

FINAL REPORT

THE EFFECTS OF HYDROLOGIC STRESSORS ON WADING BIRD FORAGING DISTRIBUTIONS IN THE EVERGLADES FROM 1985-2000

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PRINCIPAL INVESTIGATOR

Dr. Michael J. Conroy, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602-2152

CO-PRINCIPAL INVESTIGATORS

Dr. James T. Peterson, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602-2152

Dr. Clinton T. Moore, Patuxent Wildlife Research Center, University of Georgia, Athens, GA 30602-2152

POSTDOCTORAL ASSOCIATE

Dr. Jonathan Runge, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602-2152

RESEARCH COORDINATOR

Jay Howell, Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602-2152

GRADUATE ASSISTANT

Zhenyu Zhong Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602-2152,

EXECUTIVE SUMMARY

We used counts from systematic reconnaissance flights (SRF) to quantify patterns in wading bird distribution and abundance in relation to hydrologic factors from 1985-2000 in the Everglades system. We first reviewed published literature and reports describing historical changes in hydrology and wading bird distribution and abundance, and postulating factors that may have contributed to the decline. We identified four principal hypotheses: (1) distant magnets, (2) transitional habitats, (3) hydropattern alteration, and (4) estuarine degradation; in addition we describe a “food availability” hypothesis. Before developing models, we first describe the SRF data and important auxiliary data on hydrology and nesting birds, and identify strengths and weaknesses of the sampling approaches and other factors affecting data quality. We identified several important areas where survey protocols, data management, or uncontrolled factors such as heterogeneous detection may have adversely affected data quality. We also comprehensively review previous models of wading birds and other fauna of the Everglades system. Many previous models are highly complex, yet lacking in empirical support and predictive ability. We then proceeded to construct a series of models centered on the alternative biological hypotheses we identified in our literature review, and focusing on the two species for which the most data existed, White Ibis (WHIB) and Great Egret (GREG). We used both mixed model analysis in SAS and zero-inflated, random effects modeling in PyMC, a program that implements Markov chain- Monte Carlo (MCMC). Our analysis supported a global model, in which the factors postulated under all of the major hypotheses are assumed to operate. Predictions based on the global model suggested optimal water levels and drying rates for both species, with optima differing by species. We also conducted a dual-observer trial to estimation

rates of detection and source of heterogeneity in detection rates. We found that detection rates generally were below 70%, sometimes markedly so, and varied by species, observer, and position in the aircraft. Simulation modeling indicated that these rates and types of heterogeneity could profoundly affect inference obtained from models based on these data, and we recommend that detection be taken into account both in survey design and in the interpretation of data. Finally, we consider the use of SRF data as performance measures, and recommend the use of predictions under alternative models, in conjunction with adaptive management, as the best approach for utilizing these data in decision making, and reducing uncertainty through time.

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1.0 INTRODUCTION

1.1 Resource problem

The Everglades basin is one of the world's largest wetland systems (Figure 1); the Basin has undergone dramatic alterations under human impacts, starting in the early 1900s. The decline of wading bird populations in the Everglades was one of the first and most visible signs that the Everglades ecosystem had been degraded. Currently, wading birds are used as an important component of the Everglades restoration effort. The Comprehensive Everglades Restoration Plan (CERP) uses hypothesized relationships between wading birds and hydrology to shape hydrologic targets for the Everglades restoration. In addition, several CERP performance measures based on wading birds will be used to gauge the progress and success of the Everglades restoration. Candidate performance-measures include the following: the number of large flocks in the system, the number of nests in the system, the location of the nesting colonies, the occurrence of large flocks, the presence and distribution of foraging flocks, and the timing of nesting initiation. The results from this project will be used to fine-tune these hydrologic targets and develop useful performance measures to support the Everglades restoration.

The number of wading bird nests in the Everglades has decreased by an estimated 70% since the 1930s (Crozier and Gawlik 2003), but population trends appear to be species-specific. The numbers of Wood Stork (*Mycteria americana*) and White Ibis (*Eudocimus albus*) nests in the Everglades have decreased by 78% and 87%, respectively, since the 1930s. However, the number of Great Egret (*Ardea alba*) and Great Blue Heron (*Ardea herodias*) nests appears to have increased over the past 50 years, although declines in count statistics from surveys may not be directly interpretable as indicating population declines (e.g., Kushlan and Frohring 1986). The species-specific population changes emphasize the need to examine individual species and their hydrologic requirements. Accompanying

these changes in population numbers has been a substantial shift in the location of wading bird colonies in the Everglades since the 1930s (Kushlan and White 1977; Ogden 1994). The large “super colonies” that once lined the coastal mangrove fringe in the southern Everglades have been replaced by smaller colonies located in the northern freshwater portions of the Everglades.

These changes in the wading bird community have coincided with the construction of massive water control works for flood control and water supply in South Florida. This infrastructure has altered the hydroperiod, sheet flow, recession rate, and water depth within different parts of the system. Under the “food availability” hypothesis, water-management activities have changed the hydrology and decreased the extent of the Everglades reducing the availability of prey for wading birds, reducing their feeding success and ultimately their reproductive output. Prey availability may be reduced by a decrease in the density of prey and/or the vulnerability of prey in foraging areas. Thus, a major focus of this study is to identify factors, particularly those related to water management, that influence the abundance and spatial distribution of foraging birds.

1.2 Project scope

The main objectives of this study are to: (1) determine the relative contribution of short- and long-term effects of hydrologic stressors and landscape variables on the variation and trends in wading bird feeding patterns and population sizes observed over the past 17 years; (2) develop wading bird performance measures for CERP based on relationships between wading bird spatial distributions and annual nesting effort; (3) evaluate the SRF as a tool for wading bird monitoring; and (4) develop a system for displaying spatially-explicit information in a GIS framework. The main challenge of this project is to capture the realism of how wading birds use a dynamic landscape with key variables that are changing at different time scales. Landscape features, such as basin and elevation, are essentially static. Dominant

vegetation types change, but very slowly. Overlain on top of those relatively static features is water, which pulses daily and seasonally. Wading birds move across that matrix of static features and pulsing water to locate places where the combination of variables is suitable for their individual foraging apparatus (Maurer 1996). Capturing the interactions among those variables, which reflect the choices faced by birds, is the basis for our approach.

This project extends over the entire Everglades basin, because this is the scale at which wading birds use the ecosystem (Figure 1). The primary data set for the project consists of spatially-explicit aerial wading bird surveys (i.e., Systematic Reconnaissance Flight surveys; SRF). Both the spatial distribution and movement of birds across the landscape are believed to be linked to successful nesting. Preliminary analyses of the SRF data have correlated the abundance of large foraging flocks in the breeding season, indicative of high-quality foraging areas, with high nesting effort. Previous analyses of SRF data examined only the northern (Bancroft et al. 1994; 2002; Hoffman et al. 1994; Bancroft and Sawicki 1995) or the southern (Russell and Portier 1999) Everglades and found that vegetation and hydrology affected wading bird distribution and abundance patterns. A weakness of these studies was that when bird abundance was low it was unclear whether birds were simply shifting to other portions of the system or whether they left the system entirely. It is likely that the linkage between the northern and southern portions of the landscape may in fact be an important mechanism to sustain wading bird populations during short-term fluctuations in hydrologic conditions. This important link between landscape level processes and wading bird population dynamics has yet to be quantified. This project is needed to bridge this gap and provide resource managers with the tools and understanding to help restore the Everglades ecosystem.

The models derived in this work will have immediate benefit to resource managers because they will contain quantitative information related to the sensitivity of the ecosystem to management activities. The results from this project will provide the predictive link needed to formulate CERP wading bird performance measures that will help guide the Everglades restoration. The results of this research will also guide development of more robust, mechanistic models of population response to environmental change (i.e., Across Trophic Level System Simulation [ATLSS]; Huston et al. 1996).

The project has three stages: collate existing primary and ancillary data sets into a single data base, perform an initial exploration of the assembled data sets, and develop detailed empirical models and performance measures aimed at quantifying the effects of multiple hydrologic and landscape factors on wading bird populations. We describe approaches for each of these stages below after first reviewing the literature documenting the broad scale hydrological and vegetative changes that have occurred in this system, along with concomitant changes in the abundance and distribution of wading birds.

2.0 LITERATURE REVIEW

2.1 Everglades hydrology and vegetation changes

Prior to the major hydrological changes induced by human engineering during mid-century, the Everglades system was characterized by several distinct features. Key aspects of the pre-disturbance system included the following (Russell and Portier 1999; Harwell 1997): first, dynamic storage and sheet flow of water with spatially variable hydroperiod, and nutrients derived principally from rainfall resulting in an oligotrophic system; second, a large spatial scale with water flowing virtually without interruption over a nearly flat landscape extending from Lake Okeechobee to Florida Bay; third, habitat heterogeneity, with heterogeneous vegetation distribution, microtopographic relief, local climatic variation, and episodic disturbances. Seasonal recession of water created a transitional ecotone, exposing aquatic prey. Episodic

events such as hard freezes, wildfires, and hurricanes further modified this landscape. Fourth, the system was strongly influenced by natural disturbances, with fires, infrequent freeze events, prolonged droughts, and extreme winds.

By the mid 20th century, this system had been extensively altered by humans, as agriculture and urban development extended into the southern portion of the Peninsula. First, human population growth dramatically increased in South Florida, mostly concentrated along the Atlantic Coastal Ridge. An extensive system of canals, levees, and water control devices altered hydrology, and roadways, urban developments, and other human infrastructure dissected the landscape. The amplitude, spatial extent, and timing of water movements were all drastically altered, with a resulting major reduction in spatio-temporal variability. Concomitantly there occurred major changes in the scale of agribusiness south of Lake Okeechobee, the region directly in the historical path of water flow through the Everglades.

As might be expected for systems so tied to hydrologic regime, dramatic changes occurred in the natural function of the Everglades, ultimately reflected in floral and faunal communities. Increased drainage during the normally wet season, together with flooding during dry periods, influenced rates of oxidation and soil subsidence, and pumping of agricultural runoff through the system led to nutrient enrichment and eutrophication (Rudnick et al. 1999). Vegetative communities responded accordingly. For instance, cattail (*Typha domingensis*) has expanded aggressively into areas of the Everglades previously dominated by sawgrass (*Cladium jamaicense*), although there are competing explanations that revolve around increased nitrification (Newman et al. 1996; 1998). Dramatic changes occurred in vertebrate communities, much of it due to changed hydrology (Strong et al. 1997; Frederick and Collopy 1989; Bancroft et al. 2002; Russell et al. 2002) but also to eutrophication (Crozier and Gawlik 2002).

2.2 Wading bird biology and population dynamics

Concomitant with the changes in hydrologic regime, nutrient loads, and vegetation, major changes occurred in the abundance and distribution of wading birds. Before discussing alternative hypotheses that have been put forth to explain these changes, we first review relevant aspects of wading bird ecology.

The species of wading birds of interest in this system nest in large aggregations from a few dozens to tens of thousands of birds. Presumably, the birds that are observed on the SRFs (considered in more detail below) are associated with specific colonies, although the degree of association clearly will vary depending on time of year of the SRF. Important differences exist among species with respect to (1) the distribution of distances at which foraging occurs, (2) the role of social attraction in facilitating foraging (e.g., Erwin 1983), (3) fidelity to nesting site, and perhaps most relevant to the current study, (4) temporal and spatial scale of response to environmental conditions (e.g., water levels) and the prey densities (giving-up densities or GUD) below which foraging bouts are discontinued (Frederick and Ogden 1997; Strong et al. 1997; Russell et al. 2002; Frederick and Ogden 2001; Kushlan 1986; Gawlik 2002). For instance, Frederick et al. (1996a) suggested that White Ibises are nomadic breeders adapted to take advantage of food resources that are highly unpredictable at large spatial scales and at annual time scales. In contrast, wood storks appear to be more robust to hydrologic changes and will remain in an area longer following disruption of “natural” flows or other impacts.

Major declines in populations of wading birds and distributional shifts away from South Florida both occurred by the mid 20th century (Kushlan and Frohring 1986; Frohring et al. 1988). Although there clearly have been general declines in the population levels of most species, the extent to which local population declines were principally due to range-wide population declines related to vegetation changes, or the result of distributional shifts in response to changing water distribution, is largely unknown. In

particular, the expansion of impoundments in the Southeast, largely associated with aquaculture, may have had a profound influence on wading bird distribution (Fleury and Sherry 1995; Melvin et al. 1999).

2.3 Hypotheses to explain population decline and distributional changes

At least four hypotheses, involving factors operating at differing spatial scales, have been postulated as explaining the observed declines in wading bird abundance and distribution (Walters et al. 1992).

2.3.1 Distant magnets

Under this hypothesis, declines in local (i.e., Everglades system) populations of wading birds were caused not by concomitant declines in local habitat quality, but rather by attraction to superior habitats elsewhere. Support for this hypothesis is provided by increases in populations outside of Florida, for example of White Ibises in South Carolina that roughly matched concomitant decreases in Florida populations (Frederick and Collopy 1989). It appears certain that at least some species of wading birds have been able to exploit newly available shallow water habitats, for instance those centering about aquaculture (Fleury and Sherry 1995; Melvin et al. 1999). Arguing against this hypothesis are the facts that habitats have not improved in most places outside Florida, and that large numbers of wading birds still migrate to South Florida but fail to successfully reproduce (Frederick and Ogden, personal communication). As pointed out by Walters et al. (1992), even if it is demonstrated that large numbers of wading birds have been attracted to areas outside Florida, it remains to be explained why the populations that do nest in the Everglades have been unsuccessful in sustaining positive population growth.

2.3.2 Transitional habitats

Hydrological models suggest that under natural water flow (i.e., prior to 20th century impacts) there were fewer, but larger, transitional habitats that offered shallow water early in the dry season. These

areas are important for allowing birds to build metabolic reserves, in turn stimulating nesting. Implications of this hypothesis include the recommendation that water flows be restored into key areas (WCA3B, NESS, Taylor Slough) with profound long-term impacts to the eastern part of the Everglades system.

2.3.4 Hydropattern alteration

Kushlan (1987), among others, has suggested that a key requirement for successful wading bird nesting may be the occurrence of annual, relatively severe “progressive drawdowns”, with steady drops in water levels exposing fresh, transitional habitats throughout the season. Walters et al. (1992) questioned this hypothesis based on empirical evidence and model predictions and argued “if the progressive drydown arguments were correct, the birds should be doing better now than they did historically.” However, the hypothesis has received a degree of at least indirect empirical and experimental support (e.g., Gawlik 2002; Russell et al. 2002) and is the subject of further discussion under the “food availability hypothesis,” considered in more detail below.

2.3.5 Estuarine degradation

Several lines of evidence suggest that Everglades wading bird declines were due to declines in estuarine productivity associated with the reduced freshwater flows (Costanza et al. 1990; Walters et al. 1992; Sklar et al. 1990). This syndrome of decreased flows followed by estuarine degradation has also been blamed for general declines in waterfowl populations in coastal wetlands of the South. There seems to be little doubt that declines in estuarine productivity have occurred contemporaneously with declining populations of Everglades wading birds. It is not clear, however, that this factor alone is sufficient to explain the declines, and seems more likely to have acted in combination with hydropattern alteration and other factors.

Walters et al. (1992) advocated treating each of the above as mutually exclusive hypotheses, rather than as factors that may be operating in concert, and at differing spatio-temporal scales. They based this view on the fact that wading bird populations have persistently declined since the 1940's despite efforts to mitigate the decline through water management. Walters et al. (1992) also appeared to favor the “estuarine degradation” hypotheses among the four, and advocated experimental water management to discriminate among the alternative hypotheses.

We too advocate experimental and adaptive approaches but, for several reasons, are less inclined to treat these as mutually exclusive hypotheses or to dismiss individual factors. First, on general principles, we would expect any system as complex and variable as the Everglades to be influenced by many processes and operating at multiple spatial scales (Levin 1992). We think it unlikely that a single factor or explanation operating at a particular scale would overwhelm all others. We find this idea particularly unlikely when the system includes communities of nomadic birds that move over landscapes many times larger than the Everglades system and respond differentially to disturbance, food availability, and other factors. Second, even if the “mutually exclusive” formulation turns out to be true, we see nothing being lost by describing and modeling the system via multiple, interacting factors, so long as data can be used to estimate the strength of factor and interactive effects. If a single factor does dominate, then data will support the strength of that factor and the weakness of competitors, including interactive effects. As seen below, we advocate a hierarchical modeling approach to explore these relationships, in conjunction with information-theoretic and Bayesian measures of parameter and alternative model credibility.

2.3.6 The food availability hypothesis

Beyond these four general hypotheses, which operate at different spatio-temporal scales, Russell and Portier (1999) list several competing ideas that revolve around the specific issue of foraging dynamics and differ with respect to the specific mechanisms and timing of hydrologic impacts. These may be viewed as sub hypotheses within a general “food availability hypothesis.” As with the hypotheses described above, it is not obvious to us that these are, or should be considered, as mutually exclusive hypotheses, rather than as functional responses that may operate to varying degrees and at varying spatio-temporal scales. In any case, Russell and Portier (1999) propose that wading bird declines are:

- Directly related to loss of overall foraging habitat.
- Directly related to the disproportionate loss of specific (seasonal) foraging habitat types.
- Directly related to changes in the spatial configuration of foraging habitat types.
- Indirectly related to fragmentation in the continuity of water flow among foraging habitat types.
- Directly related to increased, seasonal, water level fluctuations within foraging habitat types.
- Indirectly related to alteration in the hydrologic periodicity, (including drydown frequency, magnitude and duration) of foraging habitat.

Russell and Portier (1999) also summarize what they term as a “consensus model”, and claim that the SRF data are consistent with this model. The model posits a functional relationship between hydrologic periodicity, food availability and reproductive success. Essential elements are:

- Wading birds depend on the efficient acquisition of prey to sustain nest building and egg laying activities, and to feed their hatchlings.
- This requires prey items to be “relatively concentrated” in “small areas” to avoid excessive search time.

- During the dry season of the Everglades, such high concentrations are provided by the shallow pools that develop along a variety of ‘drying fronts’ at the edges of the areas of deeper water.
- Feeding pressure reduces prey density in these pools (Kushlan 1976), so a continual supply of new shallow water areas is required. Ideal conditions, under this model, would be continuous drying at a rate of 5mm d⁻¹.

During the 1970s, correlations were established between the hydrologic function of the Everglades and wading bird feeding success (Kushlan 1976; Ogden et al. 1976; Kushlan 1977; Kushlan 1979). An effort to link nesting directly to hydrologic properties showed that nesting was affected by drying rate, but the effects were inconsistent among years and species (Kushlan 1986; Frederick and Collopy 1989; Bancroft et al. 1990; Frederick 1994; Frederick and Spalding 1994). A harmonic analysis of the annual hydrologic cycle showed that Wood Stork nesting effort and hydrology were related (Nuttall 1997). The first experimental evidence clearly linking food availability with reproductive output was for Great White Herons (*Ardea herodias occidentalis*) in Florida Bay (Powell 1983).

Gawlik (2002) explored these hypotheses with a series of experiments in artificial wetlands in which prey density and water depths were manipulated, and evaluated the numeric response of eight species of free-ranging wading birds (White Ibis; Wood Stork; Snowy Egret, *Egretta thula*; Glossy Ibis, *Plegadis falcinellus*; Great Egret; Tricolored Heron, *Egretta tricolor*; Great Blue Heron; and Little Blue Heron, *Egretta caerulea*). The giving-up-density (GUD; density of prey where the predators quit foraging) increased with increasing water depth. There was an apparent (but non-statistical) difference among species in this relationship, with the White Ibis, Wood Stork, and Snowy Egret having higher GUDs in the deepest treatment than did Glossy Ibis, Great Egret, Tricolored Heron, Great Blue Heron, and Little Blue Heron. The feeding strategy of the first three species groups appeared to be one of

searching for new high-quality food patches rather than staying and exploiting food patches that were declining in quality. The author further inferred that birds were not responding to average prey availability at large spatial scales but rather at small-scale high-quality patches. The quality of these patches is driven largely by physical features of the landscape, hydrology, and microtopography. Finally, the author noted that those species employing a searching strategy also have shown the most severe population declines, suggesting that factors affecting bird density at feeding sites also may have affected population size.

2.4 Everglades restoration

Recently, efforts have begun to develop management strategies for restoration of the Everglades system. To date, most attention has focused on “replumbing” this system so as to restore (or at least mimic) hydrologic patterns thought to have prevailed before the onset of major agricultural and developmental pressures of the 20th century. Models have been developed that seek to explore the impacts of alternative hydrologic scenarios on vegetation and animal communities of the Everglades (DeAngelis et al. 1998; Huston et al. 1996; Curnutt et al. 2000), and potentially can be combined with risk assessment (Englehardt 1998; Harwell 1998), decision theory (Lindley 1985), or other approaches to guide decision-making. All such approaches of course are limited by the degree to which policy makers have (or allow themselves) choices, and by the fact that certain impacts to the Everglades are extremely unlikely to be reversed, at least in the short term (e.g., the isolation of Lake Okeechobee from the remnant Everglades; the conversion of Atlantic Coastal Ridge habitats to Miami). Even given these constraints, decision-making must take into account the fact that biological response to any proposed alternative is subject to tremendous uncertainty. To be useful to policy makers, predictive models must honestly capture critical aspects of this uncertainty.

3.0 REVIEW OF SURVEY DATA AND OTHER DATA SOURCES

A number of sources of historical data may contribute to the construction of decision models for the wading bird component of the Everglades system. The sources most applicable to the focus of this work are data collected from the Systematic Reconnaissance Flights (SRF). These surveys are conducted annually, are extensive both in time and space, and are carried out cooperatively by participants working in pre-assigned areas of operation. In addition, we also consider how counts of birds at nesting colonies can be used as ancillary data in the construction of statistical models. Here we briefly describe principal characteristics of the two types of surveys; discuss their strengths, shortcomings, and potential for use in system modeling; and review some applications of their use to date. With few exceptions, descriptions of the surveys are found in unpublished reports housed in participating agencies.

3.1 The SRF Survey

The SRF survey is intended to record the relative abundance, flock composition, and the spatial and temporal distribution of foraging wading birds across the entire Everglades system (11,640 km²). The surveys are conducted monthly during the historically drier part of the year (December-June), which includes the nesting season, but at least one survey is usually conducted in August at the height of the wet season. The survey is also used to assess general surface water conditions throughout the survey area, and, in some survey areas, to assess vegetation conditions.

Operational surveys were initiated in 1985, following a one-year pilot study (Portier and Smith 1984). The survey area comprised the water conservation areas (WCA) of the northern and central Everglades, Everglades National Park (ENP) and southern Big Cypress National Preserve (BCNP) in the south, and BCNP proper in the west. Surveys in the northern and central Everglades (hereafter, the northern survey area) were initially conducted by the National Audubon Society (NAS) through a contract

with the South Florida Water Management District (SFWMD) (Hoffman et al. 1990; Bancroft and Sawicki 1995; Sawicki et al. 1995). In 1995, the northern survey area was expanded to include the Holey Land and the Everglades Nutrient Removal Area (Sawicki et al. 1995). Surveys in the BCNP (hereafter, the western survey area) were initially conducted by the Florida Fish and Wildlife Conservation Commission (FWCC) (J. Schortemeyer, Florida Fish and Wildlife Conservation Commission, personal communication). However, the U.S. Army Corps of Engineers (USACE) now surveys both the northern and western survey areas (unpublished reports, U.S. Army Corps of Engineers, Vicksburg, Miss.), taking over survey responsibilities from the NAS in 1996 and from the FWCC in 1998. The southern survey area has been continually surveyed by ENP personnel since 1985 (Russell and Portier 1999).

Transects oriented east-west are spaced 2 km apart throughout the surveyed region. For purposes of data organization and reporting, transects are subdivided longitudinally into 2-km segments. Georeferencing equipment (LORAN C or GPS) is used to assure consistency in line and segment location among surveys. However, some transects were evidently realigned at some point, at least in the northern survey area (compare 898 segments in Figure 2 of Hoffman et al. [1990] to 883 segments in Figure 2 of Bancroft and Sawicki [1995]). A fixed-wing aircraft flying at 148 km/h ground speed follows the transects in alternating directions. Aircraft altitude is variously identified as 45 m (D. M. Fleming et al., unpublished manuscript), 61 m (Hoffman et al. 1990; Bancroft and Sawicki 1995; Sawicki et al. 1995), and 90 m (Russell and Portier 1999). A group of observers surveys birds and habitat conditions encountered in 150-m strips on either side of the aircraft. Distance of the strips from the transect line is probably known and possibly varies by survey area, but this information was not reported in any of the survey descriptions.

Survey aircraft generally contained four occupants: the pilot, two observers of wading birds, and a front-seat observer whose responsibilities were to record water surface conditions and other ancillary data and to monitor the location of the aircraft relative to the transect. However, only two observers were used after 1995 in the northern survey area (Nelson and Theriot 1997); responsibilities taken on by the third observer were thus shared by the remaining two. Documentation for the northern survey area suggests that survey roles tended to be carried out by the same individuals, especially within a year. We know of no existing information regarding the consistency of observer assignments in the southern survey area.

Observers recorded species, number, and longitude of all wading birds sighted within the transect strips. In the northern survey area, behavior of each bird was also recorded. Surveys in all areas recorded numbers of the following species: Great Egret, Great Blue Heron, White Ibis, Glossy Ibis, and Wood Stork. In the southern survey area, counts of Great White Heron and Roseate Spoonbill (*Ajaia ajaja*) were also recorded. Individuals of smaller-bodied, dark-plumaged species were counted collectively in a “Small Dark Herons” class which included (depending on survey area) Tricolored Heron, adult Little Blue Heron, Green Heron (*Butorides virescens*), Black-crowned Night-Heron (*Nycticorax nycticorax*), Yellow-crowned Night-Heron (*Nyctanassa violacea*), and the dark phase of Reddish Egret (*Egretta rufescens*). Similarly, a class of “Small Light Herons” contained individuals of the following species (depending on survey area): Snowy Egret, Cattle Egret (*Bubulcus Ibis*), immature Little Blue Heron, and the light phase of Reddish Egret.

General surface water conditions were recorded for the segment at large. Prior to 1989, a three-category classification of “dry,” indicating absence of surface water, “wet,” indicating continuous surface water, and “transitional” was used. Starting in 1989, surface water conditions were recorded in more than three categories, but approaches differed between the northern and southern survey areas. In the north,

the “transitional” category was split into two categories: “dry transitional” (areas less than 50% flooded) and “wet transitional” (areas more than 50% flooded). In the south, both “dry” and “transitional” categories were split: “dry/dry” (absence of surface water and no groundwater visible in landscape depressions), “dry/wet” (absence of surface water, but groundwater visible in depressions), “dry transitional” (some surface water present, but area is mostly dry), and “wet transitional” (area mostly covered by water, but some dry patches remain).

