

THE RELATIVE INFLUENCES OF PREDATION AND PREY AVAILABILITY  
ON ARDEID BREEDING COLONY SITE SELECTION

By

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This thesis is dedicated to my parents Mark and Cathy, who have weathered the many twists and turns of my life's last decade with unconditional love and support, leavened with just a touch of legitimate bemusement.

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## TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS .....	iv
LIST OF TABLES .....	vii
LIST OF FIGURES .....	viii
ABSTRACT .....	ix
CHAPTER	
1 INTRODUCTION .....	1
2 METHODS .....	5
Study Area .....	5
Data Sources .....	6
Water Depth Grids .....	6
Vegetation Maps .....	6
Wading Bird Colony Locations .....	8
Distributional Relationships .....	9
Calculation of Variables .....	9
Multivariate Analyses .....	11
3 RESULTS .....	17
Distribution of Colony Sites .....	17
Bootstrap of Foraging Habitat Calculation .....	17
Multivariate Analyses .....	18
4 DISCUSSION .....	38
Effects of Site Availability .....	38
Model Performance .....	38
Responses to Hydrological Variability .....	39
Management Implications .....	40
LITERATURE CITED .....	42
BIOGRAPHICAL SKETCH .....	46

## LIST OF TABLES

<u>Table</u>	<u>page</u>
1-1 Variables and methods of calculation. ....	4
1-2 Weeks of nest initiation and duration of breeding period for three focal species .....	4
3-1 Number of colonies inhabited by each species, 1993-2000 .....	19
3-2 Values of FOR calculated in 30 randomly-chosen cells using constant proportions, compared to approximate 95% confidence intervals from a bootstrap analysis involving 1000 iterations where proportions were allowed to randomly vary. ....	20
3-3 Logistic regression models tested for Great Blue Herons and associated statistical values.....	21
3-4 Logistic regression models tested for Great Egrets and associated statistical values.....	21
3-5 Logistic regression models tested for Tricolored Herons and associated statistical values.....	22
3-6 Best models for each species and associated measures of classification performance.....	23
3-7 Relative importance of variables to each species.....	23

## LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1 Southeastern Florida showing the location of WCA3 within the larger Everglades ecosystem .....	14
2-2 Everglades Landscape Model cells in WCA3 .....	15
2-3 Algorithm for determining which models to test for each species.....	16
3-1 Distribution of ardeid colonies in WCA3 .....	24
3-2 Relationship of Great Blue Heron colonies relative to all available sites in WCA3 as shown by linearized Ripley's K (l[d]) graphs .....	26
3-3 Relationship of Great Egret colonies relative to all available sites in WCA3 as shown by linearized Ripley's K (l[d]) graphs .....	30
3-4 Relationship of Tricolored Heron colonies relative to all available sites in WCA3 as shown by linearized Ripley's K (l[d]) graphs .....	34

Abstract of Thesis Presented to the Graduate School  
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THE RELATIVE INFLUENCES OF PREDATION AND PREY AVAILABILITY ON  
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Nest predation and prey availability are two of the most important factors affecting breeding success in long-legged wading birds (Ciconiiformes). I investigated whether the breeding colony site selection of three species of herons and egrets (family Ardeidae) in the Florida Everglades was influenced by environmental characteristics that mediated these two factors. These characteristics were 1) likelihood that sites remained inundated throughout the breeding period; 2) amount of foraging habitat around sites; 3) average weekly proportional decline in water depths around sites throughout the breeding period; 4) spatial variation in water depths around sites at the time of nesting. Variables were calculated within a geographic information system using both raster and vector inputs. I used measures derived from the Akaike information criterion to select the best logistic regression model and to evaluate the relative importance of these four variables for colony site selection in each species.

Amount of foraging habitat and likelihood of remaining inundated were the most important variables influencing colony site selection by all three species. Great Blue Herons (*Ardea herodias*) also selected sites with high rates of average weekly proportional declines in water depth, but it is likely this variable was a proxy for deep water for this species rather than a reflection of prey availability. Overall, these species seemed to favor stable (rather than variable) hydrological conditions. This might also indicate that their colony site selection is based on conditions at the time of nesting rather than an attempt to predict future conditions. These results confirm the importance of managing the Everglades to maximize the extent of slough habitats, if the goal is to increase breeding populations of wading birds therein.

## CHAPTER 1 INTRODUCTION

Two of the most important factors affecting the breeding success of long-legged wading birds (Ciconiiformes) are egg and chick predation, and the availability of adequate food to raise chicks to fledging (Taylor & Michael 1971; Frederick & Collopy 1989a; Frederick & Spalding 1994; Frederick 2002). Although wading birds cannot control the behaviors of predators or their prey, it is likely that selection has favored the recognition of breeding colony sites with beneficial environmental characteristics that mediate or constrain those behaviors.

For example, wading birds nearly always nest on islands or in trees and/or shrubs that are inundated at their base, a pattern that has most often been interpreted as a strategy for deterring mammalian predators (Rodgers 1987; Bancroft et al. 1988; Frederick & Collopy 1989b; Smith & Collopy 1995). However, whether this pattern represents actual selection for this characteristic has never been quantitatively studied. With regard to prey availability, although previous studies (Gibbs et al. 1987; Gibbs 1991; Gibbs & Kinkel 1997; Baxter & Fairweather 1998; Bancroft et al. 2002) have shown that wading birds select colony sites that maximize the amount of wetland habitats within a reasonable foraging range, other environmental characteristics (e.g., water depth) are better determinants of wading birds' ability to capture prey.

If wading bird colony site selection represents an attempt to deter predators and/or maximize prey availability, then used sites should be measurably different from available unused sites with relation to environmental characteristics that affect these two factors. I

identified one characteristic that deters predators from reaching nests and three characteristics that are likely to influence prey availability around sites (Table 1-1) and make the following predictions.

**Prediction 1: Used sites will have a greater likelihood of remaining inundated throughout the breeding period than unused sites.** This characteristic seems to be a good measure of a site's ability to deter mammalian predators (Frederick & Collopy 1989b; Smith & Collopy 1995), which are generally the most destructive in their effects on wading bird colonies (Rodgers 1987; Post 1990; Smith & Collopy 1995).

**Prediction 2: Used sites will be surrounded by more open or sparsely vegetated habitats than unused sites.** Not all wetland habitats are appropriate foraging grounds for wading birds. In particular, they are known to avoid dense vegetation (such as monospecific stands of sawgrass [*Cladium jamaicense*] or cattail [*Typha latifolia*]), which interferes with their visual or tactile hunting techniques, provides prey animals with more hiding places, and could serve as a hiding place for predators of the birds themselves (Hoffman et al. 1994; Smith et al. 1995; Surdick 1998).

**Prediction 3: Used sites will be located in areas that experience greater proportional declines in water depth throughout the breeding season than unused sites.** Wading birds are generally limited to foraging in water that is shallower than the length of their bills or legs (Custer & Osborn 1978; Powell 1987). They are often attracted to areas of declining water depth where prey have been concentrated into pools or depressions that remain inundated late in the season (Kushlan 1976; Bancroft 1989; Frederick & Collopy 1989a; Smith 1995; Gawlik 2002; but see Frederick & Spalding 1994 for a critique of this idea).

**Prediction 4: Variability in water depths at the time of nesting will be greater around used sites than around unused sites.** Water levels are dynamic and unpredictable in most wetlands. Heterogeneous topography around a colony site could therefore provide a foraging advantage to wading birds as this would provide the most diversity of potential foraging sites at almost any time or water condition (Kahl 1964; Bancroft et al. 2002).

I used logistic regression models to assess the relative influence of these four variables on the colony site selection of three wading bird species in the ciconiiform family Ardeidae (Table 1-2) over a period of 8 years in the Florida Everglades. Measures derived from the models' Akaike information criteria (AIC) (Akaike 1973; Burnham & Anderson 2002) were used to choose the best model and determine the relative influence of the variables on the colony site selection for each species.

Table 1-1. Variables and methods of calculation.

Variable	Abbreviation	Method of calculation
Affecting predator deterrence		
Likelihood that a cell will remain inundated for the duration of the breeding period	INUN	Used GREATER THAN function to output number of weeks over duration of a species' breeding period that depths remained above 0; divided by number of weeks to yield values between 0.0 and 1.0
Affecting prey availability		
Amount of foraging vegetation around sites	FOR	See text for details
Average rate of proportional decline in depths around a site for the duration of a species' breeding period	FWI	Calculated proportional decline in water depths for every week during a species' breeding period (rises in depth expressed as 0); averaged these values over all weeks; used the FOCALMEAN function to average these cell averages over 3x3 cell neighborhoods, yielding values between 0.0 and 0.5
Spatial variation in water depths around a site at week of nest initiation	WV	Used FOCALSTD function to calculate standard deviation of depths in 3x3 cell neighborhoods

All calculations carried out in ESRI Arc/INFO workstation v.8.3 except FOR, which was calculated in ESRI ArcMap v.8.3. Weeks of nest initiation and duration of breeding periods are listed in Table 1-2.

Table 1-2. Weeks of nest initiation and duration of breeding period for three focal species

Species	Week of nest initiation <sup>a</sup>	Duration	Source for duration
Great Blue Heron ( <i>Ardea herodias</i> )	9th	14 weeks	Butler 1992
Great Egret ( <i>Ardea alba</i> )	9th	10 weeks	McCrimmon et al. 2001
Tricolored Heron ( <i>Egretta tricolor</i> )	12th	11 weeks	Frederick 1997

<sup>a</sup>Source is Frederick (pers. comm.)

## CHAPTER 2 METHODS

### **Study Area**

I studied ardeid colony site selection within Water Conservation Area (WCA) 3, a 2,350-km<sup>2</sup> human-made impoundment in the central Everglades (Figure 2-1). Most of the wading birds that breed within the Everglades ecosystem have selected colony sites within this impoundment since the early 1970s (Ogden 1994; Frederick & Ogden 2001). The annual hydrology of WCA3 is characterized by a decline in water depths during the dry season between November and April, and most annual rainfall occurring during a subtropical wet season between June and November. The northern end of the impoundment is shallow and quick to dry, while the southern end is almost permanently inundated. This same gradient exists to a lesser extent from west (where flow of water into the adjoining Big Cypress National Preserve is unimpeded) to east (the enclosed sub-impoundment WCA3B created by the L-67 canals, Figure 2-1). Wading birds therefore have a wide range of hydrological conditions within which to select sites in WCA3.

The vegetation of WCA3 is characterized by open “wet prairie” communities in deeper areas interspersed between narrow ridges covered in cattail and/or sawgrass (Gunderson 1994). The patches of woody or shrubby vegetation that serve as potential nesting sites for wading birds are scattered throughout. Large areas in the northern end of the impoundment are dominated by an almost complete monoculture of cattails.

## **Data Sources**

### **Water Depth Grids**

I derived hydrological variables using estimated water depths from the Everglades Landscape Model (ELM; Fitz et al. 2004), which simulates the flows and stages of water across the entire Everglades ecosystem at a resolution of 1 km<sup>2</sup>. Model output was available for the period 1993–2000, so these 8 years comprised the duration of my study. Each output layer is an Arc/Info grid (Environmental Systems Research Institute 2002) whose values are the estimated weekly average above-ground depth of water in each cell. The model generally performs well both spatially and temporally when compared to actual depths measured throughout the landscape (Fitz et al. 2004). The largest errors occur in cells containing canals, as these contain the most intracellular variation in water depths. ELM 1 km<sup>2</sup> cells, rather than discrete colony sites, were my units of analysis as these were the coarsest in resolution of all the data.

### **Vegetation Maps**

I used a polygon vector geographic information system (GIS) layer showing the distribution of vegetation in the central and southern Everglades and based on aerial infrared photography acquired in 1995 over the entire area of WCA3, Everglades National Park, and Big Cypress National Preserve. The latter two areas were included in my analysis since they are within the typical foraging range of birds nesting near the boundaries of WCA3 (Bancroft et al. 1994). The distinctive reflectance signatures of different types of vegetation within the aerial photography were used to digitize polygons representing discrete patches. These could contain up to three specific vegetative classes, assigned hierarchically. After comparing the polygon layer to 1999 United States Geological Survey (USGS) digital orthophoto quarter quads (DOQQs), I was satisfied

that this layer was an accurate depiction of the vegetation in WCA3 for the entire time period of this study.

Since all reports of nesting by ardeid wading birds are on trees or shrubs in WCA3, I defined potential colony sites as polygons that contained at least one class of woody vegetation. Among the classifications used in the vegetation map these included: all variants of forest, all variants of shrublands, Melaleuca, Brazilian pepper, disturbed fish camp sites, spoil areas, and artificial “deer islands.” I aggregated contiguous polygons that contained at least one of these vegetation types into single discrete patches, which I hereafter refer to interchangeably as “patches of woody vegetation” or “potential colony sites.”

The locations of wading bird colonies (see below) revealed that a small proportion (~1.1%) of the potential colony sites did not occur within a reasonable distance from a patch of woody vegetation. In October 2002 I visited all such sites in WCA3B and in WCA3A north of Highway I-75 (Figure 2-1), and determined that in most cases either some woody vegetation had not been included in an existing polygon, or that a single tree or small patch of shrubs was present and should have itself been digitized as a polygon. In these cases, I therefore either added a woody vegetation classification to the second or third tier of the existing polygon, or digitized the patch myself using the 1999 USGS DOQQs.

