FACTORS AFFECTING BREEDING STATUS OF WADING BIRDS IN THE EVERGLADES

2001 Final Comprehensive Report
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EXECUTIVE SUMMARY

This comprehensive final report summarizes the results of a four-year research and monitoring effort (1998 – 2001) designed to document nesting effort and success by wading birds, and to investigate the reproductive physiology and ecology of White Ibises (*Eudocimus albus*) in the Everglades ecosystem. The monitoring of nesting has been accomplished by standardized systematic aerial and ground surveys and study of nesting success of nesting colonies in Water Conservation Areas (WCAs) 2 and 3 of the central Everglades. The White Ibis work was accomplished through 1) investigation of the nutritional, behavioral, and hormonal aspects of "normal" breeding in a captive colony of Scarlet Ibises (*Eudocimus ruber*, considered by many to be the same species as the White Ibis), and 2) documenting the physiology, nutritional state, breeding phenology, contaminant load, and hormonal status of free- living adult White Ibises in the central Everglades.

Nesting effort and success

We documented a large increase in numbers of wading bird nesting attempts over the past four years in the Everglades system (ENP, WCAs combined). In 1998, we started with just over 8,800 wading bird nests, increasing to approximately 26,000 nests in 1999, 35,100 in 2000, and finally 34,500 in 2001 (Figure 3.1, Table 3.1). Over these four years, an average of 49% of all nests were constructed by White Ibises. In comparing these 4 years (1998-2001) to the previous ten years (1988-1997), all species except for Cattle Egrets have shown an average increase in nesting attempts. Black-crowned Night Herons (*Nycticorax nycticorax*) and Glossy Ibises (*Plegadis falcinellus*) showed the greatest increases in recent years, each 3.4 times above the prior ten-year average. Wood Stork

(*Mycteria americana*) nests during the study period increased by 3.4 times the ten-year average, while White Ibises increased by 2.7 times over the ten-year average. Cattle Egrets (*Bubulcus ibis*) showed a decline of 25% compared to the ten-year average, largely due to their relatively small numbers of nests during 2000. Within the recent four-year period the average for all wading bird species increased by 2.2 times the prior ten-year average. Although there were increases in most species, the most pronounced increase was among those species that forage tactilely (Wood Storks, White Ibises, Glossy Ibises) and those that forage actively in tight social flocks (Snowy Egrets; *Egretta thula*). By comparison, the birds capable of foraging in deeper water and that typically forage by stealth and vision (Great Egrets; *Ardea albus*, Great Blue Herons; *Ardea herodias*) did not have as strong increases, and in at least one year (2001) did very poorly.

The hydrological conditions in 1999, 2000 and 2001 were those that have been associated with large numbers of nesting birds in the past – relatively high initial water levels, falling rapidly and with little interruption between November and April. However, the large number of nesting birds cannot be explained by these conditions alone, since similar conditions prevailed in at least two years during the mid-1990's and nesting numbers were comparatively paltry. This suggests that there were other factors involved in the attraction of large numbers of birds in 1999 – 2001. We have suggested that an extensive and in some places severe drought in other parts of the southeastern US may have made the Everglades one of the few places that were suitable for nesting for a large number of birds. It is also possible that the marked decline in mercury contamination was related to the increase in nesting numbers. Finally, there is the possibility that some combination of hydrological conditions may have resulted in extremely dense prey populations. However, our results are largely based on association, and we are unable to isolate the combined or individual effect of these events, especially with the small sample sizes available for any given set of conditions. The basic problem is that we are attempting to understand the effects of at least five variables that may each have independent action (hydrology, weather, prey population fluctuations, contamination, and conditions outside the ecosystem), and we have no ability to vary these effects in an experimental way. These effects are likely to be isolated either through a very large number of years monitored, or through some combination of experiments with captive animals.

However, the present study has also demonstrated conclusively that while antecedent severe drought in the Everglades ecosystem may often lead to large nesting events in the years following droughts, these droughts are not the only events that can lead to large nestings. Although we maintain that droughts play a important role in the ecology of wading bird populations and the Everglades ecosystem, we believe that research should also be focused on identifying other mechanisms by which prey are made abundant and available over large areas of the marsh.

Effect of nesting date on reproductive success in ibises

Many birds show a seasonal decline in nesting success and juvenile survival in the temperate zone. We attempted to measure the effect of initiation date on nest success and juvenile survival in White Ibises, in order to understand the consequences of nesting early and late in the breeding season. In a sample of 570 nests monitored in 6 colonies during 2001, we found extreme early and late nests varied by 27-86 days among colonies. We found no significant differences in clutch size, hatchability, or overall nest success (measured through the Mayfield method) between early and late nests. However, this sample of nests showed very poor success overall (4%), the lowest so far recorded for the species, and hatchability was extremely poor. Most colonies abandoned entirely, and in colonies with some success, very few nest attempts survived to produce young. In this context, we do not believe that our comparison of early and late nesting was at all conclusive. Growth rates of late-hatching birds appear to be faster than those of early hatching chicks, but this conclusion is tentative due to small sample size.

We also marked 53 fledging ibises with radio tags equipped with mortality sensors. In 69 hours of tracking from ground and air between marking and October 2001, we found 3 of these birds died, one lost its transmitter, and we relocated 14 of the 49 birds believed to have fledged from the colony. Mean age at independence from the colony was 62.5 (SE 6.9) days. We believe there may be an opportunity to reassess survival in this group of birds as many may return to south Florida during the winter of 2001/2002.

Refinement of counting and surveying techniques.

We measured two potential sources of error in estimating numbers of birds in colonies and numbers of nesting attempts. First, we examined accuracy and observer variation in counts of large numbers (200 - 6000) of densely nesting birds in vegetated situations using a scaled model. We placed known numbers of scaled model birds on a physical scaled model of a wading bird colony. Trained biologists repeatedly estimated the numbers of birds in a series of trials. We also compared true numbers with photographic counts of the same trials. The model ensured that the numbers of actual birds were known and that the numbers of birds could be changed rapidly for multiple counts in any testing session. The overall tendency among observers was to undercount (81% of all estimates). The mean underestimate (N = 255) varied from the true value by –48.61% (SE = 1.41%). The mean overestimate (N = 59) varied from the true value by 54.92% (SE = 7.15%). When total overestimates and underestimates were combined, the mean error for all estimates by all observers was –29.16% (SE = 10.09%,), and we found no evidence of increasing error with size of aggregation. We found no significant effects of total number of surveys previously conducted, date when the observer last conducted a survey, largest number of animals previously surveyed, highest education level, or the use of corrective lens on estimation error. Counts of photographs taken of each trial resulted in a mean aggregate error (over and underestimates combined) of -13.17 % (SE = 3.65%). The absolute value of the mean error in photographic counts was 20.98% (SE = 3.94%), significantly lower than the error associated with observer counts.

We also investigated how many nest starts might have been missed by having surveys spaced one month apart. Nests might start and fail during the intersurvey interval and so not be counted. In addition, asynchronous nesting may lead to underestimates of the true numbers of nests if "peak" monthly counts are used. In order to estimate the magnitude of this error, we used a large sample of start and end dates for individually marked nests studied in the Everglades and simulated whether each nest would have been detected through monthly surveys. The counts done during "peak" periods of activity were surprisingly poor estimators of the total numbers of nests initiated, ranging between 36 and 76% of the total for any given species-year combination. This suggests initially that peak snapshot surveys were undercounting the true population by 24 – 64%. The proportion counted of any species also varied considerably among years of study.

Both snapshot survey error and counting error are independent processes, and their effect is additive. Both types of error were associated with large variation either among years (snapshot) or observers. This suggests that it will be difficult to develop correction factors for these errors. More importantly, this information suggests that past survey information may not have consistent error from year to year, and therefore may not be a good index of population change. We suggest the use of photos, documentation of observer error, and further research into renesting as ways to partially alleviate the biases introduced by these sources of estimation error.

Reproductive physiology of White Ibises

We developed several methods for trapping and handling adult White Ibises, including the use of rocket and mist nets. We used white plastic flamingos as decoys to lure birds to both kinds of sets. Although both systems captured ibises, the mist nets were quieter, safer, and quicker to set up and to re-set following capture.

We captured adult ibises during all stages of breeding, and developed predictive models both to identify sex based on body measurements, and to predict stage of reproduction based on coloration. We confirmed that ibises do develop brood patches, and that many ibises molt during the breeding cycle. The field work and the work with captive Scarlet Ibises confirmed that both sexes do put on mass immediately prior to breeding, and that mass declines significantly during later breeding stages. In addition, the captive studies indicated that ibises can put on the mass typical of breeding birds in as little as two weeks. Although the mechanistic importance of mass gain remains unclear, it does seem obvious that mass gain plays an important role in the reproductive process, implying that hyperphagy (rapid food intake) prior to breeding is a necessary precondition to initiate the reproductive process.

The control of gonadal growth in ibises appeared to be related to day length and age, and the development of other attributes (hormonal changes, color changes, body mass changes) appeared to be influenced by local conditions; we suspect that social and feeding conditions are primary among these influences.

We also radio-marked 51 adult ibises over the course of the study, and this allowed us to document both migration out of the study area, and breeding activity within the Everglades. Through this, we have demonstrated that adults can breed in successive years, and that they are not limited by energy or other constraints to breeding at some longer interval. Our results also indicated that ibises may be quite philopatric; 71% of adults marked in 1999 and relocated in 2000 bred in the same colony.

Comparisons of nesting and "nonbreeding" birds

Comparison of numbers of breeding birds and all birds estimated in the area (SRF surveys) initially suggested that there were many more birds on the marsh than were breeding in colonies. However, especially with the large uncertainty in estimating numbers of breeding and nonbreeding birds revealed by our studies, we feel that these survey-based comparisons are too inaccurate to draw any conclusions about whether birds are nonbreeding. In addition, our radio telemetry studies and the signs of breeding in captured birds suggest that during 1999 – 2001, all the adult ibises in the ecosystem were breeding. However, its also clear that we studied this phenomenon most intensively during three years when breeding numbers were considerably above normal, when nonbreeding might be expected to be at a minimum. In this light, it seems impossible to say at present whether nonbreeding occurs, or if it does, whether it occurs at high enough proportions to affect the population trajectory of any species in the south Florida ecosystem.

Mercury contamination and breeding by Everglades wading birds

During each year of study we documented mercury levels from standardized feather samples of young Great Egrets taken from representative colonies in WCA 3. Between 1994 and 2000, we documented a 73% reduction in average mercury contamination levels in feathers of young birds. By extrapolating from the feather Hg dynamics and known food/contamination relationships, we estimated a 67% decline in Hg content of the Great Egret prey items during the study. Since these young birds are raised on food resources gathered within the immediate vicinity of the colony (<25 km), we believe that this is strong evidence for a decline in mercury in the food web of the central Everglades. The cause of the decline is unknown, but we speculate that decreases in incinerator-generated mercury since 1990 is the most likely explanation.

We found a positive relationship between mercury in adult male ibises and both progesterone and corticosterone levels during incubation. The apparently stronger relationship in males may be due to the fact that males had higher circulating levels of mercury than did females, probably because females were able to excrete significant amounts of mercury through egglaying. We are aware that at higher physiological levels of mercury, progesterone receptors may be blocked. This would fit with the positive relationship between mercury and progesterone. If receptors are blocked, then the negative feedback loop would be inhibited and progesterone production would continue to compensate. What little is known about progesterone's role in avian reproduction suggests that decreased progesterone might lead to poorer nest attendance or even abandonment of nesting. In the case of the male ibis, the higher progesterone in mercury contaminated birds is thought to be indicative of blockage of progesterone reception sites, which would effectively amount to the same thing as low progesterone levels in other studies. High abandonment rates of wading birds has been noted as a characteristic of the Everglades nesting populations in the past (Frederick and Spalding 1994). However, any potential connection between nesting and mercury contamination is extremely tenuous.

CHAPTER I. INTRODUCTION

Purpose of this study

This study was initiated in January of 1998, as a continuation of a long-term monitoring and research program. The current project was designed with two general goals in mind - continued monitoring of nesting populations of wading birds in the Water Conservation Areas of the Everglades, and the pursuit of directed research questions aimed at understanding the factors associated with large proportions of the adult population of wading birds apparently not coming into reproductive condition. Continued monitoring of wading bird populations is essential, as a tool for measuring the effect of different water management strategies, as a method for better understanding the local ecology of this group of birds, and as a way to detect changes that may be due to novel influences that may be unrelated to water management (e.g., exotic fish dynamics, contaminants, etc).

The research component of the project arose because of an observation about wading bird populations in the Everglades. During the mid – late 1990's we gathered evidence that suggested large numbers of adult wading birds that were in the Everglades during the breeding season were not associating with colonies – on average over 70% during the period 1988 – 1998 (methodology, data and details that have yielded this observation are given later in this report, see Chapter V). Understanding why the majority of adult birds were apparently not coming into reproductive condition seemed to be of key importance in restoring populations of wading birds to the south Florida ecosystem.

In the third year of our research project we began to reevaluate this research pursuit. At that point, the evidence to support our hypothesis that birds were not breeding had weakened considerably, both as a result of measuring our biases in counting birds, and through studies of the reproductive activities of marked birds. In fact, most adult birds that we captured and radio-marked showed signs of reproduction or could be tracked via radio-telemetry to a breeding colony. Therefore, we proposed three alternative hypotheses to explain why the number of wading birds in breeding colonies had apparently been lower than the number of birds present on the marsh: 1) the number of breeding pairs in large colonies are underestimated by observers counting from an aerial platform, 2) many birds attempt to breed but fail early and so are not counted in our surveys, or 3) similarly, within a colony wading bird reproduction is sufficiently asynchronous and unsuccessful so that monthly surveys frequently miss many nesting birds.

In addition to evaluating the three mechanisms by which we might have mis-estimated numbers of breeding birds, we also evaluated the possibility that substantial numbers of birds were not coming into reproductive condition. In this report we will address these four possible reasons why the number of birds in breeding colonies are lower than the number of birds present in the Everglades system. To address the first hypothesis, that the number of birds at breeding colonies are underestimated, we conducted an experiment to examine observer counting error (Chapter IV). We also compared estimates of colony size by observer counts and estimates of colony size by observers counting photos of colonies.

We also hypothesized that our ability to estimate numbers of breeding birds at a colony using aerial monthly surveys was strongly hampered by asynchronous reproduction. If birds are highly asynchronous or if breeding attempts often fail, the possibility exists that a substantial number of nest attempts would start and fail between survey dates, leading to a substantial undercount of nesting attempts. Therefore, we used past records of individual nest fates to estimate how much these effects might bias our estimates of numbers of nests in a colony or season (Chapter IV).

The third possibility, that a large proportion of birds attempts to breed but usually fails early in the breeding season prompted the following two questions: 1) do we capture birds who show signs of reproduction, but then do not relocate them in a colony (Chapter IX)? 2) Do we see large numbers of birds attending colonies and then only a few occupied nests later in the season, suggesting widespread abandonment (Chapter III)?

To address the fourth possibility, that many birds do not attempt to breed in most years, we focused on White Ibises (*Eudocimus albus*). This species has made up the bulk (in many years the majority) of the wading bird biomass breeding in the Everglades. This species is also well understood biologically, is not endangered, and is one of the species whose color and nesting habits allow reasonable accuracy in identifying population fluctuations. We asked the following two questions: 1) Are there non-breeding birds in the Everglades system throughout the breeding season? By modeling external plumage and coloration changes during the breeding season and examining gonadal changes we were able to identify whether birds were reproductively active (Chapters VIII and IX). 2) Do White Ibises skip years between breeding efforts? Many birds skip years between breeding efforts because they are physiologically or energetically limited (Hector et al.

1985). Thus, if ibis reproduction is very costly it may be a natural part of ibis life history for the birds to skip years between nesting attempts. Alternatively, if the birds were adversely affected by a toxin (such as mercury) then they may be unable to reproduce. To answer this question we captured birds and examined the potential physiological constraints of ibis reproduction (i.e. body condition changes and gonad growth patterns) (Chapter VIII), observed their reproductive behavior between years with radio telemetry (Chapter IX), and recorded mercury exposure (Chapter X).

We also addressed the idea that ibises regularly do not breed by studying limitations on reproduction in what was the largest captive flock of Scarlet Ibises in the world (*Eudocimus ruber,* of which the North American White Ibis is considered by some to be a race) at Disney World's Discovery Island near Orlando Florida. Our approach with the captive birds was to manipulate factors that may affect reproduction. We experimentally examined the impact of food and body reserves on the willingness of individuals to breed.

The ensuing chapters present the results of our work, separated into cohesive units as chapters. Understanding each of these parts of our work requires some background on the history of wading bird populations, and the probable causes of breeding population decline.

History of wading bird populations in the Everglades.

The Everglades of southern Florida has historically supported very large populations of wading birds (herons, egrets, ibises, storks and spoonbills, order Ciconiiformes), numbering in the hundreds of thousands of pairs in some years (Robertson and Kushlan 1974, Ogden 1994). While there was typically large variability

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These dramatic changes in breeding dynamics and numbers have been accompanied by an intensive period of human-made hydrological changes (Gunderson and Loftus 1993, Light and Dineen 1994). In the space of approximately 30 years, the South Florida Project resulted in large portions of the freshwater marsh being diked and impounded, the majority of the northern freshwater marshes drained and put into agricultural production, and huge acreages of surface water coming directly under the control of human management. This has resulted in an outright loss of 30% of the marsh surface to other land uses (Browder 1978), a drastic cutoff of freshwater flows to the formerly productive estuarine zone of Everglades National Park (Walters et al. 1992), and the loss of the majority of short-hydroperiod marshes in the system (Fleming et al. 1994, Ogden 1994).

The record of wading bird population monitoring is both lengthy and rich (Frederick and Ogden in press), and has been summarized in detail by Kushlan et al.

(1984), and Ogden (1978, 1994). These summaries show that many heron and egret species went through a severe decline during the plume-hunting period from 1875 to 1910, after which most populations (Reddish Egret, *Egretta rufescens* excepted) rebounded quite rapidly by the 1930's. We can conclude from this history that once constraints on reproduction are removed, many wading bird species have the potential to increase rapidly and, in a healthy Everglades environment, could presumably be sustained in large numbers.

During the 1930's and 1940's, the emerging picture was one of high variability in annual nesting numbers. However, we also believe that a population of at least 100,000 pairs (all species combined) bred with some regularity (Kushlan et al. 1984, Ogden 1978, 1994). The largest colonies were located almost entirely in the mangrove zone along the coast of what is now Everglades National Park. In addition, substantial summer breeding by several species, and large summer roosting groups of White Ibises were a regular feature of this period. Another characteristic was that Wood Storks were recorded initiating breeding during the late fall (November - December). Careful analysis of breeding and hydrological records during this period suggests that larger aggregations of birds bred in wetter years, and that the size and success of breeding had only a weak association with the rapidity of drying of the interior marsh surface (Ogden 1994). In fact, the impression Ogden (1994) gives is that breeding occurred not so much under a different range of hydrological and weather conditions than at present, as under a much wider range of conditions.

The period of the 1950's and early 1960's was one of very sporadic and almost always incomplete surveys. At some point during this period Wood Storks began to decline (there is some disagreement as to the timing, see Ogden 1994). White Ibises began breeding for the first time in recorded history in South Carolina and Georgia in more than token numbers, and in central Florida in several very large colonies (Frederick et al. 1995). By the late 1970's, colonies of White Ibises in the Carolinas had grown to over 50,000 birds annually, central Florida ibis colonies were in the hundreds of thousands of birds, and Wood Storks had increased breeding numbers and numbers of colonies in north Florida, and expanded their breeding range into Georgia and South Carolina. These movements are most parsimoniously interpreted as an exodus of southern Florida breeding populations, (or at some point, the progeny of the southern Florida aggregations), in part in response to environmental degradation, rather than solely because the northern sites offered superior nesting opportunities (Walters et al. 1992).

By the late 1970's within the Everglades, the timing of Wood Stork breeding had also clearly shifted from starting in November and December to starting in February and March, and colonies of Wood Storks in Everglades National Park began to have very poor breeding success as a result (Ogden 1994). A dramatic change in nesting location within the Everglades was also obvious - the large mixed-species nesting colonies on the coast of Everglades National Park had shifted to the interior freshwater Everglades, and the size of colonies had generally decreased. Finally, the period of the late 1960's and 1970's showed a strong and previously unrecorded relationship between nesting numbers of Wood Storks and White Ibises, and the speed of drying of the marsh surface (Kushlan et al. 1975, Frederick and Collopy 1989a). Studies during the 1980's also revealed frequent interruptions in nesting during wet springs, and during any reversals in the drying trend (Frederick and Collopy 1989a, Ogden 1994).

Why have wading birds declined?

The reasons for these dramatic changes in wading bird distributions, timing of reproduction, and breeding numbers are related to changes in amount of available foraging habitat, agricultural displacement, and marsh surface hydrology and water management, all of which have affected both the robustness of prey populations (Loftus and Eklund 1994), and the ability of the birds to capture prey. The rough coincidence of massive structural changes to surface water flows in the Everglades during the 1960's, with declines in nesting, changes in timing of nesting, changes in nesting responses to hydrological variables, and movements of birds into other nesting regions certainly suggests a causal relationship with hydrology.

During the late 1970's and throughout the 1980's, considerable research was devoted to understanding the causes of poor wading bird reproduction, both within the Everglades and elsewhere. Much of this work has been summarized in various works reported in Davis and Ogden (1994), and the salient points are listed here:

1. <u>Wading bird reproduction is strongly dependent upon the availability of food.</u> Powell (1983) found that clutch size and productivity of Florida Bay Great White Herons (*Ardea herodias*) could be increased by food supplementation, and Frohring (unpublished Everglades National Park Research Center report) found that prey densities in close proximity to colonies was the environmental factor most strongly correlated with growth rate and productivity of young. Hafner et al. (1993) found that increases in productivity of Little Egrets (*Egretta garzetta*) were associated with increased food delivery rates. Hoyer and Canfield (1990) found that the number of wading bird species on Florida lakes was positively influenced by eutrophic status and attendant high secondary productivity.

Gawlik (in press) found experimentally that most species of wading birds are strongly attracted to conditions in which prey are highly available, and leave in direct proportion to the degree to which prey animals are depleted. In the central Everglades, the timing and nature of nesting abandonments in the Everglades are consistent with interruptions in the availability of food through increases in water depth, dispersal of prey, increased rainfall, and low temperatures (Frederick and Spalding 1994, Frederick and Loftus 1993). Conversely, there is direct and/or indirect evidence that predation, human disturbance, and lack of appropriate colony substrate have a minor overall effect on breeding in the Everglades (Frederick and Collopy 1989b, Frederick and Collopy 1989c, Frederick and Spalding 1994). This evidence taken together suggests strongly that numbers of nesting birds and nesting success are driven in large part by food supply, and that problems with nesting can often be traced to inadequacies or interruptions in food availability.

2. Wading bird foraging and nesting was often centered in coastal regions during the past. Of all the ecosystem habitat types, wading bird prey were probably most consistently available in the mangrove/freshwater interface during the pre-drainage period. These habitats offered pre-breeding foraging habitat and feeding alternatives during periods of high freshwater stages, that the deeper parts of interior marshes could not. This notion is supported by the few notes on the historical pattern of feeding in the ecosystem (Kushlan et al. 1984, Ogden 1994, W. B. Robertson pers. comm.), recorded densities of fishes (Loftus et al. 1986), modeling of predrainage interior marsh water depths (Walters et al. 1992) and by investigation of the foraging behavior of birds breeding on the coast (Bancroft et al. 1994).

3. The productivity of the estuarine zone has been severely compromised by a lack of freshwater flows (see review by McIvor et al. 1994). Modeling of surface water dynamics by two different groups of investigators has shown that historic flows to the estuary were vastly larger than during the postdrainage period (Walters et al. 1992, Fennema et al. 1994). Declines in sport fisheries, commercial shrimp fisheries, and a number of biological measures of Florida Bay salinity, provide further evidence that the productivity of the estuarine zone has been severely compromised by the lack of fresh water (Browder 1985, Tilmant 1989, Rutherford et al. 1989, Bowman et al. 1989, Smith et al. 1991). Lastly, Lorenz (2001) has shown direct increases in fish productivity and standing stocks in areas and during years of higher freshwater outflows in the mangrove swamps fringing the northern border of Florida Bay.