In the northern survey areas, an observer actively monitored vegetation conditions during the years 1985-1988. Each survey segment was assigned to one of eight vegetation classes (Hoffman et al. 1990). After 1995, vegetation conditions were passively monitored through videography of the survey flight.

3.2 Uses of the SRF data

Data from the SRF have been previously analyzed to model foraging distributions of wading birds in response to habitat or to hydrology. The basic observational unit in all analyses was the 0.6-km² grid cell formed by dividing the 300-m width transect strips into 2-km segments.

Hoffman et al. (1990; 1994) constructed hierarchical loglinear models (Agresti 1990:143-144) for the 3-way classification induced by combinations of bird density (represented in five categories of relative abundance), vegetation type, and surface water coverage in each cell in the WCAs. Their analyses were conducted for each of four bird species in each of 16 months from surveys conducted 1986-1988. They found that responses in bird abundance to vegetation and hydrological characteristics differed by species. Generally, however, they noted that current surface water conditions were better predictors of abundance than water conditions in the previous month when water levels were declining, but that the converse was true when water level was increasing.

Bancroft and Sawicki (1995) used a clustering rule to assign survey months and survey years into relative hydrological categories based on measures of surface water coverage from the SRF and on measures of water depth recorded at isolated gauging stations throughout the WCAs. For each hydrological category, they produced species-specific maps of bird occurrence and abundance. In particular, their maps portrayed changes in the monthly distribution of each bird species in years considered “flooded,” “wet,” “intermediate,” or “dry.” They also built a model of bird distribution based on associations between observed numbers of individuals and predictions of survey cell water depth provided by the SFWMD water depth model (Fennema et al. 1994). They found reasonably close agreement between predicted and observed bird distributions for three of the four species they investigated.

Bancroft et al. (1994) analyzed contingency tables to make assessments of preference for or avoidance of WCA subregions by foraging Great Egrets and White Ibises throughout each of four breeding seasons. They further investigated these data in conjunction with locations of breeding colonies to test hypotheses about birds’ abilities to choose nesting locations proximate to areas of sustained foraging habitat. They concluded that sites chosen for nesting generally were not good predictors of later foraging activity, primarily because the highly altered hydrological system no longer mitigates the deleterious effects of drought and spring rainfall.

Bancroft et al. (2002) fit a series of polynomial regression models to counts of birds detected in survey cells of the northern Everglades. They used output from a hydrological model and satellite imagery to assign water depth values and vegetation attributes, respectively, to survey cells. They analyzed data from two years representing extremes in hydrological pattern and concluded that water

depth and vegetation composition influenced abundance and therefore spatial distribution of several species of wading birds.

Russell and Portier (1999) constructed generalized linear models in which bird counts from the southern survey area were related to patterns in static landscape and dynamic hydrological features. Their models employed terms that helped to remove sources of variability due to seasonality, bird aggregation, and spatial autocorrelation among survey cells. They found that a landscape measure that distinguished principal basins was the best predictor of bird numbers, after removal of temporal and spatial effects. However, despite their size and complexity, no model could explain more than 15% of the total count variability for any species, most likely due to aggregation behavior of foraging birds.

Russell et al. (2002) used a technique that provided an index to water depth based on surface water coverage recorded in the SRF surveys of ENP. From each time series of water depth indices, they calculated a set of regression statistics that reflected water depth at the start of the dry season, the drying rate, and disruptions in the drying process for areas used by each bird species or species group. They fit counts of birds in May (assumed to index population-wide reproductive success) to families of models built from these derived variables, and they found similar patterns among species in bird response to water level, drying rate, and hydrological disruptions. Greater foraging numbers in May were best associated with patterns of moderate-depth water at the beginning of the dry season, continuous drying at $\sim 5\text{mm d}^{-1}$, and minimization of disruptions from this drying pattern.

3.3 Limitations of the SRF data and implications for its use

The SRF is a systematic transect survey uncorrected for bird detection rate. The survey area is fixed and overlaps an unknown proportion of the total Everglades foraging population each period. The monthly survey interval does not capture short duration, inter-survey bird movement or hydrological

events. The survey does not cover the entire November-June dry season (Russell and Portier 1999). The surveys cannot distinguish breeding from non-breeding adults, residents from temporary migrants, and species membership among smaller-bodied birds. Aggregative foraging behavior and chance fly-overs of nesting colonies raise special concerns about the statistical treatment of the data. Based on the documentation available at the time of this writing, several survey protocols appear to vary somewhat both between and within survey areas: survey altitude, location of transect lines, location of survey strips relative to transects, survey crew size and responsibilities, bird and habitat data recorded, and temporal extent of the survey season.

In our view, the greatest limitation of the survey is the fact that the proportion of birds detected is neither estimated, demonstrated to be constant across time, space, and species, nor analytically adjusted to remove confounding effects of varying survey conditions. Most accounts of the survey suggest that the counts are considered direct indices of bird abundance, in which the count total divided by the 0.15 sampling fraction is generally equated to abundance (cf. Hoffman et al. 1990; Bancroft and Sawicki 1995). The apparent belief is that the undercount is negligible, approximately 10-15% (Hoffman et al. 1990). Yet the only SRF study where estimation was attempted indicated detection rates of 0.54 for large dark birds and 0.26 for large white birds (Russell and Portier 1999). Though the estimation approach (Caughley et al. 1976) is imperfect and was based on results from the 1984 pilot study (Portier and Smith 1984), Russell and Portier (1999) and Russell et al. (2002) heed these estimates and caution against the use of the SRF as a measurement of abundance. However, they claim that the counts nevertheless serve as valid population indices, yielding unbiased estimates of relative population size and distribution (Russell and Portier 1999; Russell et al. 2002). To our knowledge, this claim is not supported by any empirical evidence, which would require confirmation that the index bears a constant, proportional

relationship abundance over time, space, or other relevant dimensions of comparison (Williams et al. 2002).

Aerial counts of bird populations are typically regarded as incomplete in that not all individuals of a species can be identified and counted (Johnson et al. 1989; Bromley et al. 1995; Dodd and Murphy 1995; Rodgers et al. 1995; Smith et al. 1995; Frederick et al. 1996*b*; Kingsford 1999). Although the sources of undercounting are varied, they can be roughly grouped into two categories: observer and visual biases. Observer bias is defined here as the differences in counts from observer to observer due to differential abilities to detect and identify individuals and is often related to the experience of the observer (Kendall et al. 1996) or visual acuity (Sauer et al. 1994). Observer bias can be minimized through the use of well-trained and experienced observers. We assume SRF observers were well trained and that many observers surveyed across multiple years. However, the changes in survey responsibilities (to the USACE) and presumably, personnel in 1996 and 1999 could have biased count data, as was described for snail kites (*Rostrhamus sociabilis plumbeus*) (Bennetts et al. 1999). Further, the reduction in the number of observers in the northern survey area after 1995 may bias comparisons of counts among areas and through time.

Visibility bias is defined here as the over- or under-counting of populations due to the ability to visually detect and identify individuals. Survey-induced bias is one source of visibility bias due to sampling protocols, such as the height and speed of the airplane as well as transect width (Pollock and Kendall 1987). Variability in visibility rates can be minimized through the use of standardized survey protocols. However as indicated above, survey protocols are apparently not consistent across the entire survey area, complicating any comprehensive analysis at the scale of the Everglades ecosystem.

Visibility can vary among bird species (Pollock and Kendall 1987). Body size or coloration can influence the ability to detect birds. For example, larger wading birds and those with bright coloration are generally more conspicuous and can be detected with greater frequency (Kingsford 1999). Species-specific behaviors, such as aggregative foraging behaviors, can also influence the ability to obtain accurate counts. Birds typically found in large (>5000) or small (<10) aggregations are more difficult to count and detect, respectively, resulting in significant undercounting of these species (Kingsford 1999). The physical habitat characteristics of survey areas also can affect the ability to detect birds (Bibby and Buckland 1987; Smith et al. 1995). Physical structures, such as tall grasses and tree canopies, can prevent aerial observers from detecting birds, thereby biasing counts. Bird detection is also influenced by a combination of behavioral traits and physical habitat structure. Species typically found foraging in shallow open water areas during non-nesting periods move to wooded habitat during the nesting season, so that detectability can change with season.

The Everglades consist of a mosaic of habitat types whose characteristics also vary temporally (i.e., among seasons and years). These characteristics presumably influence the bird population dynamics and may influence the ability to detect birds during surveys. For example, water levels affect both snail kite population sizes and detection rates (Bennetts et al. 1999). Bird communities in the Everglades also are composed of species with differing resource requirements, morphologies, behaviors and detectabilities. Failing to account for differences in detectability when making comparisons among habitats and species or through time introduces a systematic error or bias into the data that can lead to incorrect interpretations of statistical relationships and poor management decisions. For example, Bromley et al. (1995) found that visibility of arctic geese was lowest during years of highest reproduction and suggested that the use of unadjusted count data would lead to erroneous conclusions regarding the

status of populations. To minimize the influence of visual bias on estimates of population change, we believe that the methods for adjusting bird counts should be developed to ensure sound management decisions.

One method of developing bias adjustments is through the calibration of aerial surveys. This can be accomplished by comparing aerial counts with known benchmarks, such as ground counts (Frederick et al. 1996*b*; Kingsford 1999), boat counts (Conant et al. 1988), aerial photographs or videography (e.g., Dodd and Murphy 1995), and through the use of known numbers of surrogates (e.g., duck decoys; Smith et al. 1995). Evaluations are typically conducted under a variety of sampling conditions encountered in the study area and adjustments developed by relating the relative difference in counts to species traits and sampling conditions, such as water level. Russell and Portier (1999) suggested that this type of approach would be prohibitively expensive due to what they believed would be a large number of evaluations. However in our experience (e.g., Smith et al. 1995), we believe that adequate adjustments could be developed at minimal costs if evaluations are focused on factors known to influence aerial counts. Further savings would be gained by formally incorporating the results of previous studies under similar survey protocols and sampling conditions (Table 1).

Another approach to developing bias adjustments is through the use of auxiliary data (Bennetts et al. 1999). Certain types of auxiliary data collected during the survey could be used to adjust for confounding effects of varying survey conditions. Clearly, detection rate of birds farther from the airplane is lower than the rate for birds near the plane; therefore, a record of distance of each detected bird from a transect line or sampling point offers a way to adjust for this effect (Gates 1979, Burnham et al. 1980, Ramsey and Scott 1981, Buckland et al. 1993). Bird detection also varies with sunlight characteristics (e.g., time of day, month, sky conditions), vegetation type, observer experience, group size,

bird behavior, and other variables. Auxiliary data collected on these survey and response characteristics would be helpful in removing such sources of variability in detection rate (Drummer and McDonald 1987, Samuel et al. 1987).

Another fact about the SRF is that the survey cannot distinguish between birds that are and are not actively nesting. Therefore, inferences regarding linkages between the fate of particular nesting colonies and foraging activity will be indirect at best. Perhaps an approach similar to that of Bancroft et al. (1994) may prove useful in tentatively identifying such linkages.

Assuming that the above issues can be resolved, selection of an appropriate statistical model is not clear-cut. Approaches based on contingency tables or loglinear modeling methods are not appropriate as inferences from such models are not robust to the arbitrary choice of survey cell size. Methods similar to those used by Russell and Portier (1999), which account for spatial autocorrelation and extra variation induced by bird aggregation, are more appropriate for cell-based responses. By investigating survey-wide monthly bird totals, Russell et al. (2002) avoided the necessity of such complex models, though by doing so they also sacrificed any ability to derive spatially explicit types of inferences.

3.4 Nesting Data

Whereas the SRF survey tallies foraging birds in a mostly consistent manner throughout the Everglades, there is no comparable standardized system-wide survey of nesting colonies. Instead, colonies are surveyed by a number of cooperators, each adopting a unique protocol. Since 1995, descriptions and summaries of many of these surveys have been compiled annually by the SFWMD (D. E. Gawlik, SFWMD, unpublished reports; 1997-2002 reports available electronically at http://glacier.sfwmd.gov/org/wrp/wrp_ev/evg/projects/wading01). However, the level of detail contributed to these reports also varied by cooperator, and no metadata structure exists for the entire collection of

data. Therefore, utility of these data cannot be determined without contacting and interviewing each cooperator.

Nesting surveys differ appreciably in their conduct (Table 2). Surveys in the WCAs have been systematic since the late 1980s and surveys of ENP and WCAs prior to that time have been systematic only in some years. Point-to-point surveys of known colonies are usually based on the assumption of complete detection of all colonies in an area (D. Gawlik, personal communication). In some cases, colonies are visited incidentally during surveys for other wildlife organisms. Surveys of larger areas are flown, though some of these may use ground-based methods to more carefully count colonies seen from the air. Surveys differ in their timing. Some surveys are conducted only once per year whereas others are conducted monthly during the breeding season.

Nest detection rate for these surveys is unknown and most likely varies among colony size, bird species, vegetative substrate, and survey method. In a 2002 study of a single large colony, rates of aerial detection ranged from 1-28% of matched ground-based counts for nests occurring in a sample of quadrats (2002 Wading Bird Report).

4.0 MODELS FOR RELATING BIRD DISTRIBUTION AND DENSITY TO HYDROLOGY

4.1 Overview of modeling approaches

Before describing our approaches to model development for this problem, we briefly consider some alternative purposes for modeling. Many possible classifications of ecological models exist; we consider one based on the application(s) for which the model is intended (Williams et al. 2002:23-31).

First, *theoretical models* describe possible system responses under specific hypotheses or parameter values. Under this approach, scientific hypotheses express alternative ideas about how an ecological system functions and models are used to project the consequences of these hypotheses. The

purpose of theoretical models is to explore “the science of the possible” (Caswell 1988), essentially playing “what if” games with alternative (but plausible) ideas that may or may not have empirical support. Note however that “theoretical” does *not* imply that such models have no real world, management applicability. On the contrary, if contrasting, plausible views about system dynamics result in different optimal policies, resolution of which alternative is closer to “truth” suddenly becomes imperative.

By contrast, *empirical models* involve predictions of population or other system behavior, which can then be compared to observed behavior. Empirical models include statistical inference (estimation and hypothesis testing). In estimation, values for model parameters are inferred from observational or experimental data, usually under the assumption that a particular parametric model is true. Data, in turn, are used to assess the reliability of the model, via goodness-of-fit, confidence intervals, and validation (comparison of model predictions to independent observations). Whereas empirical (statistical) and scientific hypotheses can be related, they are not the same, since the former but not the latter depend not only on an underlying scientific hypothesis, but also on aspects of sampling design and data collection. This distinction is important and must be kept in mind, particularly because poor sampling designs or inadequate modeling of sampling processes can easily confound statistical inference about scientific hypotheses.

The distinction between scientific and statistical hypotheses notwithstanding, empirical models are a distinctive part of empirical science, which seeks to use data to discriminate among competing scientific hypotheses. There are two (at least) competing approaches to empirical modeling. The first, which we characterize as the “single-model approach”, is associated with Popper (1959; 1962; 1972) and Platt (1964). Under this approach, a model is used to deduce testable predictions from a scientific hypothesis; the hypothesis is compared to data, and, based on a (usually statistical) test, the hypothesis is retained

(subject to further testing) or rejected (either modified or replaced with competing hypothesis). Hypotheses that survive repeated empirical challenge by this approach are viewed (at least provisionally) as the best approximation of reality. In practice, this approach usually relies heavily on statistical null hypothesis testing to support or reject an underlying scientific hypothesis. An alternative approach, usually attributed to Chamberlin (1897) is based on multiple working hypotheses (Platt 1964). In this approach, competing scientific hypotheses and their corresponding predictions are considered simultaneously, and relative belief is revised following comparison of predictions under each empirical model to observations. In contrast to the usual emphasis on statistical null hypothesis testing, this approach fits naturally with likelihood-based updating using Bayes' Theorem (Williams et al. 2002: 25) and with information theoretical approaches for optimal model selection and multi-model inference (Burnham and Anderson 2002). Finally, information-theoretic and Bayesian approaches usefully blur the artificial (in our opinion) distinction between statistical estimation and hypothesis testing. In this view, relative (empirical) belief in alternative models becomes just another aspect of estimation, whether this is via computation of criterion-based weighting (e.g., AIC weights) or estimation of marginal posterior distributions of alternative models (Burnham and Anderson 2002).

The third type of model application involves models applied to projecting the consequences of scientific hypotheses about system behavior in order to identify an appropriate management action to achieve some objective. Thus, one needs in addition to a model (or, more appropriately *multiple* models) of system behavior, an explicit objective and a set of available management actions or controls. The models also must provide an explicit linkage between alternative management actions and the objective, which itself is usually based on some observable state of the system following management.

The use of models in this context fits naturally with previously described approaches to theoretical and empirical modeling. In ecological applications, there will nearly always be more than one alternative prediction about the consequences of any management intervention. Failure to take into account these alternative predictions can seriously degrade decision-making, because it is seldom (if ever) possible to select a single predictive model with certainty. Rather than endeavor to eliminate alternative models (the single-model approach), we endeavor to incorporate feasible, alternative models, appropriately weighted where possible to reflect empirically-based relative belief.

4.2 Review of Everglades models to date

Effects of natural phenomena, anthropogenic stressors, and water management decisions on wading bird populations in the highly modified Everglades landscape have been explored in a number of hypothetical, process simulation models. Most models are spatially explicit, presuming that spatial configuration of habitats is equally or more important than total amount of habitat in terms of bird use. Of these, many models are individual-based, allowing population response to arise as an emergent property of individual responses.

Most population modeling work has occurred within the ATLSS (Across Trophic Level System Simulation) framework (DeAngelis et al. 1998; Gross and DeAngelis 2002). ATLSS is a collection of system models, each forecasting organism response across a landscape grid of habitat squares. The organisms chosen for representation in ATLSS models are keystone or umbrella species that collectively are thought to most completely integrate the variety of energy, materials, and stressors dispersed across space, time, and trophic levels (DeAngelis et al. 1998). ATLSS models are usually individual-based in the belief that realistic population behavior emerges as a synthesis of individual behaviors operating in a highly variable, dynamic landscape (DeAngelis et al. 1998).

DeAngelis et al. (1998) describe the ATLSS implementation of a wood stork model based on work by Wolff (1994). Wolff (1994) simulated production response of a hypothetical wood stork colony exposed to varying hydrological conditions within a single breeding season; a schematic description of the model is found in Fleming et al. (1994). Elaborate decision rules governing behavior of individual adult birds were simulated in a simple environment of varying hydrological and prey base conditions. Movement, foraging, and nesting behavior of adults and survival of nestlings were determined through many specific functional forms and parameter values. The model simulated colony activity on fine spatial (250 m × 250 m) and temporal (15 min) scales. Wolff (1994) used the model to investigate colony productivity under alternative hydrological patterns.

Fleming et al. (1994) used the Wolff (1994) model to simulate colony nest initiation time and productivity response under three alternative hypotheses of system-wide wood stork productivity failure in the Everglades: (1) general loss of wetland habitat, (2) disproportionate loss of high-elevation, short-hydroperiod wetlands, and (3) increase in frequency of system wide drydowns. Their simulation results under the disproportionate-loss hypothesis were consistent with patterns of nest initiation and reproductive success observed under historical conditions of low, normal, and high early-season water levels.

Hallam et al. (1996) modified and generalized the Wolff (1994) model to simulate wood stork colony response to methyl mercury distributed across the landscape. In addition to the behavior and production rules encoded in the Wolff (1994) model, the contamination-response model required further assumptions regarding resource contamination levels and distribution, uptake and bioaccumulation of mercury by adults, lethal and sublethal effects of mercury on adults, and production and growth of offspring. The authors were unable to base many of these hypothesized relationships on empirical data,

and of those, few were derived from studies of wood storks (Hallam et al. 1996). The authors performed sensitivity analyses for the most tenuous parameters and concluded that their model was sufficiently robust to infer that mercury contamination could contribute to colony loss in the long term.

Curnutt et al. (2000) also used the ATLSS modeling framework, but unlike the individual-based approach used by Wolff (1994), they modeled “habitat potential” for the long-legged wading bird guild. They calibrated this spatially-explicit species index (SESI) model against bird foraging data collected on SRF flights. Foraging suitability of a model cell was a function of water depth, fish abundance (based on prior-year water depth), and water depth in a neighborhood of cells. By linking this model to the SFWMM, Curnutt et al. (2000) investigated spatial patterns of habitat potential under alternative hydrological management regimes. Curnutt et al. (2000) acknowledged several weaknesses and unresolved uncertainties in their model, but they defended its use for unbiased relative comparisons of alternative management plans.

In all of the preceding models, fish abundance was modeled passively, as a simple, direct function of cell hydrological status. Gaff et al. (2000) built an ATLSS component model of prey fish populations, in which prey fish were simulated in size and age functional schools. Fish functional groups were allowed to migrate among cells, evacuate cells, and repopulate cells in response to cell hydrology. Cells varied topographically, which provided refugia for fish under drydown conditions, and in food resources, determined in part by cell hydrological history and in part by fish abundance. The model used fine scales for both space (500 m × 500 m) and time (5 days) and employed many parameters and functional forms, the majority of which were not estimated using empirical evidence. By linking their model to the SFWMM, Gaff et al. (2000) compared expected prey fish distributions across the landscape in response to alternative hydrological management regimes. Although the model lacked validation or sensitivity

assessments, Gaff et al. (2000) defended the model's use for credible relative comparisons of alternative management plans.

Mooij et al. (2002) developed an ATLSS prototype model for snail kites to investigate predictions about effects of varying spatial and temporal patterns of drought on population size. Their model was spatially-explicit and individual-based, but followed bird fates over an irregular network of wetland habitats rather than over a regular grid of polygons. Water conditions in the wetlands influenced availability of prey and, in turn, determined carrying capacity for snail kites; carrying capacity influenced the probability of snail kite movement among sites and snail kite fecundity. The model suggested that the population responded negatively both to system-wide droughts and prolonged habitat inundation, but was mostly unaffected by more localized droughts.

Walters et al. (1992) built a landscape model of hydrological state to portray pre-alteration conditions of the Everglades and to provide a basis for assessing relative credibility of four alternative hypotheses of wading bird population decline. Like the SFWMM, against which they compared their model results, the model of Walters et al. (1992) provided hydrological input to other models of ecological indicators. They inferred from both models that a large pool of short-hydroperiod water once occurred to the east of the system and served as a regulator of flows through the south. They also concluded that larger volumes of water once flowed through the southern Everglades and into the estuaries and mangrove forests. Walters et al. (1992) called for an experimental approach of structural modifications and water releases to test whether restoration of the estuarine zone is a necessary condition for wading bird population recovery.

Smith (1997) constructed an energy flow model of the Lake Okeechobee Great Egret population. Unlike other models for wading birds, Smith's (1997) model was neither spatially-explicit nor individual-

based, and it was formulated in a continuous time domain. In this model, interactions among environmental forcing variables and state variables that represented the prey population, the adult bird population, and the population of recruits were expressed through a large number of parameters and functions. The parameters and functional forms of the model were chosen based on fit of model output to a time series of population data. Smith (1997) performed no model validations, but nevertheless used model predictions to support several hypotheses about the influence of hydrological and environmental characteristics on Great Egret population dynamics.

Empirical models that relate foraging bird response to hydrological conditions were reviewed above (*Uses of the SRF Data*). McCrimmon et al. (1997) analyzed trend patterns in Christmas Bird Count (CBC) data to make inferences on statewide population dynamics for several species of wading birds. Their models, however, did not link bird abundance to any variable subject to management control.

5.0 METHODS

To evaluate the proposed hypotheses explaining wading bird decline and develop predictive models under one or more of these hypotheses, we related observations of birds from the SRF to measures of hydrology from the SFWMM and indexes of abundance from the Breeding Bird Survey (BBS). In the course of compiling the data, we identified some issues with the SRF and SFWMM data that had to be addressed before modeling could proceed.

5.1 SRF observational data

The basic observations from the SRF are bird sightings from a particular flight, transect, and longitude. However, this is only one-half of the information that should be available from the survey. The areas (SRF cells) where no birds were seen also are of interest for modeling purposes. This information may be inferred by plotting the observations against the surveyed cells such that cells where no

observations occur may be assigned values of zero. To do this, we had to determine where the observations occurred and identify the cells that were being surveyed. We determined a survey extent for each region based on how each was surveyed. In the northern survey region, the extent was determined by the westernmost terminus of the surveyed transects, the eastern regional boundary, the southernmost surveyed transect, and the northern regional boundary (Figure 2). In the Big Cypress survey region, the extent was determined by the easternmost terminus of the surveyed transects, the western regional boundary, the northern regional boundary, and the southernmost surveyed transect (Figure 3). Finally, the surveyed extent for the Everglades National Park was determined based on a map provided by the park (Figure 4; Mario Alvarado, Everglades National Park, personal communication).

With the survey extents defined, we then assigned observations to SRF cells. However, we found a number of observations in the northern regions had longitude values that placed them outside of the survey extent. To address this issue, we dropped those points outside of the survey extent. This eliminated the obviously inaccurate points, but ignored the possibility of positional errors for observations within the survey area.

As noted earlier, at an unknown time, a shift occurred in the transects used to monitor the northern regions. As far as we can determine, the shift occurred sometime before 1988 in the surveys conducted by the Audubon Society for the WCAs who then presumably passed on the shifted transects to the Army Corps of Engineers. Because the shifted transects resulted in an entirely different set of SRF cells being surveyed, it was decided by the parties involved to continue using them. This had two ramifications. First, an entire transect in the middle of the Everglades was no longer surveyed. Second, the latitudes of the locations for the WCAs prior to 1988 are unknown and may be off by an entire row (i.e., 2 km). We

dealt with the first problem by editing the surveyed area for the effected years. To deal with the second problem, we assumed that the shift occurred at the beginning of the survey (1985).

In most cases, a survey for a given region occurred over a period of multiple days, with individual flights within each survey covering a subset of transects in that region. In some cases, flights within a survey re-flew transects that were surveyed by a previous flight. This occurred rarely (WCAs 27 times and BCNP 3 times). Because dealing with these overlaps would unnecessarily complicate the modeling, it was determined that only the observations from the flight that initially surveyed each transect would be retained.

Each of these issues with the SRF resulted in the final analysis data set being a subset of the total amount of data available. The steps and amount of data removed at each step are summarized in Table 3.

5.2 Hydrology data

The South Florida Water Management Model (SFWMM) is a spatially explicit computer model that simulates the hydrology of South Florida (Fennema et al. 1994; South Florida Water Management District 1997). It is regional in spatial extent and uses a 3.2km-by-3.2km fixed-resolution gridded model domain. The SFWMM assumes homogeneity in hydrologic characteristics within each grid cell and runs at a fixed time step of one day. It predicts the mean water depth relative to sea level (i.e., absolute depth) for each grid cell. This absolute depth level then is adjusted for each grid cell using the mean elevation of the cell estimated from a digital elevation model. This results in a relative measure of water depth for each cell that did not reflect variation in microtopography within a cell.