Water model cells that either contained no potential colony sites, or contained only the “clipped” edges of sites whose bulk were in an adjacent cell, were excluded from further analysis since wading birds could not have nested in them. At the scale at which I

calculated the variables (see below), this removed less than 3% of the total area of WCA3 from analysis (Figure 2-2).

### **Wading Bird Colony Locations**

Locations, species composition, and size of wading bird colonies were determined using both aerial and ground survey techniques (Frederick et al. 1996). Aerial surveys were designed such that the entire ground surface of the study area was visible along at least one east-west transect. These were spaced 2.9 km apart, flown at 245 m altitude, and were conducted monthly between January and June of each year. Dark-colored species are often not visible in aerial surveys (Frederick et al. 1996), and for these species ground-based airboat searches were conducted. All tree islands in the study area were approached and searched for signs of nesting in the middle to late part of the nesting season (April through May). Colony site coordinates were determined by handheld GPS receivers, and populations of every species present were estimated by counting nests and/or number of adults that flushed from the site. In cases where a colony was visited more than once per season, I used the peak count of nests at that colony for a given species.

I created point vector GIS layers representing the colony locations for each of the three focal species for every year. Given that point coordinates reflected the location of the airboat or airplane at the time of data collection, rather than the actual location of the colony, I used a spatial join operation to shift points to the centroid of the nearest patch of woody vegetation. In general, these shifts were not more than 100 m for points collected on the ground, or 300 m for points collected during aerial surveys. I then overlaid the water model grid and classified all cells as either used or unused by each of the species for every year.

### **Distributional Relationships**

To rule out the possibility that the distribution of these species' colonies was simply a reflection of the distribution of available sites, I calculated Ripley's K statistic for each species-year pattern of colony sites as well as for the parent pattern of all available sites, at 500 m intervals from 500 to 20,000 m. This statistic is a scale-dependent measure of spatial dispersion within a defined area (Fotheringham et al. 2000). However, it can also be used to assess whether two patterns within the same area are spatially similar, especially when one is a subset of the other. Differences between two patterns' K statistics (i.e., the linearized Ripley's K, or  $l(d)$ ) indicate that they are spatially dissimilar, with positive values of  $l(d)$  indicating a dispersed pattern relative to the parent pattern, and negative values of  $l(d)$  indicating a clustered pattern relative to the parent pattern. Since there is no significance test to determine how different from 0 an  $l(d)$  value must be to indicate that the patterns are different, I used bootstrapping to create sample-size-dependent 95% confidence intervals against which to compare each species-year point pattern (Fotheringham et al. 2000).

### **Calculation of Variables**

All variables were calculated at the scale of a 3x3 neighborhood of cells (i.e., 3 km x 3 km) centered on the cell in question except INUN, which was calculated at the scale of the cell itself. I chose these small scales to maximize the spatial independence between samples, since larger neighborhoods would have increased the distance required between two cells before their neighborhoods did not overlap. The calculation of the three hydrological variables is described in Table 1-1.

To calculate FOR I first identified all polygons in the vegetation map that contained any of the foraging habitat types. Within the map's classification system these included:

all variations of savanna; spike rush and maidencane-spike rush prairies; all variations of non-graminoid emergent marsh; open water; mixed mangrove scrub; and, buttonwood and saw palmetto scrubs.

Vegetation classes were hierarchically assigned to polygons qualitatively (e.g., a large area of wet prairie might contain some scattered shrubs), yet I needed a quantitative estimate of the areal extent of each class within polygons. Since vegetation classes could be assigned to any of the tiers within a polygon, with adjoining polygons often having the same classes in reversed order, the least biased method of estimating these extents was to allocate the same proportion to a given tier in every polygon. In polygons containing two classes of vegetation, I allocated 70% of the area to the dominant vegetation type and 30% to the secondary; in three-class polygons, I allocated 50, 30, and 20% of the area to the three tiers respectively. After allocating a polygon's area between its vegetation classes, I calculated the total extent of foraging habitat present within the polygons. I intersected these polygons with a square grid polygon layer corresponding to the ELM grid cell boundaries to assign the vegetation polygons to the cell they inhabited, and summed the areas of foraging vegetation present within every cell. I recalculated the area of foraging vegetation in polygons that had been split by cell boundaries by multiplying their new area by the same proportion of foraging vegetation calculated for the parent polygon. Finally, I calculated the 3x3 neighborhood sums for every cell in WCA3.

To ensure that the proportions I chose did not bias the ultimate values of FOR, I randomly chose 30 cells and performed a bootstrap analysis whereby the proportions allocated to vegetation classes within their polygons were allowed to randomly vary. Since the vegetation classes were originally assigned hierarchically, I constrained the

proportions such that the dominant class proportion was always greater than the secondary, and this was always greater than the tertiary. I calculated FOR for each cell 1000 times based on these randomly-determined proportions and used these values to create an approximate 95% confidence interval for the “real” value of FOR in each cell. I then determined how many of the values of FOR calculated in the 30 cells using the proportions described above fell within these confidence intervals.

### **Multivariate Analyses**

I used the Number Cruncher Statistical Systems software (NCSS, Hintze 2001) to evaluate logistic regression models where the response variable was the use (presence of at least one colony) or non-use of a water model cell by a species. Model inputs consisted of the values for all cells used by a given species in all 8 years combined with an equal number of randomly-selected unused cells from each year. I bootstrapped these randomly-selected sets for every species-year to ensure that their mean values for all four variables were within the 95% confidence interval suggested by the bootstrap.

Results of the logistic regression analyses were interpreted within the information-theoretic approach of Burnham and Anderson (2002). Multiple models were evaluated and the Akaike information criterion (AIC; Akaike 1973) calculated for each one thus:

$$\text{AIC} = -2(\log\text{-likelihood ratio}) + 2K \quad (2-1)$$

where K was the number of parameters estimated in the model. The model with the lowest AIC was the “best” model among all those evaluated. The last term in Eq. 2-1 therefore represented a “penalty” against a model’s AIC value for every variable added to the model.

The performance of a given model relative to the best one in the set was expressed using three values derived from the AIC values. The AIC difference ( $\Delta_i$ ) for model  $i$  was calculated:

$$\Delta_i = AIC_i - AIC_{min} \quad (2-2)$$

This was converted to “Akaike weights” ( $w_i$ ):

$$w_i = \exp(-\frac{1}{2}\Delta_i) / \sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r) \quad (2-3)$$

where the denominator in Eq. 2-3 was the sum of all models’  $\Delta_i$  values. The  $w_i$  for model  $i$  was a measure of the likelihood (often expressed as a percent) that it is the best model.

An analogous quantity is the evidence ratio for model  $i$ :

$$\text{evidence ratio}_i = w_i / w_j \quad (2-4)$$

where  $w_j$  was the  $w_i$  value for the best model in the set. The evidence ratio was a measure of “how much” better the best model was than model  $i$ . Because they relied on the sum of all models’  $\Delta_i$  values, the  $w_i$  and evidence ratios were recalculated every time a new model entered the set.

I followed the algorithm shown in Figure 2-3 to determine the models tested for each species. Upon identifying the best model for each species, I report three measures of its classification performance (Fielding & Bell 1997): 1) the number of used and unused cells correctly classified; 2) the Kappa statistic ( $\kappa$ ), which measures the extent to which a model’s predictions are correct above the proportion expected simply by chance; and, 3) the area under the model’s ROC curve, which measures the likelihood that the value assigned by the final model to a randomly-selected “used” cell will be greater than that of a randomly-selected “unused” cell. I also summarized the relative importance of the

variables tested for each species by adding the  $w_i$  values for all models in which a given variable is included (Burnham & Anderson 2002: 167-168).

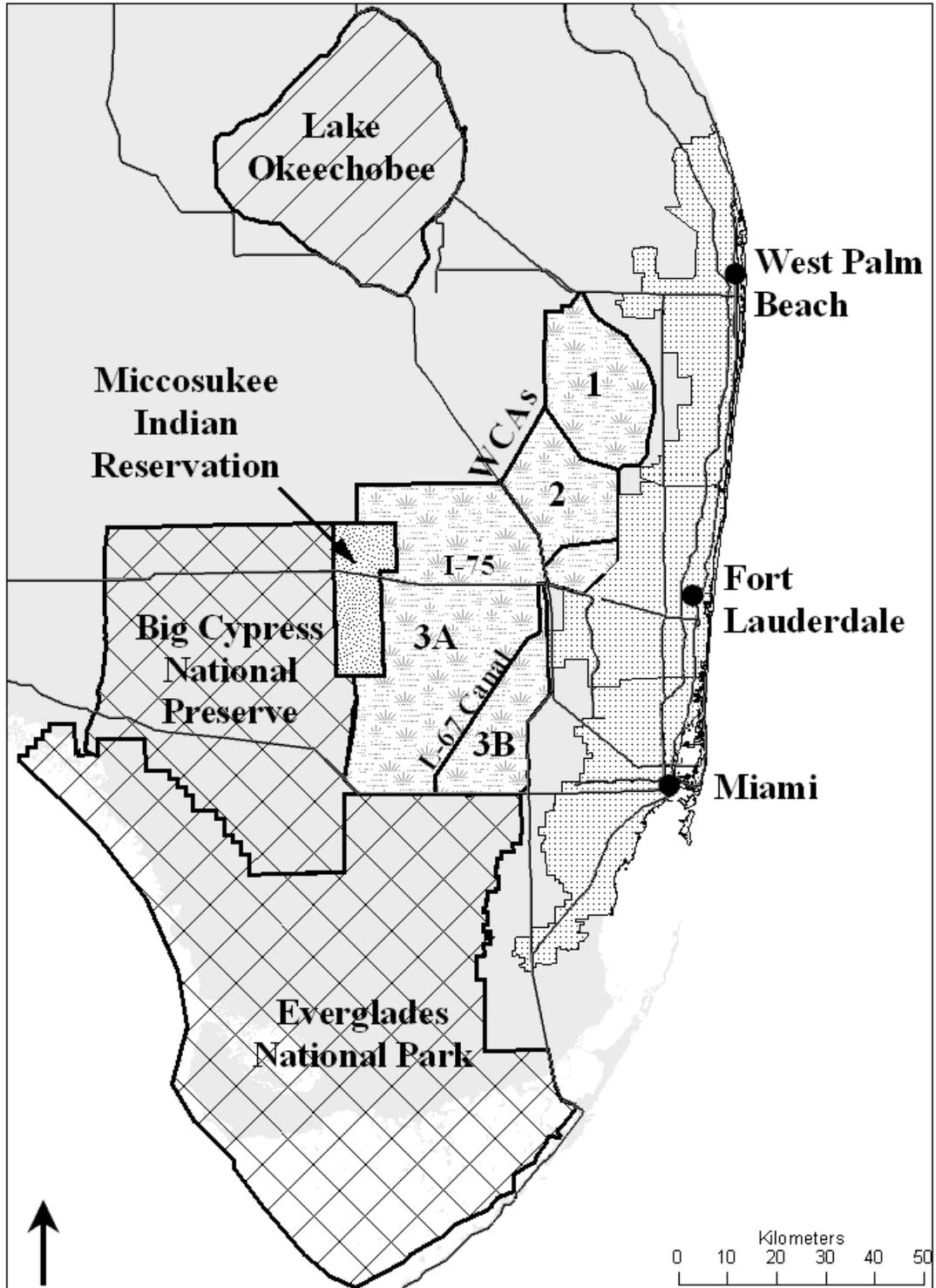


Figure 2-1. Southeastern Florida showing the location of WCA3 within the larger Everglades ecosystem. The dotted areas along the east coast show the extent of urban landscapes and their proximity to what is left of the Everglades.