4. Within some bounds, productivity of small "bird forage" fishes in the freshwater marshes is related to hydroperiod (Loftus et al. 1986, Loftus et al. 1992, Loftus and Eklund 1994). Shortened hydroperiods over much of the southern Everglades may well have reduced the productivity of the prey that wading birds feed upon, particularly in the interface between freshwater marsh and mangroves, where the large historical colonies were located. The presence of dikes is also hypothesized to impair the ability of prey fishes to travel in the freshwater parts of the Everglades, and so may obstruct recolonization between compartments, particularly from areas of long hydroperiod to those of short hydroperiod.

5. Short hydroperiod freshwater marshes were also critical pre-breeding and early - breeding season foraging habitat for wading birds (Kushlan 1974, Kushlan et al. 1984, Ogden 1994, Fleming et al. 1994). These higher-elevation marshes probably once

offered wading birds feeding opportunities during high rainfall years, as well as during reversals in drying trend. Modeling studies have suggested that these short hydroperiod marshes have decreased in abundance far more than have other marsh types. The lack of early and pre-breeding foraging habitat is consistent both with the dramatic shift towards later breeding of Wood Storks, the early departure of the majority of the wintering population in most years, and the extreme sensitivity of the current breeding efforts to minor changes in drying trend.

6. A combination of human-made ecological changes has led to instability in the production and availability of wading bird food. This hypothesis suggests that the cumulative effect of many human-induced changes has been responsible for a lack of productivity in the Everglades marsh, and eventually, for the decline of wading birds. The impoundment of much of the marsh into deeper pools, the tremendous reduction in area and hydrological isolation of short hydroperiod marshes, the shortened hydroperiod of lower Shark Slough, and the degradation of the coastal estuary, seem to have sharply reduced the conditions under which robust and continuous wading bird feeding (apparently necessary for reproduction), can occur. Such feeding opportunities now seem limited to the impounded freshwater sections of the Everglades, during years of rapid surface water drying in which there are few increases in water level, and infrequent or weak periods of cold (Bancroft et al. 1994, Frederick and Collopy 1989a, Frederick and Loftus 1993, Ogden 1994).

These conclusions have provided a new focus for restoration policy (Walters et al. 1992, Davis and Ogden 1994, Anonymous 1993), which now includes recommendations for increases in short hydroperiod habitat, increased flows to the estuary, greater hydrological connection among compartments, and restoration of long hydroperiods to northern Shark Slough as explicit components.

Low proportions of breeding birds?

In addition to low reproductive success, low numbers of nest starts and altered timing of nesting, monitoring studies between 1986 - 1997 have provided some evidence that a low proportion of birds present on the marsh attended breeding colonies. This information arose from a comparison of annual surveys of breeding wading birds, with annual estimates of all wading birds on the marsh surface through the Systematic Reconnaissance Flight (SRF) surveys. These latter surveys are designed to estimate total populations of wading birds on the marsh, and to document the geographic locations of those birds. The SRF surveys are performed monthly between January and June of each year, and have been performed variously by staff of Everglades National Park, the National Audubon Society, Big Cypress National Preserve, and the U.S. Army Corps of Engineers (Vicksburg Office).

Several adjustments must be made to derive a reasonable estimate of the proportion of adult birds breeding. First, it is likely that the Everglades hosts large numbers of migrant birds in some years (Bancroft et al. 1992). To ensure that migrants are not included in the counts, we have used estimates of the total population taken in May, when all breeding elsewhere in North America is well under way. To avoid including juvenile birds in the estimates, 10% of the birds are assumed to be juveniles. Empirical demographic modeling and SRF counts of ibises (in which age-based plumage characteristics are unambiguous) suggest that the actual figure is probably much closer to less than 1%. And at any point in time, it is assumed that one member of each breeding pair is off the nest, and therefore counted in the SRF surveys. Using only species for which identification is easy in both SRF and breeding surveys, we estimated that over the period 1986 – 1999, an average of 31.2%, 28.7%, and 28.6% of adult Wood Storks, White Ibises, and Great Egrets bred, respectively, in the WCAs. This suggests that somewhere between 69% and 72% of adult birds were not engaging in nesting activity. Several hypotheses exist to explain this apparent low breeding proportion. The first and most obvious is that there are errors in the estimation of numbers of birds. This is a real possibility, since there are errors inherent in estimates of both breeding birds and foraging birds (SRF's). For example, the existing literature suggests that nearly all estimates of groups of animals are biased low, and particularly so with large numbers of animals and in situations where some animals are cryptically colored or are hidden by vegetation (Kadlec and Drury 1969, Erwin 1982, Rodgers et al. 1995). Although we have selected only white-colored species that tend to nest in the open, there is still the potential for estimates of breeding birds to be biased low. This would tend to bias the estimation of proportion of birds breeding towards figures that are lower than actual. There is also the possibility that estimates of breeding birds are biased low because estimates are taken at times of "peak" activity. This method would ignore animals that completed or failed nesting prior to the peak date, as well as those that initiated nesting after the peak date. The size of this potential error is unknown. Thus, although many of the biases are known to be in one direction (biasing the proportion breeding too high) there are several potentially important sources of error in counting breeding birds that might lead to a low-biased proportion breeding. These sources need to be measured as closely as possible, and their effects modeled.

Assuming that the measurements are reasonably accurate, one hypothesis to explain the low proportion breeding suggests that the birds are not coming into reproductive condition because food is limiting their reproductive energy budgets. While this is certainly a frequently-cited cause of poor breeding success or of no breeding, there are several reasons why this explanation is at least partially inadequate.

First, wading birds are notoriously weak in their breeding philopatry, and movement in response to poor breeding conditions would be expected of animals in this order. Many of the approximately 70% of adults estimated not breeding in an average year should be expected to move to better areas to breed – apparently they do not. This is not predicted by the food-limitation hypothesis.

A second explanation is that nonbreeding is a typical part of the life histories of these birds. While it might not be surprising for wading birds to occasionally sit out a year, the extent of nonbreeding in this case seems extreme. If the typical adult sits out over two thirds of the available breeding years, this is likely to have an effect on reproduction. The effect of nonbreeding has been modeled using very generous fecundity, survival and life history parameters. Even small deviations from 100% of adults breeding results in negative population growth for models specific to White Ibises, Wood Storks, and Great Egrets. Thus, it seems unlikely that these large numbers of adults are foregoing reproduction as part of their natural life history.

A final possibility is that wading birds are kept from breeding by some form of environmental contamination. Although no comprehensive surveys of environmental contaminants have been accomplished in the Everglades, it is known that mercury occurs at extremely high levels throughout the Everglades aquatic food web (Frederick 2000, Frederick et al. 1999, Spalding et al. 1994, Facemeier et al. 1995, Sunlof et al. 1994, Frederick et al. 2001). Sublethal contamination of mercury is known to predispose wading birds to disease (Spalding et al. 1994). In addition, experimental work on young Great Egrets showed that ambient levels in the Everglades result in reduced red blood cell counts, reduced appetite, increased lethargy, altered maintenance behavior, and reduced hunting activity (Frederick et al. 1997, Spalding et al. 2000 1, 2, Bouton et al. 1999, Williams 1996). It seems plausible that the reduced appetite and increased lethargy that result from sublethal mercury toxicosis could contribute to decreased body condition in prebreeding adult birds. Mercury could also act as a direct suppressor or disruptor of normal hormonal systems. Finally, there could be some indirect effect of mercury on the food web – mercury contamination could be suppressing the reproductive potential of prey animal populations, resulting in food stress on wading bird populations and a decrease in breeding.

These hypotheses were completely untested upon the initiation of this project, and one of the main goals was therefore to put these hypotheses at risk in as many ways as possible. The objectives of this project were identified as the following:

1. Continue to monitor the timing, success, and location of breeding by wading birds annually in the Everglades using established techniques, and monitor the proportion of the adult population that breeds annually.
2. Estimate error in breeding bird counting techniques.
3. Quantify breeding asynchrony, and model the effect of asynchrony and breeding success on the ability to estimate numbers of breeding birds.

4. Collect information on reproductive physiology and energetics on a captive breeding flock of Scarlet Ibises, in order to provide baseline information for comparison with Everglades birds, and determine threshold energetic requirements necessary to bring captive birds into reproductive condition.
5. Develop methodologies for capturing adult wading birds on the marsh.
6. Develop techniques for identifying breeding adult wading birds.
7. Describe the reproductive physiology of free-living White Ibises and identify potential stages where birds may be vulnerable to changes in food availability or other environmental changes.
8. Monitor contaminant loads and in particular examine effects of mercury on wading bird breeding physiology.

CHAPTER II. HYDROLOGICAL AND METEOROLOGICAL CONDITIONS DURING 1998 – 2001.

The Everglades is an exceptionally flat, shallow body of water, oscillating between drought and flood according to the current mix of rainfall, evapotranspiration and upstream flow conditions. The Everglades is also at the latitudinal border between temperate and tropical biomes, in a region where the inter-freeze interval can strongly determine introgression by exotic animals, plant community dynamics, and interactions among predators and prey (wading birds and fish, Snail Kites *Rostrhamus sociabilis* and Apple Snails *Pomacea paludosus*). Virtually all biotic interactions in the ecosystem are therefore strongly affected by antecedent and current patterns of rainfall, wind, and temperature. The purpose of this chapter is to therefore to illustrate the hydrological and meteorological context for the bird dynamics recorded in later chapters.

Rainfall and weather:

The period of study was preceded (1994 – 1997) by an extended period of higher than normal rainfall, and high water stages. During the study period of January 1998 through July 2001, the rainfall patterns could be characterized neither as extreme drought nor as particularly wet. Figure 2.1 shows monthly rainfall totals during the period as deviations from long-term monthly averages. The degree to which rainfall was extreme is illustrated by one standard deviation in excess or deficit of the long-term mean. The first half of the study period (to mid-summer 1999) showed somewhat higher than normal rainfall, though generally within 95% of period-of-record observations. The only exception to this rule was June of 1998, which had nearly seven inches less rainfall

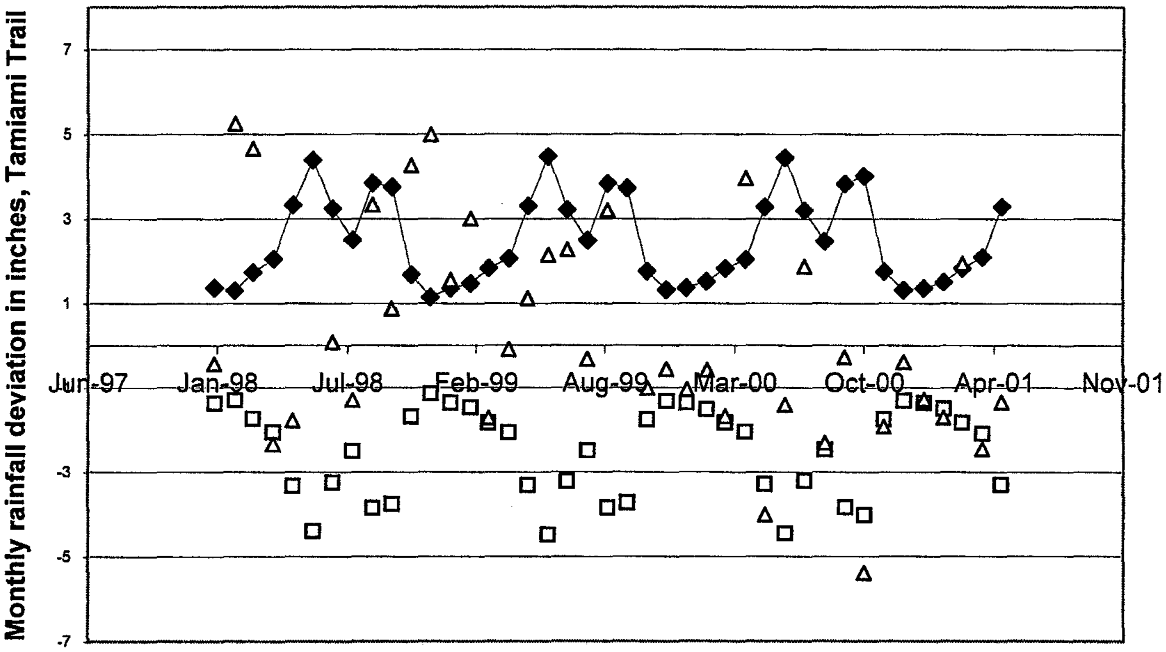

Figure 2.1. Monthly rainfall deviations (line with diamonds) at Tamiami Trail Ranger Station in Everglades National Park, January 1998 – June 2001. Mean monthly rainfall deviation for the period of record is represented as the straight horizontal line at 0; deviations of one standard deviation in excess or deficit of the mean are shown as squares and triangles, respectively.

during June than the long term average. The dry seasons of 2000 and 2001 were characterized by having below-average rainfall, though very few months were less than one standard deviation of monthly means.

Mean monthly temperatures during the study period were generally higher than normal (Figure 2.2), with no severe freezes during the period. The only exception was during February of 2001, when a single very cold week occurred.

The study period was also not a particularly windy one, at least during the winter-spring wading bird breeding season (Figure 2.3). Though January and February of 1998 were considerably windier than usual, the breeding seasons of 1999, 2000 and 2001 were either well below normal (particularly 2000), or close to normal (2001).

Hydrology:

The period of study was preceded by a lengthy period of considerably higher stages than normal (1994 – 1997), during which wading bird nesting was somewhat depressed (depending on species). In Loxahatchee NWR, stages remained consistently higher than normal being between the average maximium for any month, and one standard deviation higher than the average monthly maximum (Figure 2.4). This trend is a result of intentional management for higher stages within Loxahatchee National Wildlife Refuge.

In WCA 3, the same trend occurred, with higher than normal stages throughout the study period (Figure 2.5). This is an important point, since there have been some attempts to portray the dry seasons of 2000 and 2001 as "drought" years. Apparently, stages were high to normal in nearly every month of the study period, including the height of the dry season. Stage in WCA 3 began the winter of 2000 at very high stages

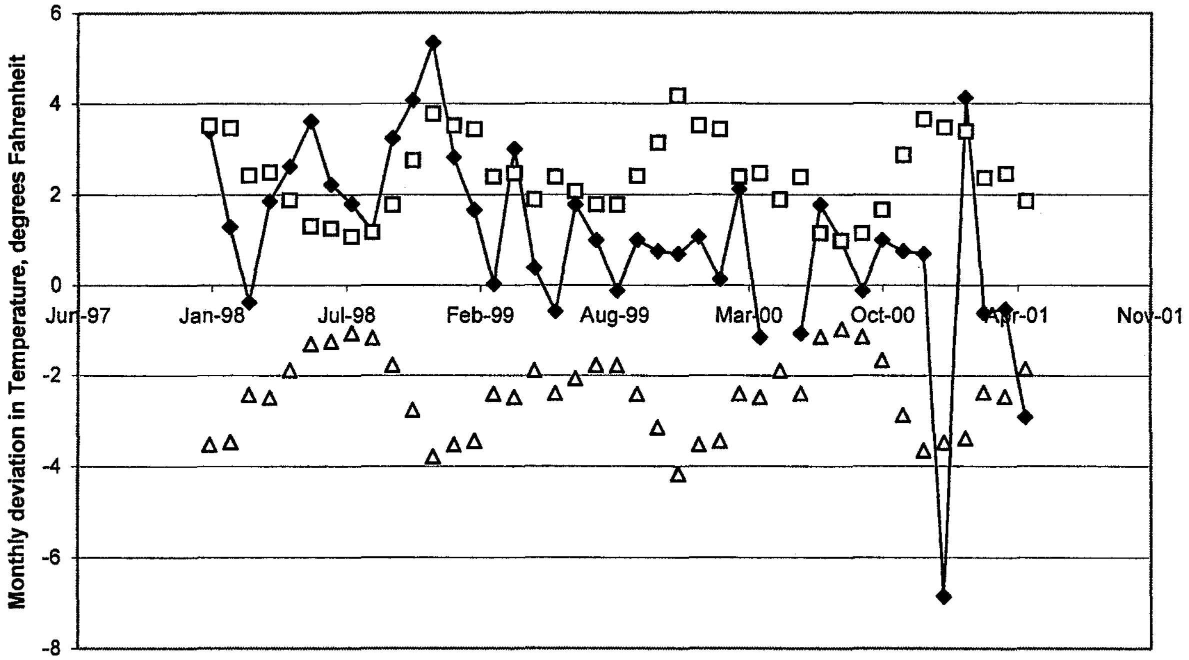

Figure 2.2. Monthly deviations in averaged temperatures (line with triangles) at Tamiami Trail Ranger Station, Everglades National Park during January 1998 – May 2001. Mean monthly temperatures for the period of record are represented as the straight horizontal line at 0; deviations of one standard deviation in excess or deficit of the mean are shown as squares and triangles, respectively.

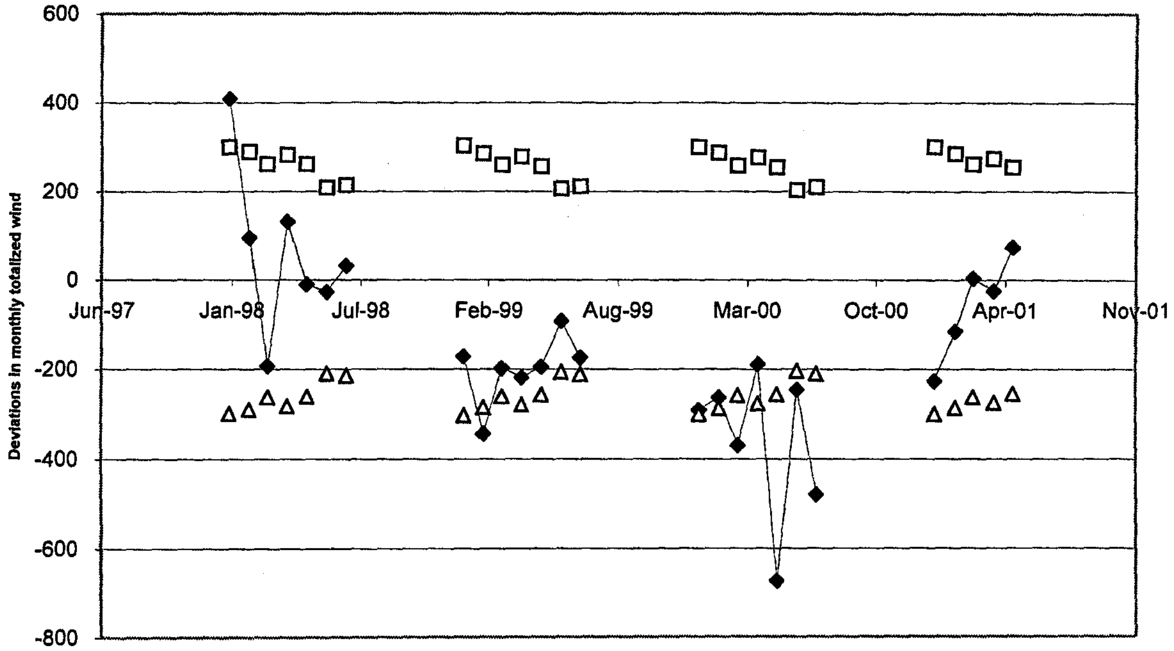

Figure 2.3. Monthly deviations in totalized wind during spring seasons (lines with diamonds) at Tamiami Trail Ranger Station in Everglades National Park, January 1998 – June 2001. Mean monthly totalized wind for the period of record is represented as the straight horizontal line at 0; deviations of one standard deviation in excess or deficit of the mean are shown as squares and triangles, respectively.

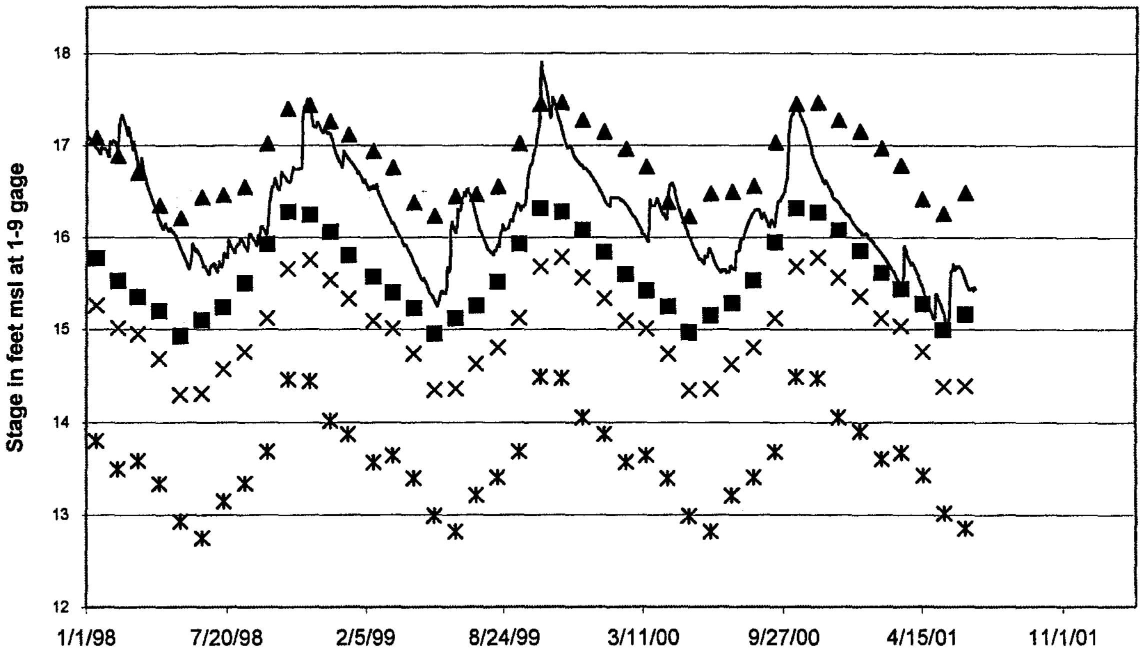

Figure 2.4. Stage at gaging station 1-9 in WCA1 (Loxahatchee National Wildlife Refuge) January 1998 through July 2001. Line represents daily stage, squares are mean monthly maxima for the period of record, triangles are mean monthly maxima plus one standard deviation, X's are mean monthly minima for the period of record, and stars are mean monthly minima minus one standard deviation.

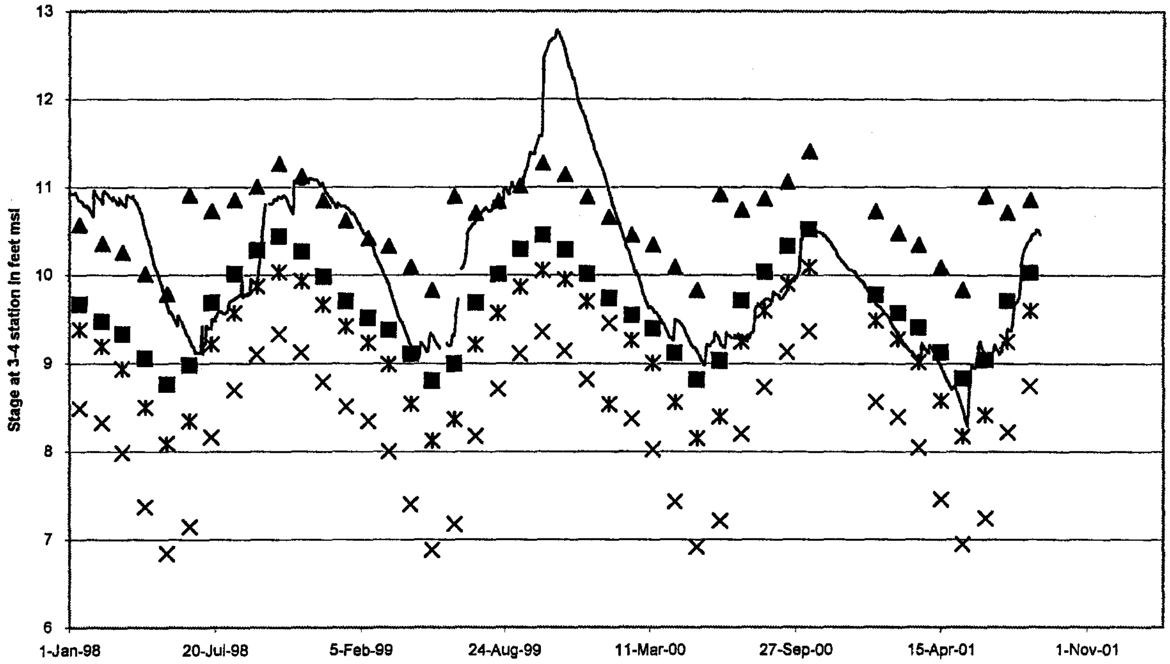

Figure 2.5. Stage at gaging station 3-4 in northern WCA 3, January 1998 through July 2001. Line represents daily stage, squares are mean monthly maxima for the period of record, triangles are mean monthly maxima plus one standard deviation, X's are mean monthly minima for the period of record, and stars are mean monthly minima minus one standard deviation.