Hydrology data from the SFWMM have gone through an extensive testing process, and water patterns predicted by the model match observed patterns well (South Florida Water Management District 1997). The hydrologic data extracted from SFWMD gages are subjected to rigid quality assessment and

control measures (Crowell and Mtundu 2000). After the raw data are retrieved, they are loaded into a Data Collection/Validation Preprocessing System (DCVP). The DCVP system verifies the station name and checks the period of record for ascending dates/times, gaps, and overlaps. The DCVP system also screens the data for values outside of the min/max and rate of change tolerances. The data are then graphically analyzed by skilled personnel trained in the interpolation of hydrologic data. During the graphical review, comparison data sources are also used to identify errors. Any inconsistencies are corrected and/or tagged by the data processors. The data are then updated and filtered against daily minimum/maximum and rate of change tolerances. Daily averages are computed, extracted, and reviewed.

The grid cells from the SRF surveys did not match the grid cells from the SFWMM. To calculate predicted water levels in each SRF cell, it was necessary to reconcile the SFWMM cells with the SRF cells. To accomplish this for each SRF cell, we recorded the water depths from the SFWMM cells that overlapped the SRF cell. We then calculated an average water depth for the SRF cell weighted by the proportion of the area of the cell within each SFWMM cell that it overlapped.

Unfortunately, portions of the area surveyed by the SRF were not encompassed by the SFWMM projections. These areas were mainly tidally influenced zones on the edges of regions ('regions' are defined in Fig. 1). Because of the lack of coverage in these areas, we were unable to generate the dynamic hydrology variables critical to testing the hypotheses in which we were interested. Therefore, these areas and the observations within were removed from the analysis data set.

5.3 Subregion classification

Previous studies of the SRF wading birds indicated substantial and unquantified variation in microtopography in the SRF area that could obfuscate wading bird-water level relationships (Russell et al. 2002). To minimize these potential influences, we develop strata (henceforth, subregions) by grouping

SRF cells based on the similarity of vegetative structure (which itself is based on the Florida Land Use and Cover Classification System [FDOT 1999]) and water level characteristics (i.e., mean, minimum and maximum of predicted water levels for period of study) via *k*-means cluster analysis. *K*-means clustering is a robust form of non-hierarchical cluster analysis that is used to group data into *k* clusters (i.e., *k* = number of clusters or groups) based on their similarity (Romesburg 1990). The optimal number of number of clusters (groups) is considered to be the smallest value of *k* that maximizes the within-group (strata) similarity and maximizes the differences among groups. This optimal number was determined by fitting *k*-means clusters for several values of *k* and plotting the overall R^2 versus the number of clusters. The overall R^2 is a measure of the predictability of the characteristics (e.g., habitat) of cluster members (e.g., streams) and is analogous to r^2 in regression analysis (Hartigan 1985). The optimal number of clusters (subregions) was considered the lowest value of *k* at which the R^2 began to level off and reach an asymptote. These candidate subregions then were plotted and the maps shown to experts familiar with the SRF area who suggested minor modifications to the subregions.

5.4 Development of a hierarchical model synthesizing major, alternative hypotheses

5.4.1 Summary of general approach

We modeled bird counts at the cell level as random outcomes of effects determined at larger scales. The parameters are hierarchically structured and consist of water depth at the cell level; the rate of drawdown (water recession); a measure of smoothness of the drawdown (i.e., severity of pattern of hydrologic reversals); availability of "optimal habitats" during a critical pre-nesting period and throughout the nesting season; and an index of annual bird abundance elsewhere in the species range. Initially we began with relatively simple, fixed-effects models that incorporate principally cell-level predictors. As the analyses and modeling continued, we added hierarchical effects that account for broad-scale

phenomena (e.g., general availability of birds); time lags (e.g., to account for recruitment impacts), and spatially and temporally auto-correlated random effects (to account both for unexplained temporal and geographic patterns in the data, as well as the effect of repeated measures over time and space). Finally, we incorporated, to the extent possible, fixed and random effects due to imperfect and presumably heterogeneous detection rates in the SRFs.

5.4.2 Alternative hypotheses of foraging patterns

We considered temporal and spatial variability in Everglades wading bird abundance under four hypotheses that were expressed as alternative simplifications of a general hierarchical model of foraging abundance N . These hypotheses – *distant magnets*, *regional recruitment*, *food limitation*, and *hydropattern alteration* – were described earlier (see literature review). We did not build models for the *estuarine degradation* or *transitional habitats* hypotheses (see literature review) because they describe phenomena that had occurred before the initiation of this survey, and their underlying mechanisms could probably not be explored without large-scale experimental manipulation (Walters et al. 1992). Furthermore, their investigation required data not available to us (water level for estuarine degradation) or required specification of somewhat conceptual conditions defined by combinations of space and time (transitional habitats).

We began by modeling the average number of birds counted in SRF cell i (of subregion j within region k) during survey s of year t as:

$$D_{i(j(k)),s(t)} = \beta_{i(j(k)),s(t)} N_{i(j(k)),s(t)},$$

where $N_{i(j(k)),s(t)}$ is the true abundance of birds in cell i at survey s and $\beta_{i(j(k)),s(t)}$ is the corresponding detection probability (generally, $\beta_{i(j(k)),s(t)} \leq 1$ and variable over space and time). Thus, in general the

expected cell count $D_{i(j(k)),s(t)} \leq N_{i(j(k)),s(t)}$ due to imperfect detection; more generally, $\beta_{i(j(k)),s(t)}$ may include random effects, including spatially and temporally heterogeneous detection.

In each model, cell counts were modeled as a random outcome of a subregional average cell density, initially

$$y_{i(j(k)),s(t)} \sim \text{Poisson}(D_{j(k),s(t)}).$$

However, initial examination of SRF counts indicated a high degree of overdispersion ($E(x) \gg \sigma_x^2$) and led us to model cell counts via a lognormal distribution $y_{i(j(k)),s(t)} \sim \text{lognormal}(\mu, \sigma)$. Thus, we log-transformed all cell counts, i.e., $Y_{i(j(k)),s(t)} = \log(y_{i(j(k)),s(t)} + 0.001)$, and we modeled $Y_{i(j(k)),s(t)}$ as a linear function of predictor variables and normally-distributed error terms.

For several reasons, we focused our modeling efforts on counts of two species, Great Egret and White Ibis. These species were seen in relatively high abundance and frequency, which was likely to be helpful in separating any signal of system drivers from the background noise of unknown phenomena. Their large size and distinct profiles suggest they were unlikely to be incorrectly or indeterminately identified (except, as noted by Russell et al. (2002), possible observer confusion between Great Egret and the far less abundant Great White Heron). Detection probability was likely to be higher and more consistent for these large, white birds than for other species, an important consideration given that our ability to account for detection probability was considerably limited. Whereas these two species are comparable in several aspects, they have distinct foraging habits (e.g., different foraging ranges, flocking behaviors, hunting tactics, and giving-up prey densities) likely to be conveyed in the models.

Water depth predictions provided by the South Florida Water Management Model (WMM) were the primary source of data used as environmental drivers in two of the following four models. The cells of the WMM overlap with approximately 2,400 SRF cells, but a significant portion of SRF coverage – the

tidally-influenced estuarine zone in the southwest – is not covered by the WMM. As noted earlier, although the SRF contains some measure of hydrology, these can only be related to water at the time of the survey, therefore it was impossible to generate the trend data needed for these models in areas of non-overlap. Therefore, we decided that the only way to deal with these portions of the study area was to drop them from the analysis.

5.4.3 Distant magnets hypothesis

Two of the hypotheses described temporal patterns at the scale of the entire study area and did not directly (i.e., through structural means) address spatial variability within the system. The *distant magnets* hypothesis (Frederick and Collopy 1988, Walters et al. 1992) suggests that bird populations overall have not declined, but that decreases observed in the Everglades have been offset by increases in bird numbers elsewhere in the southeastern U.S., perhaps as a consequence of improved conditions in those areas. We evaluated support for this hypothesis by associating (log) cell abundance with annual average Breeding Bird Survey (BBS) indices:

$$Y_{i(j(k)),s(t)} = b_{0,j(k)} + b_1^{(DM)} Q_t + \gamma_{pre,j(k)} + \gamma_{nest,j(k)} + \varepsilon_{i(j(k)),s(t)},$$

$$b_{0,j(k)} \sim \text{Normal}(b_0, \tau_0),$$

$$\gamma_{pre,j(k)} \sim \text{Normal}(\gamma_{pre}, \tau_{pre}),$$

$$\gamma_{nest,j(k)} \sim \text{Normal}(\gamma_{nest}, \tau_{nest}),$$

$$\varepsilon_{i(j(k)),s(t)} \sim \text{Normal}(0, \tau).$$

The main structural element of this model relates an annual BBS survey index, Q_t , to cell abundance through a model parameter $b_1^{(DM)}$. Whereas we treated this parameter as a fixed effect, we included other parameters as subregion-level random effects to account for spatial and within-season temporal variation

not well accommodated by the structural component. Random effects included the model intercept, $b_{0,j(k)}$, and a pair of additive terms expressing the effect of the pre-nesting ($\gamma_{\text{pre},j(k)}$) or nesting ($\gamma_{\text{nest},j(k)}$) phase of the season. Each random effect was assumed to have arisen from a normal distribution with a fixed mean (b_0 , γ_{pre} , and γ_{nest} , respectively) and precision (τ_0 , τ_{pre} , and τ_{nest} , respectively). Finally, variance not accounted for by any of these parameters was conveyed in the residual error term $\varepsilon_{i(j(k)),s(t)}$.

We constructed Q_t as a weighted average of annual BBS indices published for the period 1966-2005 (Sauer et al. 2005). We obtained annual indices for Great Egret and White Ibis within each of the BBS strata 2, 3, and 4 (Floridian, Coastal Flatwoods, Upper Coastal Plain). These strata form a region that captures the range of both species in the southeastern U.S. outside of the Everglades. Weights used in the average were (1) inverse variance of the stratum-specific BBS trend estimate from which the indices were calculated, (2) inverse distance of the stratum from the Everglades (measured ordinally as 1, 2, or 3), and (3) stratum area. We chose these weights because they relate either to the precision of the index (case 1) or to the likely influence of the stratum as a population “magnet” (cases 2 and 3). Thus, strata that are larger, closer to the Everglades, and supply indices with greater precision carried greater weight in the computation of the predictor value Q_t .

This model predicts a system-wide, average annual cell abundance as a function of bird abundance outside of the Everglades system, but, as mentioned above, there is no structural means of modeling spatial and within-year survey variability in counts. For this reason, we made use of random effects in the model to account for overall spatial variation ($b_{0,j(k)}$) and within-season temporal variation ($\gamma_{\text{pre},j(k)}$, $\gamma_{\text{nest},j(k)}$). This was also the case in all the remaining models; therefore the same random effects occur in each and are defined identically. Breeding periods are different

for Great Egret and White Ibis; therefore, the pre-nesting and nesting periods for Great Egret are December-January and February-May, respectively, whereas the corresponding periods for White Ibis are December-February and March-May.

5.4.4 Regional recruitment hypothesis

The second hypothesis that directly addressed only temporal variability is the *regional recruitment hypothesis*, which specifies that abundance in year t is principally a function of system-wide recruitment from a prior year $t-v$. We modeled this essentially identically to the distance magnets hypothesis, except the predictor ($D_{k,t-v}$) is mean region-wide count averaged over the s'_{t-v} surveys conducted at the end of the breeding season of prior year $t-v$:

$$Y_{i(j(k)),s(t)} = b_{0,j(k)} + b_1^{(RR)} D_{k,t-v} + \gamma_{\text{pre},j(k)} + \gamma_{\text{nest},j(k)} + \varepsilon_{i(j(k)),s(t)},$$

$$D_{k,t-v} = \frac{1}{s'_{t-v}} \sum_s \frac{1}{\sum_j I(J)_j} \sum_j \sum_i^{I(J)} y_{i(j(k)),s(t-v)},$$

where $b_1^{(RR)}$ specifies the relationship between prior-year abundance and current-year abundance, and $b_{0,j(k)}$, $\gamma_{\text{pre},j(k)}$, $\gamma_{\text{nest},j(k)}$, and $\varepsilon_{i(j(k)),s(t)}$ were random effects defined as before. Unfortunately, we have no way of estimating what fraction of $D_{k,t-v}$ is actually available to recruit at t , so the model parameter $b_1^{(RR)}$ implicitly involves survival and fidelity to the system from $D_{k,t-v}$. The lag period, v , was species-specific, corresponding to the time spent by most birds in a pre-reproductive stage. For Great Egret, we set $v = 2$, whereas for White Ibis, we fixed v at 3 (Dale Gawlik and Mark Cook, personal communication). In order to accommodate these lags it was necessary to use observations only from 1988 onwards as $D_{k,t-v}$ would be unavailable in 1985-1987 for White Ibis.

5.4.5 Food limitation hypothesis

The remaining two hypotheses were explored under models that incorporated structural predictors of both temporal and spatial variability of bird abundance within the system. Both hypotheses linked observed bird foraging patterns with distributions of shallow water habitats at local scales, but they differed as to whether the association is strictly contemporary or is influenced by antecedent trends in habitat availability. We refer to the former case as the *food limitation* hypothesis. It states that bird abundance in each SRF cell at each survey is a random outcome of subregion-level habitat conditions:

$$Y_{i(j(k)),s(t)} = b_{0,j(k)} + b_{1,j(k)}^{(FL)} W_{i(j(k)),s(t)} + b_{2,j(k)}^{(FL)} W_{i(j(k)),s(t)}^2 + \gamma_{\text{pre},j(k)} + \gamma_{\text{nest},j(k)} + \varepsilon_{i(j(k)),s(t)},$$

$$b_{1,j(k)}^{(FL)} \sim \text{Normal}(b_1^{(FL)}, \tau_1^{(FL)}),$$

$$b_{2,j(k)}^{(FL)} \sim \text{Normal}(b_2^{(FL)}, \tau_2^{(FL)}).$$

Under this model, bird abundance is a curvilinear (linear and quadratic) function of cell-specific water level $W_{i(j(k)),s(t)}$ with slope parameters $b_{1,j(k)}^{(FL)}$ and $b_{2,j(k)}^{(FL)}$ specific to subregion $j(k)$. The slope parameters themselves are random rather than fixed, assumed to arise from normal distributions centered at fixed means, $b_1^{(FL)}$ and $b_2^{(FL)}$, and with fixed levels of precision, $\tau_1^{(FL)}$ and $\tau_2^{(FL)}$, respectively. In addition to these structural components, the model included the same set of random effects $b_{0,j(k)}$, $\gamma_{\text{pre},j(k)}$, $\gamma_{\text{nest},j(k)}$, and $\varepsilon_{i(j(k)),s(t)}$ used in previous models.

5.4.6 Hydropattern alteration hypothesis

The *hydropattern alteration* hypothesis suggests that observed spatial patterns of abundance at time s are consequences of past trends of water depth behavior that either concentrate or disperse prey. Specifically, a given patch is expected to receive high foraging use when water depth on the patch has smoothly and continuously fallen during a short time period immediately preceding s . If water depth

reduction is too slow or has reversed at some point during the period, prey become dispersed, and birds will avoid the patch even if foraging depth is adequate. Under this model, bird abundance in a cell in subregion $j(k)$ during survey $s(t)$ is a function of the rate of drying in the subregion and the consistency of that pattern:

$$Y_{i(j(k)),s(t)} = b_{0,j(k)} + b_{1,j(k)}^{(HA)} r_{j(k),s(t)} + b_{2,j(k)}^{(HA)} r_{j(k),s(t)}^2 + b_{3,j(k)}^{(HA)} r'_{j(k),s(t)} + \gamma_{\text{pre},j(k)} + \gamma_{\text{nest},j(k)} + \varepsilon_{i(j(k)),s(t)},$$

$$b_{1,j(k)}^{(HA)} \sim \text{Normal}(b_1^{(HA)}, \tau_1^{(HA)}),$$

$$b_{2,j(k)}^{(HA)} \sim \text{Normal}(b_2^{(HA)}, \tau_2^{(HA)}), \text{ and}$$

$$b_{3,j(k)}^{(HA)} \sim \text{Normal}(b_3^{(HA)}, \tau_3^{(HA)}).$$

This model defines a curvilinear (linear and quadratic) function of the preceding 14-day average trend in water level for the subregion, $r_{j(k),s(t)}$, with model parameters $b_{1,j(k)}^{(HA)}$ and $b_{2,j(k)}^{(HA)}$. Bird abundance is also a function of degree of departure from the trend, measured as the root mean squared error $r'_{j(k),s(t)}$ of the regression, with model parameter $b_{3,j(k)}^{(HA)}$. As we did in the food limitation model, we modeled the regression parameters as random effects drawn from normal distributions with respective fixed means $b_1^{(HA)}$, $b_2^{(HA)}$, and $b_3^{(HA)}$ and precision parameters $\tau_1^{(HA)}$, $\tau_2^{(HA)}$, and $\tau_3^{(HA)}$. Lastly, the model included the same set of random effects $b_{0,j(k)}$, $\gamma_{\text{pre},j(k)}$, $\gamma_{\text{nest},j(k)}$, and $\varepsilon_{i(j(k)),s(t)}$ used in previous models.

5.4.7 Global model

Each of these hypotheses (I – IV) can be shown to be a special case of a global model:

$$\begin{aligned}
Y_{i(j(k)),s(t)} = & b_{0,j(k)} + \gamma_{\text{pre},j(k)} + \gamma_{\text{nest},j(k)} + \\
& b_1^{(\text{DM})} Q_t + \\
& b_1^{(\text{RR})} D_{t-v} + \\
& b_{1,j(k)}^{(\text{FL})} W_{i(j(k)),s(t)} + b_{2,j(k)}^{(\text{FL})} W_{i(j(k)),s(t)}^2 + \\
& b_{1,j(k)}^{(\text{HA})} r_{j(k),s(t)} + b_{2,j(k)}^{(\text{HA})} r_{j(k),s(t)}^2 + b_{3,j(k)}^{(\text{HA})} r'_{j(k),s(t)} + \\
& \mathcal{E}_{i(j(k)),s(t)}
\end{aligned}$$

(included but not shown are associated higher-order hierarchical components). Because it is unlikely that bird foraging patterns arise from any single mechanism, we used the global model to consider these hypotheses individually and in combination with others. During construction of the global model, we analyzed residuals for evidence of systematic lack of fit, for example, spatio-temporal patterns of autocorrelation or interactions among model effects, and we considered any additional model structure needed to account for it.

5.5 Model fitting

We were primarily interested in the evaluating the relative plausibility of the four hypotheses relating patterns in wading bird density to local and regional factors. Wading bird abundance, however, is known to vary seasonally. Therefore, we developed two species-specific binary (0, 1) indicators variables for pre-nesting (Great Egret: December-January and White Ibis: December-February) and nesting time periods (Great Egret: February-May and White Ibis: March-May) and included these as “nuisance” variables in all candidate models. That is, we were not interested in evaluating the relative support of hypotheses of whether or not there was seasonal variation because it was known to occur. In addition, we eliminated data for the months of October and November because they were collected inconsistently among regions and only for three years, 1985, 1992, and 1993.

5.5.1 Mixed model analysis in SAS

Previous analyses of the SRF data (Russel and Portier 1989) suggested that the data was spatially autocorrelated, which would preclude the use of traditional regression techniques (Sokal and Rohlf 1995). Thus, we initially fit a global (i.e., model containing all of the predictors) linear regression model of Great Egret and White Ibis density. An evaluation of the residual plots from each global model ordered by subregion indicated significant dependence among subregions for both Great Egret and White Ibis. To account for the spatial autocorrelation, we examined relationships between wading bird densities with hierarchical models. Hierarchical models differ from more familiar regression techniques in that autocorrelation among cells within subregions, defined as lower level units (cells) within upper level units (subregions), is incorporated by including random effects for lower level intercepts and slopes (Snijders and Bosker 1999). For our study, random effects are estimates of the variability of the effect of cell-specific (lower level unit) characteristics on wading bird density among subregions (upper level units). For example, a water level random effect estimates the extent to which the relationship between water level (i.e., the regression slope) and wading bird density varies from subregion to subregion. Fixed effects are estimates of the average effect of cell-specific characteristics across regions and the effect of annual characteristics (e.g., species-specific abundance in the breeding bird survey; Table 5) on wading bird density. All models were fit using SAS Proc Mixed (Littell et al. 1996).

Prior to evaluating the fit of our candidate models, we evaluated the relative-fit-of two different variance structures for the hierarchical model random effects using the global (all predictors) model. The first variance structure modeled each random effect as independently normally distributed and the second modeled covariances among random effects. To assess the relative fit of each model, we calculated Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989). AIC_c is an entropy-based measure used to compare candidate models for the same data

(Burnham and Anderson 2002), with the best fitting model having the lowest AIC_c . The number of parameters used to estimate AIC_c included the fixed effects, random effects, and random effect covariances when included in the error structure (Burnham and Anderson 2002). The best fitting variance structure for each species then was used during the evaluation of the relative plausibility of the candidate models. Eleven candidate models representing various combinations of our four hypotheses were fitted using hierarchical linear models for each species. The relative plausibility of each candidate model (i.e., hypothesis) was assessed by calculating Akaike weights as described in Burnham and Anderson (2002). These weights range from 0 to 1, with the most plausible candidate model having the highest weight.

To allow for ease of interpretation of the relative magnitude of fixed and random effects, we plotted empirical Bayes (shrinkage) estimates (Snijders and Bosker 1999) of the relationship between water level characteristics and Great Egret and White Ibis density for each subregion using the best fitting model. We also estimated standardized coefficients to facilitate comparisons among predictor variables. The precision of each fixed and random effect was estimated by computing 95% confidence intervals based on a t -statistic with $n-1$ degrees of freedom (Littell et al. 1996).

We evaluated goodness-of-fit for each model by examining (1) normal probability plots of the lower level residuals and (2) plots of the empirical Bayes residuals by their corresponding chi-square scores with $Q-1$ degrees of freedom, where Q is the number of upper (i.e., subregion) level effects included in the candidate model (Bryk and Raudenbush 1992).

Model evaluation.- For each species, we assessed the predictive ability of each model in the confidence set using leave-one-out cross validation. Cross validation estimates are nearly unbiased estimators of out-of-sample model performance (Funkunaga and Kessel 1971) and provide a measure of overall predictive ability without excessive variance (Efron 1983). Hence, they should provide an

estimate of the ability of the models to estimate bird density under conditions similar to those under which models were parameterized. During this procedure, the observations from one month and year combination (e.g., February 1990, May 1995) were excluded from the dataset, the composite hierarchical model was fit with remaining data, and the density of birds at each cell in the left out month and year combination were predicted using the fitted model. This procedure was repeated for each month and year combination (i.e., a total of 111 times), and error was estimated as the difference between the predicted and observed bird density. Relative accuracy was estimated as the root mean square error across samples.

5.5.2 Zero-inflated estimation using PyMC

In the majority of the cells from any given SRF survey, no birds were observed. For this reason, we believed that a zero-inflated model of abundance (Welsh et al. 1996) may prove more effective than the hierarchical linear models previously described. The complex nature of a hierarchical zero inflated model precluded the use of traditional maximum likelihood methods. Thus we fit a hierarchical zero inflated model using Markov Chain Monte Carlo (MCMC) methods as implemented in PyMC software version 1.0 (Fonnesbeck 2006).

Although advances in computing have increased the complexity of the problems that can be tackled using MCMC, problems involving large amounts of data remain intractable in some cases. Therefore, it was necessary to reduce the complexity of the problem by summarizing the data over the subregions described earlier. Since many of the hypotheses being investigated involve processes occurring at the subregion level, we believed that the impact on the model would be minimal. In fact, the predictors remained unchanged for each hypothesis except for the model representing the food limitation hypotheses. The food limitation linear hierarchical regression model used a cell level measure ('water depth during the survey') that could not be used in the zero inflated models. However, the water depth

during the surveys of cells within a region were highly correlated (Pearson $r = 0.86$) with the subregion level intercept from the hydrology regression of the 14 days prior to the survey. Therefore, we deemed it reasonable to use this value as an indicator of the availability of food on the subregion wide level.

The zero-inflated model has two parts (henceforth, sub-models). The first part predicts the percentage of the subregion occupied, which is estimated as the number of occupied cells observed in a subregion during a survey versus the total number of cells surveyed in that subregion. The second part predicts the average abundance in occupied cells only as estimated by the average abundance in occupied cells in the subregion. The combination of these two sub-models is used to predict the mean cell level abundance for each subregion.

For each part of the model, we developed 5 candidate sub-models representing each hypothesis and a global model. Model structure and parameters corresponding to each hypothesis were identical to the initial analysis except as noted above. Identical to the hierarchical linear regression model (discussed above), parameters for the food limitation and hydro pattern alteration hypotheses were allowed to vary randomly across subregions but were assumed to have common means and standard deviations. Each model was fit over 20,000 iterations with a 10,000 iteration burn in. We evaluated relative plausibility of each candidate sub-model using Akaike weights (Burnham and Anderson 2002) as described earlier. We evaluated goodness-of-fit for the sub-models using the discrepancy measure produced by PyMC and described by Gelman et al. (1996).

Model evaluation.- As discussed above, the computer intensive nature of MCMC methods precluded the use of leave one month per year out cross validation. Thus, we evaluated the relative predictive ability of the best fitting models with two methods. We first estimated the within sample prediction error by comparing model predictions using the mean parameter estimates (from the MCMC

posterior distributions) to the observations that were used during model fitting. Note that the estimate of within sample error is known to be a negatively biased (optimistic) estimator for model performance (Johnson and Wichern 1992) but provides a relatively quick estimate of model performance when examining several complex models with large data sets, such as those used here. We also evaluated out of sample predictive ability using two-fold cross validation. Here we divided the data randomly into two parts. The first part was used to fit the most plausible combined model as determined via Akaike weights (above). The posterior means of the parameters from this fitting were then used to predict the values of the held-out data, and error was estimated as the difference between predicted and observed. Relative accuracy was estimated as the root mean square error across samples.