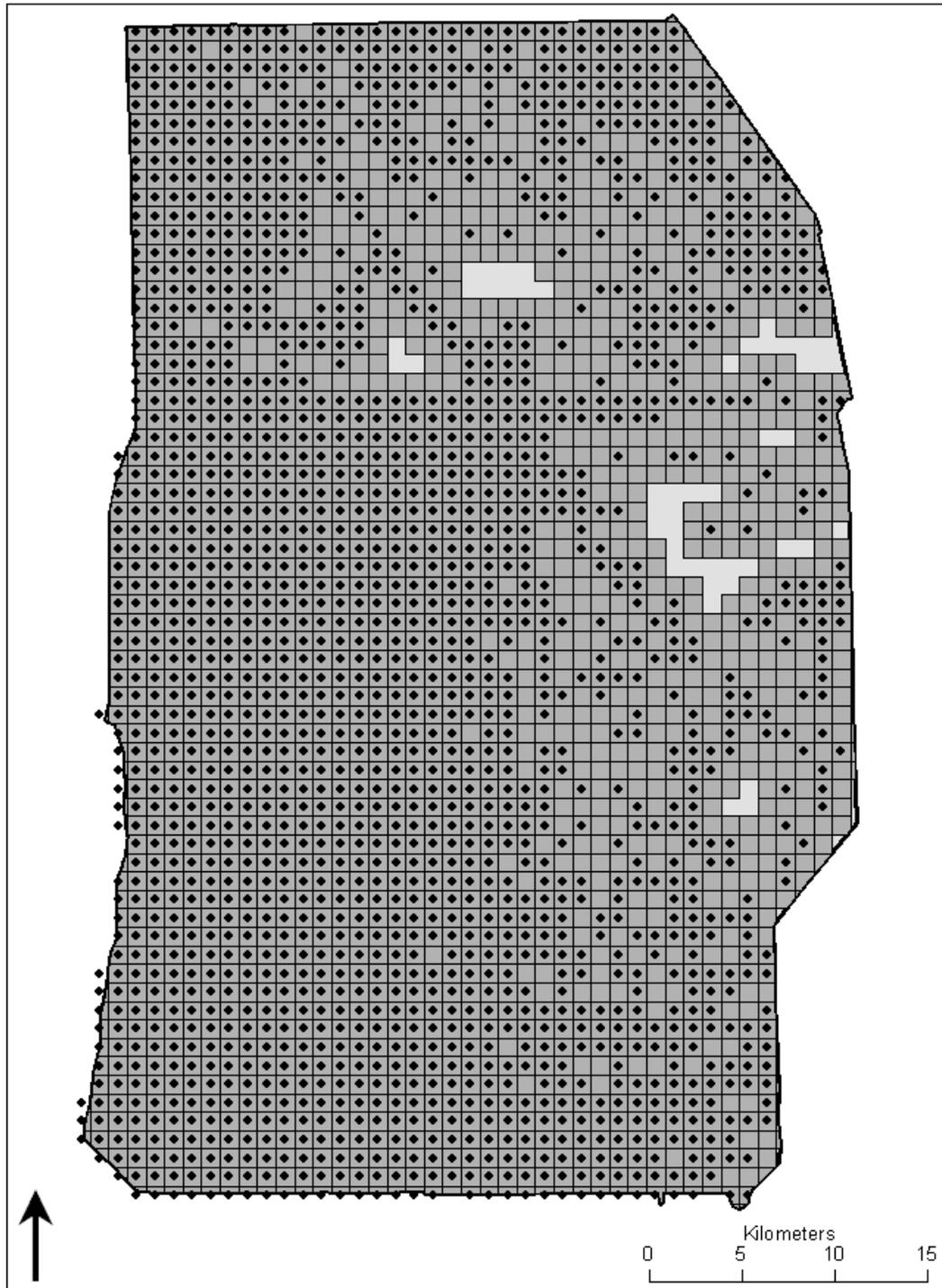


Figure 2-2. Everglades Landscape Model cells in WCA3. Black dots indicate cells that contained potential colony sites and were included in multivariate analysis. The darker shaded area indicates all cells that were within a 3x3 cell neighborhood of analyzed cells and whose characteristics were therefore included in the calculation of variables. Less than 3% of the area of WCA3, represented by the unshaded areas, was excluded from analysis.

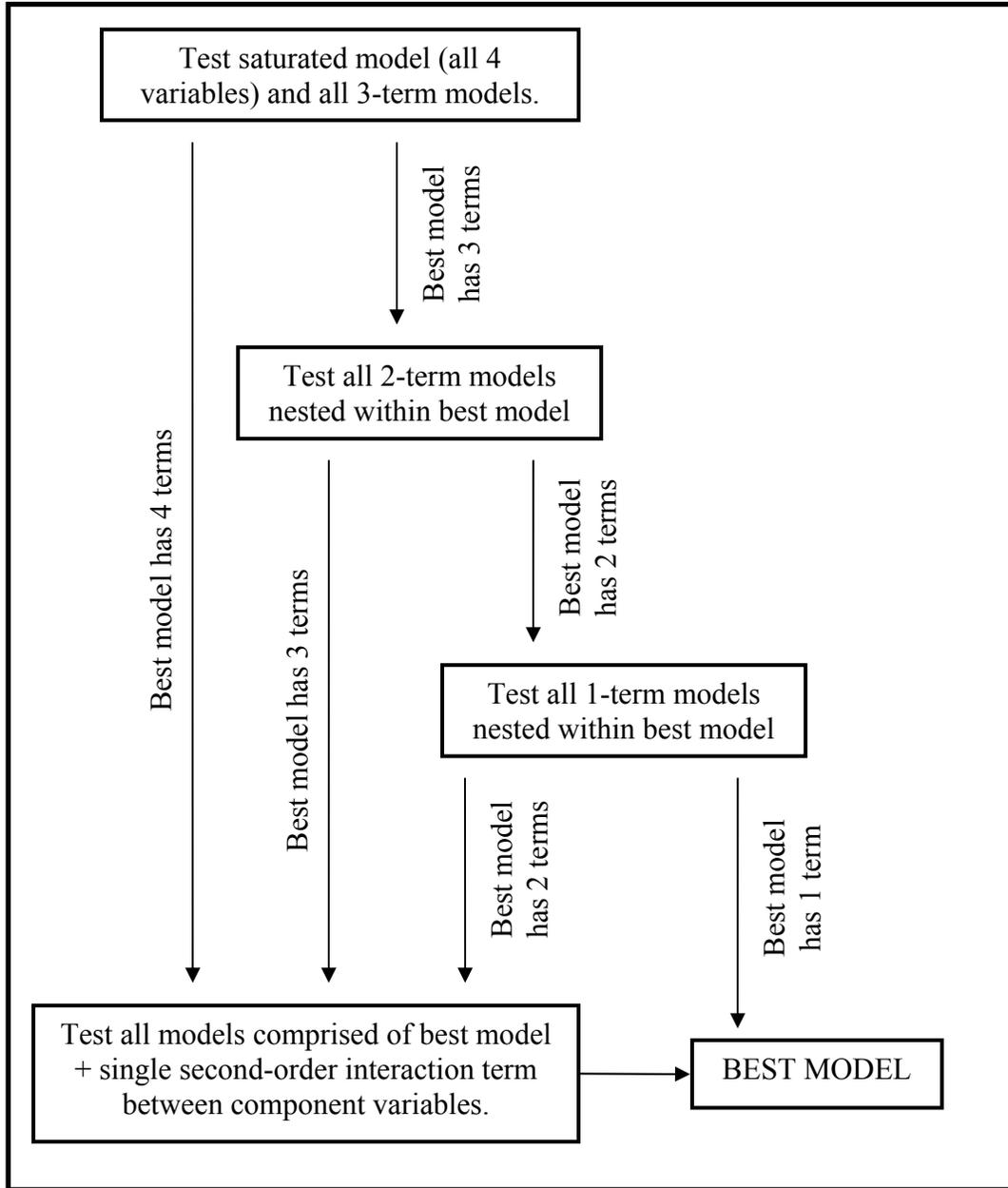


Figure 2-3. Algorithm for determining which models to test for each species. At every step the current best model competed with lower-term models comprised of its component variables. Once the best single-order model was identified, models that added a single second-order interaction term were tested.

## CHAPTER 3 RESULTS

### **Distribution of Colony Sites**

Table 3-1 summarizes the number of colonies and water model cells inhabited by each species in each year, and Figure 3-1 presents the annual maps of these distributions. Figures 3-2 through 3-4 show the  $l(d)$  graphs for each species-year combination, along with their corresponding approximate 95% confidence intervals from the bootstrap simulation. Great Blue Heron colonies were extremely clustered relative to the parent pattern of all potential colony sites in all years except 1998, when the  $l(d)$  values were closer to the lower bootstrap limit. Great Egret colonies were dispersed relative to the parent pattern at all scales in 1993, 1994, and 1995; at small scales in 1996, and at large scales in 1998. Their colony patterns were mostly indistinguishable from the parent pattern at practically all scales in 1997, 1999, and 2000. Tricolored Heron colony patterns showed the most variability: they were highly dispersed relative to the parent pattern at medium to large scales in 1993; highly clustered at all scales in 1996; slightly clustered at small scales in 1994 and medium scales in 1999 and 2000; and, otherwise mostly indistinguishable from the parent pattern in 1995, 1997 and 1998.

### **Bootstrap of Foraging Habitat Calculation**

Table 3-2 lists the values of FOR calculated for 30 randomly-chosen cells using the constant proportions described above and the upper and lower values of the approximate 95% confidence interval from the bootstrap analysis. Four of the 30 cells contained only polygons that did not vary in their values of FOR. In only one of the remaining cells was

the value of FOR calculated using the constant proportions outside the 95% confidence interval from the bootstrap; however, this cell's value was within the 99% confidence interval. This is strong evidence that the constant proportions used to calculate this variable did not bias the analysis.

### **Multivariate Analyses**

I tested 11 models for Great Blue and Tricolored Herons, and 12 for Great Egrets (Tables 3-3 through 3-5). A single best model ( $w_i > 98\%$ ) was found for the first two of these species, while the best two models for Great Egrets were nearly indistinguishable ( $w_i$  values of 29.20% and 23.18%, respectively). Table 3-6 lists the best model(s) for each species and its associated measures of classification performance. Best models correctly classified between 68.8% (Great Egrets, model 1) and 78.9% (Great Blue Herons) of the used sites, and between 36.7% (Great Egrets, model 1) and 56.7% (Great Blue Herons) of the unused sites. Kappa statistics were routinely low, ranging between 0.055 (Great Egrets, model 1) and 0.357 (Great Blue Herons). The areas under the ROC curves also indicated relatively poor model performance; these ranged between 0.524 (Great Egrets, model 1) and 0.745 (Great Blue Herons).

The amount of foraging habitat (FOR) around potential sites was always the most important variable, with all  $\Sigma w_i$  values greater than 98% (Table 3-7). It was followed by the likelihood that a site would remain inundated (INUN), with  $\Sigma w_i$  values ranging between 83.88 and 99.99%. As predicted, all three species responded to both of these variables positively, i.e., used cells had higher values overall than unused cells. The pattern for the remaining variables was less consistent across species, with Great Blue Herons responding strongly and positively to FWI, and Great Egrets responding weakly and negatively to WV (Table 3-7).

Table 3-1. Number of colonies inhabited by each species, 1993-2000. Number of water model cells inhabited in parentheses.

	Great Blue Heron	Great Egret	Tricolored Heron
1993	156 (127)	32 (32)	11 (11)
1994	200 (153)	45 (44)	46 (43)
1995	298 (229)	39 (39)	40 (39)
1996	167 (136)	45 (43)	52 (42)
1997	101 (90)	34 (33)	8 (8)
1998	110 (97)	44 (41)	23 (23)
1999	258 (206)	77 (71)	66 (63)
2000	309 (235)	71 (62)	57 (53)

Table 3-2. Values of FOR calculated in 30 randomly-chosen cells using constant proportions, compared to approximate 95% confidence intervals from a bootstrap analysis involving 1000 iterations where proportions were allowed to randomly vary.

Lower limit of 95% confidence interval	Value of FOR calculated using constant proportions	Upper limit of 95% confidence interval	Observed within confidence interval?
75	75	75	Constant value cell
251	339	644	Yes
750	750	750	Constant value cell
118	887	1,155	Yes
149	1,742	2,389	Yes
4,321	4,321	4,321	Constant value cell
5,925	5,925	5,925	Constant value cell
9,763	10,296	12,057	Yes
1,526	20,539	29,209	Yes
24,992	25,858	26,380	Yes
20,804	35,765	42,190	Yes
74,514	80,693	84,326	Yes
101,367	103,625	119,108	Yes
146,646	149,072	150,791	Yes
172,177	218,953	244,864	Yes
163,585	256,693	339,316	Yes
281,378	286,925	305,647	Yes
28,983	289,828	328,472	Yes
337,236	352,078	356,356	Yes
115,366	360,059	418,467	Yes
77,850	376,847	504,702	Yes
92,661	382,298	501,854	Yes
373,516	445,018	635,874	Yes
220,282	470,162	569,560	Yes
413,803	477,840	597,608	Yes
271,067	504,240	587,148	Yes
307,407	507,071	567,364	Yes
385,418	532,264	559,474	Yes
504,530	607,378	604,063	No, 99% confidence interval
531,142	638,535	646,606	Yes

Table 3-3. Logistic regression models tested for Great Blue Herons and associated statistical values. Italicized models are the best from their subset, while the best overall model is shown in boldface.