(well in excess of the long term monthly maximums) as a result of very high rainfall from tropical cyclones in fall 1999, and the drawdown of Lake Okeechobee in late fall of that year. The same peak in stage can be seen to a lesser degree in WCA 2 and Loxahatchee NWR.

In WCA 2A, the pattern was much less consistent than in WCAs 1 and 3, with both high peaks in stages (March 1999, November 1999), and some periods of much lower than normal stages (April - May 1999, April 2001, see Figure 2.6). This WCA is used as a water transfer unit to a much larger extent than the other two WCAs, and as such its stage behavior is likely to be more transient and "flashier".

In the past, the behavior and reproductive response of birds has been thought to be predicted in part by the rate at which surface water recedes during the dry season (Kushlan et al. 1975, Frederick and Collopy 1989), as a result of both drainage and evapotranspiration. The mechanism of influence on the birds is through the concentration of prey animals on the marsh surface by the action of decreasing depths. This has been expressed as an early season recession rate (difference between monthly highs of November and January) and a late recession rate (difference between monthly highs of January and March). Note that a fast recession rate would be a high positive number, signifying rapid recession (2 mm/d and above), and a slow rate could be represented by negative numbers (stage actually increased between the two months).

Drying rates in 1998 were quite slow, with negative late rates in WCAs 1 and 2, and no consistent trend for early rates (Table 2.1). This was due to a large pulse of water that occurred in March of 1998, effectively reversing water level trends. There were rapid recession rates during the period late March through May, however. In 1999, early

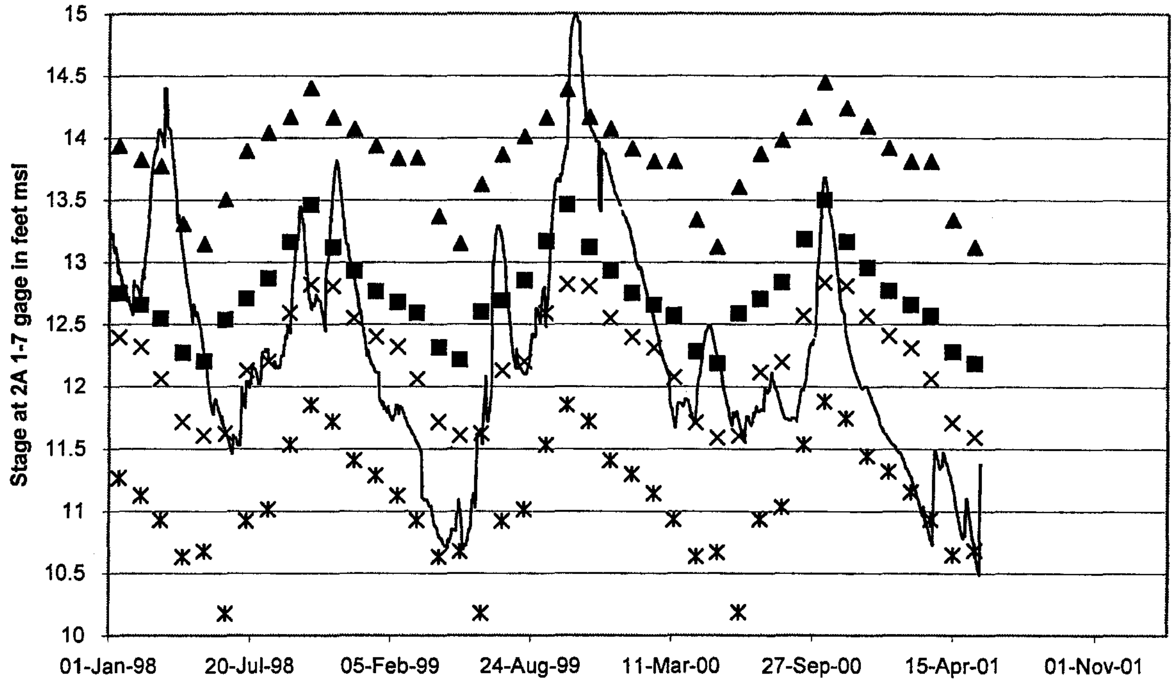

Figure 2.6. Stage at gaging station 2A 1-7 in WCA 2A, January 1998 through July 2001. Line represents daily stage, squares are mean monthly maxima for the period of record, triangles are mean monthly maxima plus one standard deviation, X's are mean monthly minima for the period of record, and stars are mean monthly minima minus one standard deviation.

Table 2.1. Water level recession rates (mm/d) in the Water Conservation Areas, with comparisons of the year in question with historical records at each station. Note that negative values indicate rising water, positive values indicate falling water. Percent exceedance refers to the percent of years in the record in which the drying rate is less than that of the current year.

Year	Station	Early Dry	Late Dry	% Exceedance Early Drying Rate*	% Exceedance Late Drying Rate*	% Exceedance Both Early and Late Drying Rate*
2001	3-4	3.098	2.43	55.6	61.1	33.3
2001	1-9	4.347	1.16	91.4	28.6	22.9
2001	2A 1-7	6.246	2.32	92.3	94.9	89.7
2000	3-4	7.935	7.70	100	100	100
2000	1-9	4.54	na	94.1	na	na
2000	2A 1-7	7.595	5.57	94.5	94.8	89.7
1999	3-4	2.13	3.83	41.7	91.7	38.9
1999	1-9	2.19	4.24	18	29	14
1999	2A 1-7	7.77	7.46	97.2	94.5	97.1
1998	3-4	n.a.	n.a.	n.a.	n.a.	n.a.
1998	1-9	1.48	-0.52	34.3	2.85	0
1998	2A 1-7	-4	-0.04	2.9	20	0
1997	3-4	2.63	1.419	57	42	36
1997	1-9	2.19	0.581	51.5	15.2	3.03
1997	2A 1-7	4.12	2.77	94.1	73.5	70.5
1996	3-4	6.99	5.68	100	100	100
1996	1-9	0.14	0.383	25.0	3.5	0.0
1996	2A 1-7	11.50	0.646	96.9	34.4	34.4
1995	3-4	-0.90	5.95	0.0	100.0	0.0
1995	1-9	0.97	0.21	32.1	10.7	3.6
1995	2A 1-7	0.55	3.50	28.1	87.5	29.0
1994	3-4	2.56	-1.08	58.6	6.9	3.6
1994	1-9	1.49	0.42	21.8	9.3	3.1
1994	2A 1-7	3.32	-4.67	90.0	3.3	3.3
1993	3-4	0.22	-0.40	10.0	10.0	3.3
1993	1-9	-0.33	3.91	14.8	7.8	0.0
1993	2A 1-7	-1.45	0.22	12.9	29.0	3.2
1992	3-4	2.29	2.63	24	38	14
1992	1-9	2.01	1.47	46	54	21
1992	2A 1-7	3.16	2.09	82.1	53.5	44.4

recession rates exceeded the 2.0 mm/d threshold thought to be associated with strong nesting by ibises and storks in all three WCAs (Kushlan et al. 1975, Frederick and Collopy 1989), and the 7.77 mm/d shown by WCA 2A exceeded nearly 95% of all other years on record. The late recession rate in WCA 2A also exceeded 95% of observations, and in WCA 3, exceeded 92% of observations. However, Loxahatchee NWR showed much slower rates, with exceedance of only 18% and 29% of observations for early and late rates, respectively. The reason for this discordant pattern was not obvious.

Drying rates in 2000 were uniformly rapid, with the fastest early and late rates on record for WCA 3, exceedance of 94% of all records for early rates in Loxahatchee, and exceedance of 95% of early and late records in WCA 2. These uniformly rapid recession rates were in large part the result of beginning the season with exceptionally high stages (December 1999 and January 2000). Under these conditions, high stages can be reduced quickly through the action of water movement or drainage alone.

During 2001, recession rates in WCA 2 were again very high, with early rates exceeding 92% and 95% of observations for early and late (respectively). InLoxahatchee, the early recession rate was rapid (greater than 91% of all years on record) but the late rate was exceeded by over 71% of years on record. In WCA 3, both early and late drying rates exceeded 2.0 mm/d, but were not particularly exceptional in the context of hydrological history. However, in all three WCAs, the recession during 2001 was largely uninterrupted by heavy rainfall during the January through March period. The exception was a large rainfall event during late March 2001, which caused significant reversal of water trend in Loxahatchee NWR and 2, and to a much lesser extent, WCA 3.

CHAPTER III. MONITORING OF BREEDING POPULATIONS OF WADING BIRDS IN THE EVERGLADES, 1998 – 2001.

Introduction

As with many birds chosen as bioindicators, long-legged wading birds are generally large, highly mobile, top-level consumers in the aquatic food web, and have high energetic needs. In addition, many species of wading birds are also strongly social, and often breed and feed in highly aggregated groups. This, combined with the white or light-colored plumage of many species, makes the finding, counting, and monitoring of these animals in a large ecosystem relatively efficient and accurate. Indeed, it is difficult to imagine any other vertebrate that can be monitored with any accuracy or without extreme cost within the approximately 4,000 km^2 landscape of the Everglades (Ogden 1993). Wading birds are also known to forage and breed almost exclusively in wetlands, and when breeding, to forage within a fairly well-defined range surrounding the colony (Bancroft et al. 1994, Smith 1995). This implies that some aspects of reproduction might be profitably used to reflect local environmental differences within the ecosystem. Breeding site fidelity is highly variable among species, ranging from some storks that may return annually to the same colony, to some ibises which may be extremely nomadic (Frederick and Ogden 1997). Nonetheless, most species seem capable of moving their breeding sites in response to consistently unfavorable conditions.

There is also a large but somewhat diffuse body of evidence that links various aspects of wading bird reproduction with the availability of food. In most large wetland ecosystems in the world, the timing of breeding of wading birds usually coincides with the greatest availability of food. In South Carolina, Bildstein et al. (1990) demonstrated that annual numbers of nesting White Ibises were in direct proportion to the availability of crayfishes in freshwater marshes. In the Everglades, Kushlan (1976d) showed that White Ibises shifted their timing of nesting to coincide with the time at which available food energy was at a maximum. Similarly, in the Everglades, the Llanos of Venezuela, the Pantanal of Brazil, and the Usamacinta Delta and Yucatan of Mexico, Wood Storks breed only during the dry season, when fishes are trapped in high densities in pools and depressions as a result of rapidly receding waters (Kushlan et al. 1975, Leber 1980, Ogden et al. 1988, Ramo and Busto 1992, Gonzalez 1999, Bouton 1999).

More mechanistic studies have also demonstrated links between the availability of food and reproductive success. For example, Powell (1983) found that food-supplemented Great White Herons (*Ardea herodias*) in Florida Bay had significantly higher clutch and brood size than did unsupplemented birds. Hafner et al. (1993) found that increases in productivity of Little Egrets (*Egretta garzetta*) were associated with increased food availability. In the Everglades, interruptions in food supply have been closely correlated with mass nesting abandonments, whether the interruptions were brought about as a result of drought (Bancroft et al. 1990), cold weather (Frederick and Loftus 1993) or flooding (Kushlan et al. 1975, Frederick and Collopy 1989a, Smith and Collopy 1995, Frederick and Ogden 1997). Growth rates of nestling herons are directly related to food intake rates (Salatas 2000), and growth rates in Snowy Egrets have been correlated with survival rates of fledglings during the first month of life (Erwin et al. 1996).

Within the Everglades, the relative effect of other potential causes of variation in reproductive success have been investigated in some detail. Losses of nest contents to predation have been found to be surprisingly rare in the central Everglades in most years (Frederick and Collopy 1989b), and effects of both researcher disturbance (Frederick and Collopy 1989c) and availability of nesting habitat (Frederick and Spalding 1994) have been found to be negligible. In a large-scale survey of the importance of disease in Everglades wading birds, only one parasitic disease was found to have any effect on reproduction (Spalding and Forrester 1991). Although this disease (eustrongylidosis, caused by the parasitic nematode in the genus *Eustrongylides*) can cause very high mortality of nestlings in some colonies, the disease seems associated only with the relatively uncommon sites of high nutrient deposition within the Everglades (Spalding et al. 1993).

Thus food availability seems to be strongly linked to nesting success in wading birds in general, and variation in food availability explains much of the variation in nesting success specifically within the Everglades. Studies linking choice of nesting site and timing of nesting with availability of food are less well established for the Everglades, but the evidence (above) suggests that location and timing of nesting may also be used as indicators of prey availability and abundance in wetland ecosystems. This information collectively suggests that the cueing and success of nesting are driven largely by the availability of prey, and that variation in reproductive effort and productivity can, within some limits, be interpreted as an indicator of those ecological and physical features that affect the abundance and availability of prey.

The conditions affecting availability of wetland prey to wading birds are probably numerous, but density of prey animals and depth of water have often been found to be primary components. Wading birds take many types of aquatic prey, using a wide variety of foraging tactics and behaviors (Kushlan 1976b, 1978). Nearly all foraging is in shallowly flooded wetlands, and foraging success is highly dependent upon appropriate conditions. Variation in foraging success may be dependent on a variety of characteristics of the foraging site, including prey density (Renfrow 1993, Surdick 1998, Gawlik in press), water depth (Powell 1987, Renfrow 1993, Gawlik in press), water temperature (Frederick and Loftus 1993), dissolved oxygen (Hafner et al. 1993) and vegetative density (Surdick 1998). Of these variables, dissolved oxygen probably plays a minor role, since the wetlands of the Everglades marshes are shallow and poorly stratified. Similarly, water temperature is only an important factor in the Everglades during relatively brief periods of cold. Within the Everglades Surdick (1998) found that water depth, prey density, and vegetative density were the factors most commonly affecting foraging success and choice of foraging sites of four species of wading birds, and that these factors often interacted.

Thus there seems to be compelling evidence that various aspects of wading bird reproduction and foraging ecology can be mechanistically linked with various aspects of the ecology of wetlands, at a variety of scales. While some of these linkages are simple enough to be revealed by short-term studies, a full understanding of the interplay of many variables (eg, hydrology, weather, vegetation, prey and fire cycles) is only possible through the use of long term records. Monitoring of wading birds in the Everglades has revealed partial or full understanding of the following patterns:

Decreasing carrying capacity of the ecosystem.

Ogden (1994) summarized a comparison of recent (1974 – 1989) wading bird nesting with that of the 1930's and 1940's. Between these two periods, the numbers of nesting birds declined by over 90% (Figure 3.1). The comparison between the two periods was biased towards finding more birds in the later period, since the more recent survey methodology was systematic and more efficient at finding birds than were the mostly ground-based estimates of the 1930's. The more recent surveys also covered vastly more area – the 1930s estimates were only of coastal colonies and did not penetrate the interior marshes. Thus the 90% reduction between the two periods seems conservative. During the period 1930 – 1946, Ogden (1994) suggested that 69,000 – 89,000 birds nested in many years, with peaks of 200,000. Current nesting numbers rarely exceed 30,000 birds, with peaks of no more than 60,000 (Frederick and Collopy 1989a, Frederick 1995).

The importance of hydrological variability in organizing pulses of productivity.

One of the most profound puzzles of the Everglades has been that a vast, nutrient-poor wetland system should be capable of supporting a large, concentrated biomass of wildlife. The wading bird monitoring programs have provided evidence of several ecological relationships that explain how the large numbers of wading birds could be supported by a system with such low energy density. The most obvious way is through annual fluctuations in water level, which serve to concentrate aquatic prey animals to the point that they are energetically profitable to consume. This process may create a

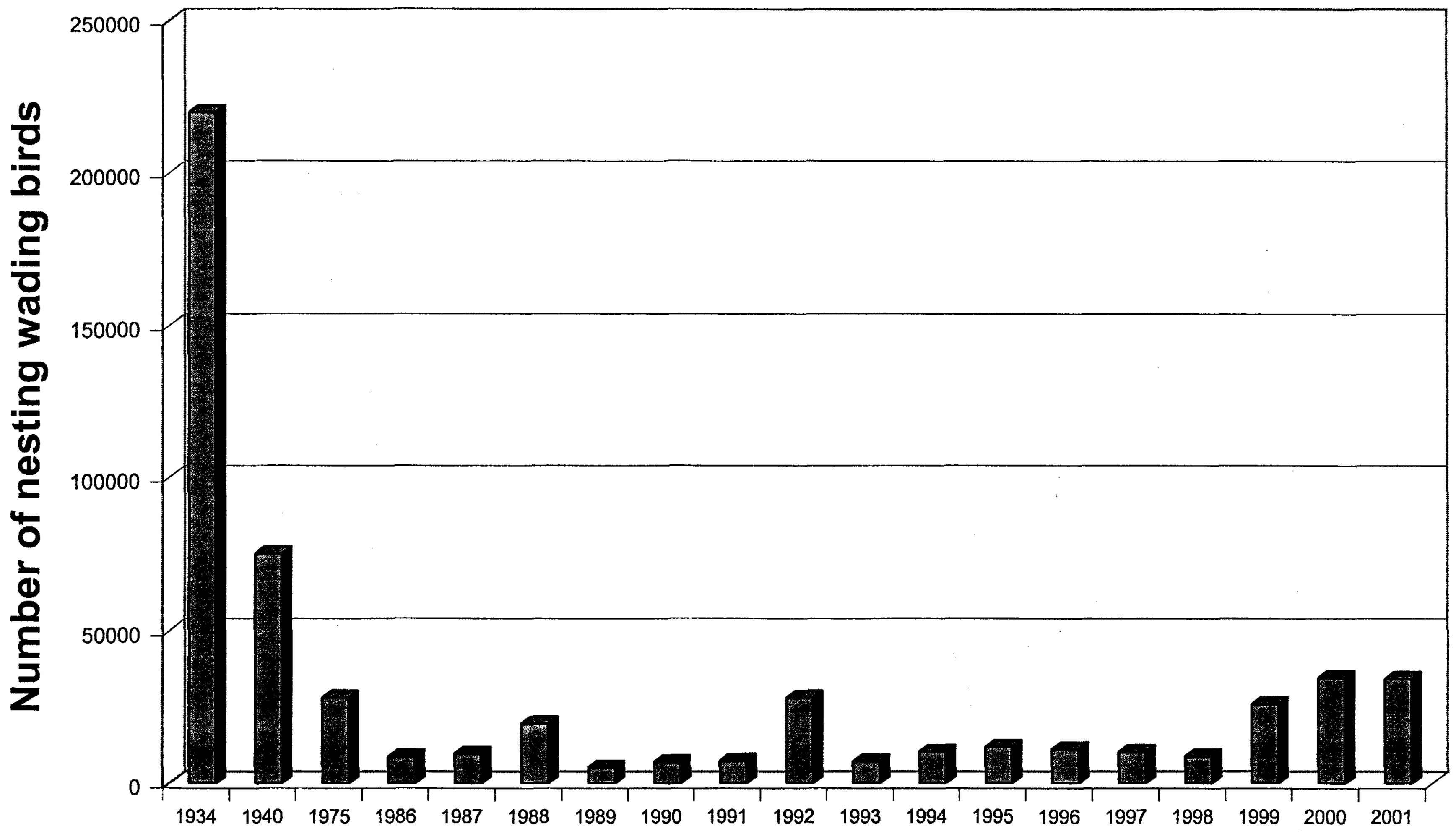

Figure 3.1. History of wading birds nesting in the Everglades ecosystem. Note that the x-axis is not a continuous scale.

"drying front", which progresses across the landscape as surface water dries during the spring nesting season, allowing wading birds (and other vertebrates) to exploit a moving wave of protein. This annual process has been well documented through aerial surveys designed to monitor numbers of birds (Kushlan 1977, Hoffman et al. 1994).

Other cycles of food availability may be less regular, with return intervals on the order of several to many years. Ogden (1994) noted that during the 1930's, there was far greater interannual variability in colony presence and size than there has been during the most recent 30 years. For instance, during the 1930's and early 1940's, alternate years often showed severe drought with little or no nesting, followed by one or more years with extremely large nestings (to over 200,000 birds). Ogden suggested that the large nestings of the 1930s and early 1940s were in part dependent upon the alternation of flood and drought. This suggested that there was something about multi-year patterns of hydrological variability that strongly affected nesting.

One prediction from this general observation is that abnormally large nesting events may be more likely following severe droughts than at other times (Frederick and Ogden 2001). Using the entire nesting record, we statistically identified eight abnormally large nesting events; all but one of these occurred within two years after severe droughts Similarly, all but two of the severe droughts during the same period were followed by abnormally large nesting events. The biotic mechanisms behind this statistically significant association are unknown, but at least three processes have been suggested: 1) Prey are temporarily superabundant following droughts as a result of liberation of nutrients, 2) Prey are superabundant following droughts because predatory fish have been killed off through desiccation (Kushlan 1976a, Walters et al. 1992), and 3) Prey are more available following droughts due to more open vegetation (Surdick 1999). These hypotheses have predictions that are specific enough to test with further monitoring of fishes and aquatic macroinvertebrates.

The idea that both prey animals and wading birds depend strongly on non-annual natural hydrological fluctuations for their pulses of productivity derives support from studies of other Everglades biota, as well as more general examples of riverine systems (Junk et al. 1989). For example, long term stable water conditions in the Water Conservation Areas have been shown to be detrimental to emergent vegetation and to both nesting and hunting success of Snail Kites, *Rostrhamus sociabilis* (Bennetts and Kitchens 1997), and rivers with flood pulses are known to have more productive fisheries than those that do not (Junk 1989).

Thus the evidence from wading bird monitoring in the Everglades has led directly to recommendations that natural hydrological fluctuation become a priority in water management, and has served as part of a growing body of evidence that hydrological fluctuation is necessary to the normal functioning of many types of wetland systems. These examples also highlight the need to understand the mechanisms involved in creating pulses of productivity. This gives further justification for monitoring populations of prey animals at a large enough scale to enable linkages with the wading bird studies.

Estuarine productivity has collapsed.

The record of early 20th century colony locations has demonstrated that there has been a major shift in the geographic location of nesting (Ogden 1978, 1994). During the latter part of the 19th century, and during the 1930's, all of the major colonies described for the Everglades were in the coastal zone or along the mangrove/freshwater marsh interface. In contrast, by the period of 1986 – 2001, an annual average of 85% of the wading bird nests were located in freshwater areas of the Everglades (Figure 3.2). Although turnover in use of colony locations is common in wading birds (Bancroft et al. 1988, Frederick 1995, Smith and Collopy 1995, Frederick and Ogden 2001), the loss of the entire region of formerly productive coastal colonies was so complete and has been maintained for such a long time (>30 years) that the abandonment of the area seemed indicative of a profound change in coastal ecosystem function.