5.6 Visibility estimation

To evaluate visibility (detection) rates on the SRF, we designed dual-observer trials, which were flown by biologists from ENP during February and March, 2004. During these trials, 1 observer was seated in the right front seat (RF) and the other observer in the right rear seat (RR). Three observers (labeled observer E, L, or M) rotated between the front and back seat positions over the course of 8 survey days. Observers independently recorded birds seen by species and did not communicate or otherwise provide cues to one another. We matched observations of the observers by synchronization of the observation times, assuming that observations taken within 10 s (approx. 400 m at aircraft speed) by 2 observers were of the same group. The observations were used to construct detection histories by each of 9 species or species groups: Great Egrets (GREG), White Ibis (WHIB), Great Blue Herons (GBH), small dark herons (SDH), small white herons (SWH), Wood Storks (WS), Glossy Ibis (GI), Roseate Spoonbills (RS) and Great White Herons (GWH) for each observer-position, with ‘11’ denoting detection by both observers, ‘10’ by the RF but not RR, ‘01’ by RR but not RF, and ‘00’ by neither. To model detection

probability we considered only observations in which birds were known to occur; that is, we conditioned on the histories 11, 10, and 01. Thus, we modeled the effects of species, observer, and position effects via a conditional, single-trial multinomial, with event probabilities as:

$$P(x_i = 10 | o_1, o_2) = \frac{p_i(o_1, 0)[1 - p_i(o_2, 1)]}{p_i(\cdot)},$$

$$P(x_i = 01 | o_1, o_2) = \frac{[1 - p_i(o_1, 0)]p_i(o_2, 1)}{p_i(\cdot)},$$

$$P(x_i = 11 | o_1, o_2) = \frac{p_i(o_1, 0)p_i(o_2, 1)}{p_i(\cdot)},$$

where $p_i(j, k)$ is the probability of encounter for species i by observers $j=o_1, o_2$ in the front ($k=0$) and rear ($k=1$) positions, respectively, and

$$p_i(\cdot) = P(x_i = 10 | o_1, o_2) + P(x_i = 01 | o_1, o_2) + P(x_i = 11 | o_1, o_2).$$

Additionally, we considered models in which probability of detection was influenced by group size and water conditions. First, we calculated C_i as the average of RF and RR observers' counts when $x_i = 11$ and as the count for the observer that detected the group otherwise. We then summarized the data by 5 group-size categories: $C_i = 1$; $1 < C_i \leq 5$; $5 < C_i \leq 10$; $10 < C_i \leq 50$; and $C_i > 50$. Finally, observers recorded water conditions in 5 categories: dry (DD), dry transitional (DT), wet-dry (WD), wet-transitional (WT), and wet (WW). We summarized detection history frequencies for each species by combinations of front and rear observers, group-size categories, and water conditions, and fit alternative models with Markov chain Monte Carlo (MCMC) (Gilks et al. 1996), using information theoretics (Akaike 1973, Spiegelhalter et al. 2002) to compare alternative models.

5.6.1 Evaluation of effect of visibility bias on bird abundance patterns

Previously cited studies suggest that the incomplete detection of birds during sampling potentially affects models of wading bird abundance and distribution and hence, statistical inferences regarding population trends and bird distribution patterns. We evaluated the influence of incomplete detection by conducting relatively simple simulations of SRF sampling protocols using known abundances and population growth rates for Great Egret and White Ibis. The simulation models began at year one with a specified number of birds in the population. The simulated sampling crew consisted of two observers in the rear seats of an aircraft that were randomly assigned prior to the survey and counted during the sampling period (i.e., the observers did not change during the survey). The number of groups (flocks) of birds foraging during the survey was modeled as a function of the total number of birds in the population (Table 4). The number of birds per flock were randomly generated assuming a negative binomial distribution with a mean equal to the population size divided by the number of groups, and variance that was modeled as a function of the mean (Table 4). During sampling, individual groups of birds were randomly assigned to an observer. The detection of individual groups then was randomly determined using a Bernoulli distribution with probability of success estimated as a function of the observer, location (rear seat), species, and group size using the best fitting model estimated above. If a group was detected, we assumed that all members were counted accurately. The observed population size was estimated as the sum of all birds detected by both observers. During the next time step, the population size changed assuming fixed population growth rate (λ) that varied with simulation scenario (Table 4). This population then was sampled using the same protocol with two randomly assigned observers. The process was repeated until the specified timeframe was reached (Table 4) and the known and observed population trend was estimated by fitting a model of the known and observed population size, respectively vs. survey year. Detection of a trend was assumed when $P \leq 0.10$.

We evaluated the relative influence of population size, rate of population change, and number of years surveyed on the detection of population change by evaluating all possible combinations of 3 initial population sizes, 9 population growth rates, and 5 survey end times. For each scenario and species, we ran 1000 replicate simulations and estimated the correct detection rate, defined as correctly detecting a positive or negative change in population change; the false detection rate, defined as falsely detected a positive population trend when it is negative or there is none and falsely detected a negative population trend when it is positive or there is none; and the bias in the slope of the regression, which was estimated as the known slope minus the observed slope.

5.7 Evaluation of the relationship between SRF counts and annual nesting effort

As indicated earlier, one of our objectives was to develop performance measures based on the relationship between wading bird distribution and nesting effort. However unlike the wading bird distribution modeling, we had no *a priori* expectation or hypotheses regarding the nature of the relationships between bird nesting effort, SRF counts, and hydrologic variables. Therefore, we conducted an exploratory analysis by fitting all subsets of models relating month and region-specific SRF bird counts and hydrologic variables to region-specific counts of nesting effort. Separate nesting effort data for WCA regions 2 and 3 were not available (i.e., counts were combined for both regions), so we combined the SRF counts for these regions and treated these as a single region in the modeling procedure. Similar to the zero-inflated modeling, we also averaged the water level regression measures across cells within regions to obtain a single value for each month and region. Nesting count data also were not available for BCNP so the SRF data for this region were not used during the modeling.

Similar to the bird distribution modeling, we used hierarchical linear models to relate bird nesting effort to SRF counts and water level statistics. Prior to exploratory data analysis, we evaluated the relative

fit of two the different variance structures (as described above) for the hierarchical model random effects using the global (all predictors) model and selected the best via AICc. The best fitting variance structure for each species then was used during the exploratory analysis. For each species, we then fit all possible subsets of predictor variables that included: total SRF counts for each month in the nesting season, the mean of 14 day water level intercept parameter, the mean root mean squared error of water level regression, mean slope of water level change for 14 days prior to survey. Goodness-of-fit for the best fitting model was assessed as described above.

6.0 RESULTS

6.1 Descriptive summary

From the cumulative SRF database of observations, we had 438,468 observations available to us from 336 surveys conducted between 1985 and 2003. In the course of preparing these observations for analysis, a number of observations were excluded due to the issues with data integrity and clarity detailed above. Additionally, the model structure required some additional editing of the data. The incorporation of data from the SFWMM required the exclusion of observations in areas where the SFWMM did not overlap with the SRF. The introduction of a three year lag for some of the parameters required excluding data from the first three years of the survey. Finally, surveys from October and November were not considered because they were only surveyed in two of the available years. The results of each of these removals and the numbers of observations removed are summarized in Table 5.

After the necessary editing, there were 14 years and 109 months of surveys. Graphs of counts of each species by month, year, and region can be found in Appendix A. The mean counts for each species by region can be found in Tables 5-7. The Everglades National Park (ENP) region was the most often surveyed, followed by the Water Conservation Areas (WCA) with Big Cypress (BCNP) surveyed the

least. Survey protocols varied between regions. Some species were not surveyed or were pooled into larger categories dependent upon that region's protocol. For example, while the WCA and BCNP regions maintained some separate observations of Cattle Egrets, ENP lumped all of those observations into the "Small White Herons" category.

Of our focal species, the White Ibis was the most abundant. There was more variation in the count of White Ibises than in the counts for Great Egrets, which were the second most abundant species in the surveys. The mean count per cell was highest for White Ibis at 6.5 birds per cell. The average count for Great Egret was 2.6 birds per cell. Despite being less abundant, Great Egrets were detected on average in 33% of cells per survey, while White Ibises were detected in only 14% of surveyed cells. White Ibises were the most abundant in the WCA region. Great Egrets were most abundant in the ENP. BCNP had the lowest mean counts for both species among the three regions.

6.2 Subregion classification

Cluster analysis of cell vegetative and water level characteristics indicated that the optimal group count based on the cell characteristics used was approximately 52. These groups were further refined based on the judgment of experts resulting in 60 subregions in the final classifications (Figure 5). These subregions were used during the modeling of wading birds detailed below.

6.3 Model fitting

6.3.1 Mixed models in SAS

An examination of the normal probability plot of lower level residuals from all candidate hierarchical linear models predicting Great Egret and White Ibis density indicated that the residuals departed from expected (i.e., the plots were curvilinear rather than linear). To normalize these data, we log transformed the data (i.e., $\ln[\text{density} + 0.001]$) and re-fit the candidate models. An examination of

normal probability plots of lower level residuals and the chi-square plots of the empirical Bayes residuals from each candidate model fit with the transformed data indicated that the fit of the models was reasonable. However, the residual plots for both species had longer lower tails than expected presumably due to the large number of zeros in the data.

Great Egret

The most plausible model of Great Egret density was the global model containing all of the predictors: SRF cell water depth during survey and quadratic term, slope of water level change for 14 days prior to survey and quadratic term, root mean squared error of water level regression for 14 days prior to survey, average abundance of Great Egrets during nesting season in year $t-2$, and the BBS index for areas outside of the SRF (Table 10). There was virtually no support for the other candidate models; hence we based all of our inferences on the global model.

Great Egret density was nonlinearly related to both cell water level during the survey and slope of water level change for 14 days prior to survey (Table 11), but relationships were highly variable among regions (Figures 6 and 7, top). The water level random effect suggested that the influence of water level (i.e., the parameter estimate) and drying rate varied by more than 82% ($\frac{\sqrt{7.341}}{3.292}$) and 99% among regions, respectively (Table 11). Great Egret density was negatively related to the root mean squared error of water level regression suggesting a negative relationship with the magnitude or frequency of drying disruptions in the 14 days prior to survey. Great Egret density also was negatively related with the BBS index for areas outside of the SRF, which was consistent with the expectations under the distant magnet hypothesis. In contrast, density was positively related to the average Great Egret density during the nesting season in year $t-2$. The standardized estimates suggest that water level during the survey had the

greatest influence on Egret observed densities, whereas BBS index for areas outside of the SRF had the least.

Predictions based on the global model (Table 11) suggested an optimal water level and drying rate for Great Egrets. On average, we predict that Egret densities are greatest at cell depths of approximately 0.6 m (Figure 6 bottom), but the optimal values varied widely among regions (Figure 6 top). The variation was presumably due to differences in microtopography and hence, error in the water-level estimates rather than a variable response by birds. Similarly, we predict that Egret densities are greatest at a drying rate of approximately 0.01 m per day (Figure 7 bottom).

White Ibis

The most plausible model of White Ibis density also was the global model containing all of the predictors (Table 12). Similar to Great Egrets, virtually no support existed for the other candidate models, so we based all of our inferences on the global model.

White Ibis density was nonlinearly related to both cell water level during the survey and slope of water level change for 14 days prior to survey (Table 13), and the relationship also was highly variable among regions (Figures 8 and 9, top). We estimate that the relationship between White Ibis density and water level and drying rate varied by more than 250% and 77% among regions, respectively (Table 13). White Ibis density also was negatively related to the root mean squared error of water level regression and was negatively related with the BBS index for areas outside of the SRF. These relationships were consistent with our expectations. However, White Ibis density was negatively related to the average White Ibis density during the nesting season in year $t-3$, which was not consistent with our expectations. In contrast to the Great Egret models, the standardized estimates suggest that water level drying rate for

the period 14 days prior to the survey had the greatest influence on White Ibis observed densities, and White Ibis density during the nesting season in year $t - 3$ had the least (Table 13).

Predictions based on the model global model (Table 13) suggested optimal water levels and drying rates for White Ibis that differed for Great Egrets. On average, we predict that White Ibis densities are greatest at cell depth at 0.01 m (Figure 8 bottom), but the optimal values varied widely among regions (Figure 8 top). As with the Great Egret, we believe that the variation is probably due to variation in microtopography. We also predict that Ibis densities are, on average, greatest at a drying rate of approximately 0.016 m per day (Figure 9 bottom).

Model evaluation.- Leave one month-year out cross-validation of the best fitting Great Egret and White Ibis models indicated that it was relatively poor at predicting wading bird densities. Root mean squared errors for Great Egret and White Ibis were 8.6 and 12.2, respectively and represented more than 200% error, on average, from the average bird density per cell. An examination of the cell by cell predictions indicated that most of the error was due to the inability of the models to predict large concentrations of birds on individual cells.

6.3.2 Zero-inflated estimation

Great Egret

The most plausible sub-models for presence and density of Great Egrets were the global models. Similar to the results from the first analysis, virtually no support existed for the individual hypothesis models. Model goodness of fit was poor for the occupancy sub-model and good for the density sub-model. Posterior estimates of the common parameter means are summarized in Tables 13-14 and are similar with the hierarchical linear models in terms of relative magnitude and direction.

White Ibis

Models for the White Ibis followed a similar pattern. The global sub-models received virtually all of the weight. Goodness of fit was again poor for occupancy and good for density sub-models. Posterior estimates of the common parameter means (Tables 15-16) were similar to the initial analysis. As in the initial hierarchical linear regression analysis, the regional recruitment parameter was negative.

Model evaluation.- Mean within sample error for both Great Egret and White Ibis was high with an RMSE of 7.46 birds or 280% of the mean density 2.87 per cell and $1.55e+16$ birds per cell, respectively. However, these errors were largely due to extreme predictions in areas with rapidly receding water levels. The median within sample error were much lower at 0.427 and 0.338 birds for Great Egret and White Ibis, respectively. These errors represented less than 5% of the mean count of birds per cell for both species. Two-fold cross validation errors also showed great increases in accuracy compared to the hierarchical linear model with medians of 0.433 and 0.230 for Great Egret and White Ibis, respectively.

6.4 Visibility trials

We successfully completed 8 survey days with dual observers during February and March 2004. Surveys generally commenced at approximately 0730h and were completed by 1500h (EST). Front and back observers were paired throughout, rotating as previously described; however, in the first (morning) portion of the 3 March survey, data for the back seat were lost due to recording error, and the front seat observations were therefore excluded from analysis. We obtained a total of 4152 detections (occasions where ≥ 1 bird were counted) by at least 1 observer, in frequencies of 1373, 1984, and 795 among the 01, 10, and 11 observer-position histories, respectively (Table 18). The most frequently detected species were GREG (2424 detections) followed by WHIB (1001), with the remaining 7 species accounting for

727 detections. Estimated size of detected groups ranged from 1 to 275, with group sizes highest for WHIB and GI.

All the MCMC models fit the data; however, a model including species, observer, and position interactive effects with additive group size effects was superior as judged by model selection criteria (Table 19). This model produced species-, observer-, and position-specific estimates of detection probability and an estimated slope on the logit scale for group size (Table 20). We used the posterior parameter values from this model to generate predictions, as follows. First, for each combination of candidate predictors (species, observer, position, and group size), we drew parameter values from normal distributions with mean and SD specified by the posterior parameter estimates. We then combined each simulated parameter value with the candidate predictor to form a prediction under the logit model, repeated this process 10,000 times to form posterior predictive distributions for each combination of candidate predictors, and summarized the results for selected combinations of predictors (Figures 10a-c). These reveal substantial variation among species, with GREG and WHIB having higher predicted detection probabilities than other species (Figures 11a; note that the prediction for GWH should be discounted, because only 5 GWH were detected in total). Detection probability also varied across observers and seemed to depend on position in the aircraft, with detection higher for observer M and in the front seat position (Figure 10b). Finally, predicted detection varied with group size, with increasing detection with increasing group sizes; however, we note that this analysis does not take into account counting inaccuracies but rather assumes that observers perfectly counted a group if it was detected (Figure 10c).

6.4.1 Evaluation of effect of visibility bias on bird abundance patterns

Simulations of the effect of incomplete detection on the evaluation of wading bird population trends indicated that the effect differed with initial population size, rate of population change, years surveyed, and species. In general, the correct detection rates were positively related to initial population size, rate of population change, years surveyed and were greatest for White Ibis (Figures 11 and 12). Correct detection rates were lowest for 3 survey years and were generally less than 60%, on average, across species and growth rates (Figures 11 and 12). After 7 years, correct detection was 100% when population growth rates were relatively high (+/- 5% and 7% per year), but were much lower for smaller growth rates. Similarly, false detection rates were highest when growth rates and number of survey years were low and the were greatest under no population change (Figures 13 and 14). The simulations suggest that false detection rates are as high as 10% even after 11 survey years for both species under no population change.

An evaluation of the bias in the parameter estimates indicated that they differed very little with initial population size (less than 10%) and with number of survey years (Figure 15). Observed estimates of the magnitude of the population change (i.e., the slope) always were less than the known and the magnitude of the bias varied with population growth rate. Under the greatest growth rates ($\lambda = 0.93$ and 1.07), the observed slope underestimated the true rate of change (+/- 0.07), on average, by 0.035 and 0.021, for Great Egret and White Ibis, respectively. This represented 50% and 30% underestimates in the true population trends, respectively.

6.5 Evaluation of the relationship between SRF counts and annual nesting effort

The best-fitting model relating Great Egret nesting effort to SRF count and hydrologic variables contained Great Egret SRF counts in February and May (Table 21). The model accounted for 44% of the

variation in Great Egret nesting effort. Interestingly, nesting effort was negatively related to SRF counts in February and positively related to counts in May. The model was fairly poor at explaining variation among regions as 62% of the remaining variation was due to differences among regions.

The best-fitting model relating White Ibis nesting effort to SRF count and hydrologic variables contained White Ibis SRF counts in March and April, the mean of root mean squared error of water level regression for 14 days prior to survey in April, and the mean of slope of water level change 14 days prior to survey in May (Table 21). In contrast to Great Egret, the model accounted for 86% of the variation in White Ibis nesting effort. Nesting effort was positively related to the March and April SRF counts, but the relationship for March varied 238% among regions (Table 21). White Ibis nesting effort was negatively related to the root mean squared error of water level regression during April suggesting a negative relationship with the magnitude or frequency of drying disruptions during April. Conversely, White Ibis nesting effort was positively related to the mean of slope of water level change 14 days prior to survey in May suggesting a positive relationship with increasing water levels.

7.0 DISCUSSION AND RECOMMENDATIONS

7.1 Modeling outcomes

Our modeling supports the belief that multiple factors described in the competing hypotheses affect wading bird abundance and distribution. Under both approaches and for both species, we found that a model that incorporated effects from all of the hypotheses was the most plausible. These models also received so much of the weight that the individual hypothesis models could be virtually ignored when making inference about the system.

We found that the impact of the factors from each hypothesis often varied widely spatially but very little temporally. Our spatial effects were based around a nested hierarchy of ownership regions and subregions that represented vegetative and hydrologic divisions within those regions. It is unsurprising then that functional relationships between birds and factors on the landscape should vary within these subdivisions.

Relationships described by the parameters of the models were generally what we expected based on the hypotheses we were investigating. However, the negative relationship to the regional recruitment parameter for White Ibis in both modeling approaches was unexpected. Whenever a statistical relationship fails to match with biological expectations, it is possible to craft plausible explanations (i.e., some unknown correlated effect or a temporal trend). It seems very unlikely that large numbers of White Ibises in the nesting season are actually having a negative impact on numbers three years later.

Tests of the ability of our models to make predictions produced mixed results. For the majority of the observations, error rates were fairly low. However, our models were unable to account for some extreme observations and areas with unusually rapid drying rates. This trend held true for our hierarchical linear models and the zero inflated models. Mean error rates were similar for both modeling approaches. We had hoped that the zero-inflated models would be more able to handle the patchy distribution of the SRF observations. However, in order to fit these models, we necessarily used summarized subregion data rather than the cell by cell information available to the hierarchical linear models. It seems likely then that the gains from zero inflating the model are mitigated by the information lost in summarizing the data.

7.2 Difficulties with the SRF

There are few surveys of similar temporal and spatial breadth as the SRF. The SRF started and continues as a decentralized effort, in which data collection and data management responsibilities are

divided between two organizations. Compared to centrally-controlled efforts, decentralization imposes fewer constraints on the survey teams, and this has undoubtedly been helpful in maintaining this ambitious scope of survey coverage. Whereas many of the day-to-day survey logistics can and must remain at the discretion of the survey teams, we believe that three components of the survey are compromised by a lack of centralized organization: (1) establishment and enforcement of consistent survey protocols, (2) flight recording and survey documentation, and (3) data assembly and quality review. Greater coordination in each of these areas would greatly enhance the value of information returned by the survey.

7.2.1 Inconsistent Survey Protocols

As mentioned earlier (see **Literature Review**), we found documented evidence of different survey protocols in use by different survey crews: e.g., aircraft altitude, georeferencing methods, and type and specificity of collected data. Furthermore, during the course of our analyses, we uncovered other evidence of inconsistent survey protocol among or within survey units. For example, the occurrence of overlapping bird locations among multiple days of a single survey or between crews working in different survey areas demonstrated the absence of a protocol that prevents multiple sampling, or at least one that describes the manner in which these cases are to be resolved at the data compilation stage.

The principal outcome of inconsistent survey protocol is the introduction of unknown sampling effects in the data. These “nuisance” effects often are confounded with biological effects of interest and are not necessarily removable through analysis. Our recommendation is that a group comprised of survey participants and other interested parties establish and document a set of survey protocols to be applied to the entire survey effort. This group should meet regularly to review the protocols, adjusting them in a consistent manner as needed. The protocols should address every aspect of the survey that influences

how the resource is observed and how the observations are interpreted. These aspects would include, but are not limited to, spatial and temporal design of the survey; allowable survey conditions; composition and roles of the crew; direction, speed, and altitude of the aircraft; rules for observing, interpreting, and recording bird and habitat data; rules for monitoring and recording aircraft, environmental, and observer conditions; and formats for the recording of data.

We were often unable to determine what protocol had been followed because of insufficient documentation about the survey flight (e.g., what altitude was flown?; how many observers were on the flight and what were their roles?), and we could not resolve ambiguities in the data because real-time conditions of the flight had not been recorded (e.g., were birds truly not seen in a cell, or was the cell not completely traversed?). We ultimately resolved some of these questionable situations by establishing arbitrary rules that altered or removed elements from the data, but filtering the data in this way introduced some unknown degree of variation. As part of the survey protocol above, we recommend the collection and central organization of data that describe the basic conditions and parameters of each flight, perhaps those recorded at the start of each flight. The changing status (time, speed, altitude, location, orientation) of the aircraft should also be recorded in a systematic fashion, either continuously or at discrete intervals, but not less frequently than at the end of each transect.

7.2.2. Data Entry and Management

The different protocols used in assembling and verifying the data also caused problems in analysis, forcing us to make arbitrary decisions about which data could be used. A database provided to us that contained numerous, obvious errors for one part of the survey was later replaced with a “cleaned” version, but how these errors were corrected (long after the surveys were flown) was not made clear to us, and it suggested the possibility of similar, unaddressed data quality issues throughout the entire survey.

We recommend that a means be developed of transmitting the data to a central location where they can be assembled and archived. While much quality checking can be performed by the survey crews themselves immediately after the survey, persons knowledgeable in the operation of the SRF should be responsible for conducting comprehensive quality checks of the data, corresponding as needed with the flight crews to resolve questionable values.

7.2.3 Heterogeneity in Detection Rates

Our dual-observer experiment indicated that detection probabilities for the SRFs may be lower than previously suggested. Previous authors have suggested that detection rates for wading birds were approximately 85% (Hoffman et al. 1990). However, Russell and Portier (1999) estimated detection rates of 0.54 for “large dark birds” and 0.26 for “large white birds.” Our data indicate rates of 40-60% or even much lower, depending on species and other factors, and are certainly more in agreement with the estimates of Russell and Portier (1999) than with previous assertions.

This under-detection of birds from the SRF would be less of a concern if detection rates could be assumed constant. Unfortunately, our analyses strongly suggest that this assumption is invalid. Use of the SRF data for comparative purposes, and modeling must take into account that detection of groups varies by species, in relation to group size (so, smaller groups tend to be missed more frequently), and in relation to operational issues (observer identity, position of observer in the aircraft). Many other controllable (e.g., aircraft altitude) and uncontrollable (e.g., year effects) factors that we were not able to examine may also affect detection rate. To the extent that these factors are unaccounted for, extreme caution must be exercised in interpreting comparisons based on raw SRF data. In particular, comparisons between species with greatly different detection rates, or combination of data across species, or inferring habitat quality

through relative comparisons of foraging group size distributions, may be strongly confounded, unless detection is estimated and accounted for.

Our dual-observer experiments could only address factors that affect the detection of groups of birds and did not address the accuracy of counting for groups that are detected. Under- or over-counting of groups obviously would bias estimates of abundance, even if group detection was 100%; therefore, our estimates of detection may, in fact, be optimistic assessments over the accuracy of the SRF as abundance measures. Finally, however, we note that technical limitations on the dual observer experiments and data recording allow the possibility that some ‘detection histories’ were misclassified, which conceivably could result in underestimation of detection. We doubt that such conditions were common enough to substantially influence our results, particularly our modeling of sources of variation in detection rates. Nevertheless, we suggest replication of these experiments, over a larger span of spatial and temporal conditions, and with improved technology for classing detection histories. Indeed, estimation of detection—by dual observer experiments, ground calibration, or other means—could be incorporated into operational surveys via a double sampling design (Thompson 1992), much in the same way as is done for surveys of waterfowl (Pospahala et al. 1974).

Our simulation modeling of the effects of incomplete and heterogeneous detection suggest that huge biases can occur in estimates of model parameters from data that have not been corrected for detection. This is apparent in even simple models of temporal or spatial difference (i.e., trends); the impacts would be even more profound in models designed to estimate and predict the impacts of physical and biotic factors, such as those that we have considered here. Only under the most fortuitous circumstances would incomplete, heterogeneous detection have a neutral effect on model parameters and predictions. We can easily envisage situations in which detection rates could interact with physical or

biotic predictors in a form of “demonic intrusion” (Hurlbert 1984) that either mask true relationships, or create apparent (but nonexistent) ones.

Our simulations were simplifications of the sampling process that did not include all of the factors that are likely to affect population estimates. For example, we assumed that all the birds in a group were counted if a group of birds were detected, whereas previous studies suggest that counts of birds can be off by as much as 70% (Frederick et al. 2003). Nonetheless, the simulations indicated that incomplete detection can have a substantial effect on the detection of population trends, particularly at relatively short time intervals (3 years or less) and small changes in population size. Given the effect of sampling error (i.e., random variation) on the detection of population trends (Thompson 1992), we expect that detection of actual trends with the SRF data would require longer time intervals and larger changes in actual population sizes.

7.3 Performance measures based on the SRF

As described earlier, one of our tasks was to develop performance measures for wading birds in the Everglades system based on the SRF survey data. More specifically, such performance measures would be used to “gauge the progress and success of the Everglades restoration (§1.1). There is also specific interest in “performance measures for CERP based on relationships between wading bird spatial distributions and annual nesting effort (§1.2). Our analyses of the latter from SRF and nesting surveys indicate a relationship between nesting effort and bird distribution for Great Egret and White Ibis. This suggests that SRF bird counts during the breeding season can be used to estimate nesting effort for gauging progress of CERP efforts using the best-fitting models. However, we caution that these models were the result of exploratory analysis and may represent spurious statistical relationships. If the performance has to directly relate nesting effort to SRF counts, we believe that better models may be

developed by incorporating additional nesting and SRF data after 2000, carefully considering the underlying biological mechanisms, and developing specific hypotheses regarding the relationship between nesting effort and wading bird abundance and distribution.