Model	Log-Likelihood	K	AIC	$\Delta$ AIC	$w_i^a$	Evidence Ratios <sup>b</sup>	Rank
FOR+WV+FWI+INUN	-1492.38	5	2994.76	16.15	—	—	3
FOR+WV+FWI	-1495.94	4	2999.88	21.28	—	—	9
<i>FOR+FWI+INUN</i>	<i>-1493.21</i>	<i>4</i>	<i>2994.42</i>	<i>15.81</i>	<i>0.04%</i>	—	2
FOR+WV+INUN	-1495.21	4	2998.42	19.81	—	—	6
WV+FWI+INUN	-1721.50	4	3451.00	472.40	—	—	10
FOR+FWI	-1496.75	3	2999.51	20.90	—	—	8
FOR+INUN	-1496.40	3	2998.81	20.21	—	—	7
FWI+INUN	-1745.57	3	3497.14	518.54	—	—	11
FOR+FWI+INUN+FOR*FWI	-1492.98	5	2995.96	17.36	0.02%	—	4
FOR+FWI+INUN+FOR*INUN	-1493.15	5	2996.29	17.69	0.01%	—	5
<b>FOR+FWI+INUN+FWI*INUN</b>	<b>-1484.30</b>	<b>5</b>	<b>2978.60</b>	<b>0.00</b>	<b>99.89%</b>	<b>1.00</b>	<b>1</b>

<sup>a</sup> “—” indicates a  $w_i$  value < 0.01%; <sup>b</sup> “—” indicates an evidence ratio > 100

Table 3-4. Logistic regression models tested for Great Egrets and associated statistical values. Italicized models are the best from their subset, while the best overall models are shown in boldface.

Model	Log-Likelihood	K	AIC	$\Delta$ AIC	$w_i$	Evidence Ratios <sup>a</sup>	Rank
FOR+WV+FWI+INUN	-498.86	5	1007.73	4.22	3.54%	8.25	8
FOR+WV+FWI	-499.97	4	1007.94	4.44	3.17%	9.20	9
FOR+FWI+INUN	-499.59	4	1007.17	3.67	4.67%	6.26	7
<i>FOR+WV+INUN</i>	<i>-498.86</i>	<i>4</i>	<i>1005.73</i>	<i>2.22</i>	<i>9.62%</i>	<i>3.03</i>	<i>4</i>
WV+FWI+INUN	-502.60	4	1013.20	9.69	0.23%	—	12
FOR+WV	-500.48	3	1006.96	3.46	5.18%	5.63	6
<i>FOR+INUN</i>	<i>-499.61</i>	<i>3</i>	<i>1005.21</i>	<i>1.71</i>	<i>12.45%</i>	<i>2.35</i>	<i>3</i>
WV+INUN	-502.69	3	1011.38	7.88	0.57%	51.35	10
FOR	-501.08	2	1006.16	2.65	7.76%	3.76	5
INUN	-503.99	2	1011.99	8.48	0.42%	69.43	11
<b>FOR+INUN+FOR*INUN</b>	<b>-497.75</b>	<b>4</b>	<b>1003.51</b>	<b>0.00</b>	<b>29.20%</b>	<b>1.00</b>	<b>1</b>
<b>FOR+WV+INUN+FOR*INUN</b>	<b>-496.98</b>	<b>5</b>	<b>1003.97</b>	<b>0.46</b>	<b>23.18%</b>	<b>1.26</b>	<b>2</b>

<sup>b</sup> “—” indicates an evidence ratio > 100

Table 3-5. Logistic regression models tested for Tricolored Herons and associated statistical values. Italicized models are the best from their subset, while the best overall model is shown in boldface.

Model	Log-Likelihood	K	AIC	$\Delta$ AIC	$w_i^a$	Evidence Ratios <sup>b</sup>	Rank
FOR+WV+FWI+INUN	-363.45	5	736.90	14.14	0.08%	—	8
FOR+WV+FWI	-364.24	4	736.48	13.72	0.10%	—	7
FOR+FWI+INUN	-363.83	4	735.66	12.90	0.16%	—	6
<i>FOR+WV+INUN</i>	-363.50	4	734.99	12.23	0.22%	—	4
WV+FWI+INUN	-387.66	4	783.33	60.57	—	—	10
FOR+WV	-364.70	3	735.40	12.64	0.18%	—	5
<i>FOR+INUN</i>	-363.92	3	733.84	11.07	0.39%	—	2
WV+INUN	-387.67	3	781.33	58.57	—	—	9
FOR	-365.35	2	734.70	11.94	0.25%	—	3
INUN	-390.82	2	785.64	62.88	—	—	11
<b>FOR+INUN+FOR*INUN</b>	<b>-357.38</b>	<b>4</b>	<b>722.76</b>	<b>0.00</b>	<b>98.62%</b>	<b>1.00</b>	<b>1</b>

<sup>a</sup> “—” indicates a  $w_i$  value < 0.01%; <sup>b</sup> “—” indicates an evidence ratio > 100

Table 3-6. Best models for each species and associated measures of classification performance.

Great Blue Herons	
Model	FOR + FWI + INUN - FWI*INUN
n, % Correct (Used)	1005, 78.9%
n, % Correct (Unused)	722, 56.7%
$\kappa$ Statistic	0.357
Area Under ROC Curve	0.745
Great Egrets	
Model 1	FOR + INUN + FOR*INUN
n, % Correct (Used)	251, 68.8%
n, % Correct (Unused)	134, 36.7%
$\kappa$ Statistic	0.055
Area Under ROC Curve	0.524
Model 2	FOR - WV + INUN + FOR*INUN
n, % Correct (Used)	274, 75.1%
n, % Correct (Unused)	152, 41.6%
$\kappa$ Statistic	0.167
Area Under ROC Curve	0.559
Tricolored Herons	
Model	FOR + INUN + FOR*INUN
n, % Correct (Used)	218, 77.3%
n, % Correct (Unused)	137, 48.6%
$\kappa$ Statistic	0.259
Area Under ROC Curve	0.654

Table 3-7. Relative importance of variables to each species.

	Great Blue Heron	Great Egret	Tricolored Heron
FOR	100.00%	98.78%	100.00%
WV	0.04%	45.50%	0.58%
FWI	99.99%	11.61%	0.34%
INUN	99.99%	83.88%	99.47%
FOR*FWI	0.02%		
FOR*INUN	0.01%	52.38%	98.62%
FWI*INUN	99.89%		

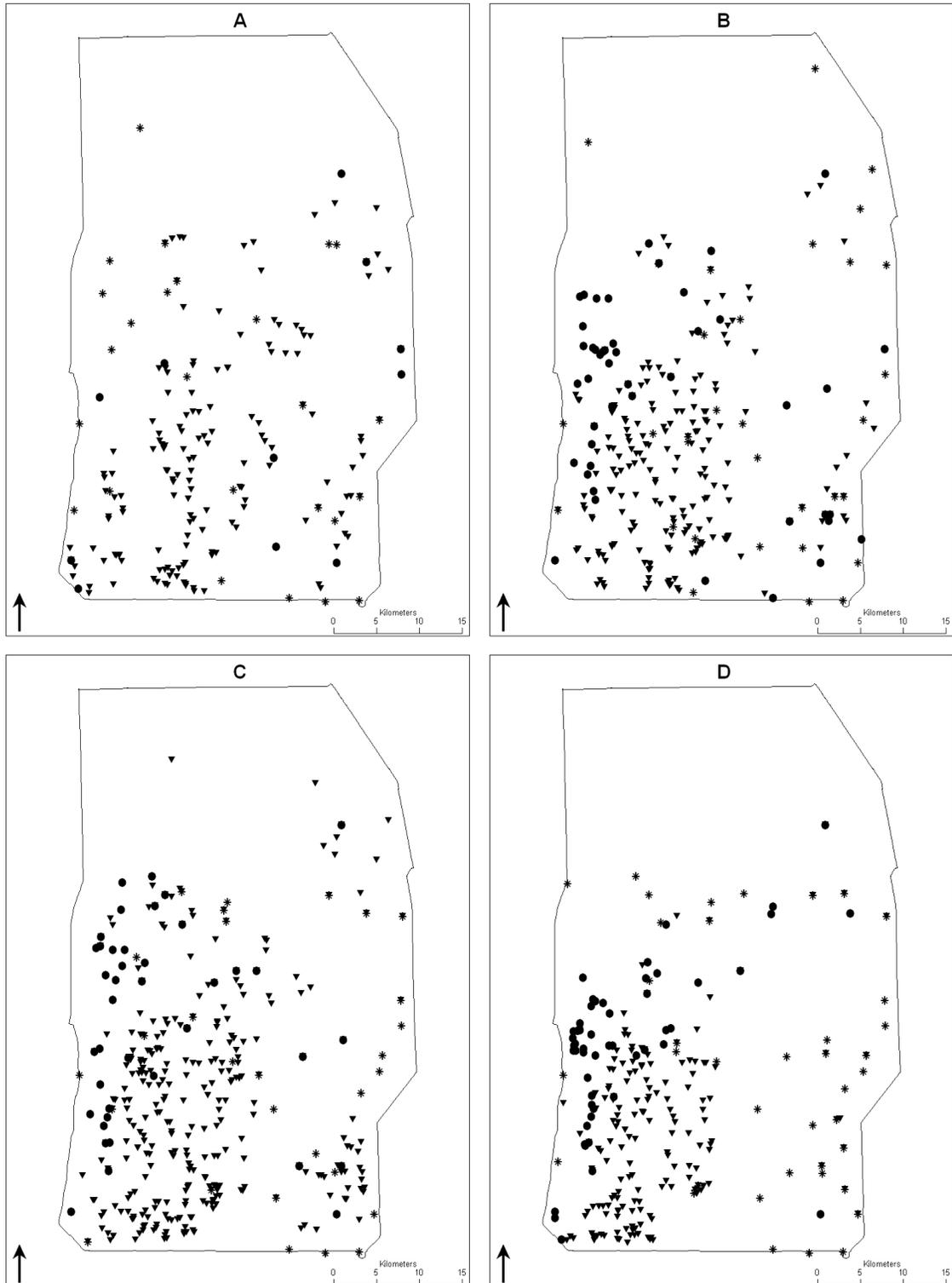


Figure 3-1. Distribution of ardeid colonies in WCA3. A) 1993. B) 1994. C) 1995. D) 1996. E) 1997. F) 1998. G) 1999. H) 2000. Triangles indicate Great Blue Heron colonies, stars indicate Great Egret colonies, and circles indicate Tricolored Heron colonies.