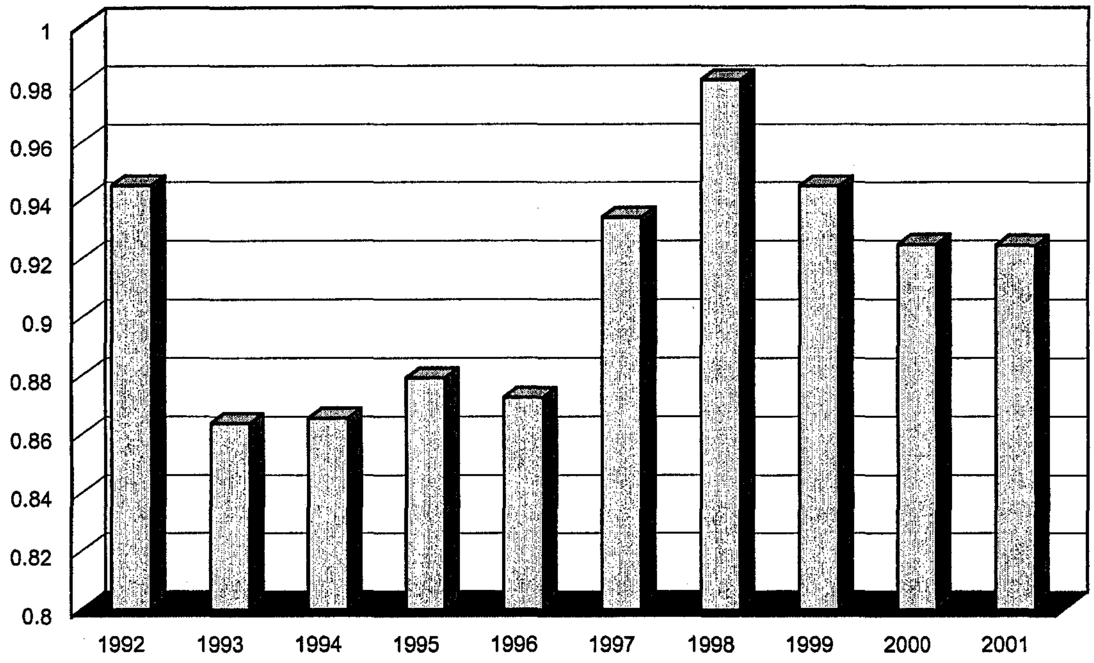

Figure 3.2. Proportion of all wading bird nests in the Everglades system located in the freshwater Water Conservation Areas.

The loss of most coastal colonies implied that the coastal foraging habitat or prey base had become degraded in some fashion, and studies initiated in the 1980's and 1990s on other aspects of the coastal ecosystem have borne this hypothesis out (McIvor et al. 1994). The most profound changes in the coastal zone have probably been driven by an extreme reduction in surface freshwater flows to the region (Smith et al. 1989, Fennema et al. 1994), and have included increases in the salinity of the estuary, decreases in shrimp production (Browder 1985), decreases in sport fish catches, and decreases in the standing stocks and densities of small "forage" fishes in the coastal marshes and mangrove ecotone (Lorenz 1997). What is most significant about the use of wading bird monitoring information in this story is that the decreases in coastal wading bird colonies were recognized as much as 20 years prior to the time when evidence from other sources suggested that the productivity of the coastal ecosystem had collapsed (Ogden 1978).

The estuarine zone may previously have been more advantageous for nesting because it offered wading birds a variety of habitat and wetland types in which to forage that would not be available in the more homogeneous freshwater marshes. The importance of heterogeneous foraging habitats for buffering birds against unpredictable water level fluctuations has been observed in modern-day studies of coastal-nesting wading birds in the Everglades (Bancroft et al. 1990, 1994), and points to the need to understand fluctuations in prey animal populations in those habitats.

Defining healthy hydrological patterns.

Wading bird monitoring studies have also demonstrated important differences in the conditions that have led to productive nesting during historical vs. modern periods, and ultimately these observations have led to fundamental changes in surface water management. Ogden (1994) noted that during the 1930s and 1940s large nesting events occurred in years with either wet or dry conditions, but that during the modern period, productive nesting occurred only during the dryer years. This pattern of nesting in dryer years has been linked to a direct relationship between annual nesting effort and rate of surface water recession, for both Wood Storks (Kushlan et al. 1975) and White Ibises (Frederick and Collopy 1989b). An analysis of nest failures in the Everglades during the recent period has similarly shown that abandonment is common whenever a drying water regime is reversed by high rainfall or surface water releases (Frederick and Collopy 1989b).

This difference between historical and modern nesting responses was something of a puzzle. However, monitoring of marsh hydrology and aquatic biota eventually showed that overdrainage of the freshwater marsh resulted in marked decreases in the abundance and standing stock of small fishes and invertebrates (Loftus and Eklund 1994, Loftus et al. 1992). Thus drainage practices have led to shortened hydroperiods in the freshwater marsh, resulting in depauperate prey animal communities. It then made sense that wading birds would show progressively greater dependence on drying events through time, because birds were relying on drying as a mechanism to concentrate the few prey present. In this case, the combination of changing bird nesting responses and fish population dynamics were required to fully realize the ramifications of long-term marsh drainage (Walters et al.1992, Fennema et al. 1994).

It is important to realize that in the absence of the long-term bird monitoring effort, our impression of suitable wading bird foraging conditions would probably be narrowly (and incorrectly) focused on the "beneficial" effects of rapidly falling water for stimulating nesting and increasing nesting success. In fact, this latter impression has been widely held, and has led to management policies that routinely dried much of the marsh surface during the dry season. Thus a negative feedback mechanism probably existed between management that favored annual drying events, and consequent increasing dependence of wading birds on drying events.

Tracking changes in aquatic contamination levels.

Wading birds are empirically good accumulators of contaminants for a number of reasons. Wading birds are known to feed at or close to the top of the aquatic food web, and show high bioaccumulation potential (Custer and Osborn 1977, Jurcyck 1993, Erwin and Custer 2000). Since the majority of the food gathered by adult wading birds such as White Ibises and Great Egrets (*Ardea albus*) is known to come from distances of 10 km or less from the colony (summarized by Bancroft et al 1994, Smith 1995), the tissues of young wading birds are known to be composed of resources from within this area. The use of young birds therefore largely avoids contamination signals that might come from other parts of the range of these migratory and nomadic birds. The sampling unit here is the colony site, and although this grain for sampling (20 km diameter circles) may seem large, it is probably appropriate for monitoring contamination in the aquatic food web of the Everglades ecosystem (rough dimensions 60 x 180 km).

To date, only mercury has been shown to consistently occur in high concentrations in wading birds in the Everglades, though there have been no systematic investigations to date of PCB's or dioxins. The Everglades aquatic food web is highly contaminated with mercury (Frederick 2000), and levels in Great Egret chicks are in some years higher than has so far been demonstrated for young of any fish-eating bird (Sunlof et al. 1994, Sepulveda et al. 1998). These levels were shown to be high enough to result in reduced health and altered hunting behavior of juvenile birds (Spalding et al. 1994, Bouton et al. 1999, Spalding et al. 2000 a,b), and there may also be effects on reproduction. Concentrations of mercury in feathers from nestlings have differed markedly and consistently among colonies, and these differences track geographic variations of mercury sampled from mosquitofish (*Gambusia holbrooki*, Stober et al. 1996, Chapter X). In addition, laboratory studies have demonstrated a clear and predictable relationship between Hg consumed, and Hg concentration in feathers of young Great Egrets (Spalding et al. 2000a). Thus there is empirical evidence from lab and field that feather tissue concentrations are a good indicator of Hg concentration in prey.

Wading birds have served an important sentinel role for contaminants in the Everglades (as much by what they have not accumulated as by what they have), and have demonstrated both geographic and temporal differences in concentrations of mercury. Further understanding of the dynamics of mercury at the ecosystem scale is likely to rely in large part on monitoring studies of top-level consumers like wading birds. The success of the mercury monitoring efforts suggests that the birds should also be monitored for other contaminants, since South Florida currently applies more pesticides per hectare, and uses a wider array of pesticides and herbicides, than any other part of the United States.

Wading birds as a linkage between the Everglades and other wetland ecosystems.

Relatively few animals move between the Everglades and other ecosystems. These include the Florida Panther (*Felis concolor coryi*), West Indian Manatee (*Trichechus manatus*), Snail Kite, migratory birds, and numerous euryhaline fishes and penaeid shrimps (Browder 1985). Of these, wading birds are probably the longest-monitored species both within and outside of the Everglades, and in many cases have been the subject of more ecological research. Thus wading birds are one of the few well-studied Everglades animal groups that have the capability of leaving the ecosystem, or of being attracted there from other locations in response to favorable ecological conditions. In this sense, wading birds can function as a true bellweather of environmental conditions among ecosystems, in a way that few other species can.

A history of statewide surveys, banding records, and other information indicates that the wading birds that utilize the Everglades are panmictic with, and demographically linked to, wading birds in other wetland areas of the southeast and the eastern Caribbean (Stangel et al. 1990, 1991, Frederick et al. 1996). The Everglades "population" then, is actually not distinct in its genetics or social organization and instead belongs to a loose grouping of animals that occur in a space perhaps as large as the eastern and southeastern U.S. and the eastern Caribbean. It is important to remember, then, that the dynamics of birds in the Everglades ecosystem may be strongly influenced by conditions in other regions, and conversely, that management in the Everglades may well influence patterns of distribution and abundance elsewhere.

For example, the Everglades probably served as an important source for the restoration of wading birds in the southeastern US during the period immediately following the decline of the plume trade (Ogden 1978). For example, the very large nesting aggregations of wading birds documented during the 1930 – 1946 period were not reported elsewhere in the US, and neither Wood Storks nor White Ibises were known to breed outside of Florida at the time. Similarly, very large colonies of Great Egrets, White Ibises, and Snowy Egrets in Florida during the 1930's immediately preceded the rapid expansion of nesting by these species in the Atlantic coastal plain and Mississippi valley.

During the last two decades, however, inter-regional monitoring indicates that this situation may have reversed itself, and the Everglades may now have become a demographic sink rather than source for many species. Wood Stork reproductive parameters in the Everglades during the recent period are exceptionally low for the species (Ogden 1994), and it is very unlikely that Everglades Wood Storks are replacing themselves). Between 1976 and 1999 the percentage of the U.S. Wood Stork population nesting in south Florida changed from 70 to 13% (Coulter et al. 1999). Although the annual numbers of breeding wading birds in the Everglades appears to be stable or slightly increasing, nonbreeding apparently occurs in some years. At this point it is not clear whether nonbreeding occurs often enough to reduce the growth rate of populations. even an apparently stable population may not be a healthy or self-sustaining one (Temple and Wiens 1989, Sadoul 1997). This example illustrates one of the ways that local monitoring, even at the ecosystem level, can be extremely misleading if not considered in the context of dynamics in other ecosystems.

The Everglades is in a geographically key position for migrating and wintering wading birds (Byrd 1978, Root 1988), and the SRF surveys have documented especially large numbers of birds using the Everglades during the winter pre-breeding season. These studies have shown that in some years the Everglades may host a substantial proportion of regional populations of some species (Bancroft et al.1992). The high usage of the area suggests that large numbers of birds are regularly able to assess conditions in the Everglades during the prebreeding period, and the large interannual variance in breeding effort suggests that these migratory birds may include the Everglades as a potential site when deciding where to nest. This scenario bolsters the notion that the numbers of birds nesting in the Everglades is indicative of conditions there, and that wading bird reproduction is a useful bioindicator of restoration.

Events in other ecosystems may also affect wading bird use of the Everglades. For example, White Ibises are known to make large scale shifts in breeding location, depending in part on comparing breeding conditions (food availablility, nesting substrate etc.) and food resources in past and prospective breeding sites (Ogden 1978, Frederick et al. 1996, Frederick and Ogden 1997). During the period 1980 – 1995, the numbers of White Ibises in Louisiana increased dramatically, probably in response to a large increase in impoundment acreage devoted to commercial production of crayfishes (*Procambarus* spp., Fleury and Sherry 1992). During the same period, a 50% reduction was documented in the total numbers of ibises nesting in Florida (Runde 1991). This strongly suggests that the increase in aquaculture in Louisiana resulted directly in decreases in ibises nesting in Florida and in the Everglades.

Thus while the monitoring of wading birds has been a powerful tool in unraveling the ecology of the birds and the ecosystem, there are excellent reasons for continuing to monitor the birds. First, the long-term nature of the record of nesting is a powerful context for comparison of any future years. Second, the long term record becomes more powerful with each passing year, particularly for the analysis of the importance of rare combinations of events. Third, a key prediction of the restoration program is that hydrological restoration will result in increased populations of wading birds, earlier nesting for some species, and increased nesting success for some species. Wading bird nesting is therefore a key criterion of restoration, and aspects of their reproductive ecology (energetics, timing, and productivity) have the potential for fine-tuning the way that the hydrology of the Everglades is managed. This chapter is divided into four main parts that provide a record of nesting in the Everglades during the years 1998 – 2001: nesting effort (numbers and species composition of nesting pairs), nesting success in relation to nesting date, effects of hydrology on nesting substrate, and effects of fire on nesting substrate.

Section A. Nesting numbers and composition of nesting pairs

Methods

Estimating numbers of breeding birds.

Over the past four years we have performed monthly systematic aerial surveys encompassing all of WCAs 2 and 3 once monthly from February through June, as well as occasional overflights of eastern ENP and Loxahatchee NWR. These aerial flights were flown as a series of east-west oriented transects throughout the Water Conservation Areas of the Everglades (Figure 3.3, 3.5), designed to provide 100% coverage of the area flown. The transects were spaced 1.6 nautical miles apart; this spacing was determined empirically by flying naïve observers at various distances from known colonies until colonies were consistently recognized. Some overlap in detectability between adjacent transects was designed into the spacing. Flights were flown at 240 meter altitude, with one observer on each side of the aircraft. Once colonies were detected, the location was circled and the colony repeatedly counted by both observers. For larger colonies, several

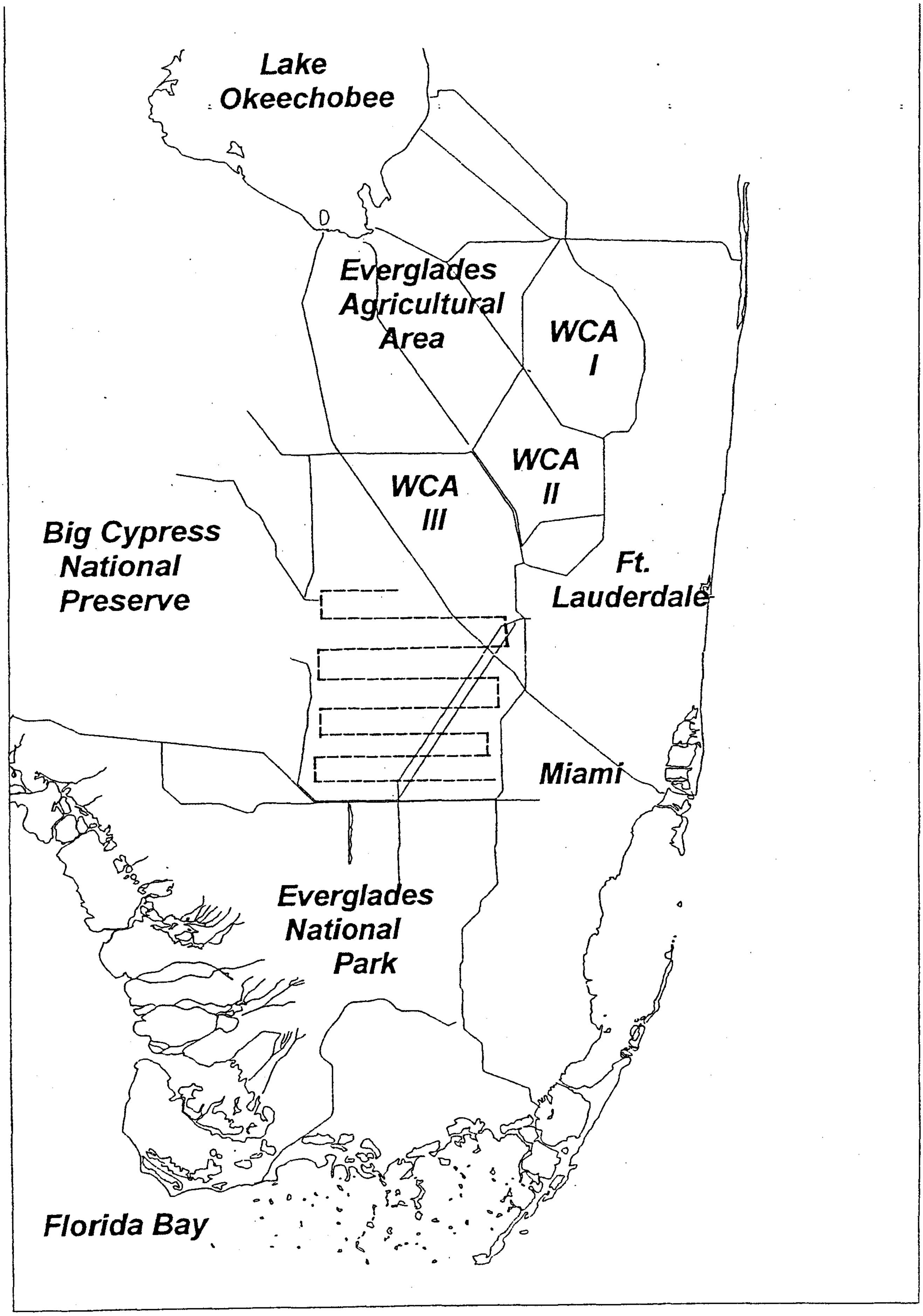

Figure 3.3. Schematic map of south Florida, showing approximate partial flight plan for breeding bird surveys (dashed line)

passes were often made at lower altitude to confirm nesting stage, species composition, or to achieve better discrimination among counts of similar species.

These aerial surveys are efficient for detecting large colonies of white birds. Aerial surveys are far less efficient at detecting and counting smaller colonies, and particularly those of dark-colored species. In the Everglades, our aerial surveys detected on average only 30% of the colonies, and 60% of the total number of birds (Frederick et al. 1996). For this reason, we also performed complete ground surveys of WCAs 2 and 3 by airboat to document small colonies and dark-colored species. These ground surveys were performed between March and June of each year. Each tree island was approached by airboat to a close enough proximity to either see or flush any nesting birds on the island. Similar airboat surveys were carried out in Loxahatchee NWR (WCA 1) by NWR staff, but the coverage there was not usually complete.

Occasionally, some areas were not completely surveyed by boat due to low water levels in WCA 2 and in the northern sections of WCA 3. In these cases, it is unlikely that any birds were nesting, as a result of the very low water conditions. In addition to monitoring the general success of nesting in most large colonies, during 2001 we also followed the fates of specific nests of White Ibises in the Tamiami West colony in ENP, and documented individual nest success and juvenile survival of White Ibises in WCAs 1, 2B and 3A.

Results

Nesting Effort

We have documented a large increase in numbers of wading bird nesting attempts over the past four years in the Everglades system. In 1998, we started with just over 8,800 wading bird nests, increasing to approximately 26,000 nests in 1999, 35,100 in 2000, and finally 34,500 in 2001 (Figure 3.1, Table 3.1). Over these four years, an average of 49% of all nests were constructed by White Ibises. In comparing these 4 years (1998-2001) to the previous ten years (1988-1997), all species except for Cattle Egrets have shown an average increase in nesting attempts. Black-crowned Night Herons (*Nycticorax nycticorax*) and Glossy Ibises (*Plegadis falcinellus*) showed the greatest increases in recent years, each 3.4 times above the prior ten-year average (Figure 3.4). Wood Stork nests during the study period increased by 3.4 times the ten-year average, while White Ibises increased by 2.7 times over the ten-year average. Cattle Egrets showed a decline of 25% compared to the ten-year average, largely due to their relatively small numbers of nests during 2000. Within the recent four-year period the average for all wading bird species increased by 2.2 times the prior ten-year average.

1998 Nesting Effort and Success

We found a total of 4,971 pairs of al21 wading birds (not including Cattle Egrets) nesting within WCA 2 and 3, and 3,227 in Loxahatchee NWR (Table 3.1, Figures 3.5 – 3.8; see Appendix I for colony specific counts by species). By comparison with the last large and successful nesting event (1992), these totals were reduced by nearly 80% (Figure 3.9). By comparison with the average of the previous five and ten years, the

Table 3.1. Numbers of nesting attempts recorded during January through July 1998 - 2001 in the Everglades ecosystem.

Year	Location	GREG*	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	Other	**Total Waders	Total - all species
1998	WCAs 2 and 3***	2,979	179	0	22	209	226	803	535	0	10	0	615	193	1,240	8	4,971	**7,019**
	Loxahatchee N.W.R.	828	123	0	0	1,036	15	352	873	0	0	0	1,682	0	0	0	3,227	**4,909**
	Everglades N.P.	607	0	25	0	0	0	0	0	0	0	0	120	0	0	0	632	**752**
	Total Everglades	**4,414**	**302**	**25**	**22**	**1,245**	**241**	**1,155**	**1,408**	**0**	**10**	**0**	**2,417**	**193**	**1,240**	**8**	**8,830**	**12,680**
1999	WCAs 2 and 3	4,808	520	320	271	509	740	1,234	4,624	0	47	0	525	25	2,172	941	14,014	**16,736**
	Loxahatchee NWR	2,037	217	0	0	1,592	470	489	5,780	0	0	0	831	0	0	0	10,585	**11,416**
	Everglades N.P.	930	4	140	0	6	0	0	0	0	0	0	250	0	0	0	1,080	**1,330**
	Total Everglades	**7,775**	**741**	**460**	**271**	**2,107**	**1,210**	**1,723**	**10,404**	**0**	**47**	**0**	**1,606**	**25**	**2,172**	**941**	**25,679**	**29,482**
2000	WCAs 2 and 3	3,064	525	500	339	475	2,388	1,278	21,117	2	15	30	243	7	1,092	0	29,733	**31,075**
	Loxahatchee NWR	535	41	0	143	557	58	147	920	1	0	69	0	0	0	0	2,471	**2,471**
	Everglades N.P.	1,110	4	1,592	2	0	150	15	20	0	0	0	130	0	0	0	2,893	**3,023**
	Total Everglades	**4,709**	**570**	**2,092**	**484**	**1,032**	**2,596**	**1,440**	**22,057**	**3**	**15**	**99**	**373**	**7**	**1,092**	**0**	**35,097**	**36,569**
2001	WCAs 2 and 3	4,168	206	450	142	584	1,884	1,050	4,540	0	14	106	224	0	682	0	13,144	**14,050**
	Loxahatchee NWR	786	152	16	472	1,937	1,395	1,161	12,622	7	0	174	1,160	0	0	0	18,722	**19,882**
	Everglades N.P.	510	0	1,585	60	0	350	2	100	0	0	0	24	0	0	0	2,607	**2,631**
	Total Everglades	**5,464**	**358**	**2,051**	**674**	**2,521**	**3,629**	**2,213**	**17,262**	**7**	**14**	**280**	**1,408**	**0**	**682**	**0**	**34,473**	**36,563**

* Species codes are: GREG = Great Egret, GBHE = Great Blue Heron, WOST = Wood Stork, BCNH = Black-crowned Night Heron, LBHE = Little Blue Heron SNEG = Snowy Egret, TRHE = Tricolored Heron, WHIB = White Ibis, YCNH = Yellow-crowned Night-heron, ROSP = Roseate Spoonbill GLIB = Glossy Ibis, CAEG = Cattle Egret, DCCO = Double-crested Cormorant, ANHI = Anhinga, Other = Green Herons and unidentified small herons

** Total waders do not include Cattle Egrets, Double-crested Cormorants, or Anhingas.

*** Tamiami Trail colony estimates are included in WCA 3 for the entire study period.

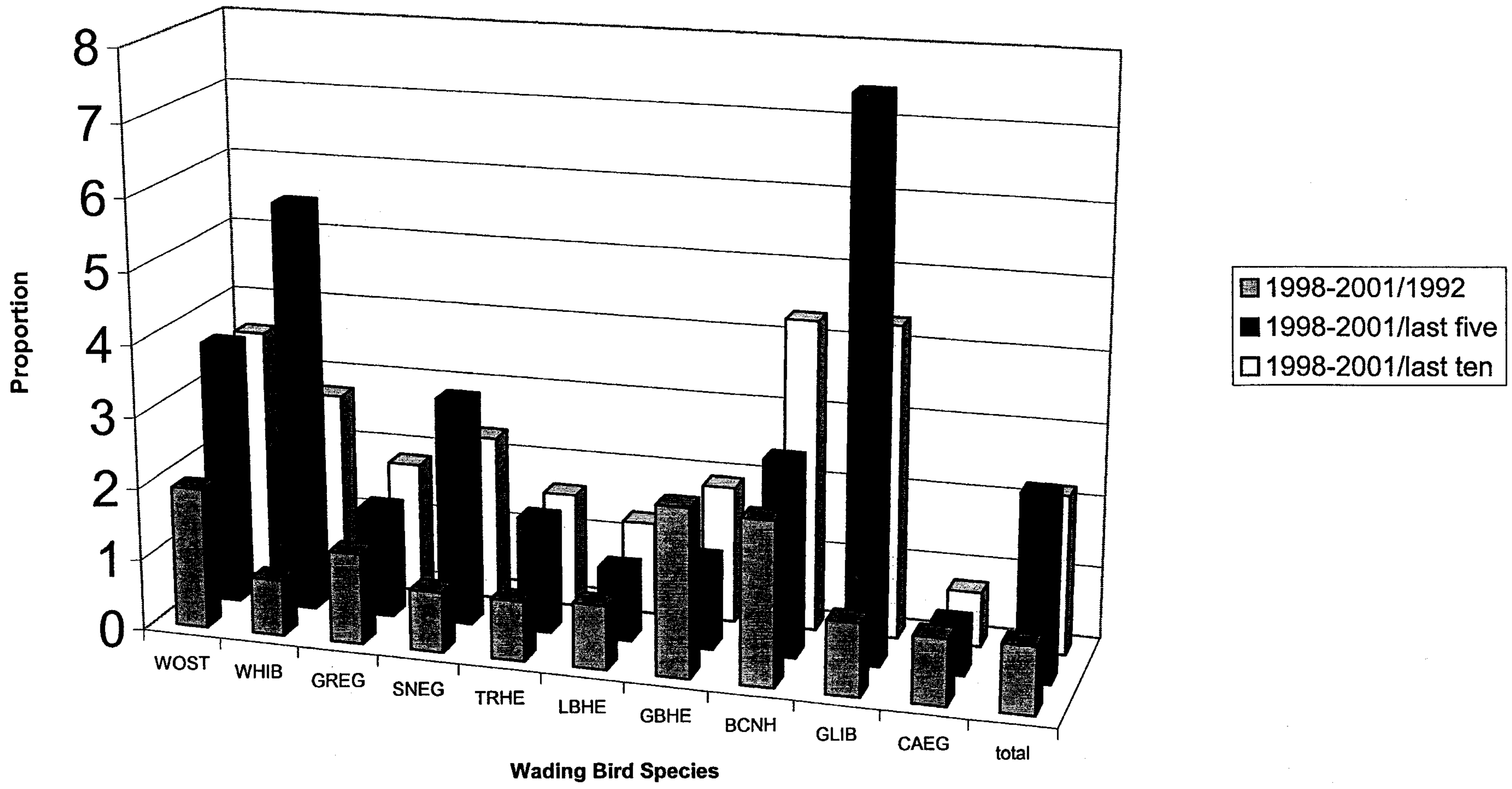

Figure 3.4. Comparison of average number of birds nesting in the entire Everglades during 1998 - 2001 with other benchmarks.