As an alternative to directly relating nesting effort to SRF counts, we think that a performance measure along the lines of the first definition—to “gauge the progress and success of the Everglades restoration”—is feasible based on our wading bird distribution models and analyses. Our best supported model is the “global” model described in §5.4.7, which predicts cell-level bird abundance assuming that all of the major physical and biological factors considered under our alternative models, are operating. Given that we now have estimates of model coefficients (or, for random effects, of mean and dispersion factors), the implementation of the models for prediction and adaptive management would be straightforward:

- A vector of initial conditions (current bird distribution and hydrologic conditions) would be specified.
- A range of alternative hydrologic scenarios would be specified that would result in spatially-explicit values for hydrologic conditions.
- The initial conditions and hydrologic conditions under each scenario would be used as inputs to our global models, and each sub-model under specific, alternative hypotheses.
- The above would result in cell-specific predicted values for bird abundance, which could be considered to be the performance measure. Under optimal decision making, these performance measures (predictions) would be aggregated to form a composite measure, possibly involving differential weighting to over or under dispersion, and a scenario selected corresponding to the highest expected, composite performance measure.

- Following implementation of the (possibly optimal) decision, the performance measure/ prediction would be compared to future SRF observations, and likelihoods computed that represent the discrepancy between predicted and observed values under each model.
- The likelihoods would then be used to update the weightings on each alternative model (and the global model), and the process repeated under new initial conditions.

Such an adaptive approach would allow for the resolution and modification of hypotheses regarding the relative effect of multiple factors influencing wading bird populations as discussed previously.

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9.0 LITERATURE CITED

- Agresti, A. 1990. *Categorical data analysis*. Wiley, New York.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In Second International Symposium on Information Theory. Edited by B.N. Petrov and F. Csaki. Akademiai Kiado, Budapest, Hungary. pp. 267-281.
- Bancroft, G. T., A. M. Strong, R. J. Sawicki, W. Hoffman, and S. D. Jewell. 1994. Relationships among wading bird foraging patterns, colony locations, and hydrology in the Everglades. Pages 615-657 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida.
- Bancroft, G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. *Waterbirds* 25:265-277.
- Bancroft, G. T., and R. J. Sawicki. 1995. The distribution and abundance of wading birds relative to hydrologic patterns in the Water Conservation Areas of the Everglades. *Final Report to the South Florida Water Management District*. National Audubon Society, Tavernier, Florida.
- Bancroft, G.T., A. Strong, and S.D. Jewell. 1990. Foraging and nesting ecology of herons in the lower Everglades relative to water conditions. *Final report to the South Florida Water Management District*, West Palm Beach, Florida.
- Bennetts, R.E., W.A. Link, J.R. Sauer, and P.W. Sykes. 1999. Factors influencing counts in an annual survey of Snail Kites in Florida. *Auk* 116:316-323.
- Bibby, C.J., and S.T. Buckland. 1987. Bias of bird census results due to detectability varying with habitat. *Acta Oecologica-Oecologia Generalis* 8:103-112.

- Bromley, R.G., D.C. Heard, and B. Croft. 1995. Visibility bias in aerial surveys relating to nest success of arctic geese. *Journal of Wildlife Management* 59:364-371.
- Bryk, A.S., and S.W. Raudenbush. 1992. *Hierarchical linear models: applications and data analysis methods*. Sage, Newbury Park, California.
- Buckland, S., D.R. Anderson, K. P. Burnham, and J. L. Laake. 1993. *Distance sampling: estimation of biological populations*. Chapman and Hall, New York.
- Burnham, K. P, G. C. White, D.R. Anderson and J. L Laake. 1980. Estimation of density from line-transect sampling of biological populations. *Wildlife Monographs* 72: 1-202.
- Burnham, K., and D. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- Caswell, H. 1988. Theory and models in ecology: a different perspective. *Ecological Modelling* 43:33-44.
- Caughley, G., R. Sinclair, and D. Scott-Kemmis. 1976. Experiments in aerial survey. *Journal of Wildlife Management* 40:290-300.
- Chamberlin, T. 1897. The method of multiple working hypotheses. *Journal of Geology* 5:837-848.
- Conant, B., J.G. King, J.L. Trapp, and J.I. Hodges. 1988. Estimating populations of ducks wintering in southeast Alaska. Pages 541-551 in M.W. Weller, editor. *Waterfowl in Winter*. University of Minnesota Press, Minneapolis.
- Costanza, R., F. H. Sklar, and M. L. White. 1990. Modeling coastal landscape dynamics. *BioScience* 40:91-107.
- Crowell, M. L., and N. D. Mtundu. 2000. Vol. 2: Data management. Guidelines for quality control and quality assurance of hydrologic and meteorologic data. *Report by the South Florida Water Management District*. West Palm Beach, Florida.

- Crozier, G.E., and D.E. Gawlik. 2002. Avian response to nutrient enrichment in an oligotrophic wetland, the Florida Everglades. *Condor* 104:631-642.
- Crozier, G.E., and D.E. Gawlik. 2003. Wading bird nesting effort as an index to wetland ecosystem integrity. *Waterbirds* 26:303-324.
- Curnutt, J.L., J. Comiskey, M.P. Nott, and L.J. Gross. 2000. Landscape-based spatially explicit species index models for Everglades restoration. *Ecological Applications* 10:1849-1860.
- Deangelis, D.L., L.J. Gross, M.A. Huston, W.F. Wolff, D.M. Fleming, E.J. Comiskey, and S.M. Sylvester. 1998. Landscape modeling for Everglades ecosystem restoration. *Ecosystems* 1:64-75.
- Dodd, M.G., and T.M. Murphy. 1995. Accuracy and precision of techniques for counting great blue heron nests. *Journal of Wildlife Management* 59:667-673.
- Drummer, T. D. , and L.L. McDonald. 1987. Size bias in line transect sampling. *Biometrics* 43: 13-22.
- Efron, B. 1983. Estimating the error rate of a prediction rule: improvement on cross-validation. *Journal of the American Statistical Association* 78:316-331.
- Englehardt, J.D. 1998. Ecological and economic risk analysis of Everglades: phase I restoration alternatives. *Risk Analysis* 18: 755-771.
- Erwin, R.M. 1983. Feeding habitats of nesting wading birds - spatial use and social influences. *Auk* 100:960-970.
- FDOT 1999. Florida land use, cover and forms classification system. Florida Department of Transportation Surveying and Mapping Office Geographic Mapping Section, Florida Department of Transportation. Tallahassee, Florida.
- Fennema, R. J., C. J. Neidrauer, R. A. Johnson, T. K. MacVicar, and W. A Perkins. 1994. A computer model to simulate natural Everglades hydrology. Pages 249-289 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida.

- Fleming, D. M., W. F. Wolff, and D. L. DeAngelis. 1994. Importance of landscape heterogeneity to wood storks in Florida Everglades. *Environmental Management* 18:743-757.
- Fleury, B.E., and T.W. Sherry. 1995. Long-term population trends of colonial wading birds in the southern United States: the impact of crayfish aquaculture on Louisiana populations. *Auk* 112:613-632.
- Fonnesbeck, C.F. 2006. PyMC- Markovian analysis in python, version 2.4. available online at <http://trichech.us/?page_id=3>
- Frederick, P. C. 1994. Wading bird nesting success studies in the Water Conservation Areas of the Everglades. *Final Report to the South Florida Water Management District*, West Palm Beach, Florida.
- Frederick, P.C., K.L. Bildstein, B. Fleury, and J. Ogden. 1996a. Conservation of large, nomadic populations of White Ibises (*Eudocimus albus*) in the United States. *Conservation Biology* 10:203-216.
- Frederick, P. C., and M. W. Collopy. 1988. Reproductive ecology of wading birds in relation to water conditions in the Florida Everglades. Tech. rep. 30, Fla. Coop. Fish and Wildlife Research Unit, School of Forest Resources and Conservation, Univ. of Fla., Gainesville.
- Frederick, P.C., and M.W. Collopy. 1989. Nesting success of five species of wading birds (*Ciconiiformes*) in relation to water conditions in the Florida Everglades. *Auk* 106:625-634.
- Frederick, P.C., B. Hylton, J. A. Heath, and M. Ruane. 2003. Accuracy and variation in estimates of large numbers of birds by individual observers using an aerial survey simulator *Journal of Field Ornithology* 74:281- 287.

- Frederick, P.C., and J.C. Ogden. 1997. Philopatry and nomadism: contrasting long-term movement behavior and population dynamics of White Ibises and Wood Storks. *Colonial Waterbirds* 20:316-323.
- Frederick, P.C., and J.C. Ogden. 2001. Pulsed breeding of long-legged wading birds and the importance of infrequent severe drought conditions in the Florida Everglades. *Wetlands* 21:484-491.
- Frederick, P.C., and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (*Ciconiiformes*) in the Everglades Ecosystem. Pages 659- 692 in S. M. Davis and J. C. Ogden, editors. *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, Florida.
- Frederick, P.C., T. Towles, R.J. Sawicki, and G.T. Bancroft. 1996b. Comparison of aerial and ground techniques for discovery and census of wading bird (*Ciconiiformes*) nesting colonies. *Condor* 98:837-841.
- Frohring, P.C., D.P. Voorhees, and J.A. Kushlan. 1988. History of wading bird populations in the Florida Everglades - a lesson in the use of historical information. *Colonial Waterbirds* 11:328-335.
- Fukunaga, K., and D. Kessell. 1971. Estimation of classification error. *IEEE Transactions on Computers* C-20:1521-1527.
- Gaff, H., D. L. DeAngelis, L. J. Gross, R. Salinas, and M. Shorrosh. 2000. A dynamic landscape model for fish in the Everglades and its application to restoration. *Ecological Modelling* 127:33-52.
- Gates, C.E. 1979. Line transect and related issues. Pp. 71-154 in R.M. Cormack, G.P. Ptil, and D. S. Robson (eds.). *Sampling biological populations*. International Cooperative Publishing House, Fairland, MD, USA.
- Gawlik, D.E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72:329-346.

- Gelman, A.B., J.S. Carlin, H.S. Stern, and D.B. Rubin. 1995. *Bayesian data analysis*. Chapman and Hall, Boca Raton, Florida.
- Gilks, W.R. S. Richardson, S. and D. J. Spiegelhalter. 1996. *Markov Chain Monte Carlo in Practice*. Chapman and Hall, London.
- Gross, L. J., and D. L. DeAngelis. 2002. Multimodeling: new approaches for linking ecological models. Pages 467-474 in Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D.C.
- Hallam, T. G., T. L. Trawick, and W. F. Wolff. 1996. Modeling effects of chemicals on a population: application to a wading bird nesting colony. *Ecological Modelling* 92:155-178.
- Hartigan, J.A. 1985. Statistical theory in clustering. *Journal of Classification* 2: 63-76.
- Harwell, M.A. 1997. Ecosystem Management of South Florida. *BioScience* 47:499-512.
- Harwell, M.A. 1998. Science and environmental decision making in South Florida. *Ecological Applications* 8:580-590.
- Hoffman, W., G. T. Bancroft, and R. J. Sawicki. 1990. Wading bird populations and distributions in the Water Conservation Areas of the Everglades: 1985-1988. *Report to South Florida Water Management District*. National Audubon Society, Tavernier, Florida.
- Hoffman, W., G. T. Bancroft, and R. J. Sawicki. 1994. Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. Pages 585-614 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 5: 187-211.

- Hurvich, C.M., and Tsai, C. 1989. Regression and time series model selection in small samples. *Biometrika* 76: 297-307.
- Huston, M., J. Comiskey, and L. Gross. 1996. Current Approaches and Suggested Modifications ATLSS Modeling Project. Online at: <http://atlss.org>
- Johnson, F. A., K. H. Pollock, and F. Montalbano III. 1989. Visibility bias in aerial surveys of mottled ducks. *Wildlife Society Bulletin* 17:222-227.
- Johnson, R. A. and D. W. Wichern. 1992. *Applied Multivariate Statistical Analysis*, 3rd edition. Prentice-Hall, Englewood Cliffs, New Jersey.
- Kendall, W.L., B. G. Peterjohn, and J. R. Sauer. 1996. First-time observer effects in the North American Breeding Bird Survey. *Auk* 113:823-829.
- Kingsford, R. 1999. Aerial survey of waterbirds on wetlands as a measure of river and floodplain health. *Freshwater Biology* 41:425-438.
- Kushlan, J.A. 1976. Wading bird predation in a seasonally fluctuating pond. *Auk* 93:464-476.
- Kushlan, J.A. 1977. Population energetics of the American White Ibis. *Auk* 94:114-122.
- Kushlan, J.A. 1979. Feeding ecology and prey selection in the White Ibis. *Condor* 81:376-389.
- Kushlan, J.A. 1987. External threats and internal management - the hydrologic regulation of the Everglades, Florida, USA. *Environmental Management* 11:109-119.
- Kushlan, J.A. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. *Colonial Waterbirds* 9:155-162.
- Kushlan, J.A., and P.C. Frohring. 1986. The history of the southern Florida Wood Stork Population. *Wilson Bulletin* 98:368-386.

- Kushlan, J.A., and D. A. White. 1977. Nesting wading bird populations in southern Florida. *Florida Scientist* 40:65-77.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Lindley, D. V. 1985. *Making decisions*. John Wiley and Sons, New York.
- Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Institute, Cary, N.C.
- Maurer, B.A. 1996. Energetics of avian foraging. Pages 250-279 in C. Carey, editor. *Avian energetics and nutritional ecology*. Chapman and Hall, New York, New York.
- McCrimmon, D. A., Jr., S. T. Fryska, J. C. Ogden, and G. S. Butcher. 1997. Nonlinear population dynamics of six species of Florida *Ciconiiformes* assessed by Christmas Bird Counts. *Ecological Applications* 7:581-592.
- Melvin, S.L., D.E. Gawlik, and T. Scharff. 1999. Long-term movement patterns for seven species of wading birds. *Waterbirds* 22:411-416.
- Mooij, W. M., R. E. Bennetts, W. M. Kitchens, and D. L. DeAngelis. 2002. Exploring the effect of drought extent and interval on the Florida snail kite: interplay between spatial and temporal scales. *Ecological Modelling* 149:25-39.
- Morgan, M. G., and M. Henrion. 1990. *Uncertainty: a guide to dealing with uncertainty in quantitative risk and policy analysis*. Cambridge University Press, Cambridge.
- Nelson, D. A., and C. T. Theriot. 1997. *Distribution and abundance of wading birds in the Water Conservation Areas of the Florida Everglades, 1996*. U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi.

- Newman, S., J.B. Grace, and J. W. Koebel. 1996. Effects of nutrients and hydroperiod on Typha, Cladium, and Eleocharis: implications for everglades restoration. *Ecological Applications* 6:774-783.
- Newman, S., J. Schuette, J., J. B. Grace, K. F. Rutchey, T. Fontaine, K. R. Reddy, and M. Pietrucha, M. 1998. Factors Influencing Cattail Abundance in the Northern Everglades *Aquatic Botany* 60:265-280.
- Nuttie, W.K. 1997. Measurement of wetland hydroperiod using harmonic analysis. *Wetlands* 17: 82-89.
- Ogden, J.C. 1994. A comparison of wading bird nesting colony dynamics (1931-1946 and 1974-1989) as an indication of ecosystem conditions in the southern Everglades. Pages 533- 570 in S. M. Davis and J. C. Ogden, editors. *Everglades: The Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, Florida.
- Ogden, J.C., J.A. Kushlan, and J.T. Tilmant. 1976. Prey selectivity by Wood Stork. *Condor* 78: 324-330.
- Platt, J. 1964. Strong inference. *Science* 146:347-353.
- Pollock, K.H., and W.L. Kendall. 1987. Visibility bias in aerial surveys: a review of estimation procedures. *Journal of Wildlife Management* 51:502-510.
- Popper, K. R. 1959. *The logic of scientific discovery*. Hutchinson, London.
- Popper, K. 1962. *Conjectures and refutations*. Basic Books, New York.
- Popper, K. 1972. *Objective knowledge*. Clarendon Press, Oxford.
- Portier, K. M., and A. R. C. Smith. 1984. *Evaluation of sampling methodology – systematic flight/pilot wading bird survey*. Technical report. Everglades National Park, Homestead, Florida.

- Posphala, R.S., D.R. Anderson, and C.J. Henny. 1974. Population ecology of the mallard: {II}. Breeding habitat conditions, size of breeding populations, and production indices. U.S. Fish and Wildlife Service Resource Publication. 115.
- Powell, G.V.N. 1983. Food availability and reproduction by Great White Herons, *Ardea herodias*, a food addition study. *Colonial Waterbirds* 6:139-147.
- Ramsey, F. L. and J. M. Scott. 1981. Analysis of bird survey data using a modification of Emlen's methods. Pp. 483-487 in Estimating numbers of terrestrial birds. C. J. Ralph and J. M. Scott (eds). Studies in Avian Biology 6. Allen Press, Lawrence, KS, USA.
- Rodgers, J.A., S.B. Linda, and S.A. Nesbitt. 1995. Comparing aerial estimates with ground counts of nests in wood stork colonies. *Journal of Wildlife Management* 59: 656-666.
- Romesburg, H. C. 1990. Cluster Analysis for Researchers. Krieger Publishing, Malabar, Florida.
- Rudnick, D.T., Z. Chen, D.L. Childers, J.N. Boyer, and T.D. Fontaine. 1999. Phosphorus and nitrogen inputs to Florida bay: the importance of the Everglades watershed. *Estuaries* 22: 398-416.
- Russell, G. J., and K. M. Portier. 1999. *Report on the Systematic Reconnaissance Flight Wading Bird Survey in Everglades National Park, 1985-1998*. [Draft report.] National Park Service, Homestead, Florida.
- Russell, G. J., O. L. Bass, Jr., and S. L. Pimm. 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. *Animal Conservation* 5:185-199.
- Samuel, M., E. Garton, M. Schlegel, and R. Carson. 1987. Visibility bias of aerial surveys of elk in north central Idaho. *Journal of Wildlife Management* 51:622-630.

- Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, results and analysis 1966-2005. Version 6.2.2006. USGS Patuxent Wildlife Research Center, Laurel, MD [URL – <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>].
- Sauer, J.R., G.W. Pendelton, and B.G. Peterjohn. 1994. Observer differences in the North American Breeding Bird Survey. *Auk* 111:50-62.
- Sawicki, R. J., W. Hoffman, and G. L. Hasty. 1995. *Wading bird abundance and distribution in the Water Conservation Areas of the Everglades: the 1995 season*. Technical Report to the South Florida Natural Resources Center, Everglades National Park. National Audubon Society, Tavernier, Florida.
- Sklar, F. H., R. Costanza, and J. W. Day, Jr. 1985. Dynamic spatial simulation modelling of coastal wetland habitat succession. *Ecological Modelling* 29:261-281.
- Smith, D.R., K. J. Reinecke, M. J. Conroy, M. W. Brown, and J. R. Nassar. 1995. Factors affecting visibility rate of waterfowl surveys in the Mississippi alluvial valley. *Journal of Wildlife Management* 59:515-527.
- Smith, J. P. 1997. An energy-circuit population model for Great Egrets (*Ardea alba*) at Lake Okeechobee, Florida, U.S.A. *Ecological Modelling* 97:1-21.
- Snijders, T., and Bosker, R. 1999. Multilevel analysis: an introduction to basic and advanced multilevel modeling. Sage, Thousand Oaks, Ca.
- Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. Freeman, New York.
- South Florida Water Management District. 1997. *South Florida Water Management Model*. Hydrologic Systems Modeling Division, Planning Department, West Palm Beach, Florida.

- Spiegelhalter, D. J., N.G. Best, B.P. Carlin and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society*. 64: 583-639
- Strong, A.M., G.T. Bancroft, and S.D. Jewell. 1997. Hydrological constraints on Tricolored Heron and Snowy Egret resource use. *Condor* 99:894-905.
- Thompson, S. K. 1992. *Sampling*. Wiley, New York.
- Walters, C., L. Gunderson, and C.S. Holling. 1992. Experimental policies for water management in the Everglades. *Ecological Applications* 2:189-202.
- Welsh, A. H., R. B. Cunningham, C. F. Donnelly and D. B. Lindenmayer. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling* 88:297-308.
- Williams, B.K., J.D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, California.
- Wolff, W.F., 1994. An individual-oriented model of a wading bird nesting colony. *Ecological Modelling* 72:75-114.

10.0 TABLES

Table 1. Data sources and variables available for inference on Everglades wading birds.

Scale(s)	Type	Data source	Variable(s) observed
Regional	Abundance- ancillary	Christmas bird counts	
Peninsular Florida	Abundance- ancillary	Christmas bird counts	
		State surveys, Audubon(?)	
	Vegetation-ancillary	Florida Gap	
	Hydrology, wetlands- ancillary	USGS, NWI	
Everglades, WCA	Abundance-ancillary	Nesting surveys	Relative abundance and location of nest colonies
SRF	Abundance at foraging sites	SRF	abundance count at time t, coordinates x, y

Table 1. continued.

		Composition of SRF	<u>Large herons</u> Great Blue Heron Great White Heron Great Egret Wood Stork White Ibis Glossy Ibis Roseate Spoonbill <u>Small light herons</u> Little Blue Heron, Snowy Egret <u>Small dark herons</u> Tricolored Heron Little Blue Heron
SRF	Hydrology	Model predictions	
	Elevation	USGS	
	Surface water classifications	?	
	Vegetation (ENP and WCA3)		

Table 2. Mean aerial counting efficiency and colony detection estimates (\hat{p}) and standard errors (se) by sampling detection group. Estimates are relative to ground counts and were from reported values or were calculated using data provided in Dodd and Murphy (1995), Rodgers et al. (1995), Frederick et al. (1996b), and Kingsford (1999).

Sampling group	Species	<u>Nest count efficiency^a</u>		<u>Nesting colony detection^b</u>		<u>Non-nesting count efficiency</u>	
		\hat{p}	se	\hat{p}	se	\hat{p}	se
Large heron	Great Blue Heron	0.787	0.631	0.743	0.037	0.46	0.075
	Great White Heron						
	Great Egret						
	Wood Stork						
	Roseate Spoonbill						
Small light heron	Cattle Egret	0.773	0.268	0.732	0.332	0.712	0.612
	Snowy Egret						
	White Ibis						

Table 2 (continued)

	Yellow-crowned						
	Night-Heron	0.211	0.256	0.243	0.267	0.187	0.038
	Black-crowned						
	Night-Heron						
Small dark heron	Reddish Egret						
	Tricolored Heron						
	Little Blue Heron						
	Green Heron						
	Glossy Ibis						
Anhinga	Anhinga					0.289	0.045
	Double Crested Cormorant						

^a Excluding great blue heron estimates in Frederick et al. (1996b) otherwise \hat{p} (se) is 0.464 (0.602).

^b Excluding great blue heron estimates in Frederick et al. (1996b) otherwise \hat{p} (se) is 0.296 (0.384).

Table 3. Summary of wading bird nesting efforts, as reported in SFWMD Annual Wading Bird Reports, 1995-2002.

<u>Survey Area</u>	<u>Land area (km²)</u>	<u>Years Reported^a</u>	<u>Reporting Organization^b</u>	<u>Nests/ year</u>	<u>Survey frequency and timing</u>	<u>Type^c</u>	<u>Mode</u>
WCA 2 & 3	2,980	1995-2002	UF	16,929	M ^d : Jan-Jun	systematic / aerial and ground	FW ^e , airboat
Loxahatchee NWR	620	1995-2002	USFWS	8,903	irregular	PTP (1995-1998) and systematic (1999-2002) / aerial and ground	FW, helicopter, airboat
Everglades NP	4,300	1995-2002	NPS	2,181	M: Jan-Jul	PTP / aerial	FW
Florida Bay	NA ^f	1996-2001	NOAA	2,567	M: Jan-Dec	PTP (islands) / aerial	helicopter

Table 3. continued.

Southwest Coast	NA	1996, 1998-2002	NAS, RBS	1,276	once/year	PTP / aerial or ground	walk, canoe, powerboat, FW
Big Cypress NP	2,570	1996-97, 2000-2002	NPS	NA	once/year	systematic (1996) or incidental / aerial	FW, helicopter
Holey Land, Rotenberger WMAs	260	1996-2002	FFWCC	NA	irregular	incidental / aerial	FW, helicopter
Ding Darling NWR	25	1998-2002	USFWS	1,587	M: Apr-Aug	PTP / ground	motorboat
Solid Waste Authority of PB County	NA	2000-2002	SWAPBC	4,543	M: Mar-Jun	PTP / ground	boat
NF St. Lucie R.	NA	2000-2002	SFWMD	NA	once/year	PTP or incidental / ground	motorboat, kayak

^a Reported in Annual Wading Bird Reports; additional and unreported surveys may have occurred prior to these years.

^b UF = University of Florida, USFWS = U.S. Fish and Wildlife Service, NPS = National Park Service, NOAA = National Oceanic and Atmospheric Administration, NAS = National Audubon Society, RBS = Rookery Bay Sanctuary, FFWCC = Florida Fish and Wildlife Conservation Commission, SWAPBC = Solid Waste Authority of Palm Beach County, SFWMD = South Florida Water Management District.

^c Surveys classified as systematic, point-to-point (PTP), or incidental, and as aerial or ground-based.

^d Monthly; ^e Fixed-wing; ^f Not reported, not available, or not calculated.

Table 4. Parameters used during the simulation of SRF sampling protocols. The coefficients of determination (r^2) values are for models fit to SRF data of observed bird counts and group sizes.

Simulation component	Great Egret	White Ibis
Initial population size	5000, 7000, 10000	5000, 10000, 15000
Population growth per year	No change ($\lambda = 1$), increase or decrease of: 0.01, 0.03, 0.05, 0.07	
Number of years sampled	3, 5, 7, 9, 11	
Number of groups ¹	$0.478 + 0.818 \cdot \ln(\text{population size})$, $r^2 = 0.81$	$199.82 + 0.050 \cdot (\text{population size})$, $r^2 = 0.71$
Variation in group size ²	$0.420 + 1.461 \cdot \ln(\text{mean group size})$, $r^2 = 0.71$	$0.323 + 1.208 \cdot \ln(\text{mean group size})$, $r^2 = 0.88$

¹ Estimate for number of Great Egret groups requires exponential transformation.

² Variation is expressed as a standard deviation and requires exponential transformation for both species.

Table 5. Observations eliminated at various steps in the database management process to generate final data set for analysis.

Region	Raw Data	Outside of Survey Area		After Year 2000 ^a		Eliminated Due to Survey Overlap		Final
Big Cypress	26273	2938	11%	1167	4.4%	64	.24%	22104
WCAs	180676	10319	5.7%	8879	4.9%	2987	1.6%	158491
Everglades NP	231519	7537	3.2%	60285	26%	NA		163697

^a Observations after 2000 eliminated because that is the time cut off for the analysis.