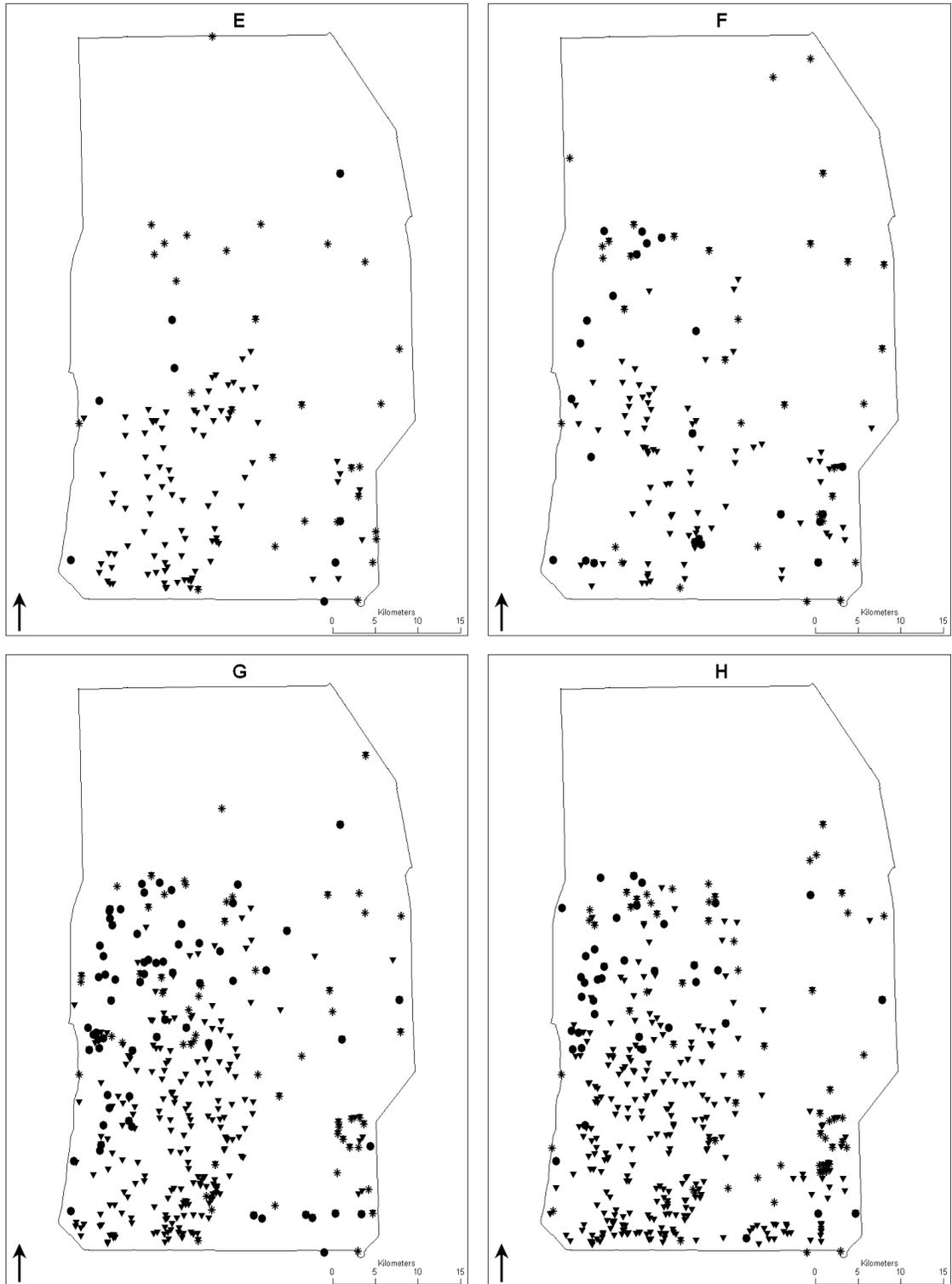


Figure 3-1. Continued

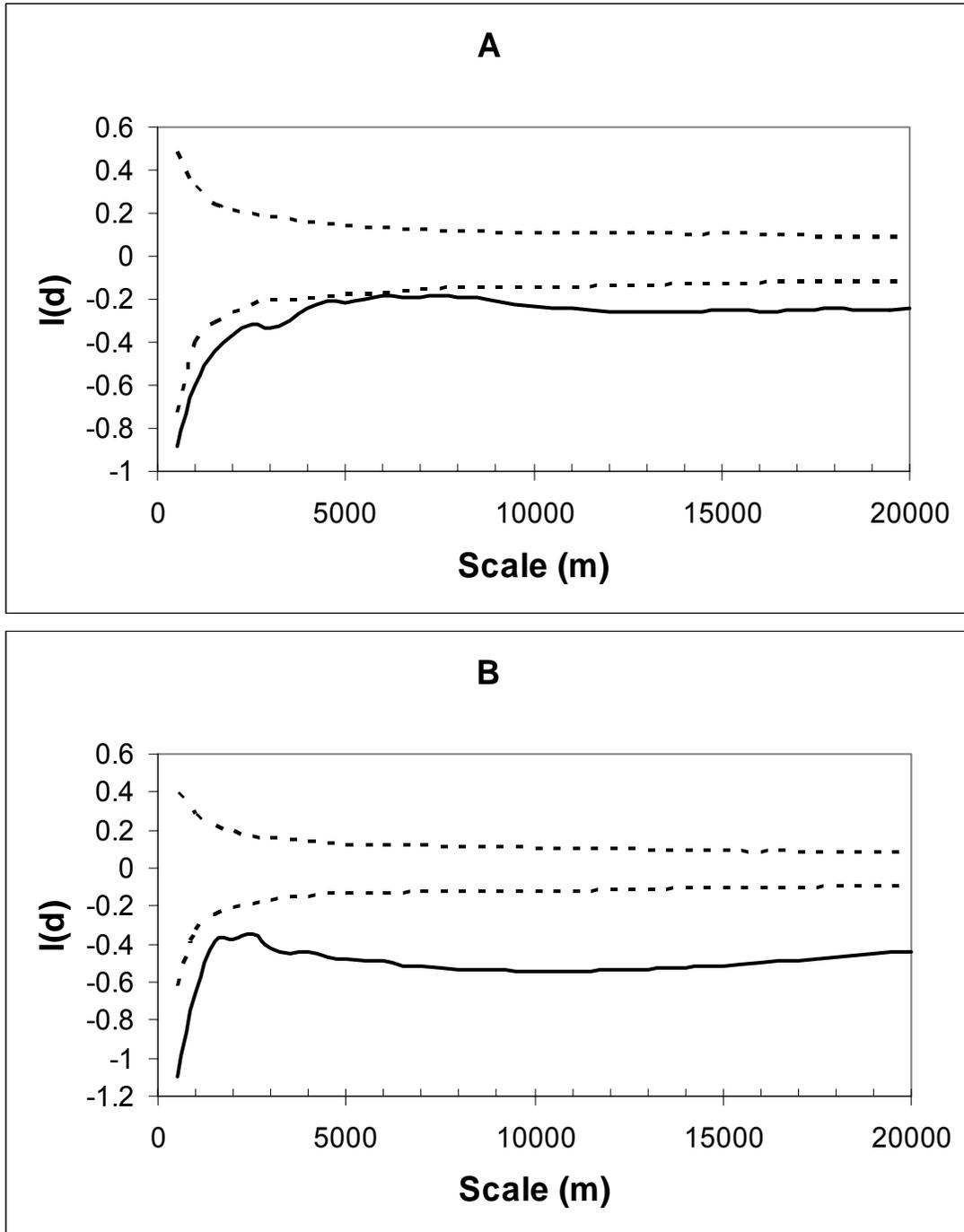


Figure 3-2. Relationship of Great Blue Heron colonies relative to all available sites in WCA3 as shown by linearized Ripley's K ( $I(d)$ ) graphs. A) 1993. B) 1994. C) 1995. D) 1996. E) 1997. F) 1998. G) 1999. H) 2000. Sample sizes for each year listed in Table 3-1. Dashed lines: 95% confidence intervals from Monte Carlo simulations of 999 identically-sized, randomly-selected samples from each year; solid line:  $I(d)$  graph for used sites.

