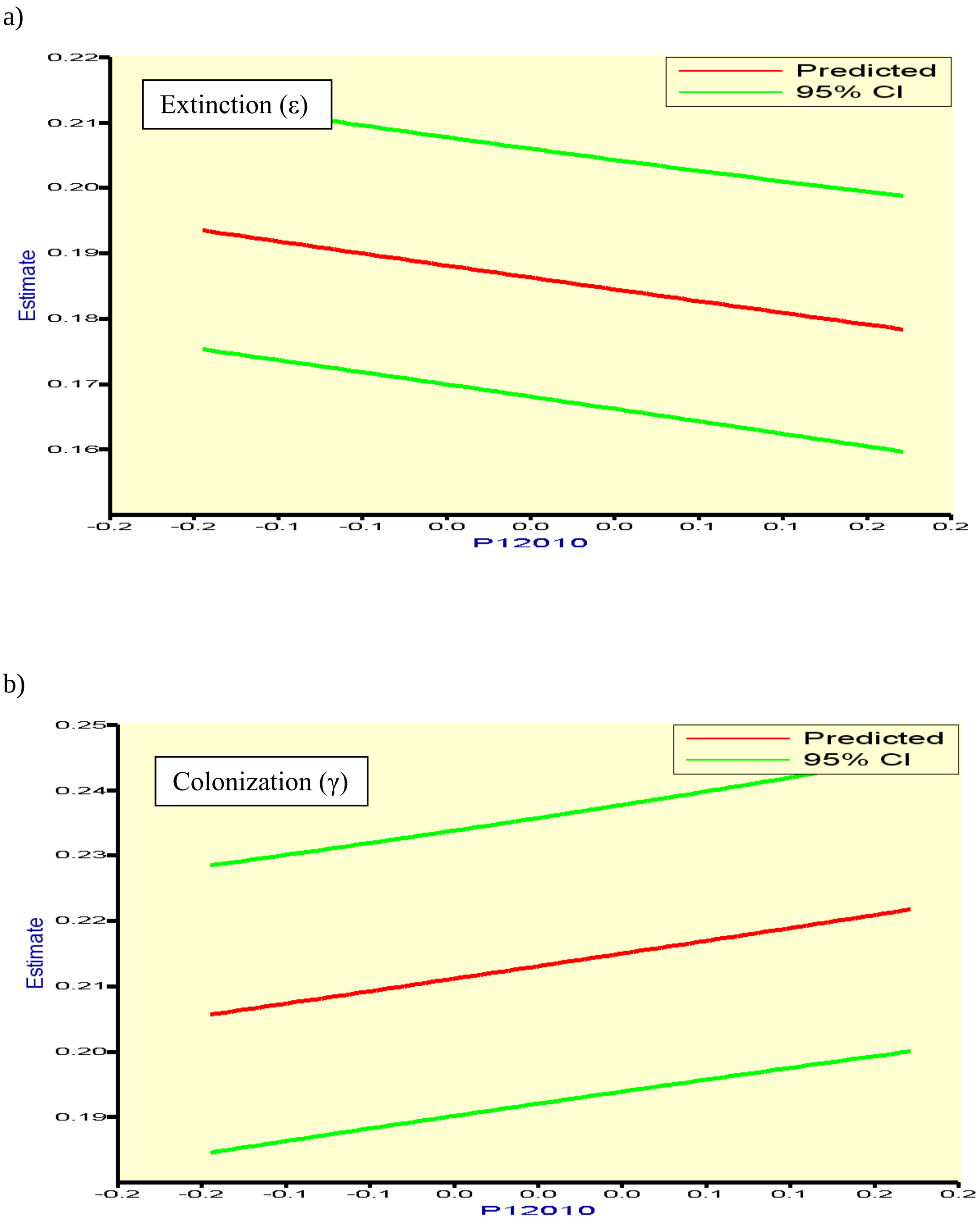

Figure 11. Relationship between precipitation 12 months before nest initiation and rates of Wood Stork colony a) local extinction and b) colonization from 1970-2010 in the southeastern United States.