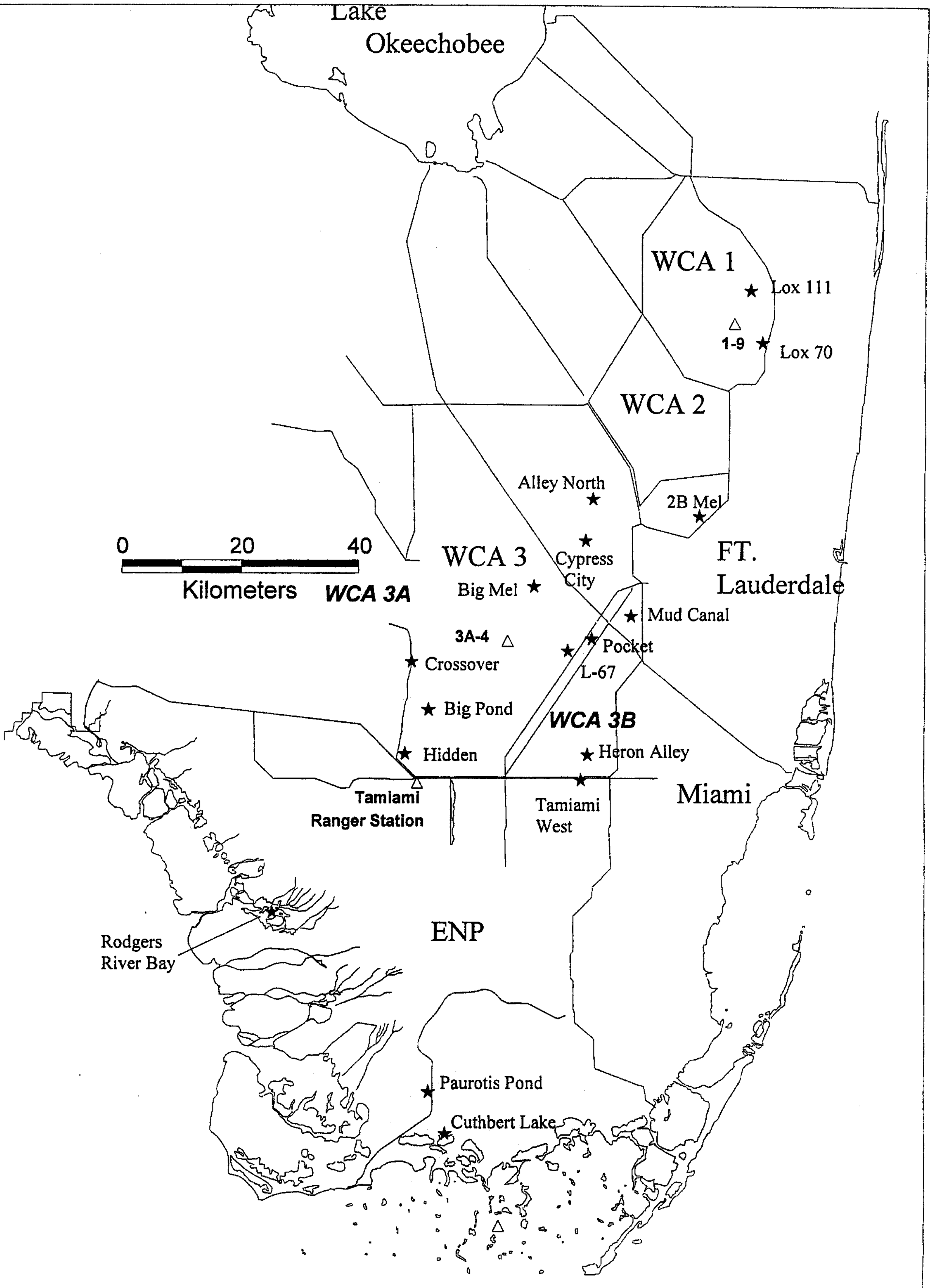

Figure 3.5. Map of south Florida, showing water management units, major colonies (stars) and water gaging stations (triangles).

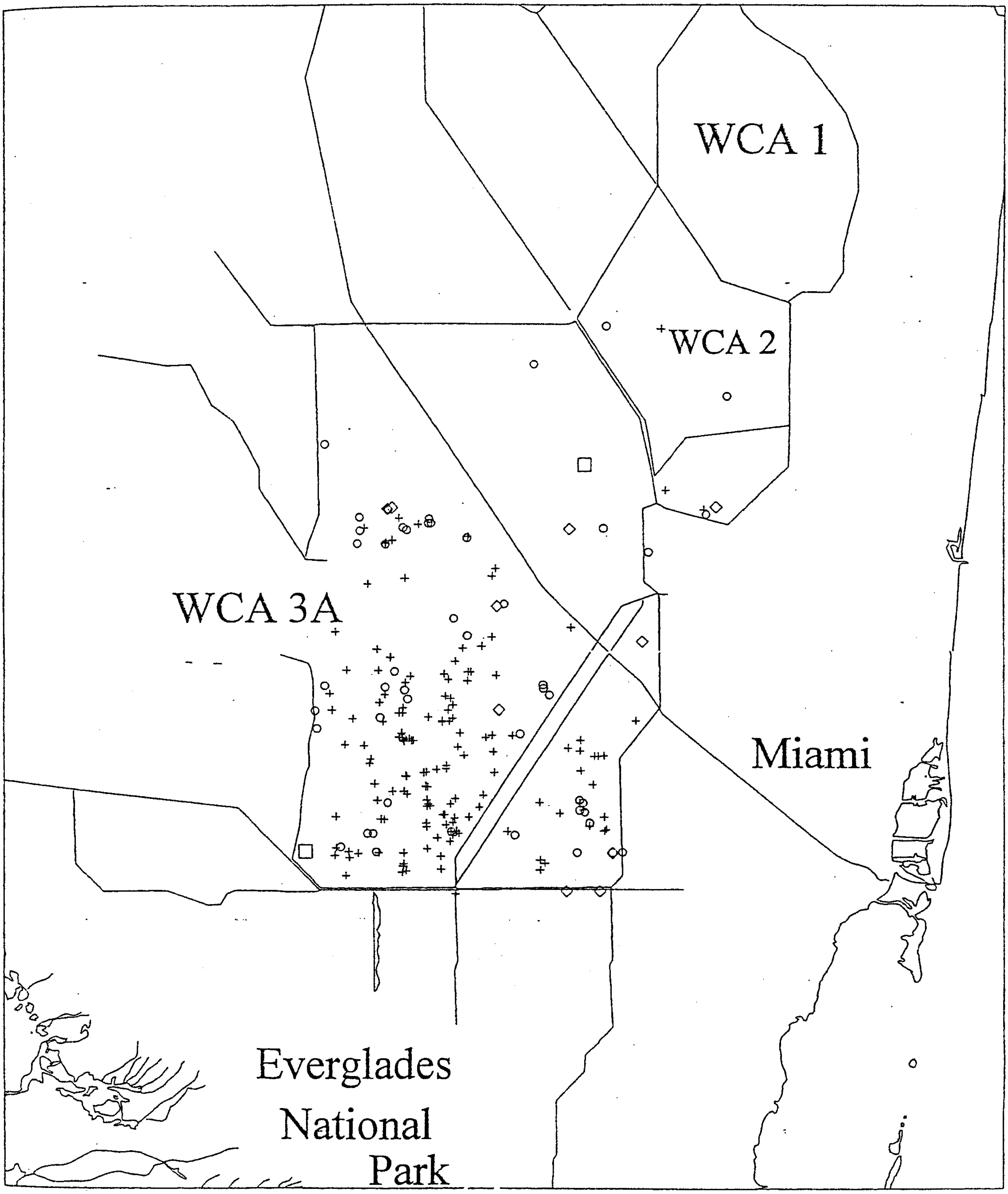

Figure 3.6. Map of the study area, showing the locations of all WCA colonies in 1998, by size of colony. Squares represent colonies of over 1,000 pairs, diamonds are colonies of 100-1,000 pairs, circles are colonies of 10-100 pairs, and crosses are colonies of 1 – 10 pairs.

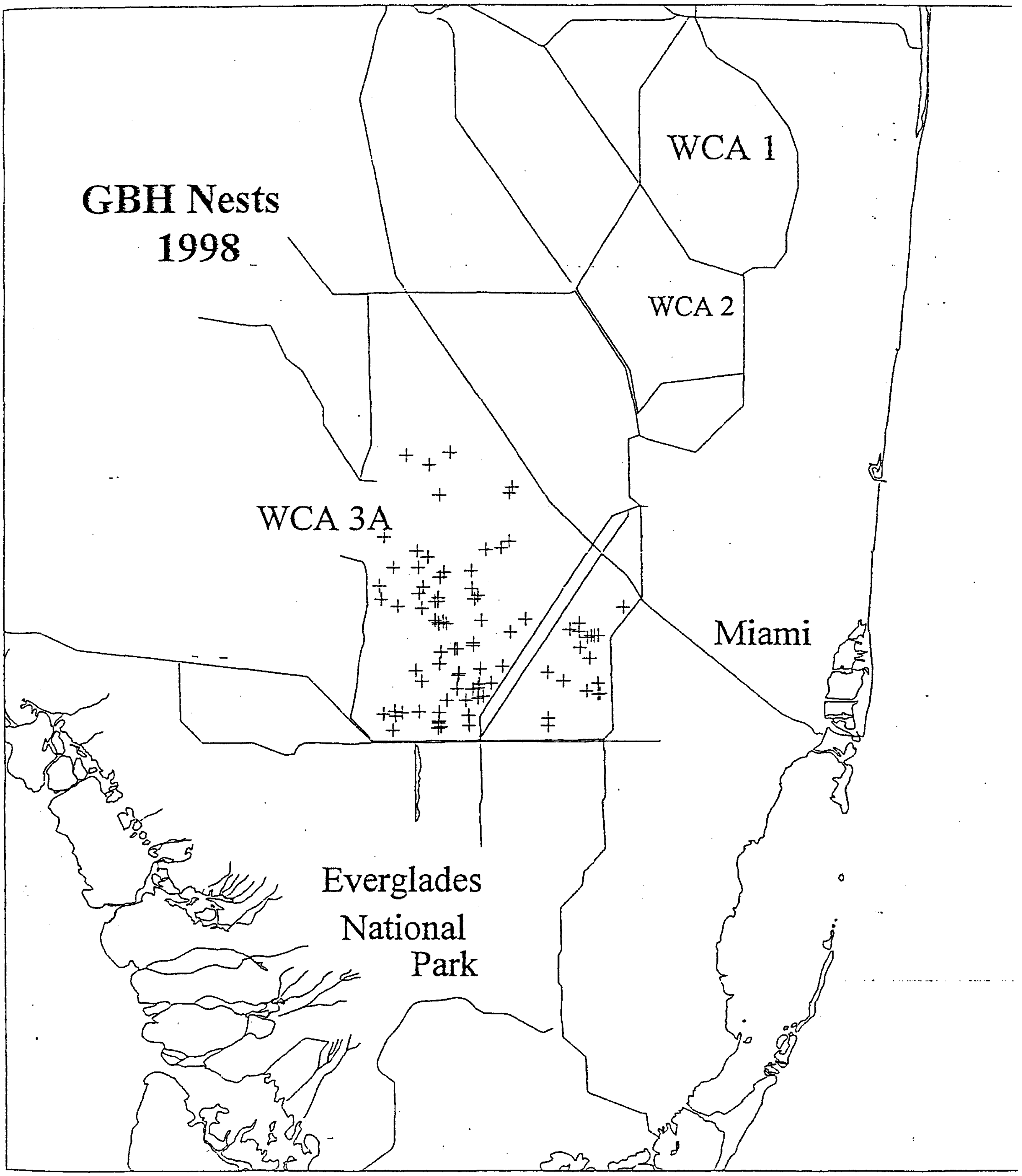

Figure 3.7. Locations of all nests and colonies of Great Blue Herons during 1998.

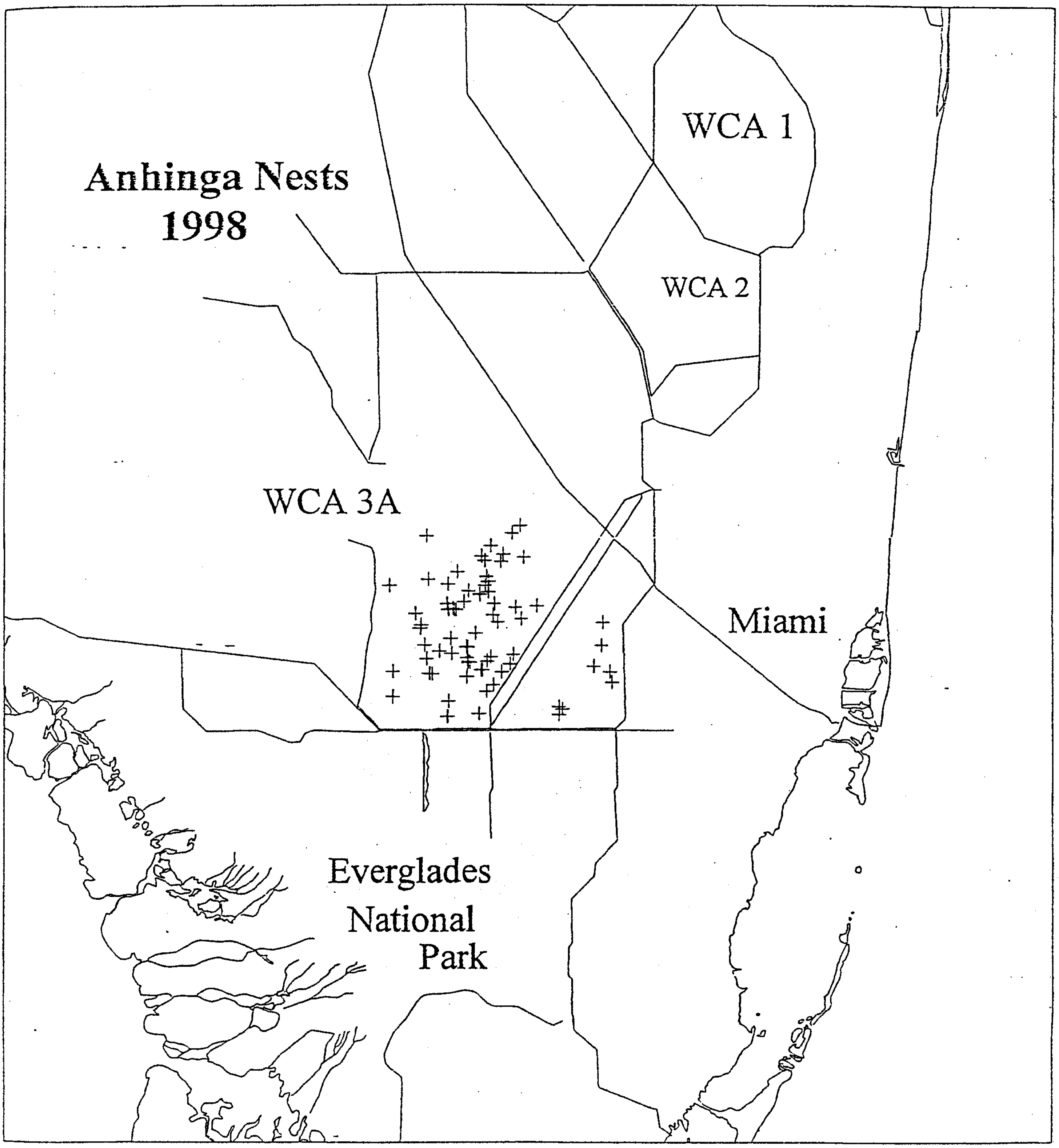

Figure 3.8. Locations of all nests and colonies of Anhingas during 1998.

1998 ecosystem totals were down by between 16 and 25%, respectively. By comparison with 1986/7 (hydrologically "average" years), the 1998 ecosystem totals were down by only 7%.

These patterns were not necessarily reflected in all parts of the ecosystem. In particular, nesting in Everglades National Park continued the decline characteristic of the previous 20 years. By comparison with the last five and ten years, the 1998 nesting effort was decreased by 42 and 50%, respectively. By comparison with 1986/7, the 1998 season produced a nesting cohort in ENP that was down by nearly 80%. As a partial result of these low numbers in ENP, the percentage of the total ecosystem population that nested

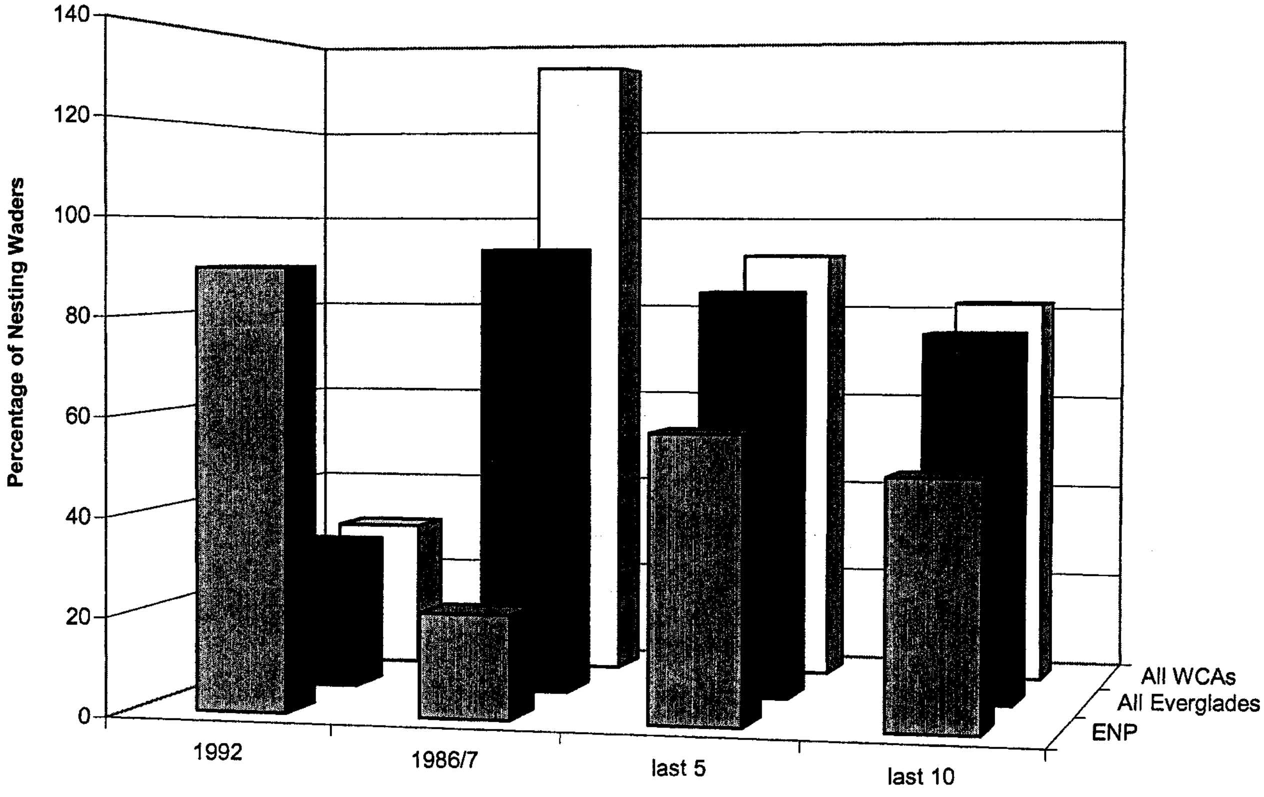

Figure 3.9. Numbers of pairs of all wading birds nesting in 1998 in the Everglades

ecosystem, expressed as a percentage of nesting totals for previous years, by geographic location.

in the WCAS was 96%, continuing a trend of increasing percentages nesting in the WCAs, that has continued over the last 15 years.

The species composition of nests also continued some trends noted earlier in the 1990's. Wood Storks nested only in small numbers in Everglades National Park, and did not nest anywhere else in the ecosystem. Numbers of breeding White Ibises and Snowy Egrets were down by 40 and 60% by comparison with the average of the previous five years. Snowy Egrets in particular seemed to be almost as rare as Wood Storks in recent years. Great Egrets continued to increase both in absolute numbers and in their proportional representation in the wading bird community. Their numbers increased dramatically since the mid-1980s and stabilized during the 1990's. Tricolored Herons (*Egretta tricolor*) appeared to be stable, though it is difficult to compare population size of this dark-colored species with any counts prior to 1992, when systematic ground surveys were initiated. Similarly, Little Blue Herons (*Egretta caerulea*) also appeared to be stable, but similar problems in earlier counts of this species make more detailed statements of population trend impossible. A small cohort of Roseate Spoonbills (*Ajaia ajaia)* nested in Alley North, but their success was not recorded.