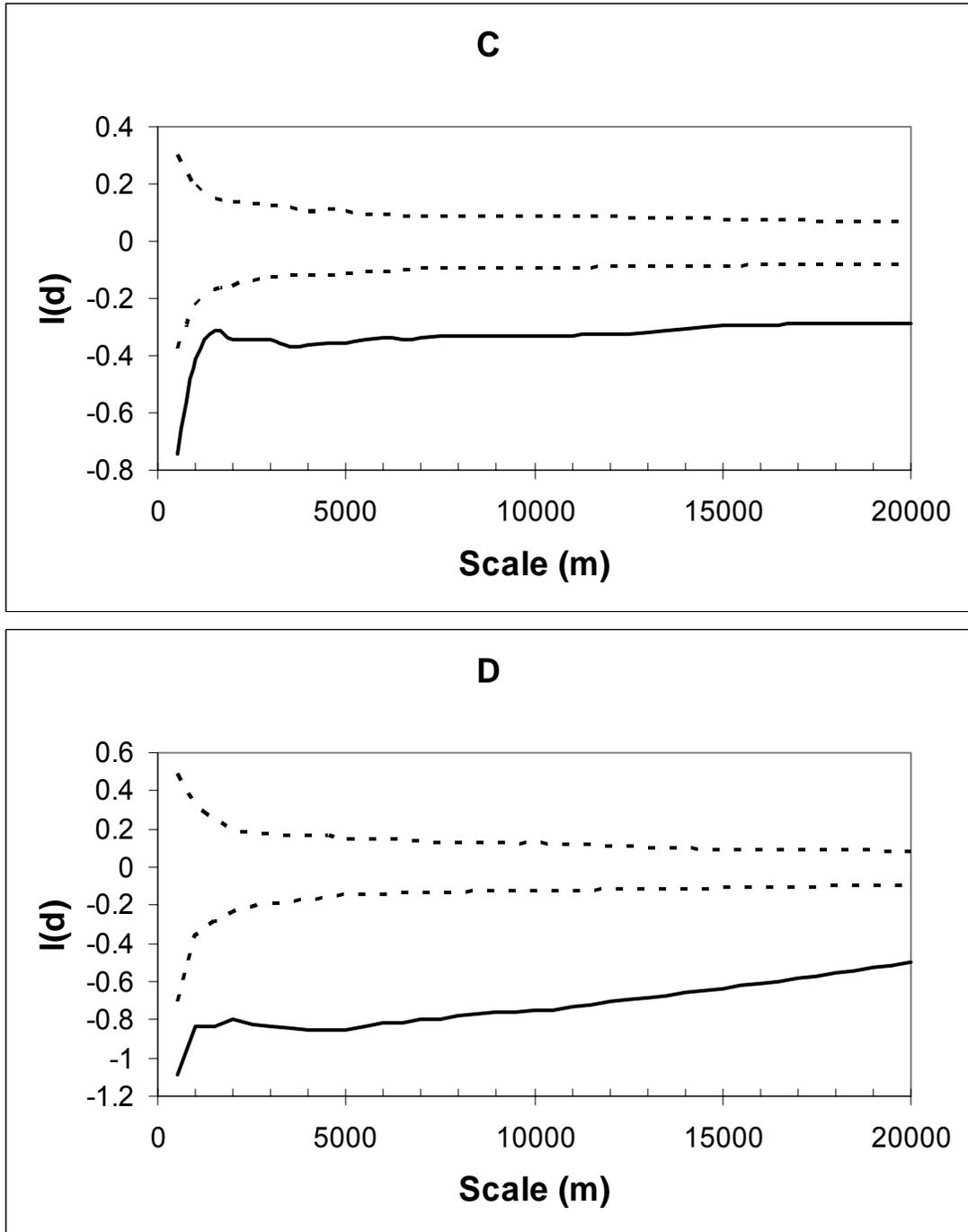


Figure 3-2. Continued

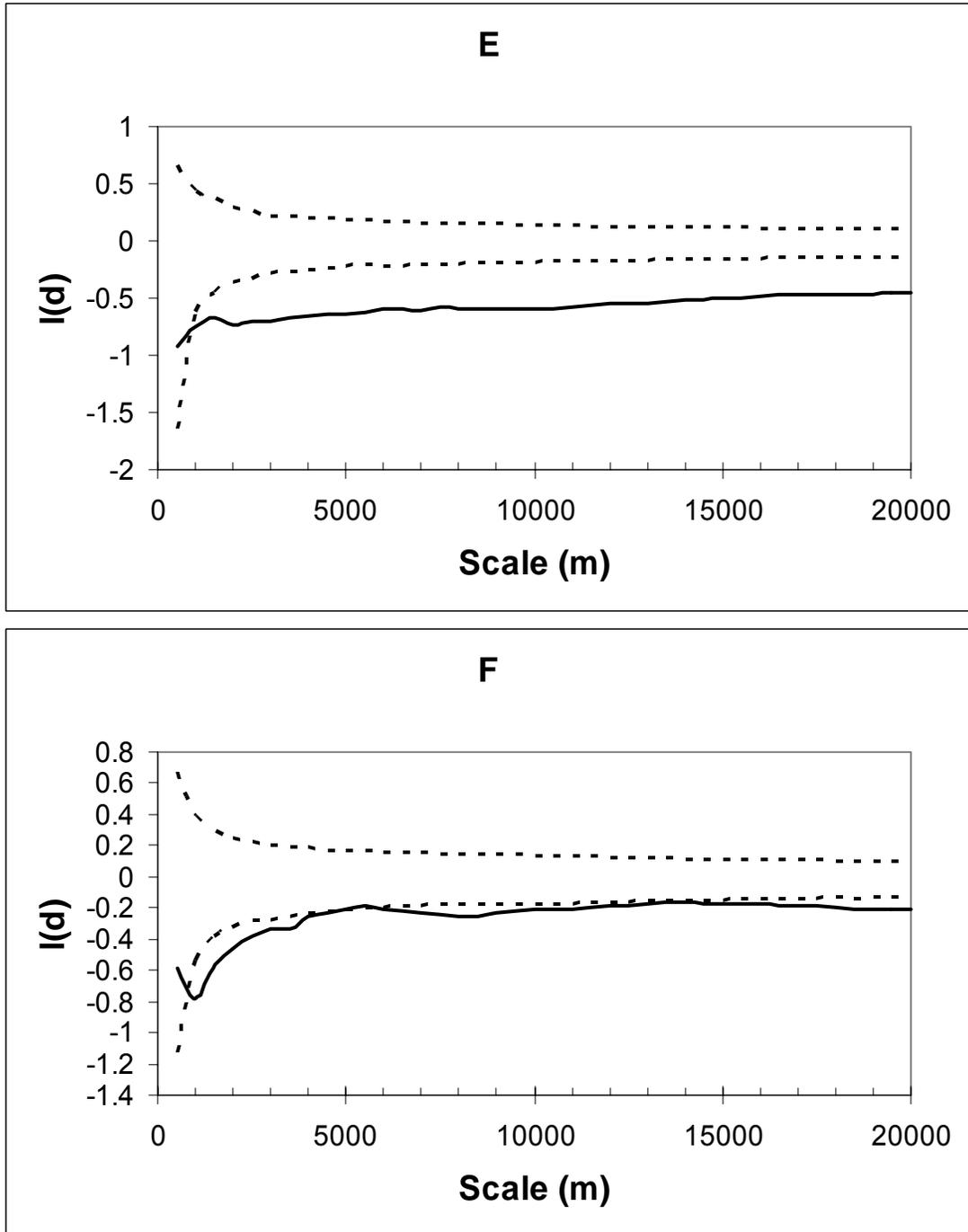


Figure 3-2. Continued

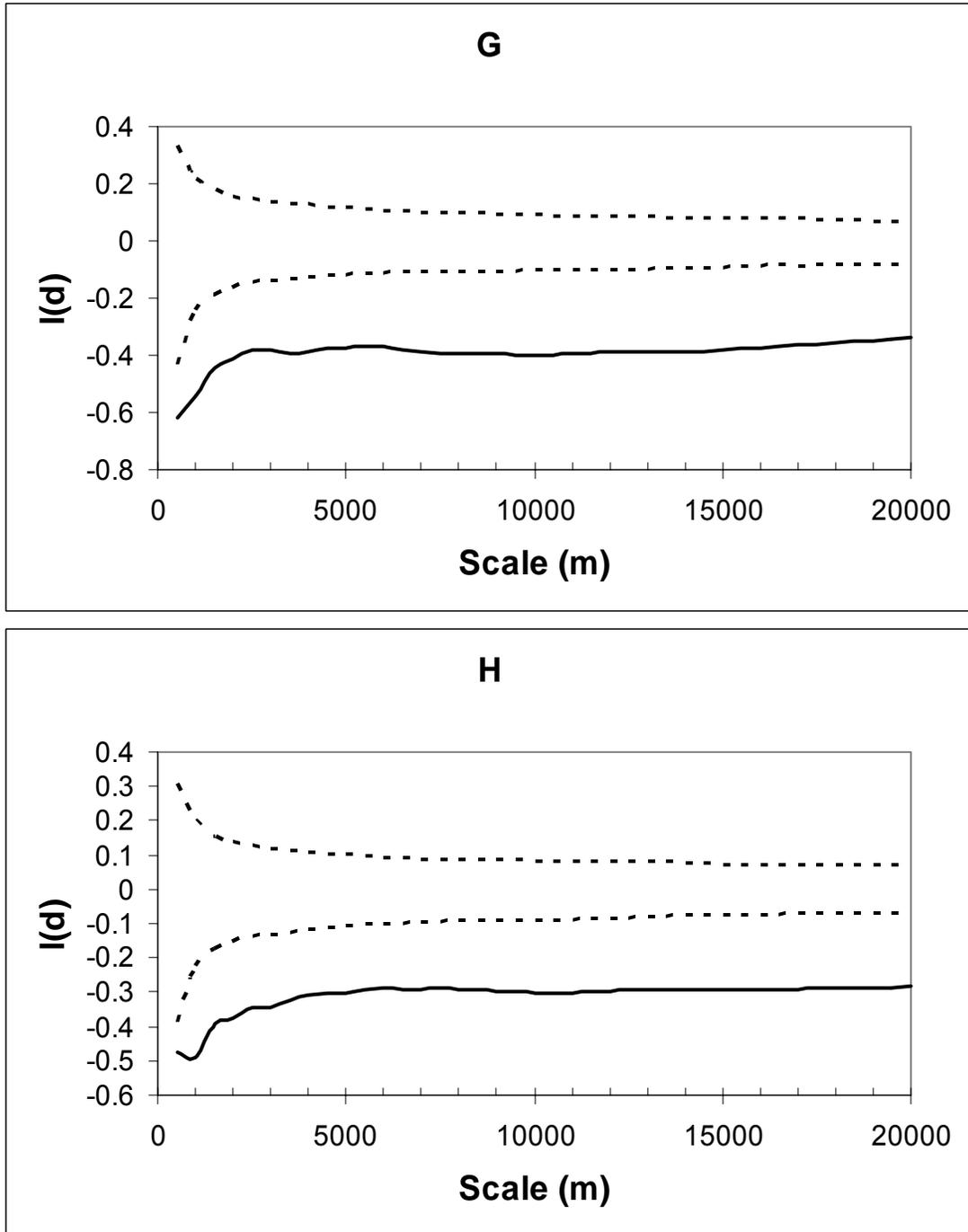


Figure 3-2. Continued

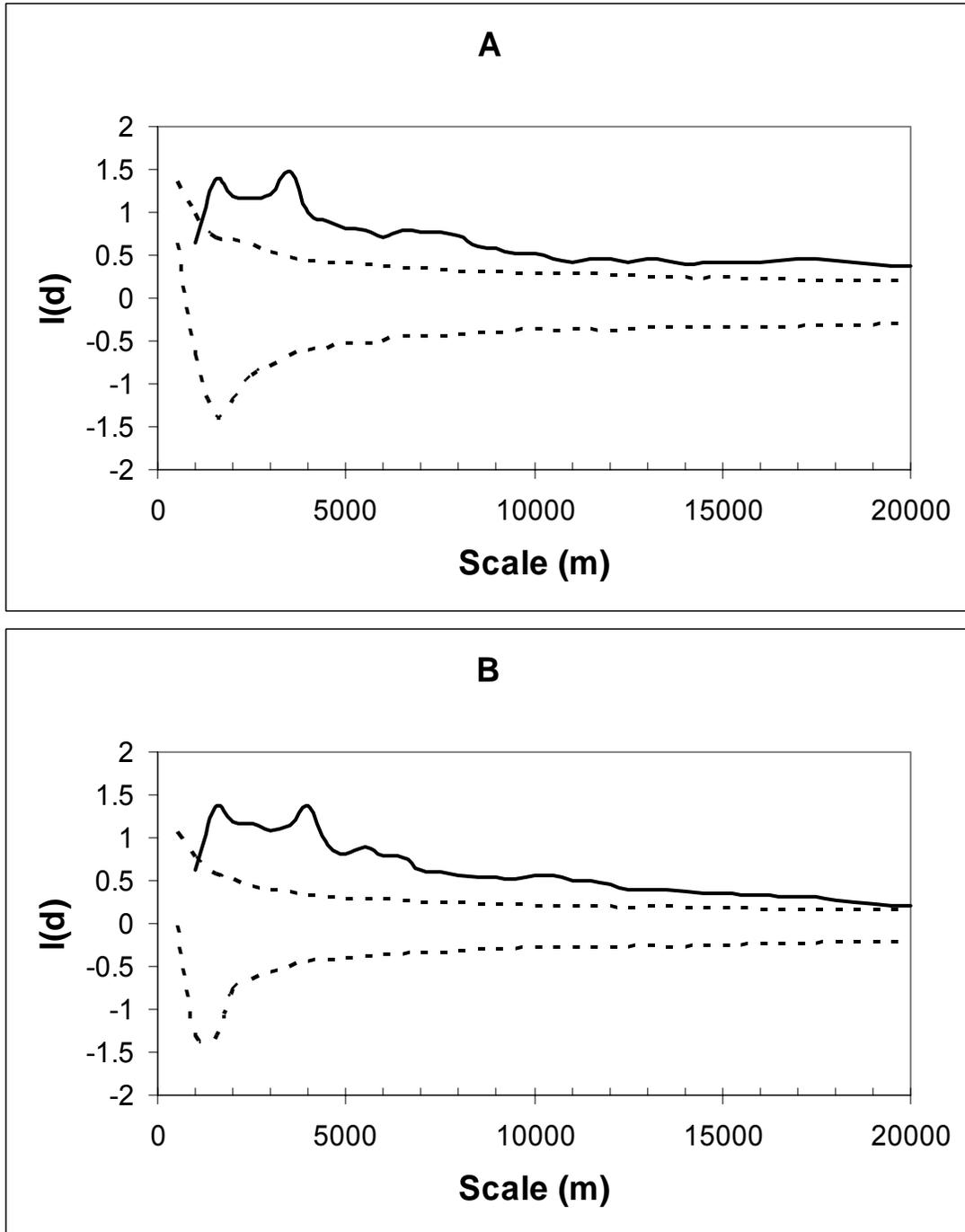


Figure 3-3. Relationship of Great Egret colonies relative to all available sites in WCA3 as shown by linearized Ripley's  $K$  ( $I[d]$ ) graphs. A) 1993. B) 1994. C) 1995. D) 1996. E) 1997. F) 1998. G) 1999. H) 2000. Sample sizes for each year listed in Table 3-1. Dashed lines: 95% confidence intervals from Monte Carlo simulations of 999 identically-sized, randomly-selected samples from each year; solid line:  $I(d)$  graph for used sites.