Table 6. The number of surveys, mean counts, standard deviation (SD), minimum, and maximum count of species in the Systematic Reconnaissance Flights for the Northern Survey region.

Species	Surveys	Mean Count	SD	Minimum	Maximum
Black-crowned Night Heron	79	2.924050633	7.710752	0	46
Cattle Egret	79	7.392405063	22.35404	0	153
Glossy Ibis	79	221.1392405	310.7332	0	1394
Great Blue Heron	79	197.4050633	162.3771	30	924
Great Egret	79	1910.949367	1058.863	150	5901
Great White Heron	79	1.189873418	1.901929	0	9
Little Blue Heron	79	89.50632911	126.5877	0	753
Reddish Egret	79	0.012658228	0.112509	0	1
Roseate Spoonbill	79	10.96202532	26.40292	0	148
Small Dark Heron	79	113.9746835	184.6656	0	1026
Small White Heron	79	316.6202532	340.4543	3	1742
Snowy Egret	79	27.84810127	56.17237	0	335
Tri-Color Heron	79	72.50632911	117.1239	0	818
White Ibis	79	4093.177215	5219.684	0	32668
Wood Stork	79	158.0253165	236.5086	0	1241
Yellow-crowned Night Heron	79	0.518987342	4.387806	0	39

Table 7. The number of surveys, mean counts, standard deviation (SD), minimum, and maximum count of species in the Systematic Reconnaissance Flights for Big Cypress.

Species	Surveys	Mean Count	SD	Minimum	Maximum
Black-crowned Night Heron	34	0	0	0	0
Cattle Egret	34	63.7058824	118.1934	0	617
Glossy Ibis	34	5.47058824	7.844069	0	23
Great Blue Heron	34	43.1764706	99.55917	1	477
Great Egret	34	576.323529	460.2426	47	2238
Great White Heron	34	0.70588235	2.431229	0	13
Little Blue Heron	34	24.7352941	32.73522	0	124
Reddish Egret	34	0.02941176	0.171499	0	1
Roseate Spoonbill	34	0.26470588	0.790428	0	3
Small Dark Heron	34	13.9705882	26.35364	0	130
Small White Heron	34	147.5	158.5302	0	838
Snowy Egret	34	8.88235294	23.49954	0	130
Tri-Color Heron	34	7.02941176	8.200093	0	37
White Ibis	34	951.5	1091.583	23	4767
Wood Stork	34	90.1764706	137.422	0	508
Yellow-crowned Night Heron	34	0	0	0	0

Table 8. The number of surveys, mean counts, standard deviation (SD), minimum, and maximum count of species in the Systematic Reconnaissance Flights for Everglades National Park.

Species	Surveys	Mean Count	SD	Minimum	Maximum
Black-crowned Night Heron	86	0	0	0	0
Cattle Egret	86	0	0	0	0
Glossy Ibis	86	116.4186047	180.4619	0	939
Great Blue Heron	86	133.1744186	102.4392	7	480
Great Egret	86	2202.104651	1398.345	59	7261
Great White Heron	86	33.73255814	57.1877	0	425
Little Blue Heron	86	0	0	0	0
Reddish Egret	86	0	0	0	0
Roseate Spoonbill	86	96.12790698	83.21097	3	459
Small Dark Heron	86	222.0697674	195.2775	6	819
Small White Heron	86	379.9418605	347.3703	17	1517
Snowy Egret	86	0	0	0	0
Tri-Color Heron	86	0	0	0	0
White Ibis	86	3112.290698	2769.443	93	14718
Wood Stork	86	274.3372093	328.5695	0	2197
Yellow-crowned Night Heron	86	0	0	0	0

Table 9. Mean, standard deviation (SD), range for predictor variables used in fitting log-linear hierarchical model models of Great Egret (GREG) and White Ibis (WHIB) counts during the SRF.

Predictor	Mean	SD	Range
SRF cell water depth during survey (m)	0.09	0.36	-1.53 - 1.94
Slope of water level change for 14 days prior to survey (dm)	0.01	0.06	-0.45 - 0.19
Root mean squared error of water level regression for 14 days prior to survey (dm)	0.11	0.11	0.00 - 1.14
Average density of WHIB during nesting season in year t-3	3.01	1.07	0.84 - 5.02
BBS ^a index for WHIB outside SRF	12.25	4.42	7.88 - 20.49
Average density of GREG during nesting season in year t-2	1.51	0.28	0.94 - 1.95
BBS ^a index for GREG outside SRF	5.44	1.03	4.16 - 8.33

^a Breeding Bird Survey

Table 10. Hypotheses AICc, Δ AICc, and Akaike weights (w) for the set of candidate models (i) for predicting Great Egret density during the SRF. Akaike weights are interpreted as relative plausibility of candidate hypotheses.

Hypothesis	AICc	Δ AICc	w_i
Global (all hypotheses)	1085633.8	0.0	1.0
Food limitation + Hydrologic alteration	1085709.6	75.8	0.0
Food limitation + Regional recruitment	1087237.6	1603.8	0.0
Food limitation	1087274.9	1641.1	0.0
Food limitation + Distant magnet	1087276.8	1643.0	0.0
Hydrologic alteration + Regional recruitment	1100057.6	14423.8	0.0
Hydrologic alteration + Distant magnet	1100087.3	14453.5	0.0
Hydrologic alteration	1100128.1	14494.3	0.0
Distant magnet + Regional recruitment	1105691.6	20057.8	0.0
Distant magnet	1105711.6	20077.8	0.0
Regional recruitment	1105838.6	20204.8	0.0

Table 11. Estimates, standard errors, upper and lower 95% confidence intervals of fixed and random effects from best fitting log-linear hierarchical model of Great Egret (GREG) density for the SRF. Fixed effects are interpreted as the average effect for the SRF area and the random effects as the variability of the effects from subregion to subregion.

Fixed effects	Standardized			
	Estimate(SE)	estimate (SE)	Upper	Lower
Intercept	-4.109 (0.179)	-3.966 (0.150)	-3.751	-4.466
SRF cell water depth during survey	3.292 (0.364)	1.019 (0.146)	4.022	2.563
SRF cell water depth squared	-2.633 (0.879)	-0.348 (0.115)	-0.873	-4.392
Slope of water level change for 14 days prior to survey (negative values indicate drying)	-5.801 (0.831)	-0.363 (0.050)	-4.137	-7.464
Slope of 14 day water level change squared	-24.952 (3.766)	-0.074 (0.011)	-17.416	-32.488
Root mean squared error of water level regression for 14 days prior to survey (large values indicate large or frequent disruptions)	-3.183 (0.377)	-0.341 (0.042)	-2.428	-3.938
Pre-nesting season	0.361 (0.089)	0.359 (0.089)	0.538	0.183
Nesting season	0.373 (0.082)	0.372 (0.082)	0.536	0.209
Average abundance of GREG during nesting season in year t-2	0.265 (0.031)	0.074 (0.009)	0.325	0.205
BBS ^a index for GREG outside SRF	-0.014 (0.008)	-0.015 (0.009)	0.002	-0.031

^a Breeding Bird Survey

Table 11. continued.

Random effects	Standardized			
	Estimate(SE)	Estimate (SE)	Lower	Upper
Intercept	1.696 (0.321)	1.299 (0.246)	2.555	1.208
SRF cell water depth during survey	7.341 (1.413)	1.183 (0.229)	11.141	5.203
SRF cell water depth squared	43.468 (8.468)	0.736 (0.144)	66.334	30.690
Slope of water level change for 14 days prior to survey	33.125 (7.555)	0.121 (0.027)	54.833	22.171
	548.530			
Slope of 14 day water level change squared	(157.160)	0.005 (0.001)	1055.490	335.520
Root mean squared error of water level regression for 14 days				
prior to survey	6.668 (1.450)	0.082 (0.018)	10.751	4.539
Pre-nesting season	0.360 (0.081)	0.358 (0.081)	0.592	0.242
Nesting season	0.325 (0.074)	0.325 (0.074)	0.538	0.217
Residual error	11.525 (0.036)	11.525 (0.036)	11.596	11.455

Table 12. Hypotheses AICc, Δ AICc, and Akaike weights (w) for the set of candidate models (i) for predicting White Ibis density during the SRF. Akaike weights are interpreted as relative plausibility of candidate hypotheses.

Hypothesis	AICc	Δ AICc	w_i
Global	1028062.4	0.0	1.0
Food limitation + Hydrologic alteration	1028276.2	213.8	0.0
Food limitation + Distant magnet	1029113.4	1051.0	0.0
Food limitation + Regional recruitment	1029169.6	1107.2	0.0
Food limitation	1030922.3	2859.9	0.0
Hydrologic alteration + Distant magnet	1035460.7	7398.2	0.0
Hydrologic alteration + Regional recruitment	1035748.1	7685.7	0.0
Hydrologic alteration	1035818.2	7755.8	0.0
Distant magnet + Regional recruitment	1036792.7	8730.3	0.0
Distant magnet	1037122.0	9059.6	0.0
Regional recruitment	1037490.3	9427.9	0.0

Table 13. Estimates, standard errors, upper and lower 95% confidence intervals of fixed and random effects from proposed global model of White Ibis (WHIB) density for the SRF. Fixed effects are interpreted as the average effect for the SRF area and the random effects as the variability of the effects from subregion to subregion.

Fixed effects	Estimate(SE)	Standardized		
		estimate (SE)	Lower	Upper
Intercept	-5.049 (0.110)	-5.903 (0.082)	-4.828	-5.270
SRF cell water depth during survey	-0.073 (0.258)	-0.218 (0.095)	0.445	-0.590
SRF cell water depth squared	-3.012 (0.598)	-0.396 (0.078)	-1.815	-4.209
Slope of water level change for 14 days prior to survey (negative values indicate drying)	-4.021 (0.502)	-0.239 (0.030)	-3.017	-5.025
Slope of 14 day water level change squared	-11.466 (2.531)	-0.035 (0.007)	-6.402	-16.530
Root mean squared error of water level regression for 14 days prior to survey (large values indicate large or frequent disruptions)	-1.980 (0.285)	-0.211 (0.032)	-1.409	-2.551
Pre-nesting season	0.713 (0.108)	0.707 (0.108)	0.930	0.497
Nesting season	0.576 (0.068)	0.571 (0.069)	0.713	0.439
Average abundance of WHIB during nesting season in year t-3	-0.087 (0.007)	-0.093 (0.008)	-0.073	-0.101
BBS ^a index for WHIB outside SRF	-0.023 (0.002)	-0.101 (0.008)	-0.019	-0.026

^a Breeding Bird Survey

Table 13. continued.

Random effects	Estimate(SE)	Standardized		
		estimate (SE)	Lower	Upper
Intercept	0.593 (0.116)	0.367 (0.072)	0.906	0.418
SRF cell water depth during survey	3.591 (0.698)	0.480 (0.095)	5.476	2.537
SRF cell water depth squared	19.640 (3.935)	0.335 (0.068)	30.375	13.742
Slope of water level change for 14 days prior to survey	9.718 (2.452)	0.036 (0.009)	17.101	6.262
Slope of 14 day water level change squared	200.910 (67.053)	0.002 (0.001)	439.890	114.640
Root mean squared error of water level regression for 14 days prior to survey	3.550 (0.880)	0.047 (0.012)	6.179	2.303
Pre-nesting season	0.630 (0.127)	0.623 (0.125)	0.976	0.441
Nesting season	0.222 (0.050)	0.224 (0.050)	0.364	0.150
Residual error	8.712 (0.027)	8.711 (0.027)	8.765	8.658

Table 14. Posterior mean, standard deviation and upper and lower 95% confidence intervals of common means and standard deviations of parameters from zero-inflated global sub-model for average cell density of cells occupied by Great Egrets for the SRF.

Parameter	Mean	Standard		
		Deviation	Lower	Upper
BBS index for GREG outside SRF	-0.038	0.000	-0.039	-0.038
Mean of Intercept parameter	0.152	0.076	0.000	0.294
Mean of Nesting Season parameter	0.036	0.109	-0.167	0.250
Mean of Pre-Nesting Season parameter	0.103	0.105	-0.103	0.305
Mean of Root mean squared error of water level regression for 14 days prior to survey parameter	0.975	0.431	0.167	1.837
Mean of Slope of water level change 14 days prior to survey parameter	2.030	1.290	-0.401	4.645
Mean of Slope of water level change 14 days prior to survey squared parameter	3.519	9.770	-14.618	23.527
Mean of 14 day water level intercept parameter	0.017	0.028	-0.042	0.067
Mean of 14 day water level intercept squared parameter	-0.004	0.005	-0.013	0.005
Regional Recruitment of GREG parameter	0.228	0.007	0.216	0.240
Standard deviation of Intercept parameter	0.572	0.058	0.466	0.690
Standard deviation of Nesting Season parameter	0.820	0.084	0.659	0.981

Table 14. continued.

Standard deviation of Pre-nesting Season parameter	0.819	0.080	0.670	0.980
Standard deviation of Slope of water level change 14 days prior to survey parameter	3.327	0.363	2.697	4.065
Standard deviation of Slope of water level change 14 days prior to survey squared parameter	9.761	0.978	7.917	11.629
Standard deviation of 14 day water level intercept parameter	73.984	9.482	56.052	92.381
Standard deviation of 14 day water level intercept squared parameter	0.208	0.024	0.159	0.251
Standard deviation of Slope of water level change 14 days prior to survey parameter	0.035	0.005	0.026	0.045

Table 15. Posterior mean, standard deviation and upper and lower 95% confidence intervals of common means and standard deviations of parameters from zero-inflated global sub-model of occupied area for Great Egrets for the SRF.

Parameter	Standard			
	Mean	Deviation	Lower	Upper
BBS index for GREG outside SRF	-0.030	0.005	-0.039	-0.019
Mean of Intercept parameter	-0.653	0.099	-0.842	-0.460
Mean of Nesting Season parameter	0.179	0.054	0.079	0.285
Mean of Pre-Nesting Season parameter	0.178	0.050	0.082	0.277
Mean of Root mean squared error of water level regression for 14 days prior to survey parameter	-2.143	0.270	-2.739	-1.666
Mean of Slope of water level change 14 days prior to survey parameter	-1.252	0.563	-2.377	-0.176
Mean of Slope of water level change 14 days prior to survey squared parameter	0.016	0.012	-0.008	0.037
Mean of 14 day water level intercept parameter	0.290	0.029	0.229	0.344
Mean of 14 day water level intercept squared parameter	-0.041	0.006	-0.053	-0.029
Regional Recruitment of GREG parameter	0.240	0.019	0.198	0.276
Standard deviation of Intercept parameter	0.781	0.081	0.621	0.941

Table 15. continued.

Standard deviation of Nesting Season parameter	0.365	0.041	0.287	0.443
Standard deviation of Pre-nesting Season parameter	0.335	0.037	0.268	0.409
Standard deviation of Slope of water level change 14 days prior to survey parameter	1.846	0.242	1.403	2.331
Standard deviation of Slope of water level change 14 days prior to survey squared parameter	3.921	0.770	2.352	5.366
Standard deviation of 14 day water level intercept parameter	0.025	0.012	0.006	0.046
Standard deviation of 14 day water level intercept squared parameter	0.220	0.022	0.180	0.266
Standard deviation of Slope of water level change 14 days prior to survey parameter	0.046	0.005	0.037	0.055

Table 16. Posterior mean, standard deviation and upper and lower 95% confidence intervals of common means and standard deviations of parameters from zero-inflated global sub-model for average cell density of cells occupied by White Ibises for the SRF.

Parameter	Standard			
	Mean	Deviation	Lower	Upper
BBS index for WHIB outside SRF	-0.043	0.002	-0.045	-0.039
Mean of Intercept parameter	1.275	0.178	0.915	1.611
Mean of Nesting Season parameter	0.324	0.163	-0.006	0.633
Mean of Pre-Nesting Season parameter	0.245	0.166	-0.077	0.564
Mean of Root mean squared error of water level regression for 14 days prior to survey parameter	1.135	0.927	-0.745	2.873
Mean of Slope of water level change 14 days prior to survey parameter	2.422	2.333	-2.315	6.759
Mean of Slope of water level change 14 days prior to survey squared parameter	-22.041	16.669	-54.745	10.476
Mean of 14 day water level intercept parameter	-0.021	0.052	-0.130	0.078
Mean of 14 day water level intercept squared parameter	-0.018	0.008	-0.035	-0.002
Regional Recruitment of WHIB parameter	-0.010	0.009	-0.022	0.007
Standard deviation of Intercept parameter	1.229	0.128	0.994	1.501

Table 16. continued.

Standard deviation of Nesting Season parameter	1.273	0.131	1.035	1.542
Standard deviation of Pre-nesting Season parameter	1.315	0.124	1.089	1.561
Standard deviation of Slope of water level change 14 days prior to survey parameter	6.994	0.760	5.547	8.413
Standard deviation of Slope of water level change 14 days prior to survey squared parameter	18.004	2.034	14.405	22.029
Standard deviation of 14 day water level intercept parameter	128.845	14.977	99.940	156.662
Standard deviation of 14 day water level intercept squared parameter	0.401	0.042	0.323	0.483
Standard deviation of Slope of water level change 14 days prior to survey parameter	0.063	0.008	0.048	0.079

Table 17. Posterior mean, standard deviation and upper and lower 95% confidence intervals of common means and standard deviations of parameters from zero-inflated global sub-model of occupied area for White Ibises for the SRF.

Parameter	Mean	Standard		
		Deviation	Lower	Upper
BBS index for WHIB outside SRF	-0.072	0.001	-0.074	-0.070
Mean of Intercept parameter	0.000	0.000	0.000	0.000
Mean of Nesting Season parameter	0.090	0.114	-0.132	0.310
Mean of Pre-Nesting Season parameter	0.234	0.125	-0.005	0.476
Mean of Root mean squared error of water level regression for 14 days prior to survey parameter	-0.001	0.000	-0.001	0.000
Mean of Slope of water level change 14 days prior to survey parameter	0.841	0.474	-0.078	1.726
Mean of Slope of water level change 14 days prior to survey squared parameter	-0.007	0.004	-0.015	0.000
Mean of 14 day water level intercept parameter	0.082	0.033	0.013	0.147
Mean of 14 day water level intercept squared parameter	-0.101	0.010	-0.121	-0.081
Regional Recruitment of WHIB parameter	-0.264	0.004	-0.273	-0.257
Standard deviation of Intercept parameter	0.000	0.000	0.000	0.000

Table 17. continued.

Standard deviation of Nesting Season parameter	0.867	0.085	0.713	1.033
Standard deviation of Pre-nesting Season parameter	0.945	0.106	0.737	1.144
Standard deviation of Slope of water level change 14 days prior to survey parameter	0.000	0.000	0.000	0.000
Standard deviation of Slope of water level change 14 days prior to survey squared parameter	3.098	0.364	2.434	3.807
Standard deviation of 14 day water level intercept parameter	0.011	0.006	0.005	0.026
Standard deviation of 14 day water level intercept squared parameter	0.250	0.025	0.202	0.299
Standard deviation of Slope of water level change 14 days prior to survey parameter	0.074	0.008	0.059	0.088

Table 18. Summarized detection histories by species for dual-observer detection trials.

Species	Detection history				Group size		
	01	10	11	Total detections	Mean	SE	range
Great Egret	745	1093	586	2424	1.770833	2.344148	1- 75
White Ibis	348	485	168	1001	6.876083	18.87498	1- 275
Great Blue Heron	83	95	17	195	1.037915	0.191444	1- 2
Small dark herons	40	49	5	94	1.56701	1.079228	1- 6
Small white herons	77	145	2	224	1.491071	1.497355	1- 15
Wood Stork	53	85	11	149	2.322785	3.12636	1- 28
Glossy Ibis	12	13	2	27	4.241379	5.047313	1- 20
Roseate Spoonbill	12	17	4	33	1.837838	1.802984	1- 10
Great White Heron	<u>3</u>	<u>2</u>	<u>0</u>	<u>5</u>	1.000000	0.000000	1- 1
Total	1373	1984	795	4152			

Table 19. Model comparison and fit statistics for dual-observer detection trials.

Model	AIC	DIC	GOF
Species*observer*position + count	8366.63	8291.42	0.13588
Species*observer*position	8381.789	8304.816	0.134355
Species + count	8408.54	8393.771	0.136813
Species*position*count	8422.866	8269.527	0.160073
Species*observer	8423.611	8390.043	0.150219
Species + observer + position	8425.873	8412.742	0.172165
Species*observer*count	8462.871	8233.252	0.152433
Species + observer	8514.606	8502.374	0.185109
Species	8564.473	8552.986	0.105304
Species*observer*position*count	8597.444	8112.944	n/a
Null	8715.749	8714.799	0.104672
Species*observer*count*water*position	10931.95	8293.495	0.157543

Table 20. Parameter estimates for best fitting detection model (Species*observer*position + count).

Parameter ^a	Species ^b	Observer	Position	Mean	SE	Lower	Upper
count	----			0.023718	0.005972	0.012145	0.035783
p	GREG	E	Front	0.406542	0.023769	0.359678	0.449259
			Rear	0.397895	0.018822	0.361089	0.435661
		L	Front	0.38409	0.025457	0.337014	0.435144
			Rear	0.279873	0.017339	0.245628	0.31113
		M	Front	0.46524	0.021403	0.426249	0.510942
			Rear	0.317848	0.022115	0.272342	0.358331
	WHIB	E	Front	0.243006	0.032407	0.176894	0.300549
			Rear	0.244483	0.024924	0.186175	0.290946
		L	Front	0.230158	0.026997	0.170753	0.274001
			Rear	0.175687	0.025816	0.126958	0.222367
		M	Front	0.374615	0.035614	0.293622	0.442022
			Rear	0.277699	0.033619	0.185992	0.336345
	GBH	E	Front	0.210022	0.063806	0.105834	0.337501
			Rear	0.201464	0.055663	0.111779	0.368021
		L	Front	0.129609	0.058962	0.034883	0.254418
			Rear	0.230051	0.061691	0.127844	0.337782
		M	Front	0.246324	0.052102	0.137498	0.329371
			Rear	0.093203	0.045341	0.024211	0.218527
	SDH	E	Front	0.176057	0.069821	0.06607	0.320785
			Rear	0.139406	0.045455	0.063069	0.228554
		L	Front	0.085055	0.055516	0.013207	0.218646
			Rear	0.362259	0.077972	0.242044	0.507653
		M	Front	0.236127	0.069776	0.094842	0.358199
			Rear	0.109946	0.072528	0.017212	0.261166

Table 20. continued.

SWH	E	Front	0.081665	0.044357	0.016218	0.176641
		Rear	0.030459	0.010708	0.012768	0.053711
	L	Front	0.027453	0.018444	0.003002	0.071825
		Rear	0.187613	0.075609	0.040711	0.321074
	M	Front	0.284359	0.065192	0.162202	0.412054
		Rear	0.06911	0.044391	0.008798	0.179794
WS	E	Front	0.143116	0.081128	0.032359	0.301077
		Rear	0.109348	0.03491	0.054441	0.184845
	L	Front	0.178451	0.071613	0.059021	0.302302
		Rear	0.161565	0.081594	0.04255	0.304036
	M	Front	0.270177	0.06365	0.149632	0.403924
		Rear	0.094496	0.036496	0.031366	0.162511
GI	E	Front	0.40454	0.200689	0.039332	0.699257
		Rear	0.271654	0.083025	0.152542	0.436123
	L	Front	0.08382	0.058539	0.005121	0.205146
		Rear	0.513556	0.115136	0.341839	0.70712
	M	Front	0.520645	0.093028	0.372452	0.67895
		Rear	0.161112	0.068163	0.03021	0.325586
RS	E	Front	0.526156	0.183045	0.248043	0.837708
		Rear	0.130677	0.049271	0.028209	0.245679
	L	Front	0.458684	0.093238	0.292354	0.683648
		Rear	0.500869	0.060447	0.397854	0.636333
	M	Front	0.190035	0.067689	0.044575	0.303294
		Rear	0.454308	0.200512	0.138309	0.698587

Table 20. continued.

GWH	E	Front	0.448209	0.105761	0.302704	0.643725
		Rear	0.234103	0.123388	0.028892	0.441037
L	Front	0.115842	0.080807	0.00468	0.299027	
	Rear	0.609987	0.1617	0.335258	0.808154	
M	Front	0.582625	0.17104	0.191325	0.812719	
	Rear	0.340924	0.123494	0.13524	0.541426	

^aModel predicts detection as $\log it(p) = \log it^{-1}(\hat{p}_{spp,obs,pos}) + \beta \times X$, where X is median group size in each of 5 categories : $C = 1$; $1 < C_{ij} \leq 5$; $5 < C \leq 10$; $10 < C \leq 50$; and $C > 50$.

^bGREG=Great Egret, WHIB=White Ibis; GBH=Great Blue Heron; SDH=Small dark herons; SWH=Small white herons; WS=Wood Stork; GI=Glossy Ibis; RS=Roseate Spoonbill; GWH=Great White Heron.

Table 21. Estimates, standard errors, upper and lower 95% confidence intervals of fixed and random effects from exploratory analysis of the relationship between nesting effort and SRF counts and hydrologic variables for Great Egret and White Ibis. Fixed effects are interpreted as the average effect for the SRF area and the random effects as the variability of the effects from region to region.