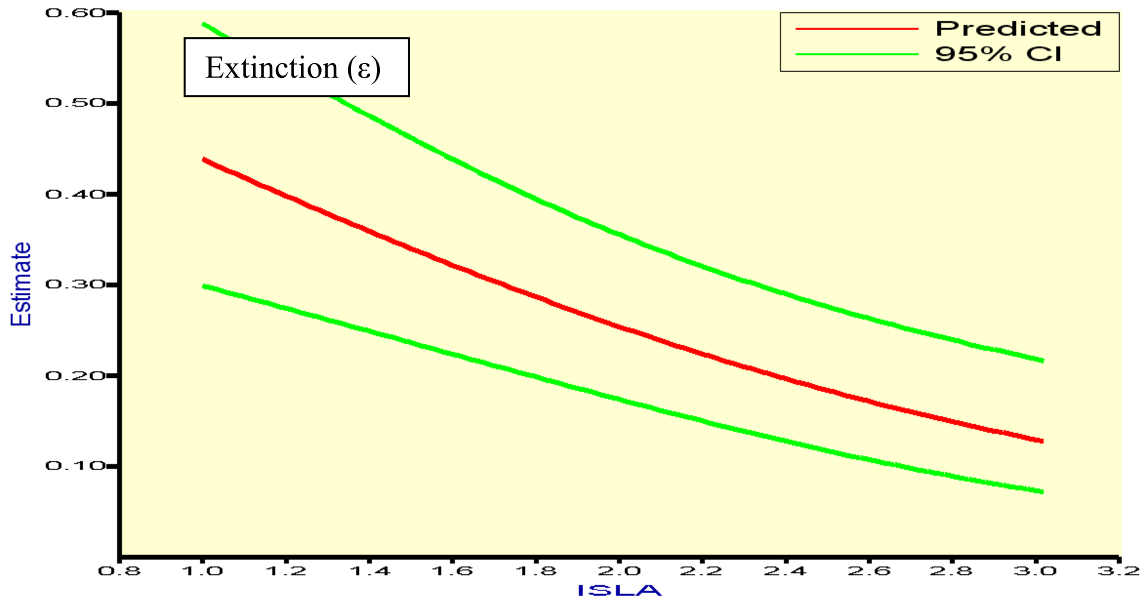

Figure 12. Relationship between degree of isolation of colony islands from mainland edge and Wood Stork colony local extinction rate from 1997-2007 in Florida. Higher values of ISLA indicate less connectivity with the mainland.

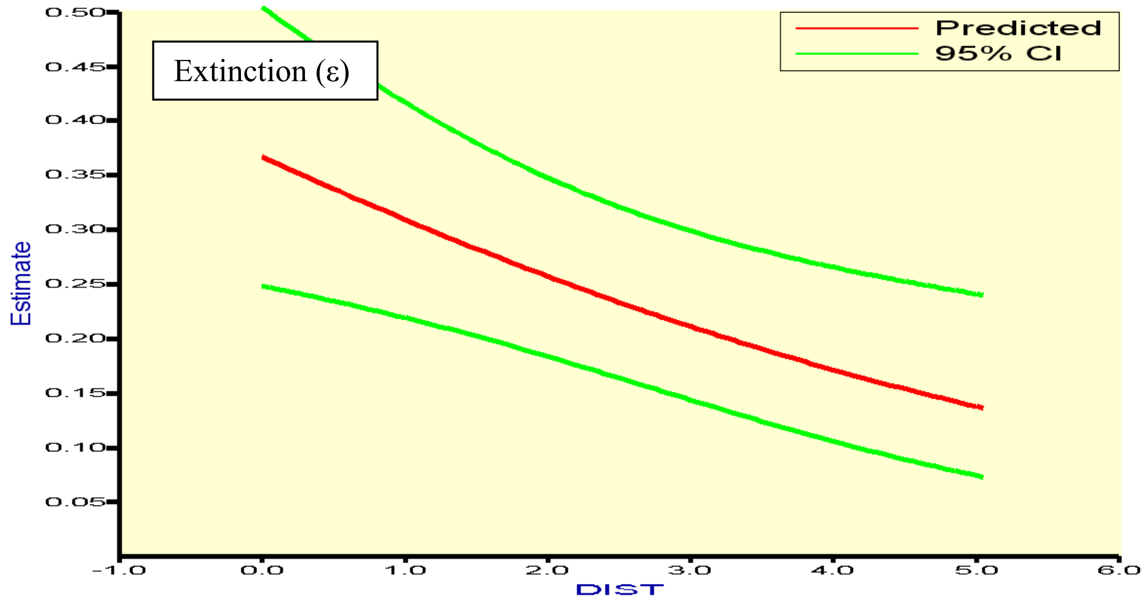

Figure 13. Relationship between human activity close to Wood Stork colony and colony local extinction rate from 1997-2007 in Florida. Higher values of disturbance indicate more human activity close to stork colonies.