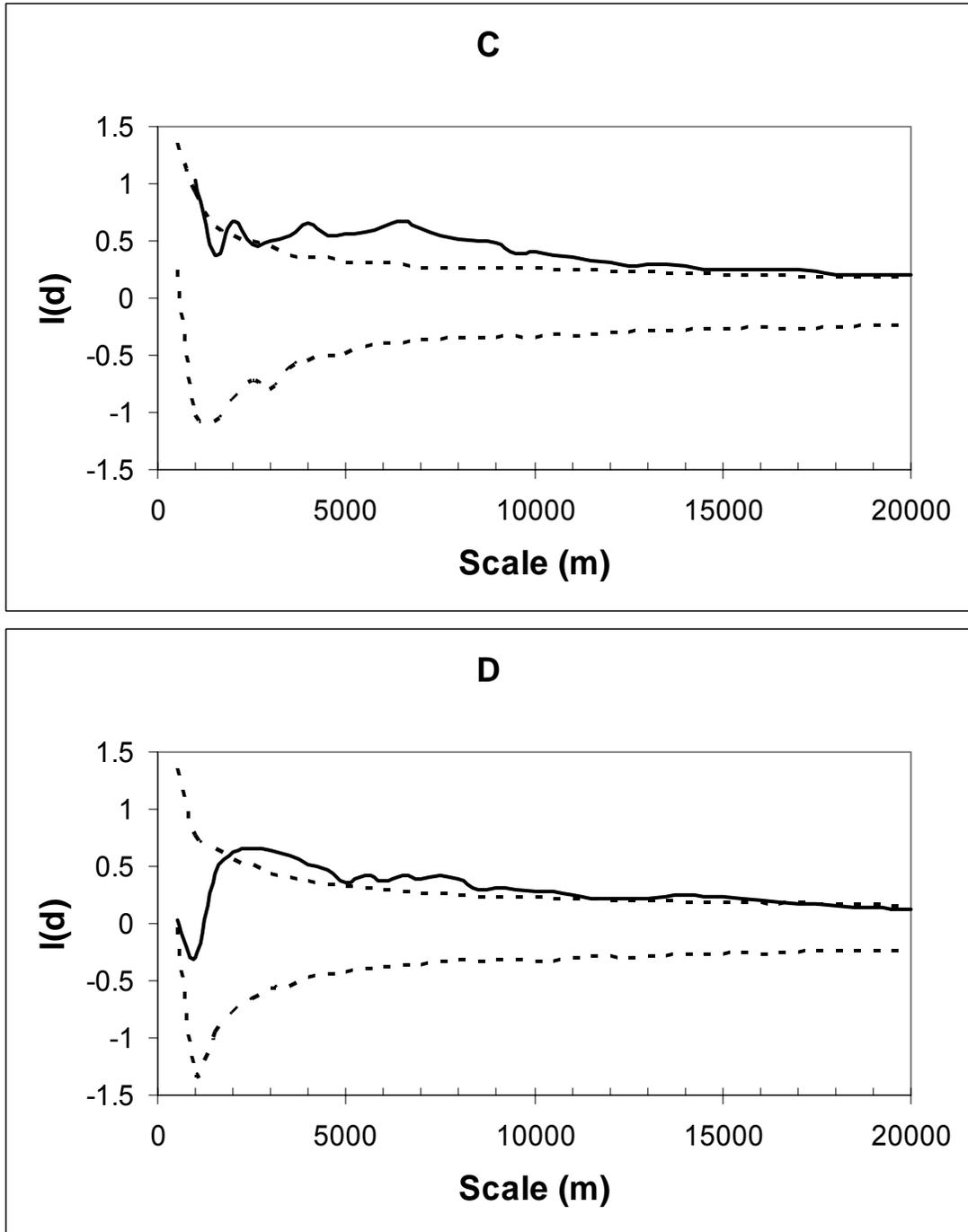


Figure 3-3. Continued

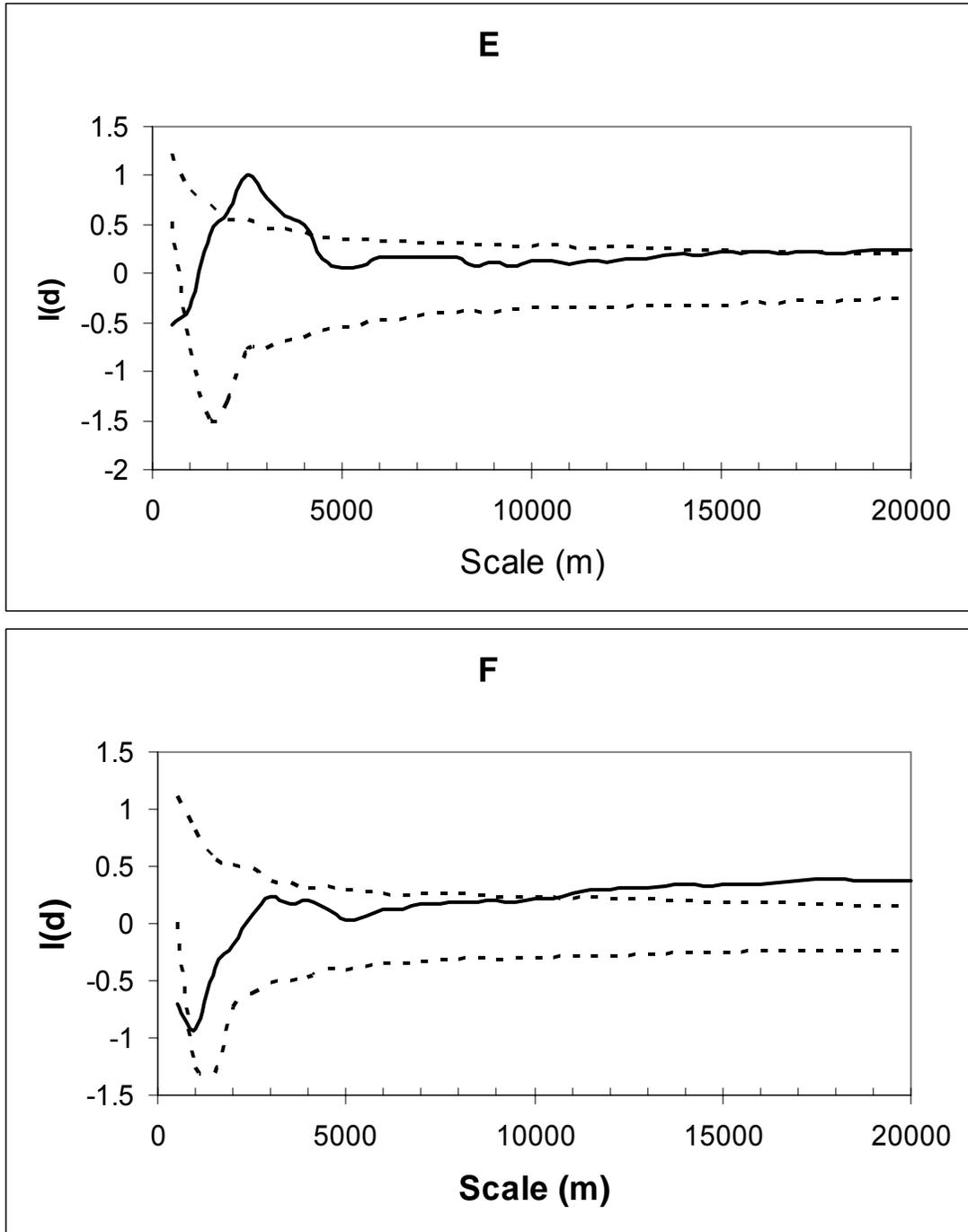


Figure 3-3. Continued

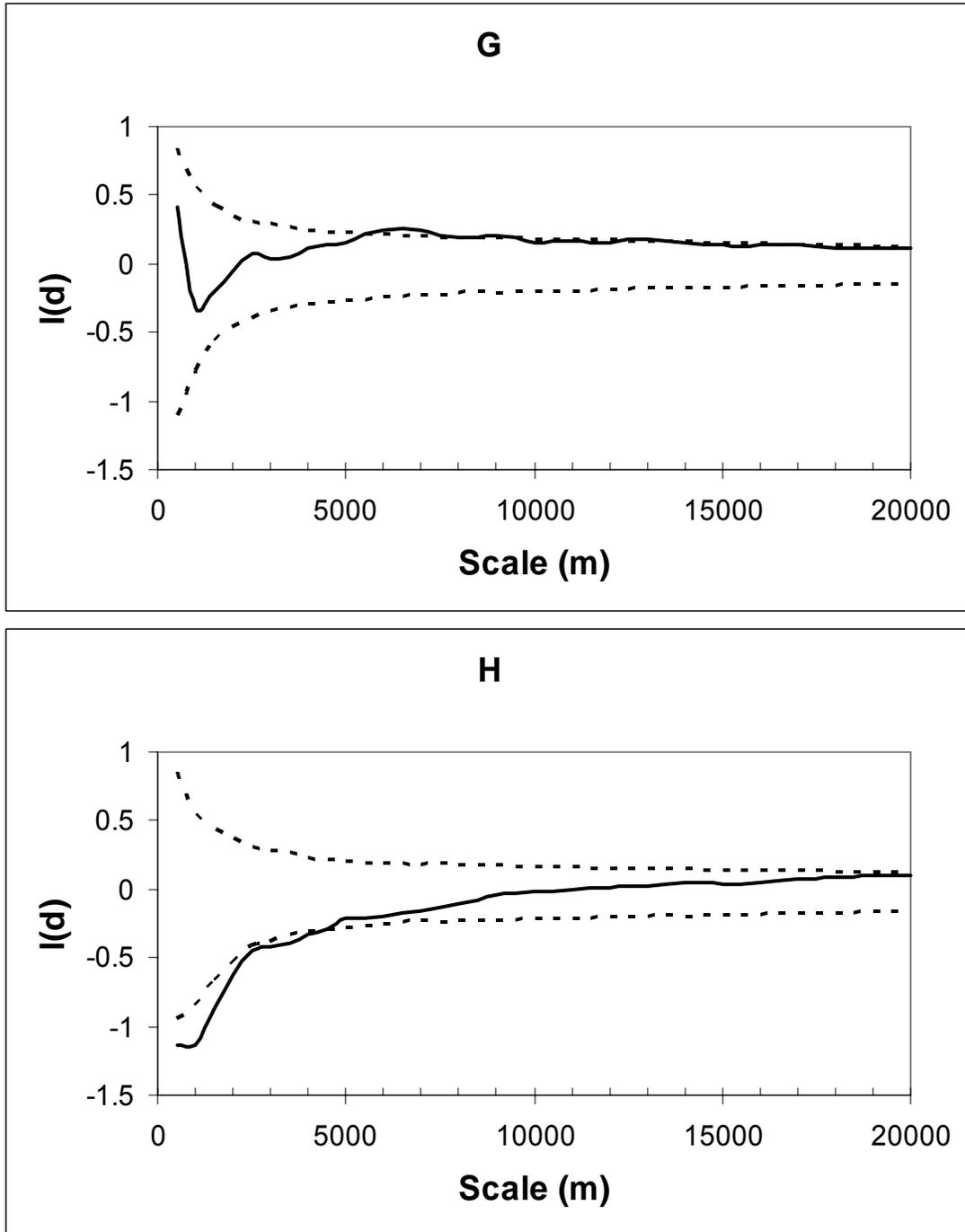


Figure 3-3. Continued

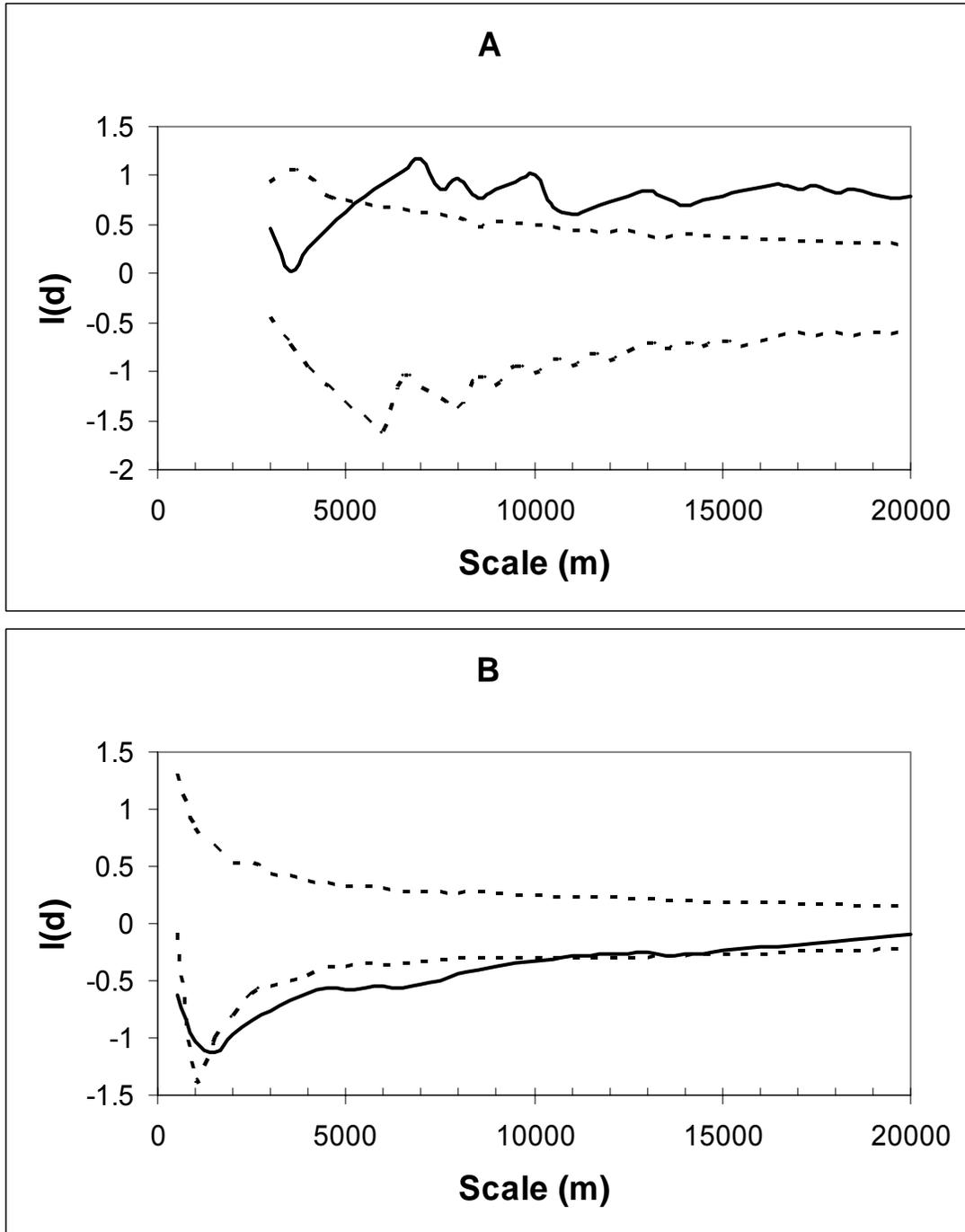


Figure 3-4. Relationship of Tricolored Heron colonies relative to all available sites in WCA3 as shown by linearized Ripley's  $K$  ( $I[d]$ ) graphs. A) 1993. B) 1994. C) 1995. D) 1996. E) 1997. F) 1998. G) 1999. H) 2000. Sample sizes for each year listed in Table 3-1. Dashed lines: 95% confidence intervals from Monte Carlo simulations of 999 identically-sized, randomly-selected samples from each year; solid line:  $I(d)$  graph for used sites.