Parameter	Estimate	SE	Lower	Upper
<u>Great Egret</u>				
<i>Fixed effects</i>				
Intercept	1151.97	411.01	346.39	1957.55
GREG SRF counts in February	-0.55	0.1475	-0.84	-0.26
GREG SRF counts in May	0.97	0.2181	0.54	1.40
<i>Random effects</i>				
Intercept	374043	334318	111490	7855205
Residual error	225814	68272	134904	453366
<u>White Ibis</u>				
<i>Fixed effects</i>				
Intercept	-270.12	389.89	-1034.30	494.06
WHIB SRF counts in March	0.54	0.15	0.26	0.83
WHIB SRF counts in April	1.47	0.77	-0.04	2.97
Mean of Root mean squared error of water level regression for 14 days prior to survey parameter in April	-9222	2102	-13342	-5102
Mean of Slope of water level change 14 days prior to survey parameter in May	16256	4181	8062	24450
<i>Random effects</i>				
WHIB counts in March	1.67	1.41	0.52	26.56
Residual error	675524	214048	395028	1411159

11.0 FIGURES

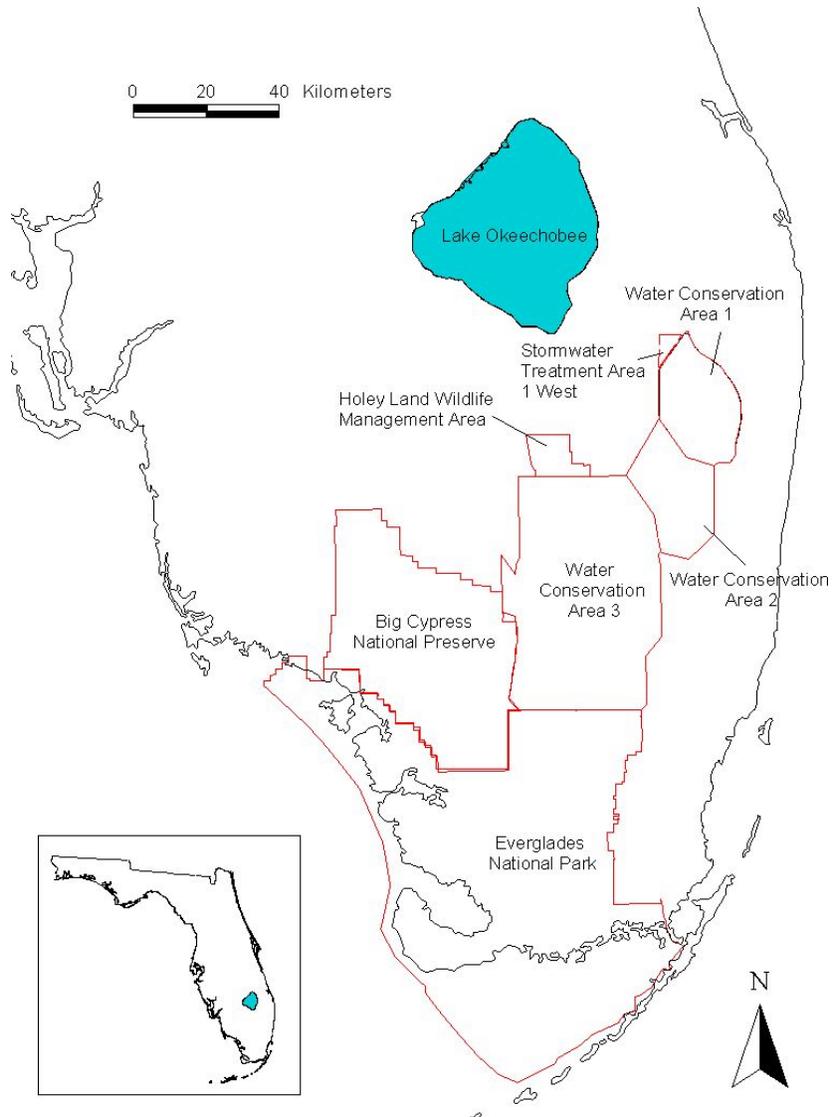


Figure 1. Location of Everglades study areas and Systematic Reconnaissance Flights (SRF).

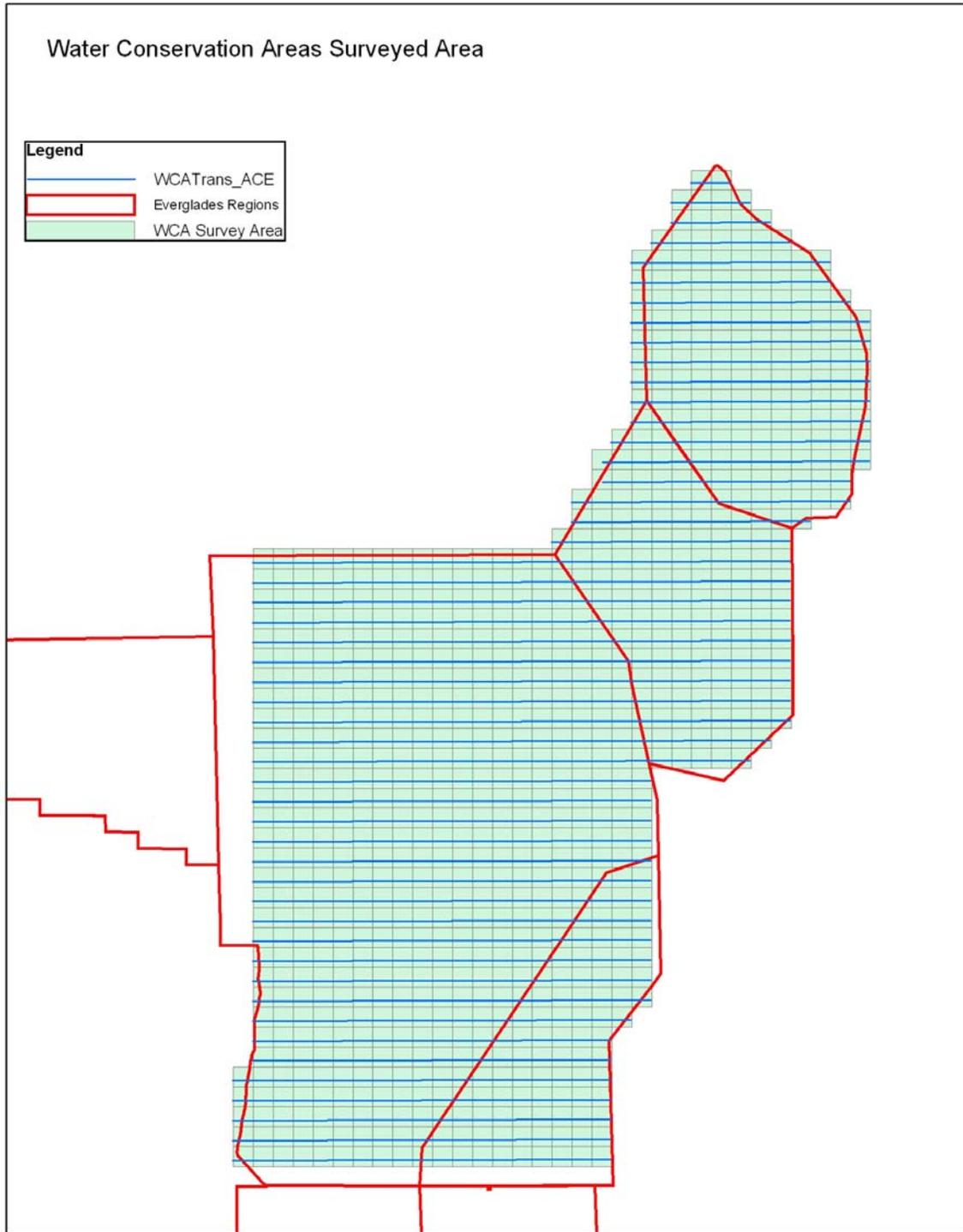


Figure 2. Northern Survey region with transects flown by the SRF.

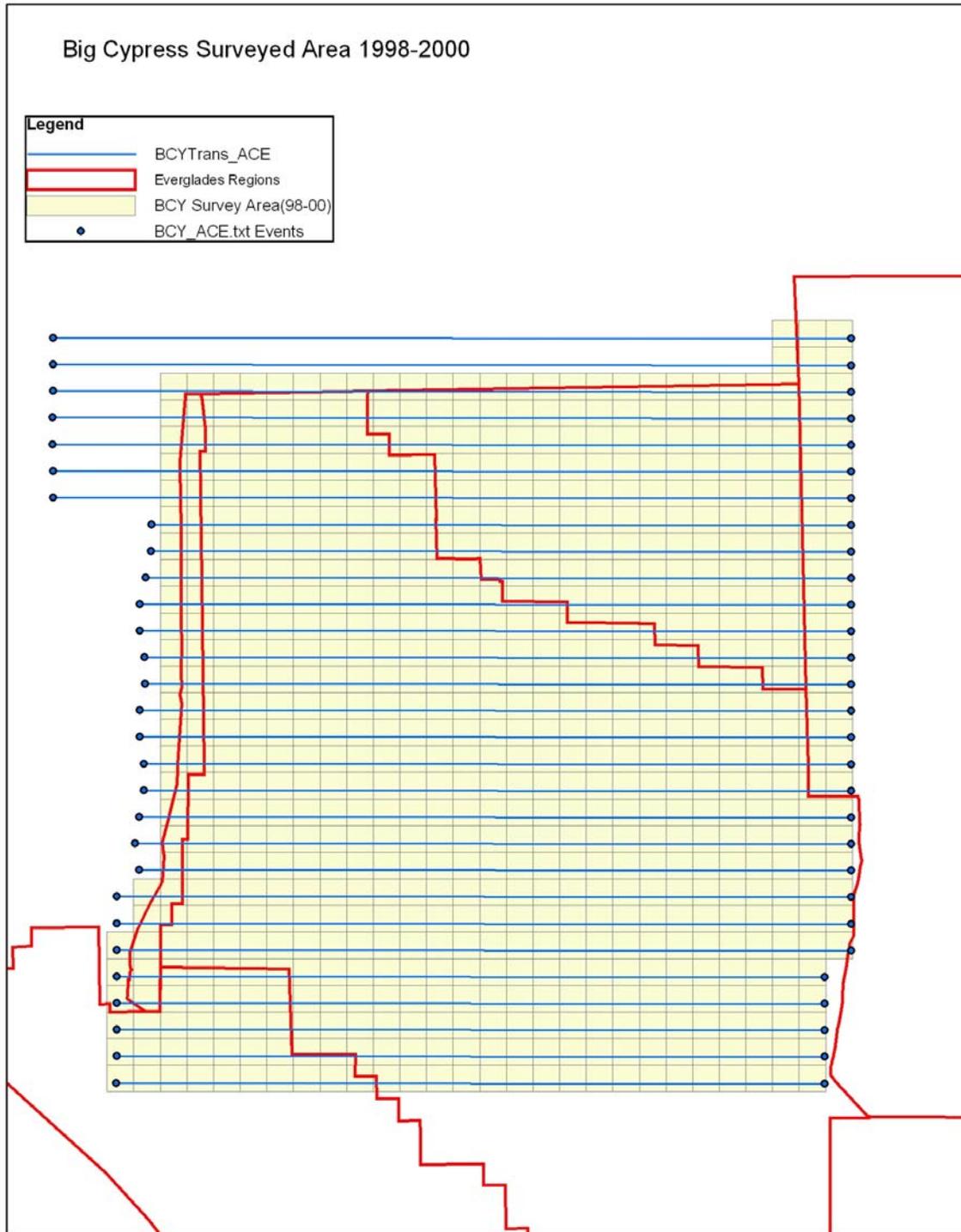


Figure 3. Area of Big Cypress surveyed by the SRF with transect and SRF cells.

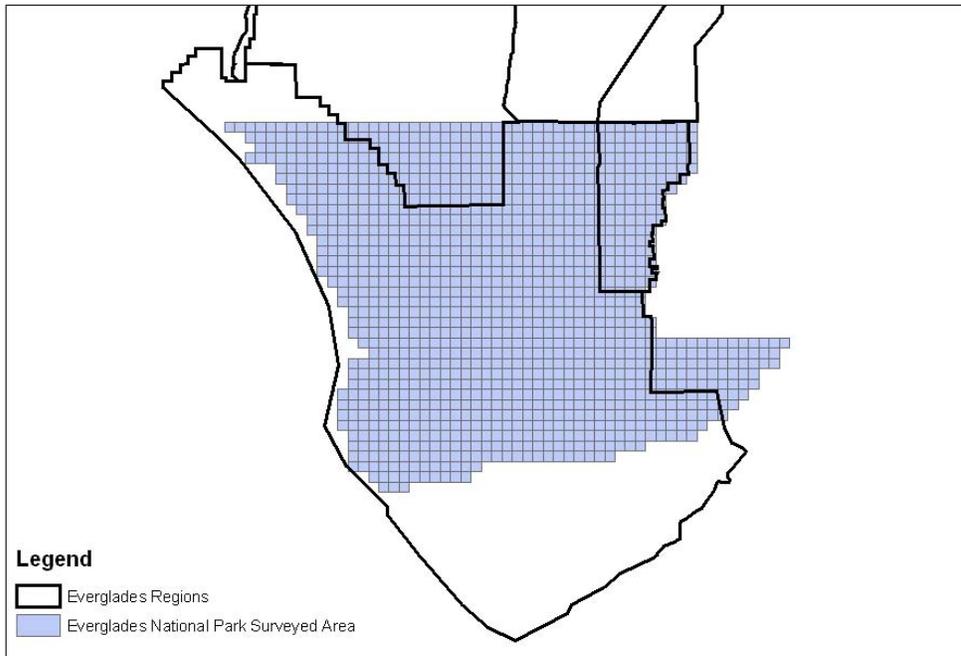


Figure 4. Area of the Everglades National Park surveyed by the SRF.

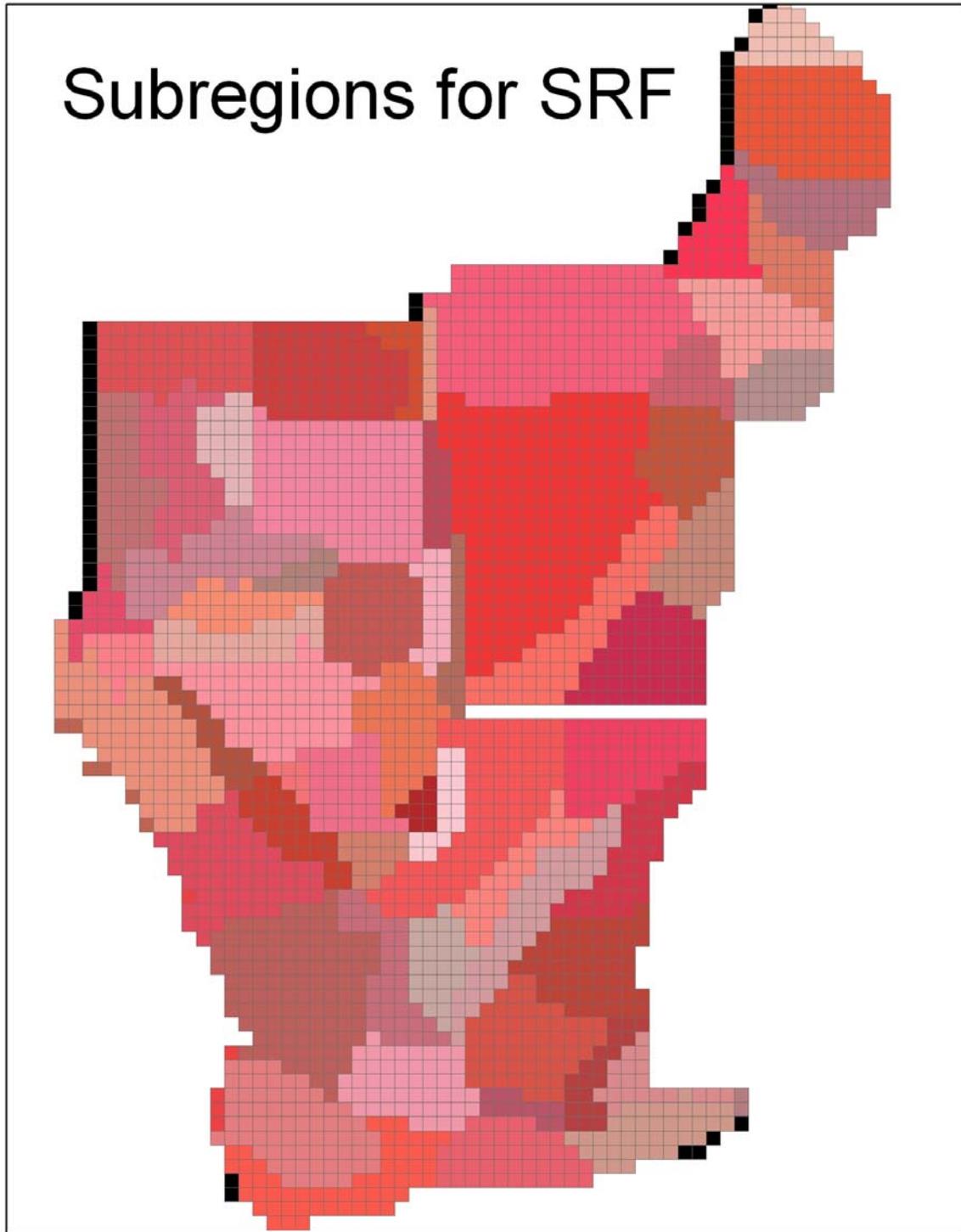


Figure 5. Subregions based on cluster analysis of vegetative and hydrologic factors for analysis and modeling of the SRF.

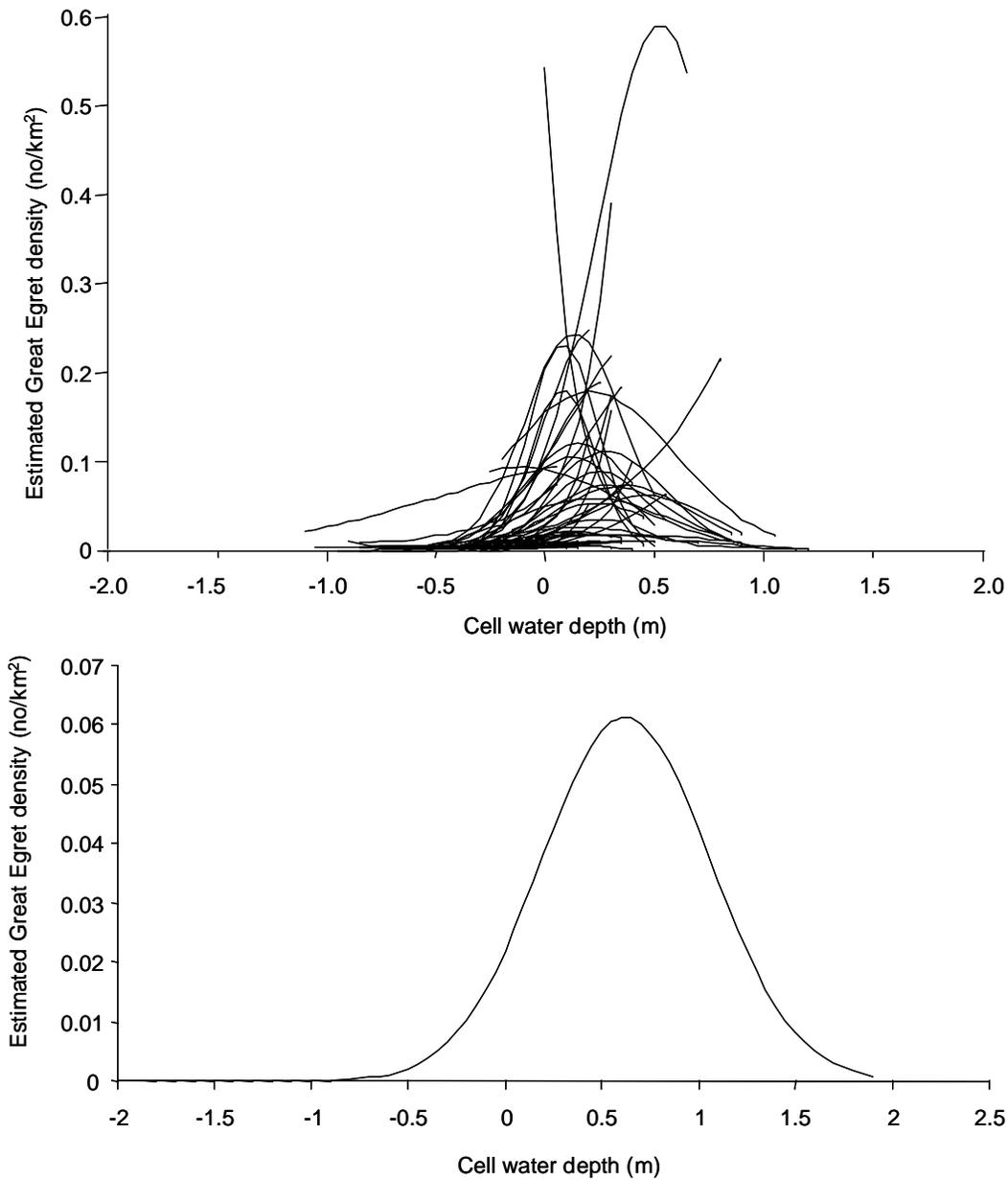


Figure 6. Empirical Bayes estimates of the relationship Great Egret density versus cell depth during the nesting season for each subregion (top) and the average relationship between cell depth and Great Egret abundance (bottom). Subregion-specific relationships (top) are only plotted for the sampled range of cell water depths predicted for each subregion. The average relationship (bottom) is based on the best fitting hierarchical model of Great Egret density using average values observed during the study for other parameters in the model (Table 9).

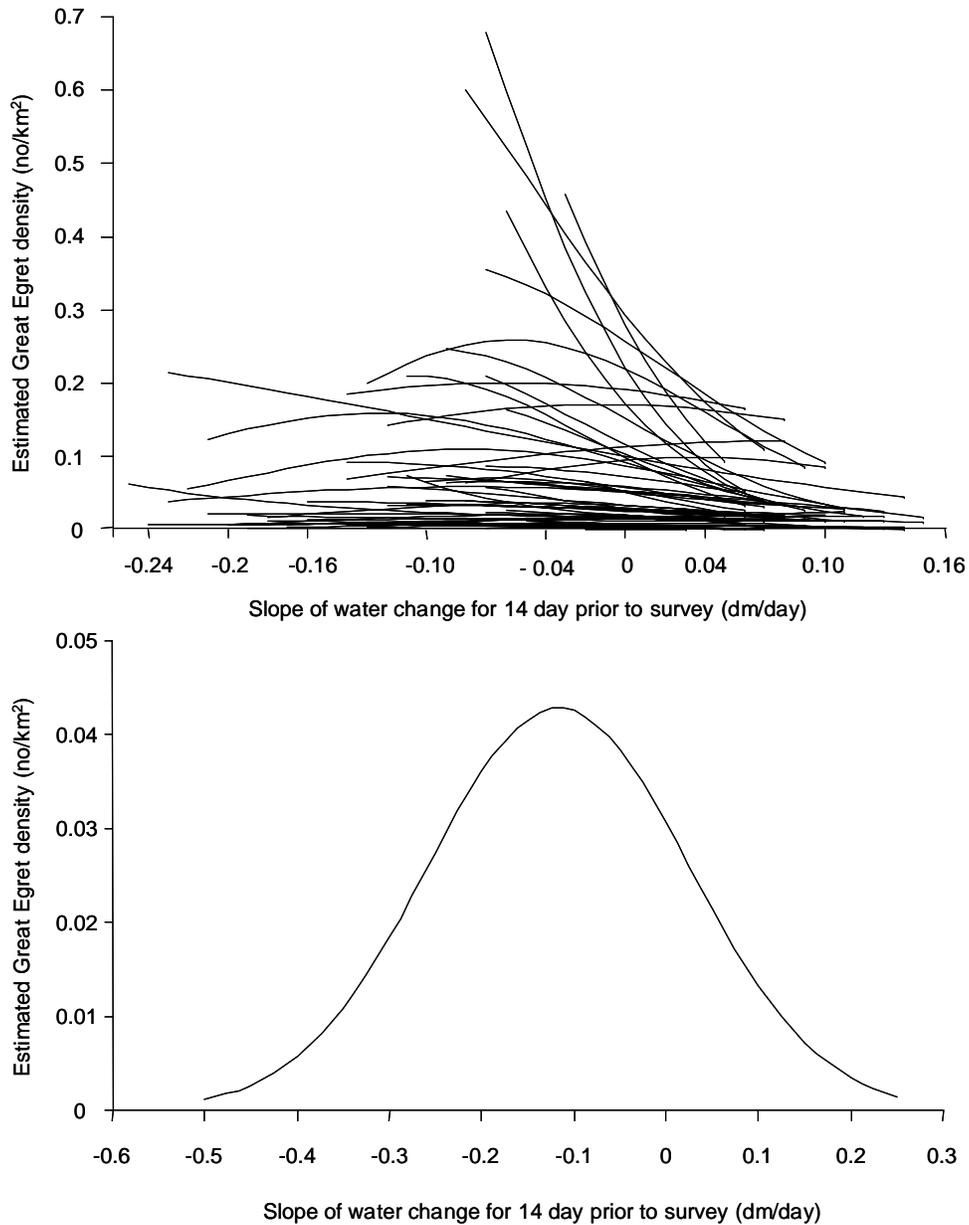


Figure 7. Empirical Bayes estimates of the relationship between Great Egret density versus the slope of water level change for 14 days prior to survey during the nesting season for each subregion (top) and the average relationship between cell depth and Great Egret abundance (bottom). Subregion-specific relationships (top) are only plotted for the sampled range of slopes predicted for each subregion. The average relationship (bottom) is based on the best fitting hierarchical model of Great Egret density using average values observed during the study for other parameters in the model (Table 9).

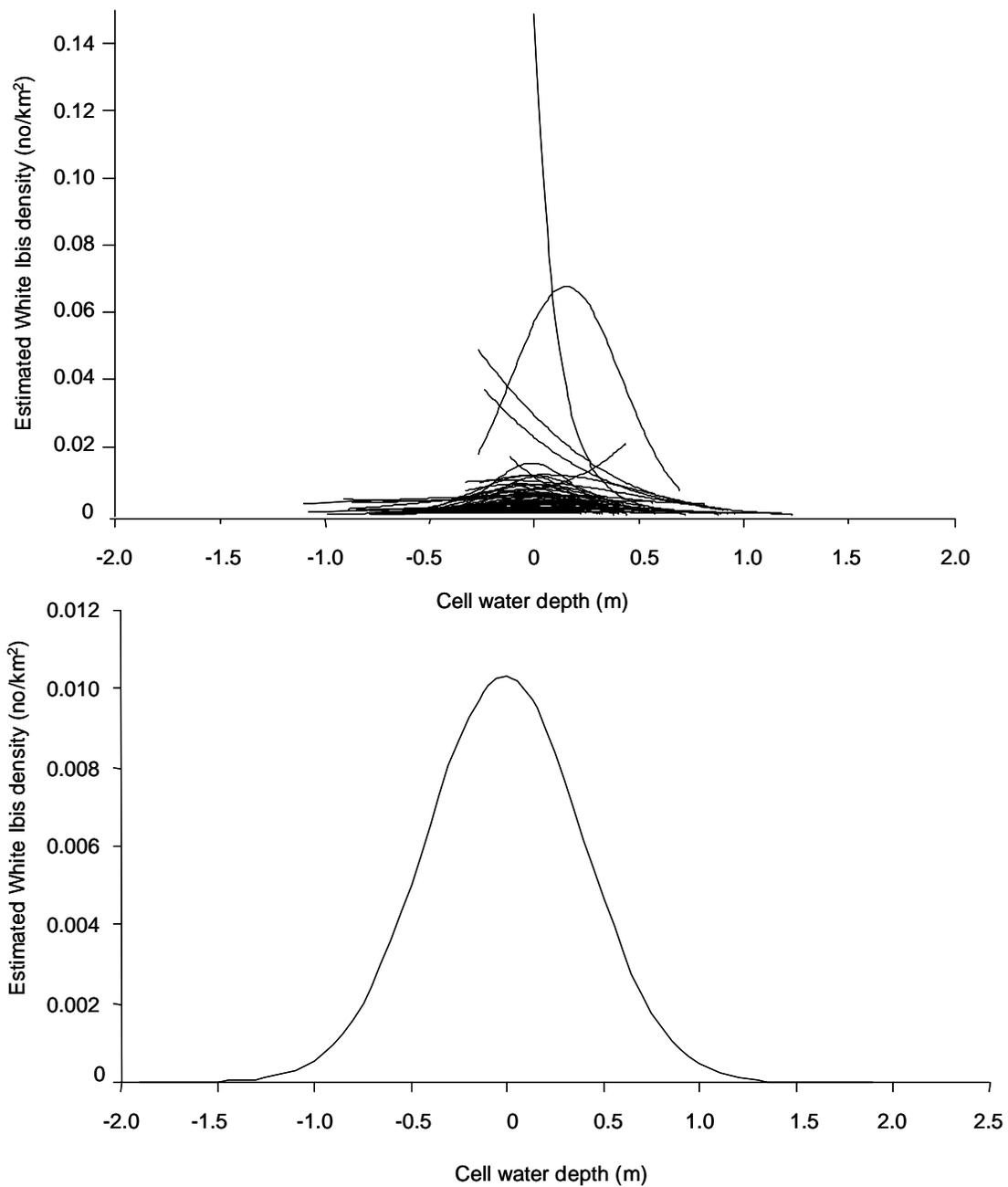


Figure 8. Empirical Bayes estimates of the relationship White Ibis density versus cell depth during the nesting season for each subregion (top) and the average relationship between cell depth and White Ibis abundance (bottom). Subregion-specific relationships (top) are only plotted for the sampled range of cell water depths predicted for each subregion. The average relationship (bottom) is based on the best fitting hierarchical model of White Ibis density using average values observed during the study for other parameters in the model (Table 9).