Numbers of Great Blue Heron nests have been counted systematically in WCA 3 since 1992. Their numbers built steadily to a peak of about 500 nests in 1995, with a slow decline thereafter. There are now enough data to suggest that this species' population fluctuates slowly across years. As with most previous years, nesting by this species was predominantly concentrated in WCA 3.

1999 Nesting Effort and Success

During the period January – June 1999, we documented a total of 14,014 wading bird nesting attempts in WCA 2 and 3 (Table 3.1, Figure 3.10, and see Appendix 2 for colony specific counts by species). Note that this estimate did not include Cattle Egrets, Anhingas (*Anhinga anhinga*), or Double-crested Cormorants (*Phalacrocorax auritus*). In cooperation with Loxahatchee National Wildlife Refuge staff, we documented 10,585 nests in Loxahatchee NWR, and Everglades National Park staff reported 1,080 pairs nesting in mainland Everglades National Park. The 1999 nesting season was a large nesting event by almost any recent standard (Figure 3.11). It is the second highest count of nests on record for the WCAs during the prior period of systematic monitoring (1986 – 1999). By comparison with the 1986 – 1988 period (one of high, low, and intermediate water stages), total numbers of nests in the entire Everglades ecosystem during 1999 showed an overall increase of over 100%. This trend was also true for each species individually, with most increases of greater than 50%.

By comparison with the last large nesting event (1992), the 1999 nesting was slightly lower (10% lower for total nests). Nearly all species individually also showed slightly lower nesting effort in 1999 than in 1992. By comparison with the last five years, the total numbers of nests were over 150% greater in 1999, and all species showed an increase ranging from Little Blue Herons (18%) to White Ibises (320%).

Wood Storks nested at three colonies – Tamiami West, Crossover, and a new colony discovered in WCA 2B (see Appendix 2). Although we did not measure nesting success directly by monitoring marked nests, storks were largely successful at each of

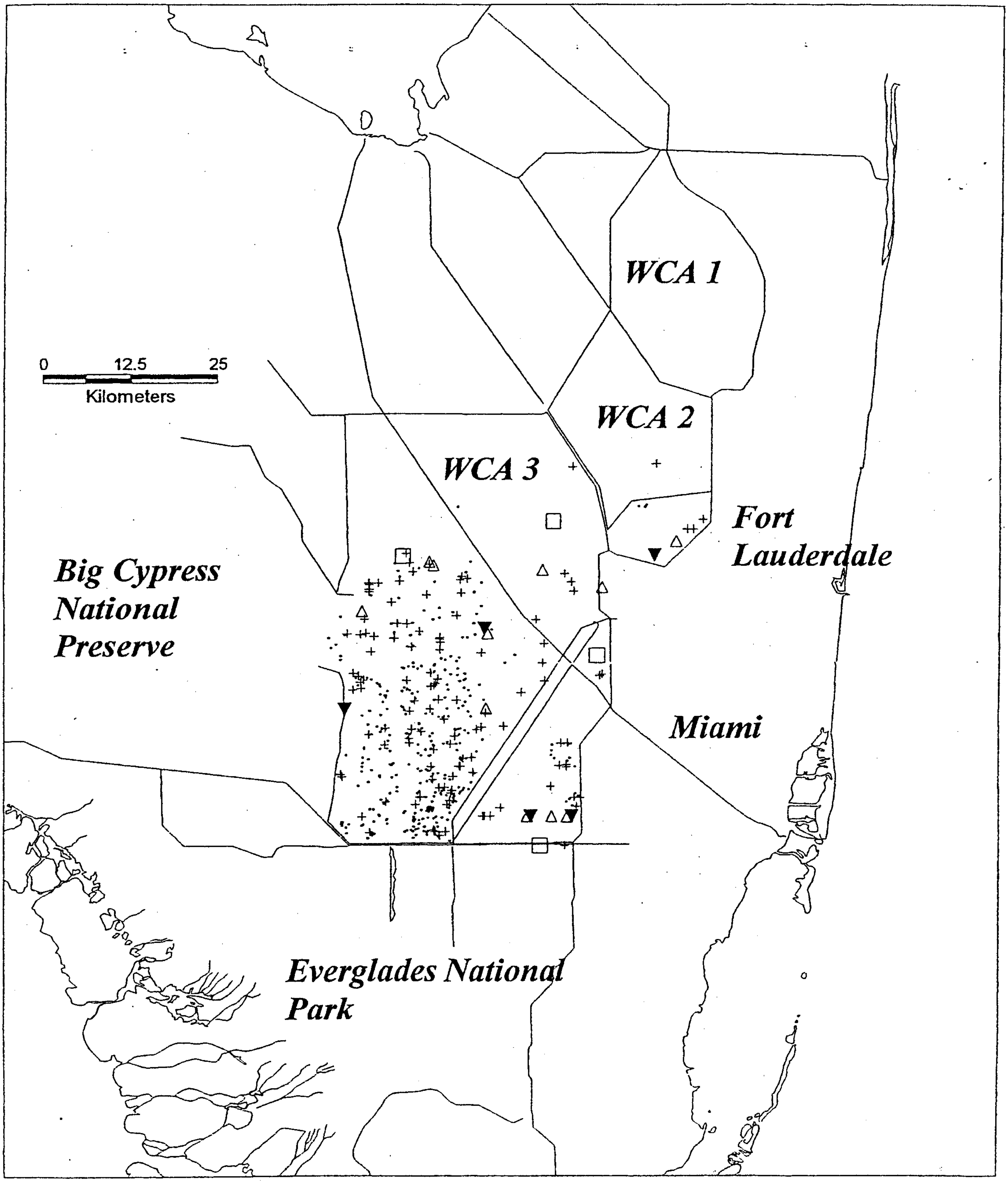

Figure 3.10. Map showing colonies active in 1999. Large squares are colonies of >500 pairs, solid triangles are 250 – 499 pairs, open triangles are 100 – 249 pairs, crosses are 10 - 99 pairs, and dots are colonies of 1 – 9 pairs.

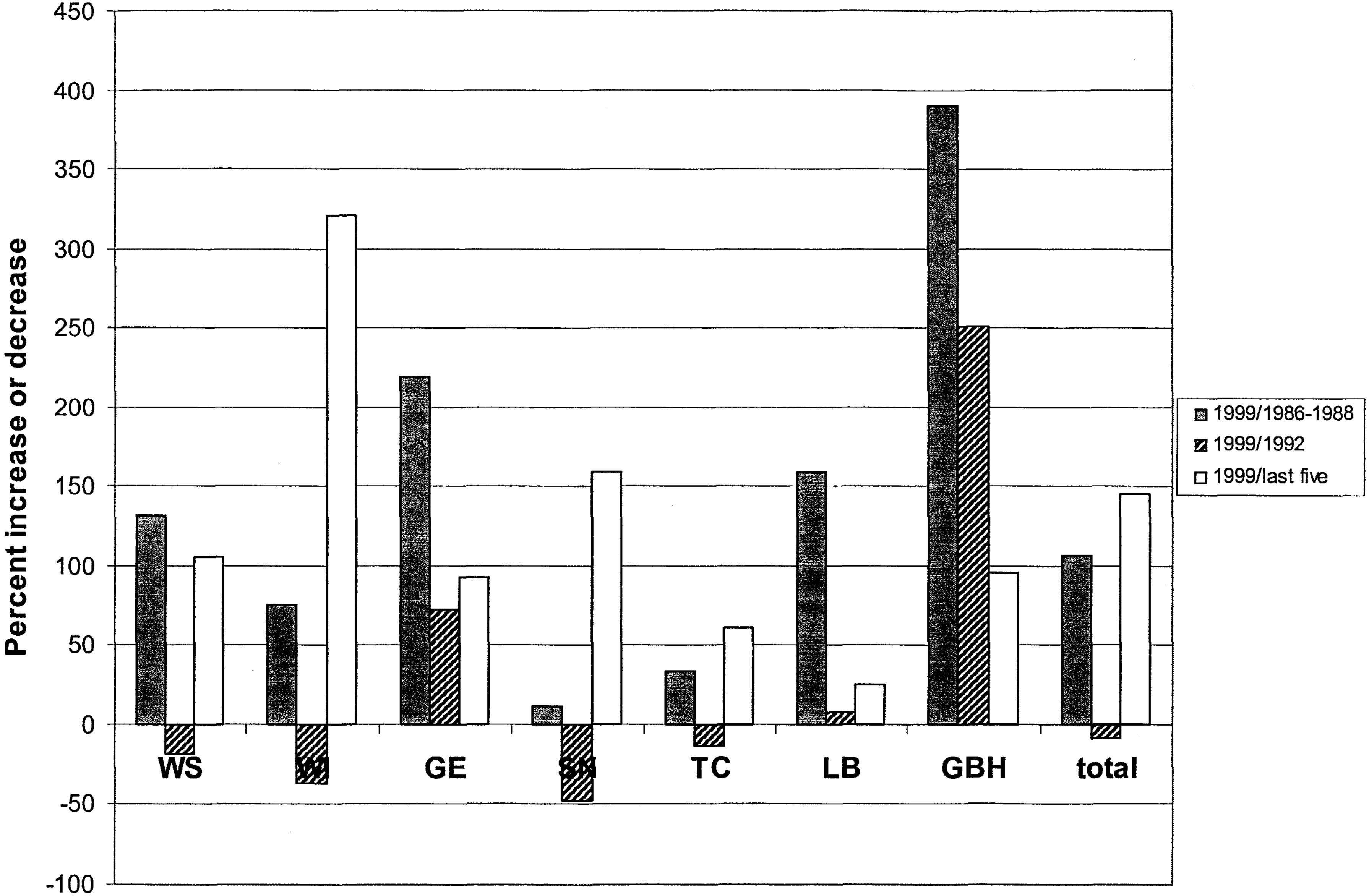

Figure 3.11. Comparison of numbers of birds nesting in the entire Everglades during 1999 with other benchmarks. Solid gray bars are proportional increase or decrease in 1999 by comparison with average of 1986 - 1988; cross hatched bars are comparison of 1999 with 1992, the last large nesting event, and white bars are comparisons of 1999 with the average of the last five years.

these colonies, even though they started in February, which usually results in large scale nest failure because of the late start date. This kind of nesting success and effort by Wood Storks has not been documented in the WCAs since 1992. White Ibises nested in large numbers (>4,000 pairs) at the Alley North colony, as well as at Tamiami West, Hidden, Big Melaleuca, and one location in WCA 3B. Large numbers of ibises (56% of the total) also nested at several locations in Loxahatchee National Wildlife Refuge. This suggests that the very high stages that have been kept in Loxahatchee NWR during the past several years have not resulted in unsuitable conditions for White Ibis reproduction. Although there was some abandonment of the late nesters after the onset of the rainy season, the vast majority of the ibis nesting attempts appeared to have been successful at each of the colonies.

We also noted no large abandonment events at any of the colonies that we monitored through aerial surveys. Although we did not measure reproductive success directly, this observation suggests that the nesting season was largely successful for most if not all of the other species. This impression was confirmed by the large numbers of young Great Egrets, Snowy Egrets, Tricolored Herons, Little Blue Herons, and Roseate Spoonbills that we saw in colonies that we entered on foot, or monitored either through aerial or ground surveys.

Small numbers (8 – 15) of Roseate Spoonbills have been nesting at the Alley North colony since 1992, when they were first discovered there (Frederick and Towles 1995). This year, however, the number jumped to 35, and we found an additional 12 nests at a new colony in WCA 2B. This pattern could be explained by young birds recruiting to these colonies as they come into reproductive status after 3 – 4 years as juveniles.

The proportion of the adult wading birds present which actually nested also appeared to increase by comparison with previous years. For Great Egrets, it was the highest proportion in the 13-yr record, and we estimate that nearly 100% of the adults bred. Similarly, the proportion of White Ibises that bred was higher than any other year except for 1995 and possibly 1988. The proportion of Wood Storks that bred was higher than any year since 1990. These high proportions are not simply the result of small numbers of adults present, since relatively large numbers of birds were found in the WCAs during Systematic Reconaissance Flights in spring of 1999.

The numbers of nesting birds in 1999 was an encouraging trend, since any increase in nesting effort or nesting success was a step in the direction of restoration goals (Ogden et al. 1997). Numbers of pairs of Great Egrets for 1999 (7,775) were at or exceeding the target for the ecosystem (4,000 pairs breeding regularly), while the 3-year running average was 5,084 (again, slightly above the target). Nesting effort by White Ibises in 1999 (10,404 pairs) was at the bottom end of the restoration scale, and the running 3-year average remains well below the target range for restoration. Similarly, although the largely successful nesting by Wood Storks was a hopeful sign, the nesting effort remains both late (beginning in February), and token in magnitude (low hundreds of pairs vs. the thousands that are restoration targets). The numbers of pairs of small herons in 1999 (5,105) and during the past three years (1,862) remained well below target levels (10,000 – 20,000 pairs), the nesting during 1999 was a considerable increase over recent years.

One of the restoration targets for wading birds is a higher proportion of nesting in coastal regions of the Everglades. There was no evidence of any movement of nesting colonies to the coastal regions of the Everglades during 1999. In fact, 1999 continued the long trend of much higher proportions of wading birds in the Water Conservation Areas than are in Everglades National Park (Figure 3.2). During 1999, the proportion of nesting in the WCAs was 94.4%.

2000 Nesting Effort and Success

Between January and June 2000, we found many more wading birds nesting than usual in the central Everglades (Table 3.1, Figure 3.12, see Appendix 3 for colony specific counts by species). During the spring, we estimated 32,204 nests of all waders (not including Cattle Egrets, Anhingas or Double-crested Cormorants) in WCAs 2 and 3. For comparison, this level of total nesting effort in 2000 was 33% greater than in 1999, 2.8 times greater than the 10-year running average, and 20% greater than the last exceptionally large nesting in 1992 (Figure 3.13). The level of nesting in 2000 in the WCAs was about half the estimate for the Everglades as a whole during several years in the late 1940's.

In the Everglades as a whole, there were apaproximately 35,100 nests found during 2000. The 2000 nesting was truly exceptional nesting event, and was over 2.5 times as large as the ten-year average, 2 times the five-year average, and 14% greater than the very large nesting event in 1992.

The vast majority of the abundance in the WCAs (almost two thirds) was made up by White Ibises, most of which nested at the Alley North colony (approximately 20,000 pairs). However, ibises also nested in several locations that were novel for ibises in the

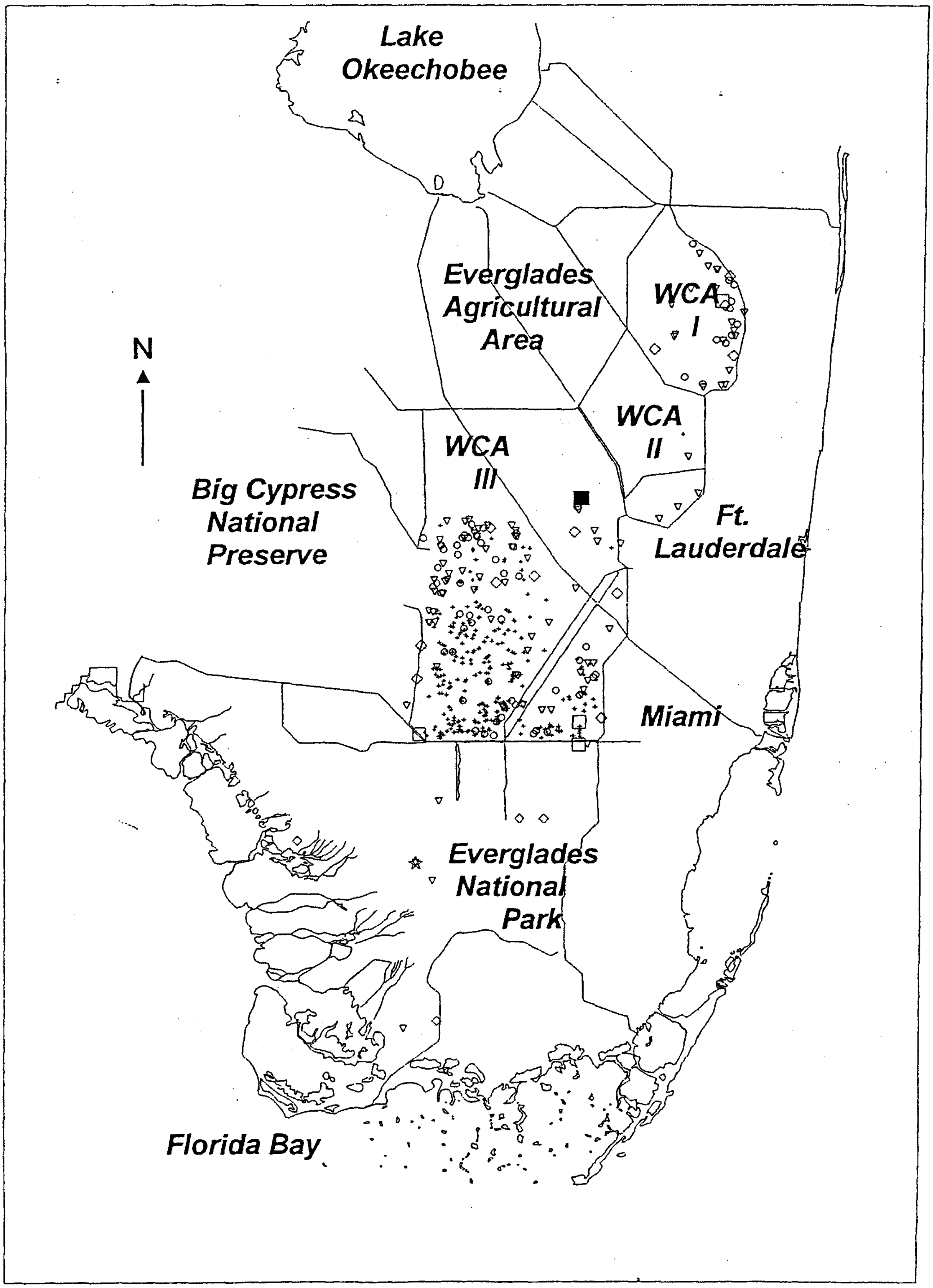

Figure 3.12. Map showing colonies active in 2000. Solid squares are colonies > 20,000 pairs. Open squares are colonies 1000 - 3000 pairs, open diamonds are 100 – 999 pairs, open triangles are 10 – 99 pairs, and circles are colonies of 3 – 9 pairs, and crosses are colonies of 1 – 2 pairs.

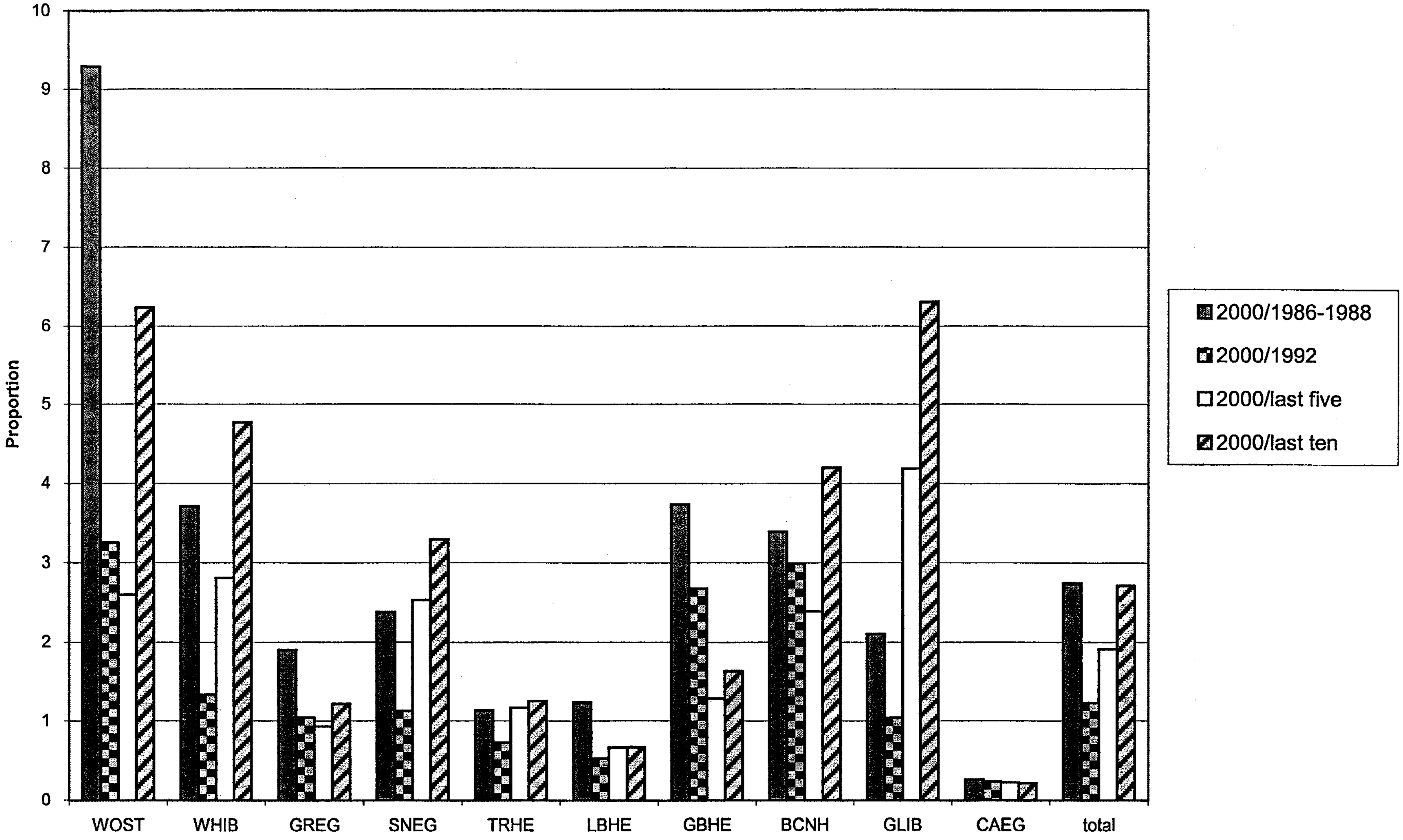

Figure 3.13. Proportion of birds, by species, nesting in the Everglades system in 2000 in relation to previous benchmarks. A proportion of 1 would be the same number of nests in both years or periods being compared.

recent past, including Hidden colony, Heron Alley colony, and a new colony at the Shark Slough tower in Everglades National Park. Numbers of White Ibises were 4.7 times the ten-year average, and 2.8 times the five-year running average.

Wood Storks also nested in much larger than normal numbers - over 1,800 pairs nested in a number of locations, including over 1,300 pairs at the Tamiami West colony, and 500 at a novel location in southwestern WCA 3. This level of nesting effort by storks had not been seen in the Everglades since the mid-1970's, almost 30 years, and the 2000 nesting was over six times the ten-year running average for the Everglades. The storks nested in early February, and were able to fledge large numbers of young this year, despite a large rainfall event in April. Summer rains were late to normal this year, resulting in a protracted drydown. We hypothesize that this further enhanced survival chances for these young storks.

Snowy Egrets numbers were also up considerably this year, with at least three times the ten-year average nesting in 2000. The largest colony was at Alley North, but there were also sizeable aggregations at Hidden colony, and Tamiami West.

Not all species showed obvious increases this year. Numbers of Little Blue Heron nests were less than 66% of the ten year running average. Numbers of Great Egrets and Tricolored Herons were similar to the ten-year mean, and showed no increase in 2000 over other years.

Within the Everglades ecosystem, the vast majority of nesting was concentrated in the Water Conservation Areas (92%), and the vast majority of the remainder in Everglades National Park was in freshwater areas and not in coastal locations. Within the Water Conservation Areas, the vast majority of nesting was concentrated in WCAs 2 and

3 (92%), and the vast majority of that (96%) was in WCA 3. In LNWR, nesting was about half the 8-year average.

Although we did not measure reproductive success through documentation of individual nest histories, we were able to monitor the success of nesting colonies in a coarser way by noting large abandonment events, and general level of productivity. Nesting was largely successful throughout WCA 3 and 2 - we found no complete failures in any colonies, and large numbers of young were produced, particularly at Alley North. However, in Loxahatchee NWR, the strong pulse of rains in mid-April resulted in widespread abandonment, including up to two-thirds of the nests destroyed in closely monitored colonies.