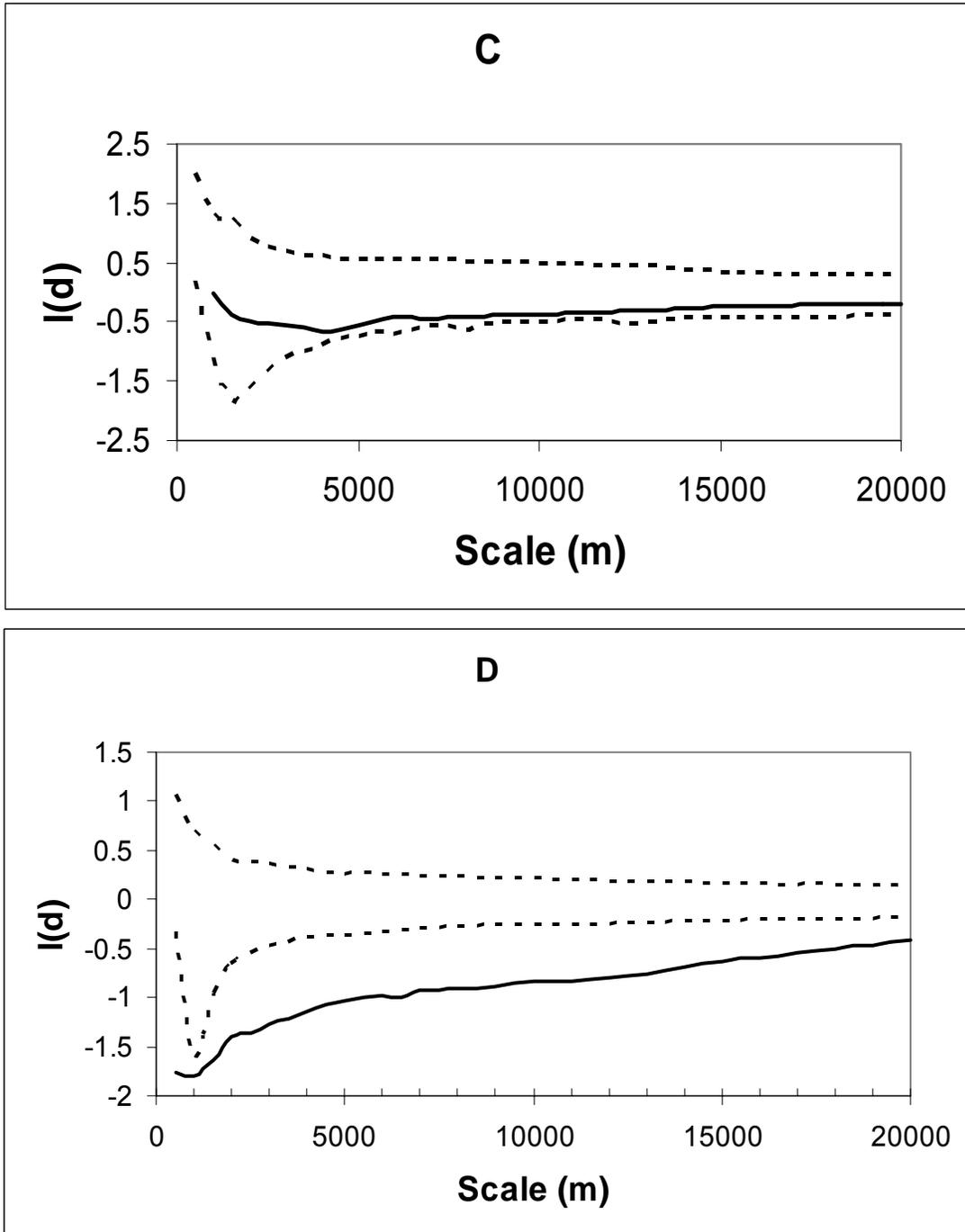


Figure 3-4. Continued

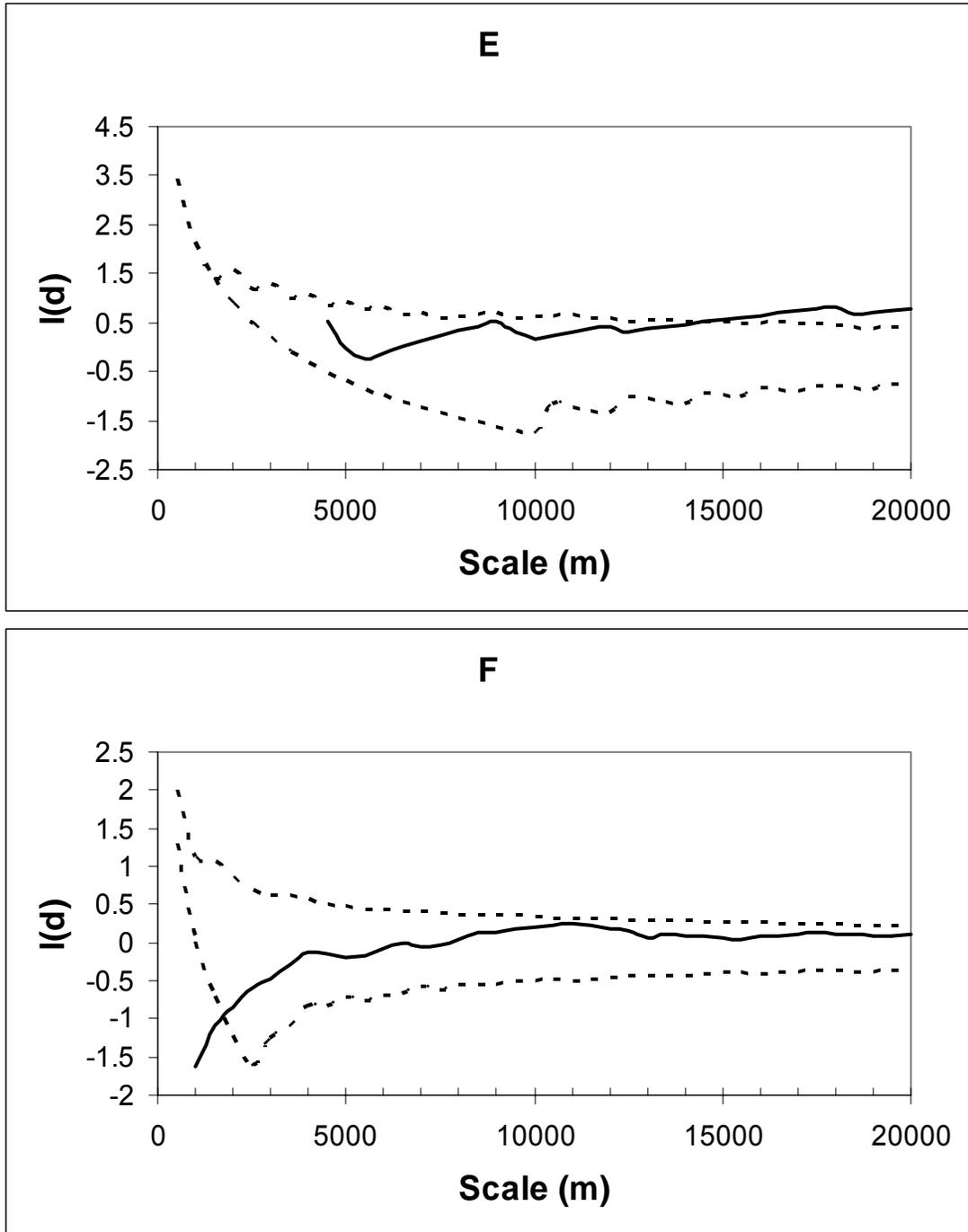


Figure 3-4. Continued

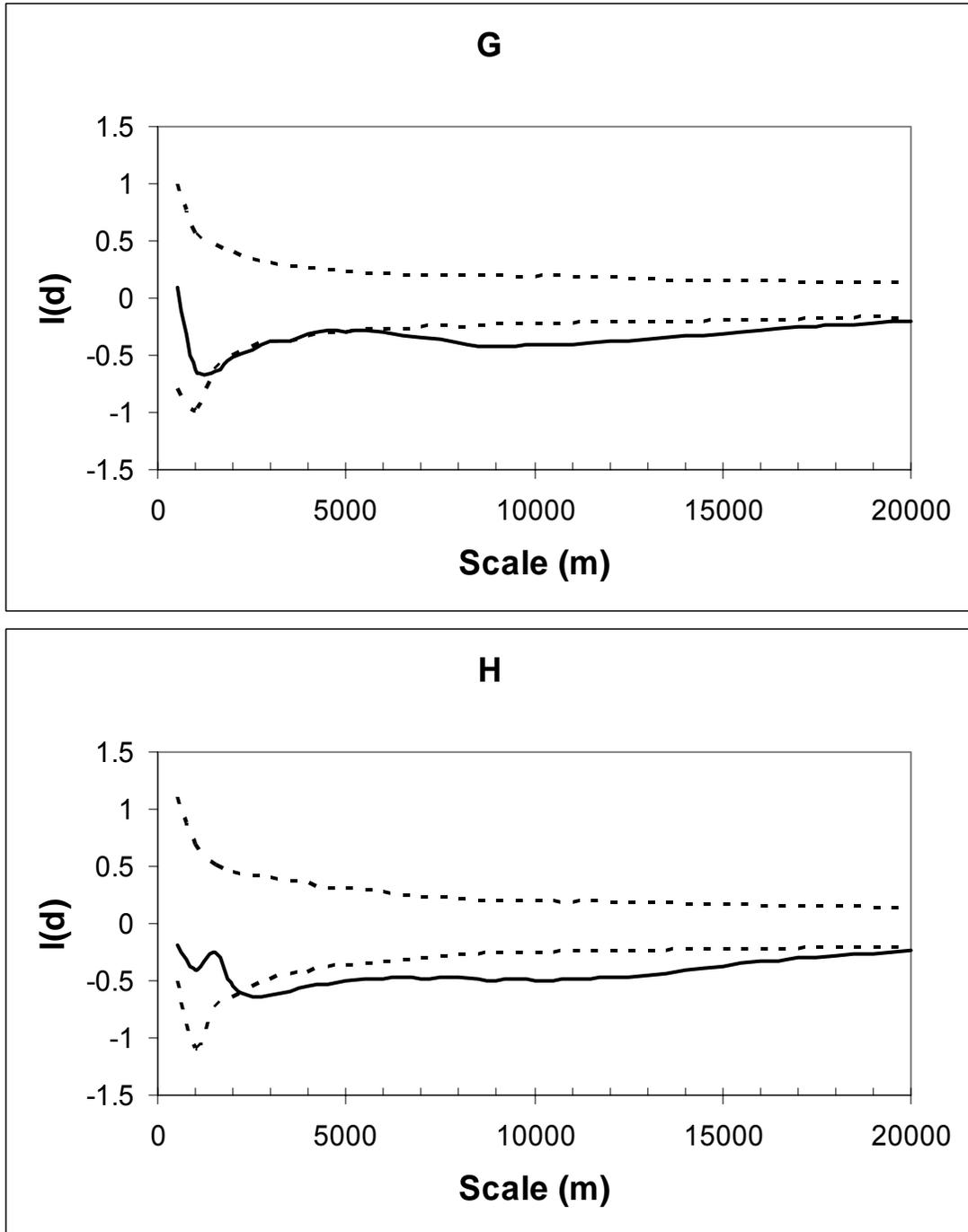


Figure 3-4. Continued

## CHAPTER 4 DISCUSSION

### **Effects of Site Availability**

The spatial patterns of colony sites used by these three species during the study period were in general dissimilar from the overall pattern of available sites (Figures 3-2 through 3-4). This was always true for Great Blue Herons, and was true at most scales for Great Egrets and Tricolored Herons in 4 and 5 of the 8 years, respectively. These two species exhibited both clustered and dispersed patterns, which likely reflects responses by the birds to different hydrological conditions in each year. These results indicate that site selection by these three species was probably independent of overall site availability or distribution.

### **Model Performance**

Although there was very strong evidence supporting the best models for Great Blue and Tricolored Herons, relative to the total set of models I tested, model classification performance was poor overall. None of the best models achieved a Kappa statistic of 0.4, which is often considered to be the minimum value for “good” performance (Fielding & Bell 1997), and only the best model for Great Blue Herons had an area under its ROC curve of at least 0.7. Models always did a better job of classifying used than unused cells (Table 3-6), which suggests that there were more appropriate sites available than were used (Fielding & Bell 1997). A major limitation of this analysis was the coarse spatial resolution of the hydrological data, which prevented me from including variables that operate at the scale of the sites themselves such as vegetation type or patch size. Finally,

simply classifying cells as used or unused ignored the enormous variation in the number of Great Egret pairs nesting at sites within WCA3, which is probably why the models for this species performed the worst.

Despite these limitations, these results clearly show that the amount of foraging habitat around sites, and the likelihood that they would remain inundated throughout the breeding season, were important influences on the colony site selection for these three species. This is the first study to quantitatively establish the importance of deterring mammalian predators as an influence on colony site selection in this group. These results also establish that the distribution of foraging habitats is as important to wading birds in an enormous wetland-dominated landscape such as the Everglades, as it is in more typical terrestrial landscapes where wetlands are part of a habitat mosaic (Gibbs et al. 1987; Gibbs 1991; Gibbs & Kinkel 1997).

### **Responses to Hydrological Variability**

In general, neither the average weekly proportional decline in water depths (FWI) nor the spatial variation in water depths (WV) were important influences on colony site selection in these three species. WV was weakly selected against by Great Egrets, and not included in the best models for either of the other two species. Only Great Blue Herons selected cells with large values of FWI. However, areas that began the breeding season with deeper water were likely to have the largest values of for this variable, since they could experience proportional declines for much longer before going dry. Thus it is unclear whether FWI actually represented prey availability for Great Blue Herons or was instead a proxy for deep water. Great Blues also selected against cells that had both rapid declines in water depths and a high likelihood of remaining inundated (i.e., the INUN\*FWI interaction term). These could represent either permanently shallow areas

(such as on the west side of WCA3, where water flow westward into Big Cypress National Preserve is unimpeded), and/or areas near canals, both of which were mostly avoided by this species (Figure 3-1).

These results suggest that ardeid wading birds are selecting colony sites that are characterized by stable, rather than variable, water depths. Another possible interpretation is that colony site selection by these species does not reflect an attempt to predict future conditions (i.e., a “bet hedging” strategy), but is rather simply a response to conditions at the time of nesting (Bancroft et al. 1994). These three species are known to be less dependent on concentrated patches of prey created by declining water depths than tactile/social foragers such as Wood Storks (*Mycteria americana*), White Ibises (*Eudocimus albus*), and Snowy Egrets (*Egretta thula*) (Kahl 1964; Gawlik 2002), so it is also possible that they have not experienced any selective pressure to recognize or respond to this environmental characteristic.

### **Management Implications**

Previous authors have speculated that the size of wading bird breeding populations in the Everglades is dependent on the extent of open slough habitat available to them (Bancroft et al. 1994; Bancroft et al. 2002), and the results of this study establish that this is the most important environmental characteristic determining where the birds nest. Hydroperiod and fire are the two largest factors controlling the distribution of wetland vegetation (Gunderson 1994), so water management can play an important role in maximizing the extent of open slough habitat within the Everglades. Water depths should be maintained at a deep enough level to prevent most breeding sites from going dry, but shallow enough for wading birds to forage. Using these guidelines could make a major

contribution to re-establishing historical breeding populations of wading birds in the Everglades.

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## BIOGRAPHICAL SKETCH

Matthew John Bokach completed his Bachelor of Science degree with a double major in biology and chemistry at Adrian College (Adrian, Michigan) in 1994. He fled the sciences for 2 years in a master's program in student affairs administration at Michigan State University, then returned to them as a U.S. Peace Corps Volunteer at Lukosi Government School in Hwange District, Zimbabwe. While teaching general science at Lukosi, Matthew fell in love with the southern African avifauna and spent an additional 2 years in Zimbabwe, mostly so he could continue watching them. He returned to the United States in 2000 and began a master's degree in interdisciplinary ecology at the University of Florida in 2002. He plans to move to the San Francisco Bay area, pursue a career in GIS application development, and eventually flee the sciences once again to pursue a career in popular music.