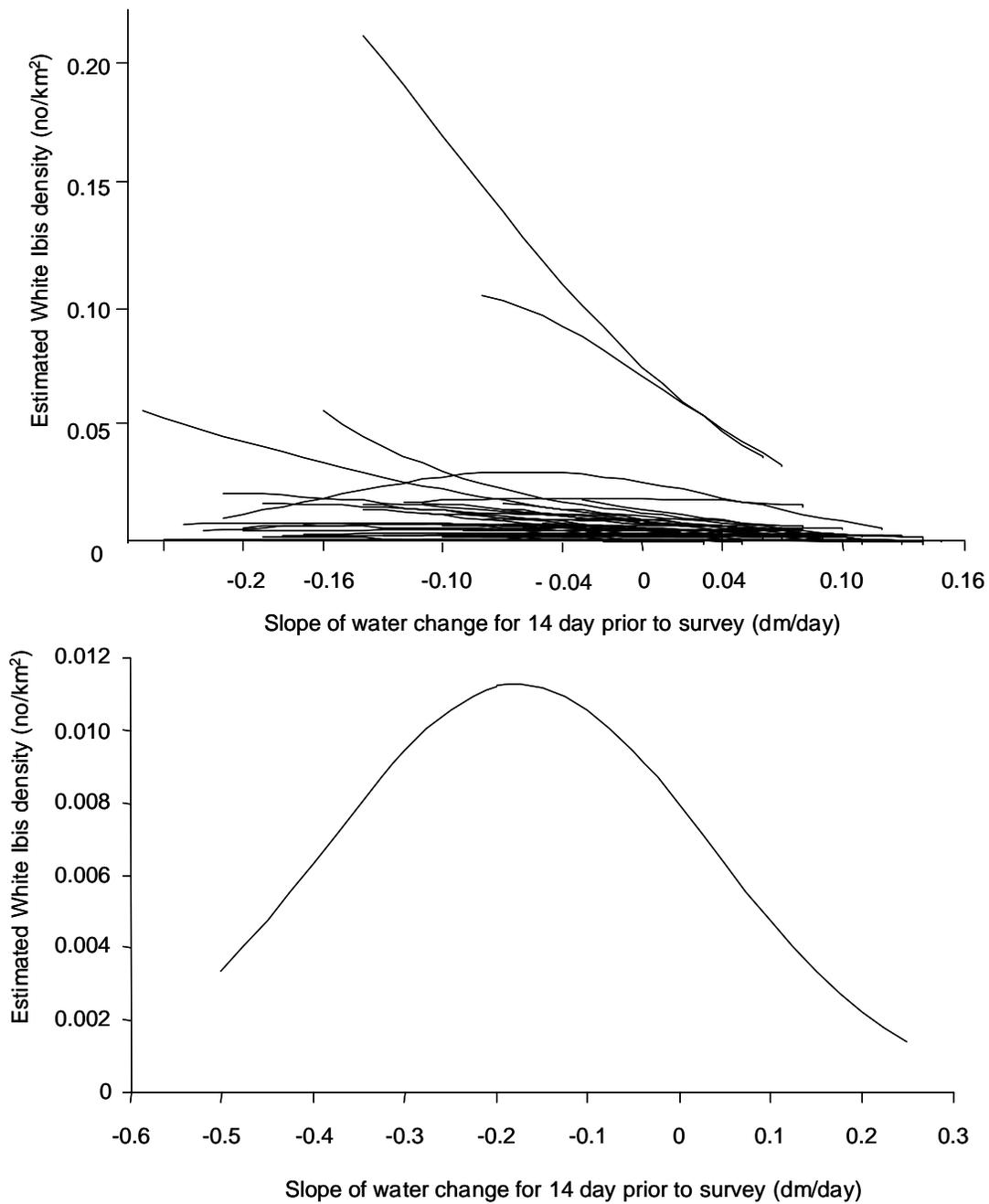


Figure 9. Empirical Bayes estimates of the relationship between White Ibis density versus the slope of water level change for 14 days prior to survey during the nesting season for each subregion (top) and the average relationship between cell depth and White Ibis abundance (bottom). Subregion-specific relationships (top) are only plotted for the sampled range of slopes predicted for each subregion. The average relationship (bottom) is based on the best fitting hierarchical model of White Ibis density using average values observed during the study for other parameters in the model (Table 9).

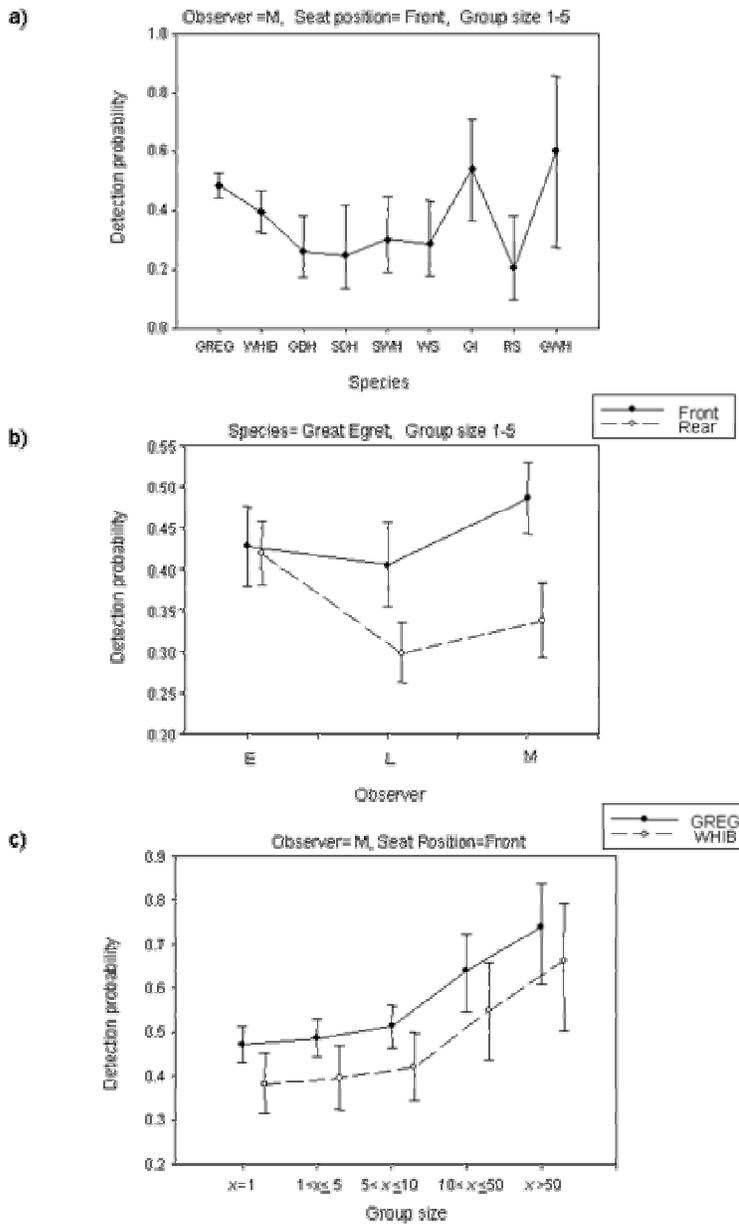


Figure 10. Predicted detection probabilities in relation to selected combination of species, observer, and group size from dual-observer trials. (a) Detection in relation to species or species group, conditioned on Observer = M, Position = Front, and 1 < Flock Size ≤ 5; (b) Detection in relation to observer and position in aircraft, conditioned on Species = GREG and 1 < Flock Size ≤ 5. (c) Detection in relation to group size for Great Egret (GREG) and White Ibis (WHIB), conditioned on Observer = M, Position = Front. GBH = Great Blue Heron; SDH = Small dark herons; SWH = Small white herons; WS = Wood Stork; GI = Glossy Ibis; RS = Roseate Spoonbill; GWH = Great White Heron.

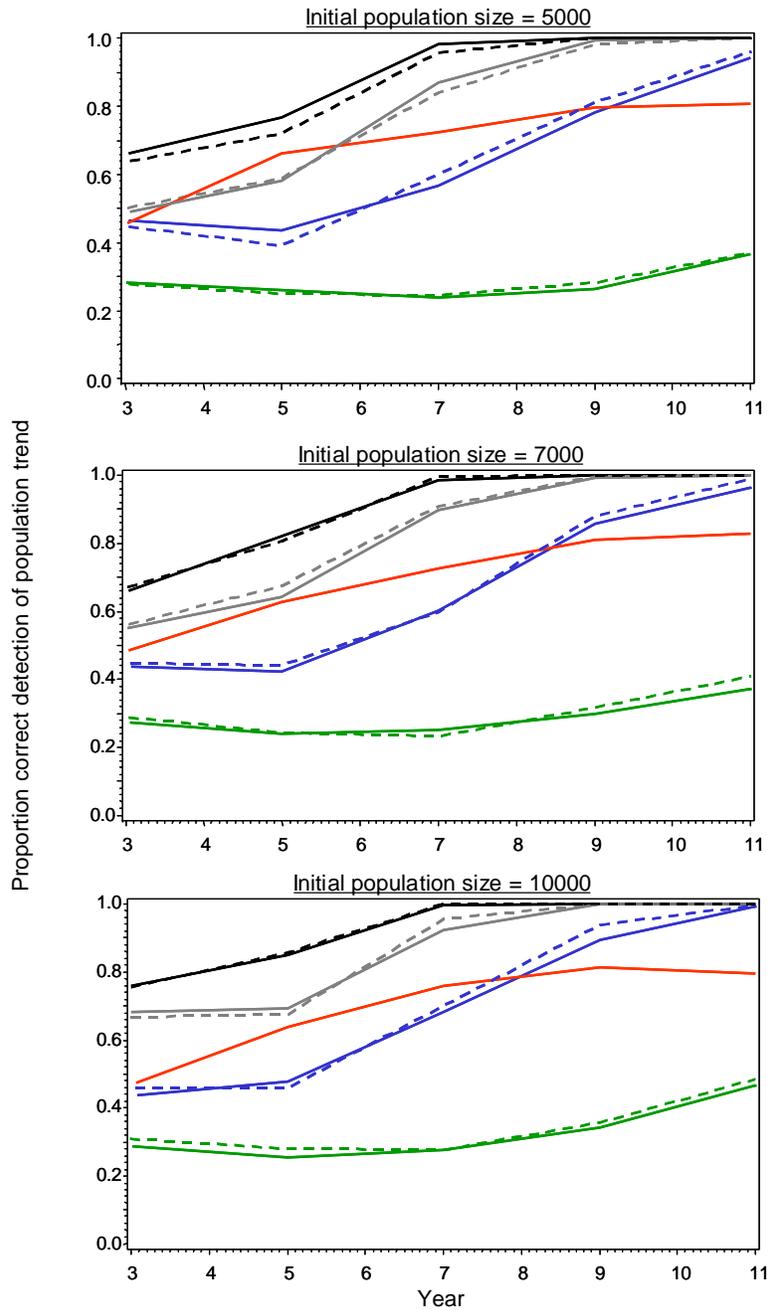


Figure 11. The proportion of simulations that detected the correct population trend by number of simulated sampling years using linear regression and $\alpha = 0.10$ for simulated positive (solid) and negative (broken) changes in annual population growth of 0.07 (black), 0.05 (gray), 0.03 (blue), 0.01 (green), and no change (red) and 3 initial population sizes for Great Egret. Proportion based on 1000 simulations of two randomly assigned rear observers during SRF surveys.

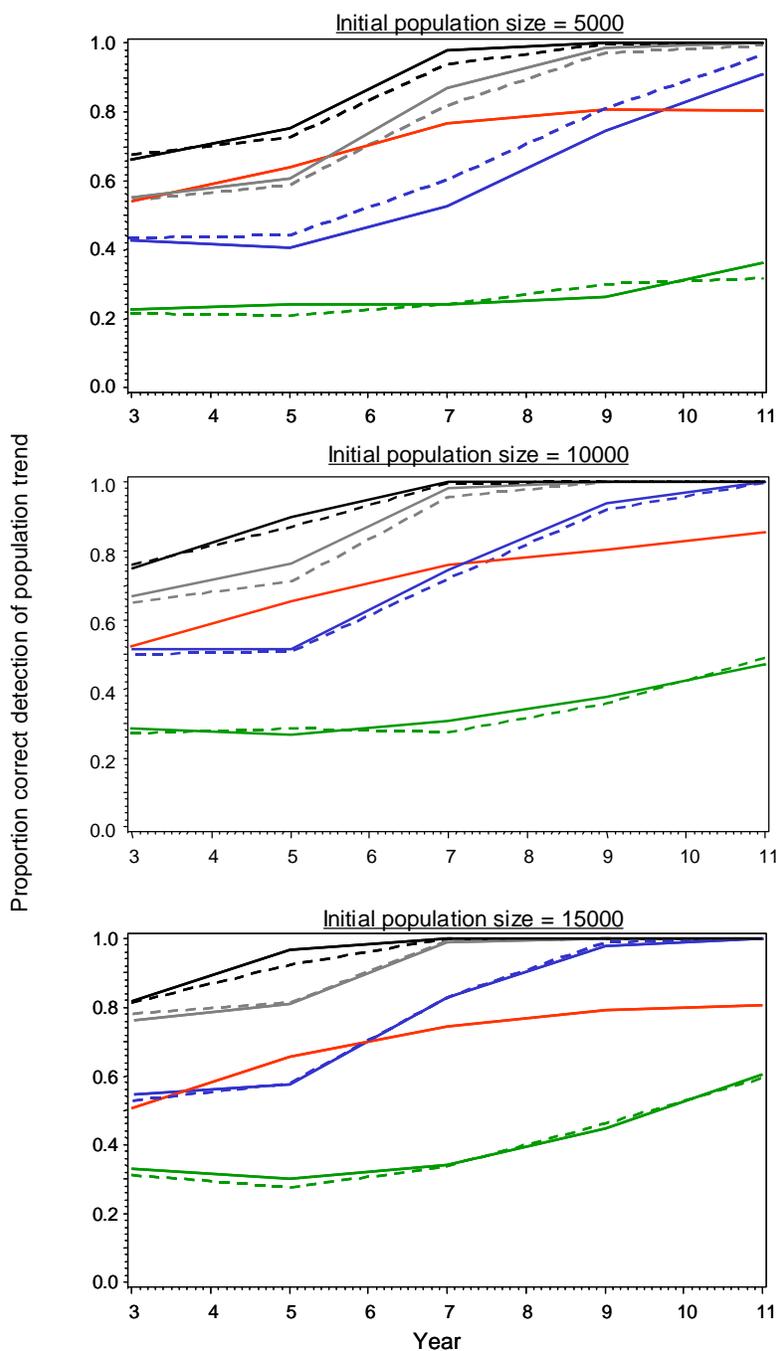


Figure 12. The proportion of simulations that detected the correct population trend by number of simulated sampling years using linear regression and $\alpha = 0.10$ for simulated positive (solid) and negative (broken) changes in annual population growth of 0.07 (black), 0.05 (gray), 0.03 (blue), 0.01 (green), and no change (red) and 3 initial population sizes for White Ibis. Proportion based on 1000 simulations of two randomly assigned rear observers during SRF surveys.

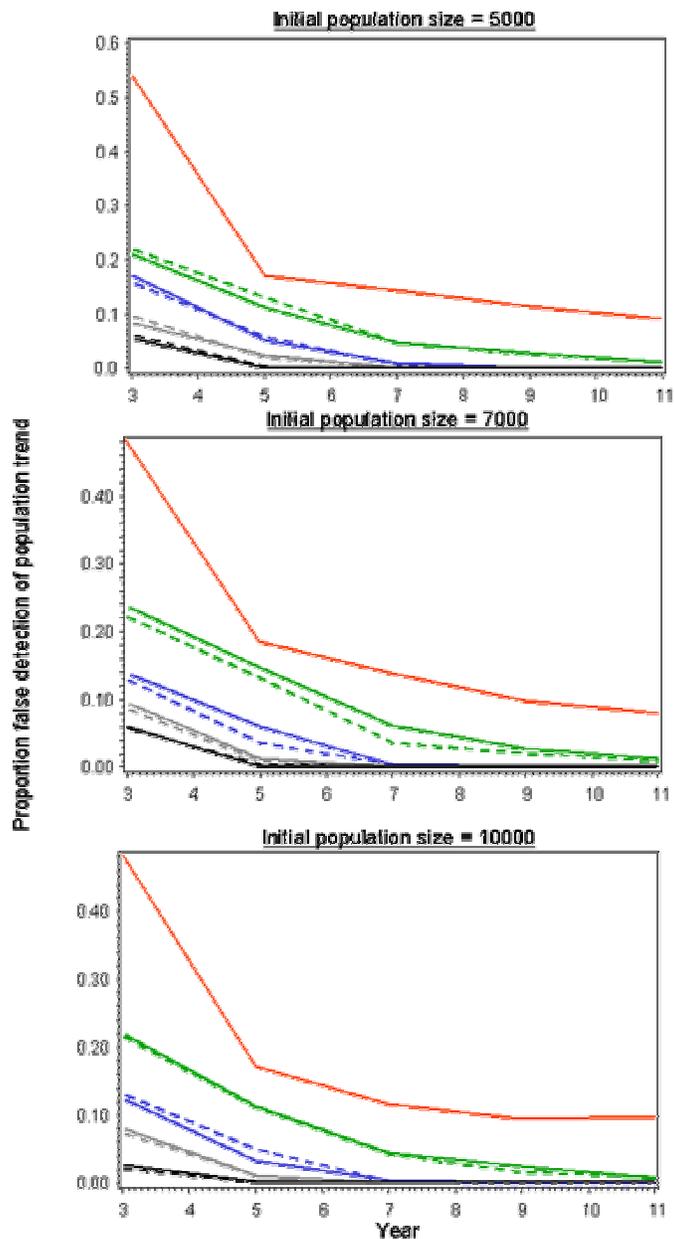


Figure 13. The proportion of simulations that falsely detected a population trend by number of simulated sampling years using linear regression and $\alpha = 0.10$ for simulated positive (solid) and negative (broken) changes in annual population growth of 0.07 (black), 0.05 (gray), 0.03 (blue), 0.01 (green), and no change (red) and 3 initial population sizes for Great Egret. Proportion based on 1000 simulations of two randomly assigned rear observers during SRF surveys. False detections were defined as determining a significant decrease in population size ($\alpha = 0.10$) when there was a simulated increase and vice versa.

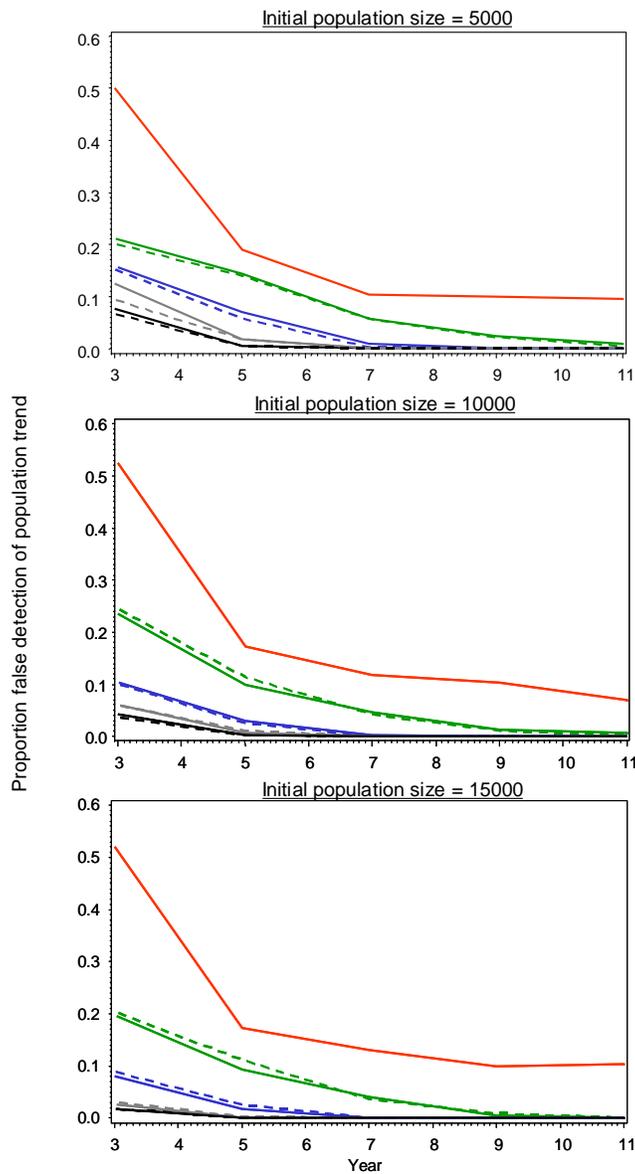


Figure 14. The proportion of simulations that falsely detected a population trend by number of simulated sampling years using linear regression and $\alpha = 0.10$ for simulated positive (solid) and negative (broken) changes in annual population growth of 0.07 (black), 0.05 (gray), 0.03 (blue), 0.01 (green), and no change (red) and 3 initial population sizes for White Ibis. Proportion based on 1000 simulations of two randomly assigned rear observers during SRF surveys. False detections were defined a determining a significant decrease in population size ($\alpha = 0.10$) when there was a simulated increase and vice versa.

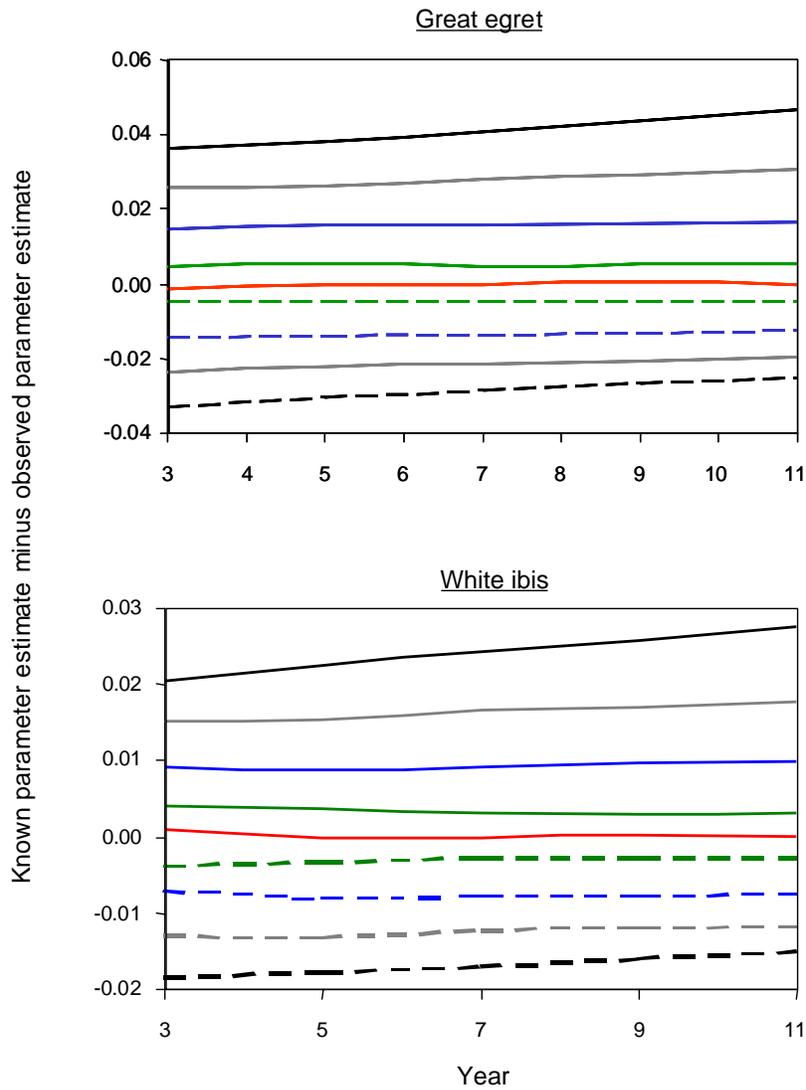


Figure 15. Estimated bias in population trend using linear regression by number of simulated sampling years for simulated positive (solid) and negative (broken) changes in annual population growth of 0.07 (black), 0.05 (gray), 0.03 (blue), 0.01 (green), and no change (red) for Great Egret and White Ibis, averages across initial population sizes. Bias is estimates as known parameter estimate (population growth rate) minus simulated observed estimate. Proportion based on 1000 simulations of two randomly assigned rear observers during SRF surveys.

12.0 APPENDICES

APPENDIX 1

[Graphs of counts for birds by year, month, and region.](#)

APPENDIX 2

[Project Orientation report](#)

APPENDIX 3

[Work Plan](#)

APPENDIX 4

[Count Statistics Report](#)

APPENDIX 5

Graphics File (on CD previously submitted)

APPENDIX 6

[SAS Model Code](#)

[SAS Library for Model Code](#)

APPENDIX 7

[PYMC Model Code](#)

[PYMC Data Files](#)

PyMC available at http://trichech.us/?page_id=3

Python (necessary for running PyMC) available at <http://code.enthought.com/enthon/>

APPENDIX 8

[Dual Observer Code](#)

[Dual Observer Data File](#)