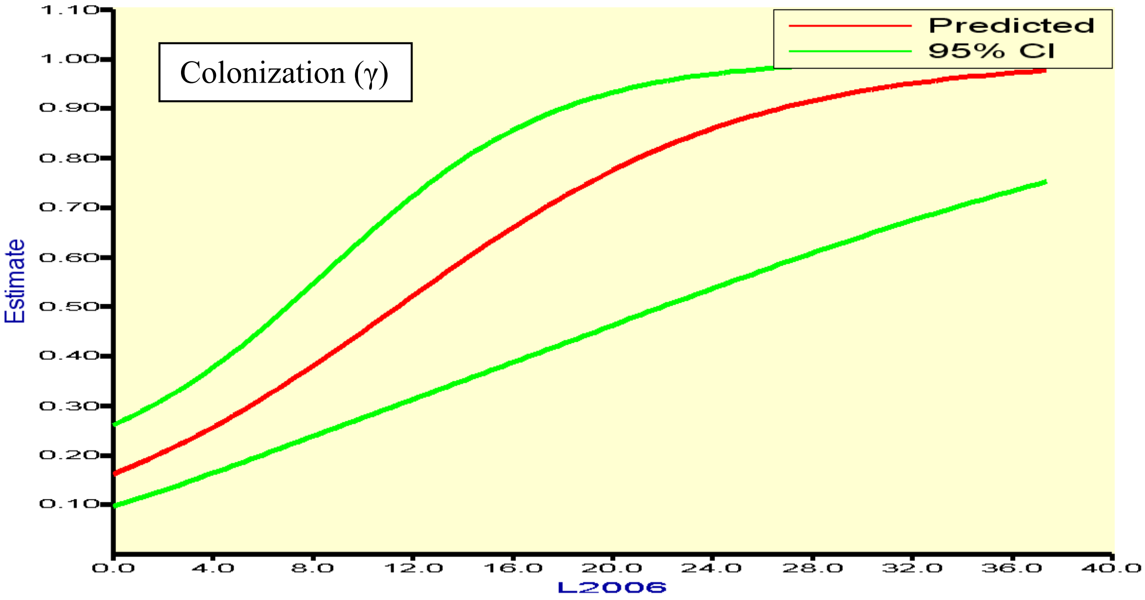

Figure 14. Relationship between Wood Stork colony longevity and colony colonization rate from 1997-2007 in Florida.

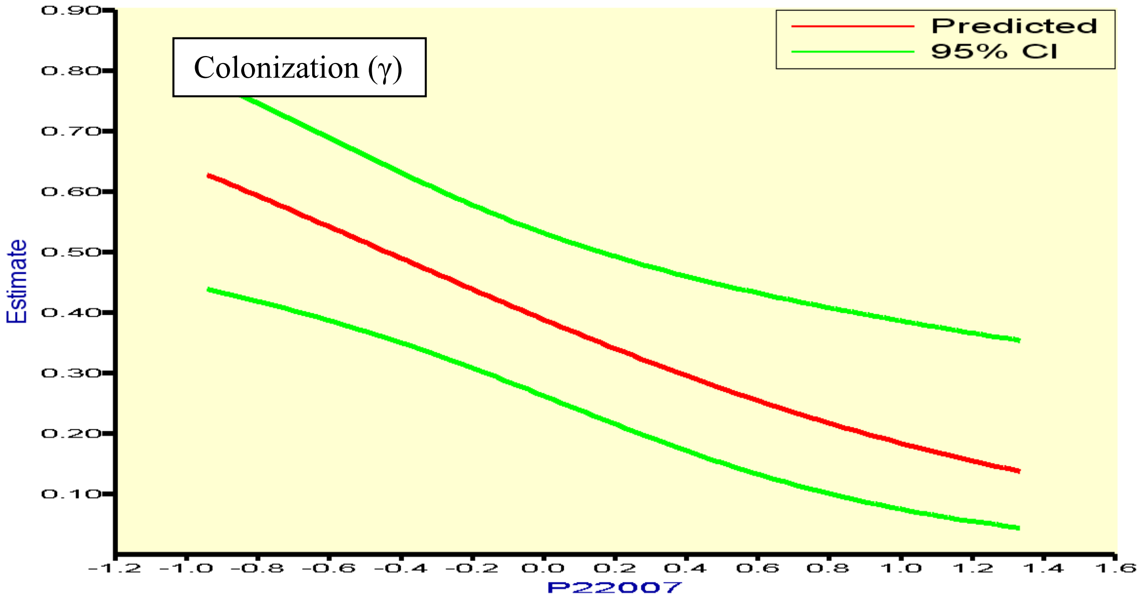

Figure 15. Relationship between precipitation 36 months before nest initiation and Wood Stork colony colonization rate from 1997-2007 in Florida.

Appendix 1. Explanation and legend for attached Microsoft Excel 2007 data sheet of Wood Stork colonies dataset in the southeastern United States from 1970-2010.

Under column “Status”, colonies were classified into High, Low, Redundant, only1, and empty. Definition of each category as following:

High quality: Colony with at least 2 active observations and these observations occurred in consecutive years or were connected with confirmed inactive observation(s).

Low quality: Colony with at least 2 active observations and these observations did NOT occur in consecutive years or were NOT connected with confirmed inactive observation(s).

Redundant: Colony registered as separate colony in the dataset but was actually the same as another colony.

Empty: Colony had no active observations.

Only 1: Colony with only one active observation.

Colonies with High and Low status were considered usable while colonies with redundant, only 1, and empty were considered unusable in the occupancy analysis.

Cell color notations under year column from 1970-2010:

State

Indicated newly indentified colonies in the dataset

Active

Indicated colony was active in particular year/colony cell.

Inactive

Indicated colony was inactive in particular year/colony cell

Not checked or unknown

Indicated colony was not checked or unknown in particular year/colony cell

First year

Indicated colony was confirmed as first year colony was observed as active

Active with conflict observations

Indicated particular year/colony cell had both active and inactive observations. However, it is treated as active considering different survey timing within a breeding season.