In WCA 3, however, the April rainfall did not result in widespread abandonment, probably as a result of lower initial stages and less increase in stage than was experienced in Loxahatchee. The difference in stage increase in Loxahatchee and WCA 3 may have been partly because of inpumping at Loxahatchee from local agricultural fields.

2001 Nesting Effort and Success

Between January and July 2001, we estimated 13,144 nests for all waders (not including Cattle Egrets or Anhingas) in WCAs 2 and 3 (Table 3.1, Figures 3.14 – 3.16, and see Appendix 4 for colony specific counts by species). For comparison, this level of total nesting effort in 2001 was 46% lower than during the spring of 2000. For a broader view of wading bird nesting effort in the Water Conservation Areas during 2001, the waders in Loxahatchee NWR, Loxahatchee N.W.R., were also considered. Approximately 54% of the waders nesting in the entire WCA region nested in

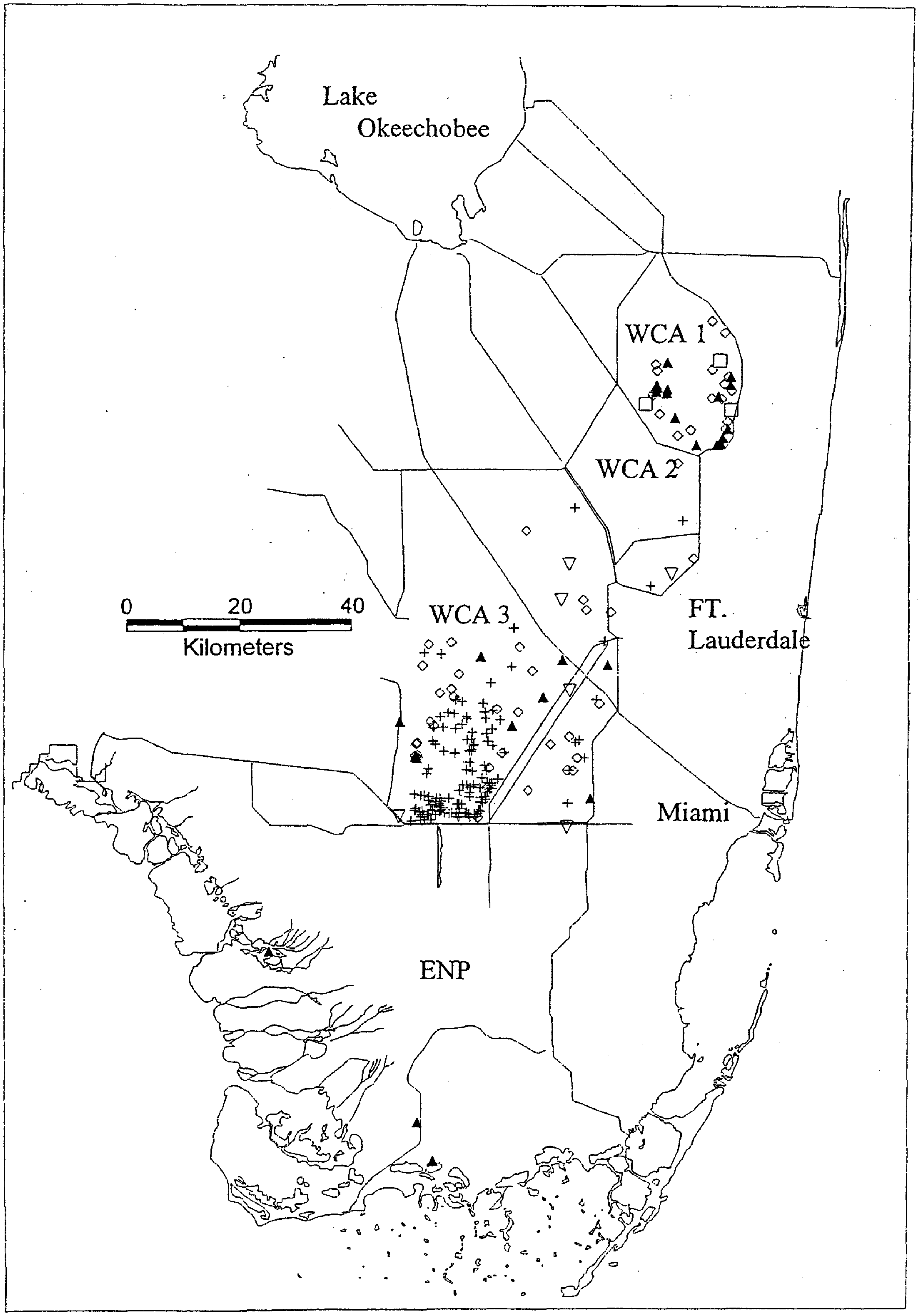

Figure 3.14. Map showing all colonies active in 2001. Open squares are colonies > 3,000 pairs, open triangles are colonies 1,500 – 3,000 pairs, solid triangles are 100 – 1,499 pairs, open diamonds are 10 – 99 pairs, and crosses are colonies < 10 pairs.

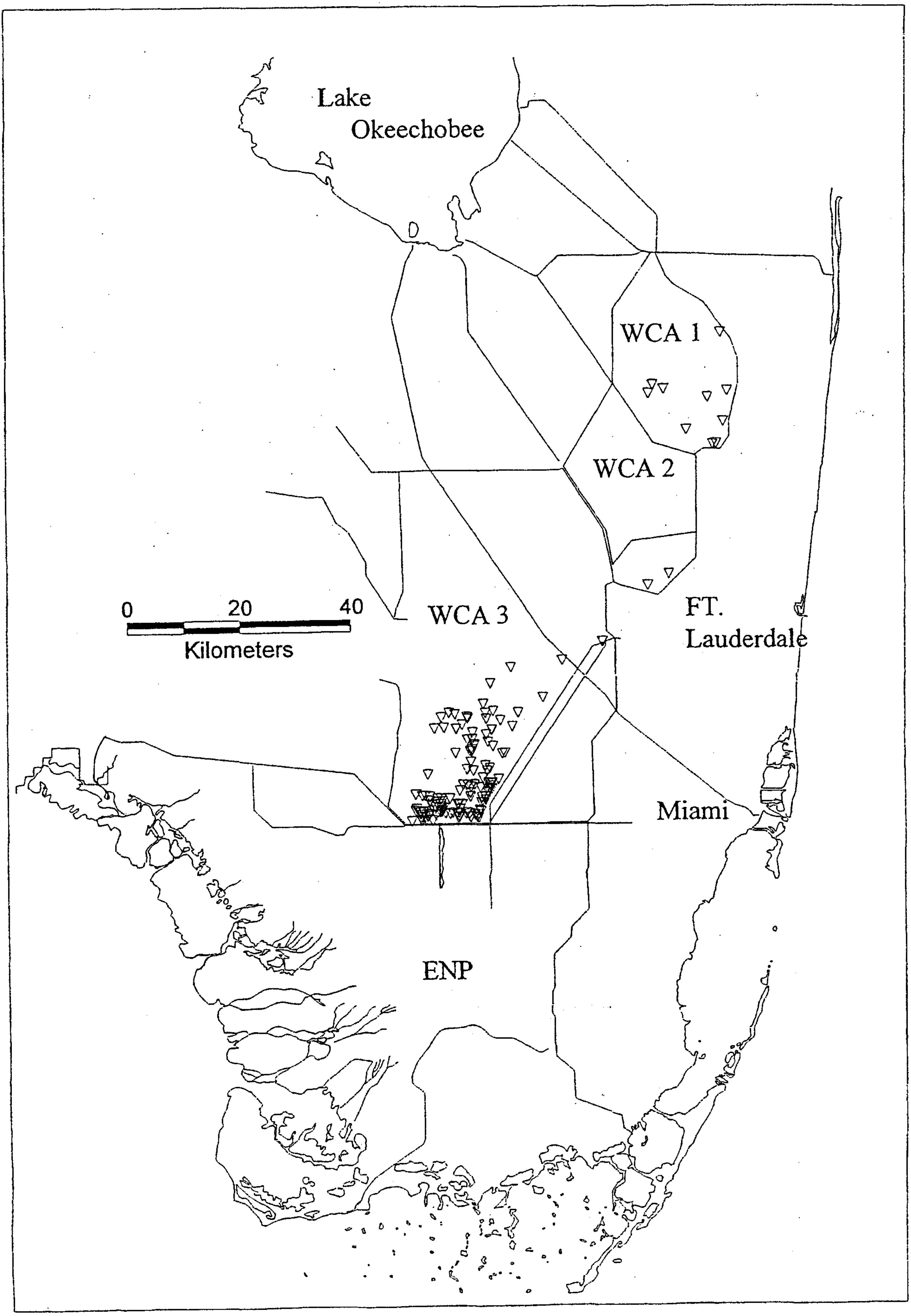

Figure 3.15. Locations of all nests and colonies of Great Blue Herons during 2001.

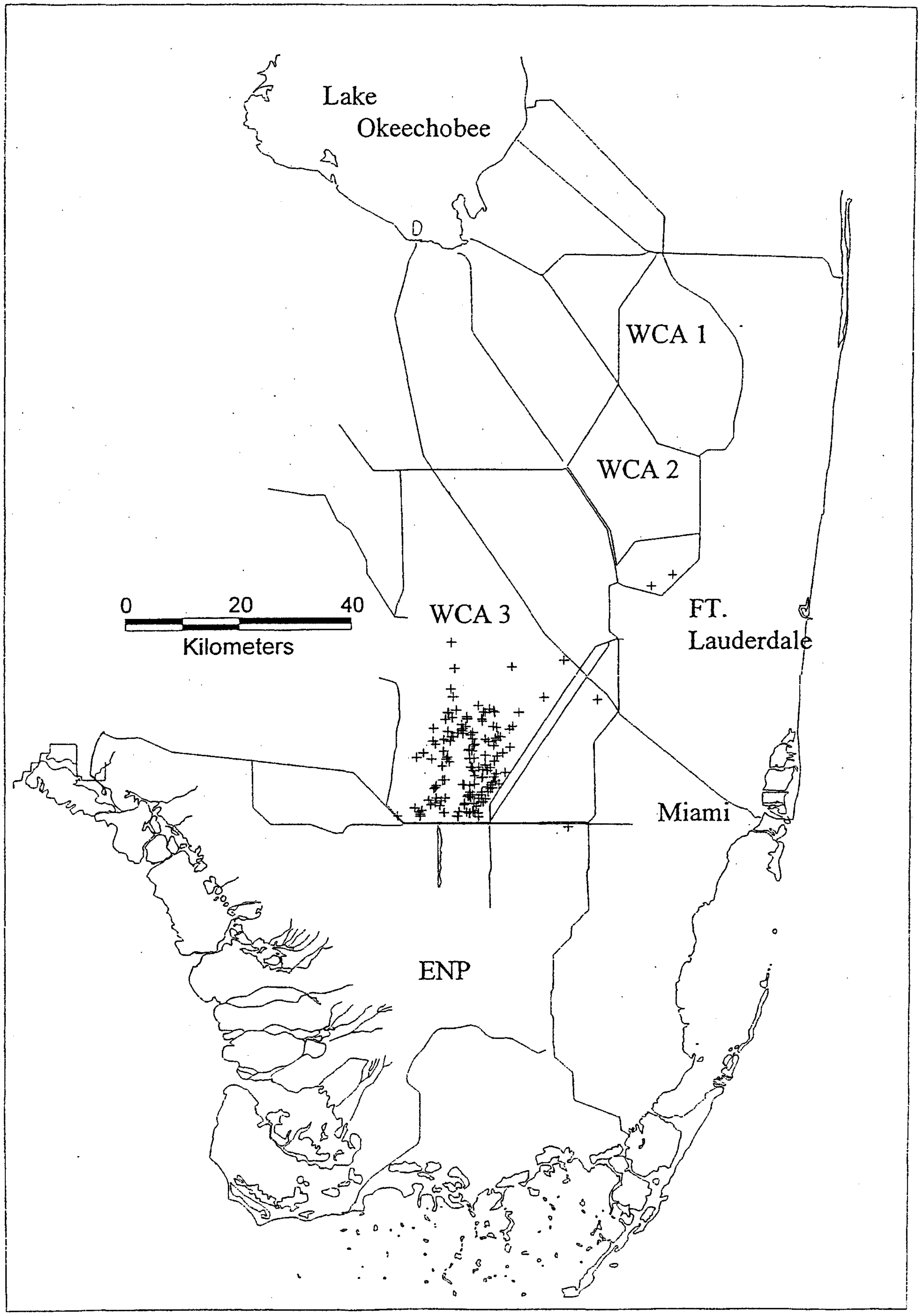

Figure 3.16. Locations of all nests and colonies of Anhingas during 2001.

Loxahatchee NWR this year, a total of 18,722 nests. This level of nesting in Loxahatchee NWR was 3.3 times the ten-year average for that water management unit. Combining the totals for all 3 WCAs yielded 31,866 total nesting attempts. This combined total was similar to the 32,204 nests estimated in 2000 for all 3 WCAs.

In the Everglades as a whole, there were over 34,400 nests located during 2001. Similar to the 2000 nesting effort of 35,100 nests, this was again an exceptional nesting event in the context of recent history. This nesting effort was 2 times as large as the ten-year average, 1.9 times the five year average, and 12% greater than the very large nesting event of 1992 (Figure 3.17). Approximately 50% of the abundance of wading bird nests in the WCAs was composed of White Ibises, most of which nested in 2 colonies in Loxahatchee NWR. In WCA 3, the majority of White Ibises nested in the colonies Pocket, 2B Melaleuca, Cypress City and L67. The number of White Ibises in 2001 was 22% smaller than during 2000, but 2.4 times the ten-year average, and 2.2 times the five-year average.

Wood Storks had an exceptionally large number of nests this year, with a total of 2,051 nest starts within the entire Everglades region. The majority of Wood Stork nests, 1,585, were located in Everglades National Park. Within ENP, the Tamiami West colony hosted approximately 1,400 nests, which comprised almost 70% of the entire stork population. Note that this colony is located at the border between WCA 3 and ENP, and that the nesting at this colony is probably reflective of foraging opportunities in both management units. A total of 450 Wood Stork pairs nested in WCAs 2 & 3. In addition, 16 Wood Stork pairs nested in Loxahatchee NWR, an area that typically has not supported any Wood Stork nests. The overall nesting by storks was approximately 10%

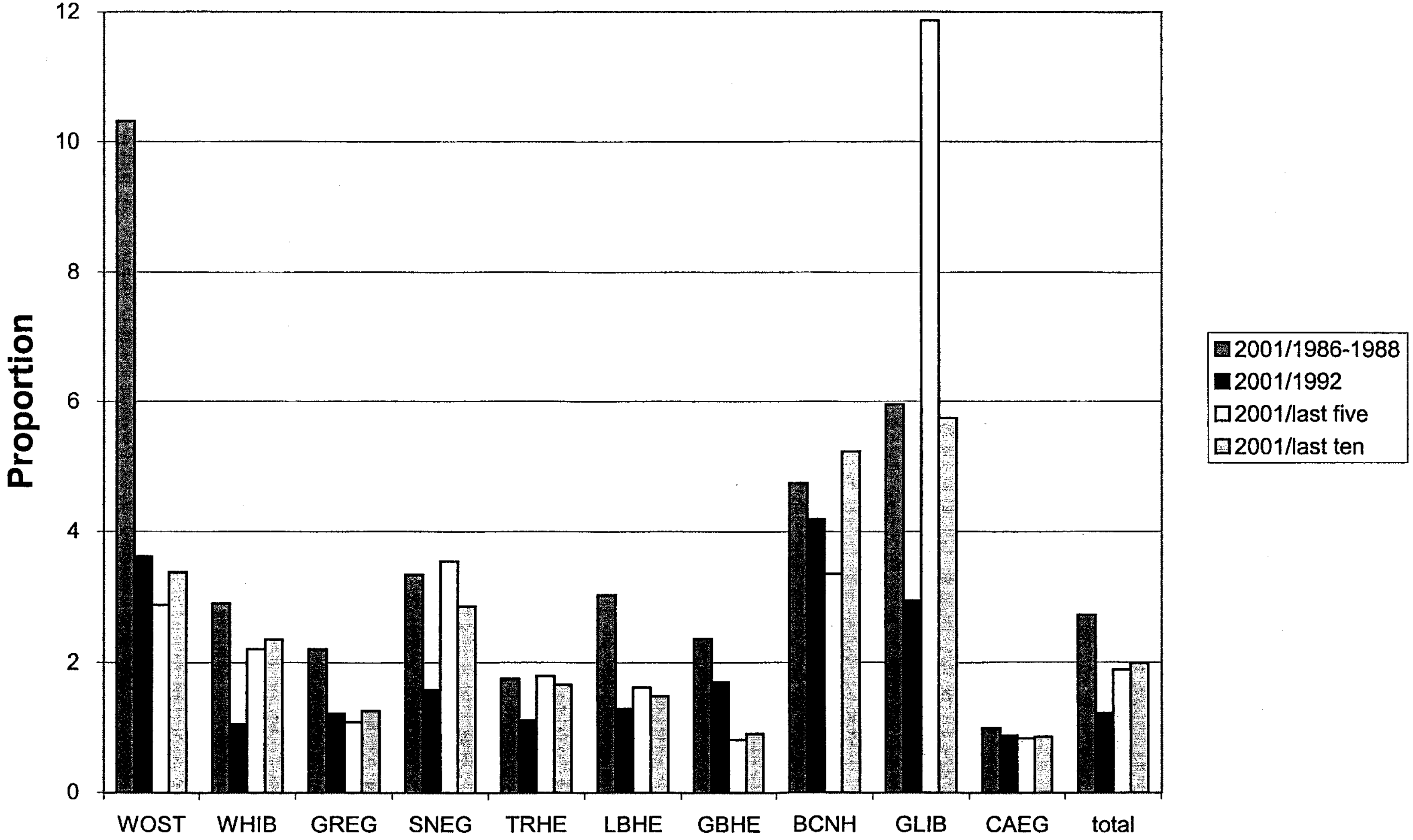

Figure 3.17. Proportion of birds (all species combined) nesting in the Everglades system in 2001 in relationship to previous benchmarks. A proportion of 1 would be the same number of nests in both years or periods being compared.

greater than the large 2000 effort. Both years hosted greater numbers of nests than had previously been seen since the mid-1970's. The 2001 nesting by storks was 3.4 times the ten-year running average for the Everglades as a whole. As in 2000, the storks nested in February and were able to fledge large numbers of young prior to the onset of rains. Overall stork nesting in the Everglades during 2001 was 3.4 times the ten-year running average, 2.9 times the five-year average, and over 10 times the average from the late 1980s.

Two species showed record highs for their nesting effort in 2001. An unprecedented 280 Glossy Ibises nests were recorded in the Everglades this year, all of which were located in the WCAs. This number is almost 12 times the five-year average and almost 6 times the ten-year average for the entire region. This relatively large number of Glossy Ibises was the highest record reported for the Everglades during the past 15 years. Additionally, numbers of Black-crowned Night-heron nests were the highest reported in the past 15 years, with over 650 nests. This nesting effort was 3.2 times the ten-year average. It should be noted however, that our ability to detect these and other dark species is relatively poor, so comparisons with previous years is somewhat weak.

Numbers of small herons were also up this year. Snowy Egret nests were almost 3 times the ten-year average, Little Blue Heron nests were 1.5 times the ten-year average, and Tricolored Heron nests were over 1.6 times the ten-year average.

Within the Everglades ecosystem, the vast majority of nesting was concentrated in the Water Conservation Areas (92%), and the remainder of nests that were in Everglades National Park were primarily in freshwater areas, not in coastal locations (Figure 3.3).

Within the Water Conservation Areas, approximately 45% of the nests were located in Loxahatchee NWR, a record high over the past 15 years. Although the level of nesting in WCAs 2 and 3 was very similar to the ten-year average, total numbers of waders was down by 126% in WCAS 3 and 2 by comparison to the large 2000 nesting event. This could be accounted for in large part by the apparent movement of ibises into two large Loxahatchee colonies.

The large number of nest initiations this year was at odds with the poor nesting success that ensued. We saw repeated abandonments of entire colonies of Great Egrets and White Ibises, and large reductions in numbers of nests at colonies that continued. Of the 4,168 Great Egret nests that initiated in WCAs 2 and 3, we estimate that 80% were abandoned or failed during the early nesting season (prior to the middle of April). The total nesting effort for all species in 2001 was quite similar to the average of the last five years (108%), however, the pattern of abundance by species was quite different from many past years. In general, we saw increases in numbers of nesting attempts in species that are highly social foragers, and whose foraging strategies are adapted for shallow water foraging (White Ibises, Wood Storks, Glossy Ibises, and Snowy Egrets). We also saw decreases in nesting by Great Blue Herons (35% fewer than the five year average), a species which forages solitarily in deep water. Great Egrets also forage in deeper water, and although they showed a 30% increase in nest starts over the five-year average, their nest success was extremely poor by comparison with previous years. These trends may suggest that as we have suspected, there are important tradeoffs in foraging strategies depending on foraging conditions, and that extreme conditions tend to favor species with one set of foraging habits, while others may be at a disadvantage (Gawlik in press).

However, the deep-water foraging species were not the only ones that had poor nesting success. We saw a complete abandonment of the Crossover colony by Wood Storks, of the Big Pond colony by White Ibises, and near-complete (>90%) abandonment of Tamiami West, Pocket and L-67 colonies by ibises. Wood Storks were successful at the Tamiami West colony and produced young, but we estimated that of 1,400 nest starts, only about 450 nests survived, producing perhaps 900 young. There may have been multiple causes for the poor success rates we observed in WCA 2 and 3. The most obvious cause was the strong drying trend, which dried out a number of the colony sites. For example, WCA 3B was without surface water for much of the season (mid-March onward), resulting in abandonment of the majority of nests of Great Egrets at the 3B Mud Canal East colony, and the Heron Alley colony never formed. We believe that many of the early abandonments by Great Egrets were in response to drying conditions. In addition, a large storm event occurred in March, causing water levels to increase dramatically in some areas. Shortly after this event, we found over 90% of Great Egrets abandoned the Alley North colony, and we found considerable wind damage to Great Egret and small heron nests in this colony. However, the physically larger young of Black-crowned Night-herons at this colony seemed to have fared better, perhaps due to initiating their nesting season earlier (January) than the other herons. Rising water has produced large-scale abandonment in many years during the past (Frederick and Collopy 1988), presumably because food becomes temporarily unavailable due to the rising water. Following this rainfall event, the few Great Egret nests which survived seemed to be persistent, and most made it to fledging.

Among White Ibises we saw a repeated pattern of large colony initiations followed within two weeks by complete or near complete abandonment (Tamiami West, Alley North, Big Pond, Pocket, and L67). These were not always in conjunction with periods of rising water, and it was unclear what caused the birds to leave. It is tempting to associate the abandonments with colony drying but we saw examples (Cypress City) where ibises had apparently good nest success despite there being little or no surface water under nests or near the colony for much of the nesting period.

As a result of this pattern in 2001, we had many cases in which it was difficult to know how to estimate nest starts in a colony. For example, we counted several hundred ibises in the Alley North colony in early March this year, engaged in courtship. Yet the site was abandoned prior to the laying of eggs or full construction of nests. We therefore attributed no ibises to that colony. Similarly, we counted several thousand ibises in the Tamiami West colony in early March, and saw courtship and nest building. In the end, the site was abandoned by ibises after only about 100 nests with clutches were completed.

Birds that abandon before clutches are completed may be more likely to attempt a second nesting effort than birds that abandon during incubation or chick rearing . Therefore, it is difficult to describe one nesting effort pattern for the Everglades ecosystem. The timing of abandonments and initiations suggests that many large numbers of birds attempting to nest at Tamiami West and Alley Northmay have moved in March and April to form the large colonies in Loxahatchee. Similarly, later in the season the abandonment of Big Pond by ibises was closely followed by the formation of the Pocket and L67 colonies, suggesting the new colonies may have been renesting attempts by these birds. However, we captured three radio-marked ibises near Tamiami West early in the season showing morphological signs of breeding, but these birds were never relocated in the WCA system following abandonment by ibises at Tamiami West. This suggested that the birds that had attempted to breed then left the ecosystem without renesting. If renesting was frequently occurring in the Everglades, there could have been many fewer nesting pairs than there were nesting attempts.

Analysis of nesting effort and success during 1998 – 2001.

The dramatic changes in nesting effort during the period of study were large enough and sufficiently unprecedented to demand explanation, even if the explanations are partly speculative. The period of 1994 – 1997 was one of generally high water conditions, during which very few storks, ibises, or Snowy Egrets nested, and both numbers and nesting success of Great Egrets and Great Blue Herons increased. During this time, there were no years in which large portions of the marsh surface dried, at least within WCAs 3, 2, and the southern half of Loxahatchee NWR. In contrast, the marsh surface was considerably drier during the period 1999 – 2001, with only about half the WCAs being wet by May of 2000 and 2001, and slightly more during 1999. Nonetheless, this idea of drier conditions is only by comparison with the very wet conditions of the mid-1990's. As outlined in Chapter II, neither stage nor rainfall during 2000 and 2001 could be considered low by comparison with long-term records, and in most water management units, stages were high to normal.

Nesting effort of storks (Kushlan et al. 1975) and ibises (Frederick and Collopy 1989a) has been linked in a statistical way with the rapidity of drying of the marsh surface (drying rates, see Chapter II). This correlation between nesting effort and drying rate certainly held true for the period of 1998 – 2001. In 1998, water levels were high and drying rates low, and nesting effort was the lowest of the four years. Drying rates were substantially higher in 1999, 2000 and 2001, with nesting increasing almost in direct proportion to the drying rate. Although drying rate is therefore correlated with nesting effort during the study period, there may be other important factors that led to the high nesting effort in 1999 – 2001.

First, there is evidence that drying rate alone is a poor explanation for nesting effort in many other years in the record. During 1995, for example, drying rate was virtually the highest on record in many WCAs, yet a very poor nesting year ensued; this was a very high water year, however, and despite the rapid drying, surface water was still quite deep by the middle of the nesting season. Similarly, during 1988, 1989 and 1990, drying rates were extremely rapid, yet little or no nesting occurred in these years. These were years in which most or all of the marsh surface dried during the spring and early summer, and although drying was fast, there was apparently too little water to support foraging in most areas. Thus rapid drying apparently must be accompanied by water levels that are neither extremely deep, nor extremely shallow over much of the marsh. It is possible that the rapid drying of the 2000 and 2001 seasons was accompanied by water levels at or close to some optimum in this regard.

The effect of antecedent drought conditions on fish community dynamics and fish abundance is another possible explanation for the nesting pattern observed. This theory suggests that some aspect of drought conditions causes a flush of exceptionally high densities of small "forage" fishes. Although the mechanism is unclear, the predicted pattern of exceptionally large nestings immediately following the cessation of droughts has been well supported by the historical nesting record (Frederick and Ogden in press). However, the 2000 and 2001 nesting seasons did not conform to the predictions of this hypothesis. Both years qualified as exceptionally large nestings in the context of recent history, yet neither nesting event was preceded by any exceptionally strong drying event. Instead, these years were preceded by an exceptional period of high water (1994 – 1997), with less exceptional, but higher than normal stages through 1999. It therefore seems unlikely that the antecedent drought hypothesis offers much explanation for why 2000 and 2001 had such high nesting effort. However, the 2000 and 2001 nesting seasons offer an important perspective on the antecedent drought hypothesis – although antecedent periods of drought are apparently sufficient to produce extremely large nesting events in the Everglades, they are not the only conditions that will necessarily produce big nesting events.

During 2000 and to a lesser extent 2001, drought conditions prevailed throughout much of the southeastern U.S. This drought resulted in the drying of many marshes, streams and even lakes, leaving much of the habitat typically available to wading birds with little or no surface water. In most cases, wading bird colonies were not even initiated in these dry or drying areas. For example, by late March 2000 only one of the 11 known Wood stork colonies in Georgia had initiated nesting. In north Florida, most wading bird colonies did not initiate, and those that did were not successful. The drought in 2000 was severe enough to affect large areas of freshwater wetlands in Georgia, parts of South Carolina, north Florida and Alabama. South Florida was therefore one of the only places in the region that held water during the drought. Thus most of the wading birds in the southeastern U.S. were left with little habitat during spring 2000, and it is quite likely that the large numbers of birds in south Florida included many birds that typically nest in other states. In support of this hypothesis, Corkscrew Swamp sanctuary also had many more storks attempt to nest than usual during 1999 and 2000; this area was also wet, but has obviously not had the same water management history as the Everglades. Although the drought conditions in 2001 were not as extensive throughout the southeast as in 2000, much of peninsular Florida remained too dry for nesting. It is also possible that there was an effect of prior experience that resulted in many birds returning to nest in the Everglades in 2001, as a result of having had excellent nesting success there in 2000. The influence of prior experience on choice of nesting location is poorly documented.

Finally, there is the possibility that the large nesting events of 2000, 2001, and the somewhat smaller event of 1999 were related to the decrease in mercury contamination recorded over period 1994 – 2001 (see Chapter X). Over this period, a standardized measure of mercury contamination in Great Egret nestling feathers decreased by over 75%, possibly as a result of reduced atmospheric inputs of mercury from local waste-burning facilities (Frederick et al. 2001, in press). This reduction in contamination has been quite significant in predatory fish as well, suggesting that the entire food chain has become considerably less contaminated.

Mercury has many potential sublethal effects on wading birds, including lethargy, altered immunology and blood chemistry, lower fledging weights, altered adult reproductive and parental behavior, altered chick behavior, reduced survival, and effects on hormone levels. Evidence presented in Chapter X suggests that feather mercury levels in adult ibises are associated with elevated progesterone levels at particular stages of reproduction. Although this evidence is suggestive of a causal relationship between mercury and endocrinology, this does not constitute hard evidence of mercury-related effects. Nonetheless, experimental work with other species has indicated a causal relationship between mercury and progesterone production, and it therefore seems likely that the correlative evidence we have presented is indicative of a causal relationship.

Although stage-specific effects have yet to be measured, it is not implausible that mercury contamination could have an effect on the ability of birds to come into reproductive condition. The interplay between day-length, body condition, and endocrinology as causative agents in the initiation of breeding is not very well worked out in many birds. However, if mercury is likely to disrupt the production or reception of hormones, and is likely to alter appetite, health and body condition, it seems quite possible that at some concentration, mercury could alter the thresholds of physiological and ecological cues used by birds to breed. Although the available evidence from the Everglades does not allow us to conclude that reductions in mercury were a contributing factor to the large nestings of the last several years, we are certainly unable to reject this hypothesis, and believe it should be retained as one of a suite of explanatory variables.

Section B. Consequences of nesting date on nesting success and juvenile survival in White Ibises

Introduction

Many species of temperate breeding birds show a decline in nesting success and offspring survival as a breeding season progresses, either due to deteriorating environmental conditions (Verhulst and Tinbergen 1991; Odgen 1994; Brinkhof 1997; Lepage 1999), degrading food sources (Odgen 1994; Frederick and Collopy 1988,1989), poor experience in late nesting birds, or some combination of these factors (Norris 1993; Perrins 1965; Tinbergen and Daan 1990; Daan et al. 1990; Martin 1987). Most research regarding seasonality and offspring survival in birds has been conducted in temperate regions. The models of explanation devised for temperate bird species may not be applicable to the different conditions experienced by subtropical and tropical species. In the Everglades, we know that this pattern (decreasing success over a season) holds for Wood Storks (Frederick and Collopy 1988; Ogden 1994; Kushlan and Frohring 1986; Kushlan et al. 1975). In the case of storks, the primary mechanism is obvious—late-nesting storks must raise their young during the onset of the rainy season, when prey become extremely dispersed and unavailable during rising water (Ogden 1994). However, it is unclear whether other species also suffer the same seasonal decline in nesting success, and if so, if the same mechanisms apply.

An understanding of the generality of this phenomenon and its specific sources has relevance for the success of Everglades restoration since the timing of nesting in several species of wading birds may be related to seasonal hydro-pattern. White Ibises levels in adult ibises are associated with elevated progesterone levels at particular stages of reproduction. Although this evidence is suggestive of a causal relationship between mercury and endocrinology, this does not constitute hard evidence of mercury-related effects. Nonetheless, experimental work with other species has indicated a causal relationship between mercury and progesterone production, and it therefore seems likely that the correlative evidence we have presented is indicative of a causal relationship.

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Introduction

Many species of temperate breeding birds show a decline in nesting success and offspring survival as a breeding season progresses, either due to deteriorating environmental conditions (Verhulst and Tinbergen 1991; Odgen 1994; Brinkhof 1997; Lepage 1999), degrading food sources (Odgen 1994; Frederick and Collopy 1988,1989), poor experience in late nesting birds, or some combination of these factors (Norris 1993; Perrins 1965; Tinbergen and Daan 1990; Daan et al. 1990; Martin 1987). Most research regarding seasonality and offspring survival in birds has been conducted in temperate regions. The models of explanation devised for temperate bird species may not be applicable to the different conditions experienced by subtropical and tropical species. In the Everglades, we know that this pattern (decreasing success over a season) holds for Wood Storks (Frederick and Collopy 1988; Ogden 1994; Kushlan and Frohring 1986; Kushlan et al. 1975). In the case of storks, the primary mechanism is obvious—late-nesting storks must raise their young during the onset of the rainy season, when prey become extremely dispersed and unavailable during rising water (Ogden 1994). However, it is unclear whether other species also suffer the same seasonal decline in nesting success, and if so, if the same mechanisms apply.

An understanding of the generality of this phenomenon and its specific sources has relevance for the success of Everglades restoration since the timing of nesting in several species of wading birds may be related to seasonal hydro-pattern. White Ibises are of particular interest both because they represent the majority of the avian biomass in the wetland (Ogden 1994), and because they display very long reproductive windows (nest initiation ranges from January to September). This flexible breeding schedule, coupled with the nomadic movements of this species, may allow ibises to exploit favorable and spatially unpredictable breeding conditions. The consequences of this flexibility on nest success, juvenile survival, and demographic recruitment in White Ibises are unknown.

Mechanisms for a seasonal decline in nest success

Two possible reasons why early breeders are generally more successful than late breeders have been identified. First, early and late breeders may experience differences in environmental conditions (Verhulst and Tinbergen 1991; Odgen 1994; Brinkhof 1997; Lepage 1999), possibly resulting in a profound influence on the life-history optimization and reproductive decision-making in some species of birds (Daan et al. 1990; Tinbergen and Daan 1990). Lepage et al. (1999) found that growth rates of Greater Snow Geese (*Anser caerulescens*) goslings were slower later in the season compared to earlier in the season with no apparent effects on survival. They attributed the differences in growth rates to environmental factors that were directly related to the date of the season. Great Tits (*Parus major*) were found to have reduced fledgling success later in the season (Verhulst and Tinbergen 1991), attributable to a decline in food resources during the season. In the colonial nesting Guillemot (*Uria aalge*), the onset of nesting was sometimes highly synchronous with other colony conspecifics, regardless of the calendar date (Hatchwell 1991). This strategy may be advantageous due to a decrease in predation through swamping.

Second, quality of parental care may be different in early and late breeders (Price et al. 1988; Brinkhof 1997; Perrins 1970). An association between early breeding and high nutritional state in adults has been established, and females in good nutritional condition typically have higher reproductive success (Perrins 1970; Lack 1968). In many species, older parents tend to nest earlier and achieve higher reproductive success than younger parents (Dow and Fredga 1984; Finney and Cooke 1978). Hughes et al. (1994) found that earlier nesting Greater Snow Geese had smaller home ranges and used better quality feeding habitats than later nesting geese. If parents in poorer condition have to leave the nest more frequently than better-conditioned birds to forage, their young could be left exposed for longer periods of time to any harsh environmental conditions that may exist. This could result in lower offspring success for poorer conditioned parents.

Differences in temperate and tropical bird reproduction

Differences in temperate and tropical bird reproductive success probably exist, making it difficult to apply temperate models of life history strategies to tropical species. For example, tropical birds tend to grow 23% slower than temperate species (Ricklefs 1976; Drent 1975). The tropics also tend to be less seasonal than temperate zones, which may aid in increasing adult survival and decreasing reproductive effort (Martin 1996). Yet, species in tropical areas that experience dry periods tend to breed as seasonally as temperate species (Deshmulch 1986). Inter-specific competition for food is increased in the tropics, which has been shown to lead to increases in niche specializations (Deshmulch 1986). If food is less available in the tropics (Ricklefs 1976) then nestling periods may increase, favoring a reduction in number of broods per year (Martin 1995).

This reduction can lead to an overall reduction in reproductive effort for tropical species (Martin 1995). However, other studies (Skutch 1985) have argued that food is not a limiting factor in the tropics. In addition, young mortality is as high or higher in tropical birds as in temperate birds (Ricklefs 1969).

We proposed to accurately describe the reproductive events of a subtropical breeding bird, the White Ibis, nesting at early and late times of the breeding season in the fresh water wetlands of south Florida. We set out to address the following question: does the timing of breeding affect the condition and survival of fledgling White Ibises within their first year of life? We hypothesized that hatching late in a breeding season negatively affects White Ibis offspring survival compared to hatching early in the season.

To test this hypothesis it was necessary to assume that all nests within a colony are roughly equally affected by environmental constraints at a particular moment in time. If true, we expected to see significantly more eggs surviving to hatching, faster chick growth rates, higher survival rates of nestlings to fledging, higher survival rates of fledglings to independence, and higher survival rates of juveniles for the first year following independence for early compared to late hatched chicks.

To test egg survival rates to hatching and survival rates of nestlings to fledging, we used both the traditional and Mayfield's method of estimating success. We achieved this through monitoring the contents of marked nests in both early and late nesting colonies. Chick growth rates were obtained by taking measurements of first-hatched chicks from marked nests during colony visits. We were unable to devise a method for monitoring survival of fledglings between the time they were mobile until independence from the colony. However, we used fledglings marked with radio transmitters to determine first year survival of juveniles following independence.

By examining the relationships among environmental conditions and reproductive effort of White Ibises in the Everglades we hope to better understand both why ibises breed at different times, and what the consequences of this variable timing of breeding are. Few studies of breeding synchrony have attempted any measurement beyond the clutch or nesting stage. Our objective is to measure the magnitude of the difference in the costs and benefits of breeding early versus late in the season. We expect to find a similar seasonal decrease in survival of White Ibis offspring as observed in temperate species.

Methods

Reproductive success

To monitor nest success in ibises, we first located nesting ibis colonies by systematic flights in fixed wing aircraft (Chapter III), and we confirmed nesting stage during visits on the ground. If the majority of nests in a colony contained fewer than two eggs during our ground visits, we left the colony and returned at a later date. If most nests contained two or more eggs we marked study nests with strips of numbered surveyors flagging. Marked nests were monitored through repeated visits to the colony every five days during incubation and every three days after hatching until the oldest nestlings in the colony were 14 days old. At this point nestlings became too mobile for us to associate with specific nest sites, and at this point we stopped colony visits. Our concern with colony disturbance at this time was that younger birds in the colony might not be able to return to the nest on their own. During every visit to each nest we recorded the nest contents and any evidence of abandonment or failure. The following criteria were used in determining nest abandonment: all eggs in the nest were cold to the touch, all eggs or nestlings were missing from the nest (with no evidence of predation), the eggs were intact on the ground or chicks were dead outside the nest, or the nest was destroyed. Efforts were made to determine if nest contents had been scavenged (post-abandonment) or preyed upon, using signs at the nest and evidence of particular predators (eg Raccoons and other larger mammals) and scavengers (eg blackbirds, crows, grackles). In addition, we weighed the chicks and measured the wing chord, tarsus, and bill lengths of the first hatched chick (=largest chick if hatching order not known) in as many marked nests as could be monitored during the one-hour period we allotted for colony visits.

To determine which nests were initiated early compared to late in the season we first obtained the mean nest initiation date for all marked nests for which we could determine an accurate initiation date, within each colony. We then found the midpoint of the nesting season, using the earliest and latest mean nest initiation dates from marked nests for the season. We then placed a two week buffer around this midpoint and any nests that were initiated during this two week period were not used in the comparison of nest success and hatchability during early and late periods.

Nest success (the probability of any nest start producing at least one young to 14 days old) was estimated using both the traditional method (# successful nests/total # nests for which success or failure could be determined), and Mayfield's (Mayfield 1961, 1975) method of estimating success by pro-rating daily survival for the nesting period. The latter method evolved because nests are more likely to be found if they survive; those that fail early are less likely to be found, and the traditional nest success measure therefore tends to overestimate success, sometimes by some tens of percentage points (Frederick and Collopy 1988). Mayfield's method pro-rates the daily survival of nests found at various stages and integrates these stage-specific survival rates over the entire nesting cycle to achieve an overall estimate of nest success. Nest survival rates were estimated separately for the egg-laying and incubation periods. These rates were then combined to give an overall estimated nest success probability. Nest success rates given are only through the period that the young spend in the nest.

Hatchability of eggs is defined in this study on a per-egg basis, as the number of eggs hatching/number of eggs surviving to a date at which they would normally hatch. This measure is an indicator of eggs which fail to hatch due to embryonic death, infertility, or inattendance of adults. Only nests that hatched at least one chick by the end of the incubation stage were used in determining hatchability. Nests that were abandoned or failed prior to hatch date were not included in the estimation of this measurement.

Juvenile survival

To monitor the survival of fledged juveniles we went back to the colonies when the majority of young were determined to be large enough to safely return to the nest by themselves (oldest chick in a nest >18 days old). Up to 12 people entered the colony simultaneously, capturing juveniles by hand that were large enough to safely carry a radio transmitter, usually 18-21 days old. Captured birds were first inspected to see if they had enough back feather growth to allow for transmitter attachment. Birds were held in cloth bags until processed and all processing took place inside the colony.

For each captured bird we recorded weight, length of tarsus, bill and wing chord, collected scapular feather samples for mercury content and blood samples for sexing, and fitted (see description below) each individual with a 17 gram, 6 volt radio transmitter (American Wildlife Enterprises, Monticello, FL) with mortality sensor for radio tracking. Blood samples were taken from the brachial vein with a 27-gauge needle. Radio-tagged birds were then relocated on a bi-weekly basis through both aerial (fixed-wing aircraft) and ground telemetry tracking (see description below).

Transmitter design and attachment

Our studies have successfully utilized a figure-8 leg loop method to attach transmitters to adult White Ibises (Chapter IX). In order to monitor the survival of fledged juvenile White Ibises we needed a method of transmitter attachment that would allow for the continued growth of the birds. Juvenile ibises fledge the nest at approximately 90% of adult size (Kushlan 1977). However, an ibis' fledge date is at about 28 days and we lose the ability to capture juveniles by day 21-22, a period when the birds are still growing. Another concern was that a growing bird would develop sores as it grew into any pre-fit harness attached before it was fully grown. Adding to the complications of fit, White Ibises are sexually dimorphic, with males requiring larger U.S.F.W.S. leg bands and larger harnesses for radio transmitter attachment.

We modified the figure-8 harness used with adult White Ibises and designed an expandable figure-8 leg loop harness to attach 53 transmitters to juvenile White Ibises. One-half inch wide Teflon ribbon leg loops were precut to the average White Ibis adult harness setting (~34 cm) (Heath pers. comm.). A ¼ inch knit polyester elastic (56% polyester, 44% rubber) thread was then sewn into four places on the ribbon: both anterior and posterior sections of each leg loop. Before knotting the elastic thread, the ribbon was pulled into small bundles ('accordion' style), formed by holding onto the free end of the elastic and pushing the Teflon loop through which the elastic was threaded up against the body of the transmitter. This greatly reduced each leg loop's size, actually pulling the loops closer into the body when placed on a bird, reducing the chance of a bill or leg becoming entangled in the harness. The low tension in the elastic should allow for the expansion of the harness to the adult setting as the bird grows.

We then cut a chiffon patch to the shape of the transmitter leaving an extra ¼ inch around the edges. The chiffon piece was attached to the bottom of the transmitter using 5-minute epoxy and allowed to dry. The loops were sewn together with cotton thread at the point of the adult setting (making the total leg-loop length ~34cm), providing a "weak link" that will allow the transmitter to detach within 1-3 years. Transmitters placed on adult ibises have been retained for over 18 months (Chapter IX).

With one person holding the bird in 'standing' position, another person looped the harness around the top of each leg and across the back. We used epoxy, both along the bottom of the transmitter and on the ¼ inch chiffon overlap, to glue the transmitter in place on the bird's back feathers. This should keep the transmitter fixed in place until the bird has time to grow into the adult setting of the leg loops. With practice two people (one holding the bird) could take measurements, collect feathers and blood samples, and attach a transmitter in less than 8 minutes. Actual transmitter attachment time, including drying of the epoxy, was estimated at less than 4 minutes.

Relocating tagged birds

From the time we attached transmitters, we attempted to relocate all radio-tagged birds on a bi-weekly basis through both aerial (fixed-wing aircraft) and ground telemetry tracking. When we detected a signal, we recorded the general location of the bird(s), their status (either 'alive' or 'dead' according to the mortality sensor), and if possible, tried to visually locate the bird. All transmitters were equipped with a mortality sensor that is motion sensitive. If there is no movement from a tagged bird for 18-24 hours, the transmitter's signal increases to double-time (mortality mode). Attempts were also made to recover all birds with a 'mortality' code. As soon as possible after receiving a mortality signal we would attempt to recover the transmitter from the ground.

Before ibises began fledging from a colony, we relocated tagged birds from the ground. On the ground, signals were received either from on top of dikes (1.5-3.0 km from the colony location) or from an airboat positioned outside (<150m) the colony. Most flights were 5-6 hours in duration and consisted of both flying directly over all colonies with marked birds and flying transects over selected wetland areas in Water Conservation Areas 1, 2A, 2B, 3A, 3B, Everglades National Park, Big Cypress National Preserve, coastal zones from Biscayne Bay to Everglades City, and numerous agricultural fields south, west and east of Lake Okeechobee. A list of each flight's search area is listed in Table 3.3 (see also Figure 3.18). Once all birds had fledged from a particular colony (determined by not receiving any signals from marked birds within the colony on two successive visits), we only flew over that colony if our transect route crossed that area. Transects were spaced 7-9km apart and flown at an altitude of 300-400m and a ground speed of ~100mph.

Results and Discussion

During the 2001 breeding season, the difference in the timing of early and late nesting birds from marked nests within a colony ranged from 27-86 days. We marked and monitored 570 White Ibis nests between 2 March and 7 June 2001 from six colonies

Table 3.3. Area covered on each radio-telemetry flight. Colonies checked each flight are coded as 1=Loxahatchee 111, 2=Loxahatchee 70, 3=2B Melaleuca. See Figure 3.18 for location of Zones 1-5.

Flight Date	Colony	Transect area
4-May	1,2	Only over colonies
16-May	1,2	Only over colonies
31-May	1,2	Only over colonies
4-Jun	1,2,3	Everglades Agricultural Area, Loxahatchee NWR
8-Jun	1,2,3	Palm Beach Co. landfill, Zones 3 and 4.
11-Jun	1,2,3	Coastline of Lk. Okeechobee, Everglades Ag area, Lox NWR
12-Jun	2,3	Palm Beach Co. landfill, Zones 3 and 4.
18-Jun	2,3	Zones 1 and 2
22-Jun	2,3	Zones 2, 3 and northern half of zone 4
25-Jun	2,3	Zones 3 and 4
2-Jul	2,3	Northern half of Zone 3, Zone 5, coastline from Biscayne Bay to Everglades (
3-Jul	2,3	Zone 1, southern half of Zone 2, Lox NWR
9-Jul	2,3	Zone 3 and northern half of Zone 4, coastline from Key Largo to Everglades (
10-Jul	3	Palm Beach Co. landfill, western shoreline of Lk. Okeechobee, Zone 2
13-Aug		Eastern half of the peninsula from Sebring north to New Smyrna
14-Aug		West coast of the peninsula from Tampa north to Cedar Key
21-Aug		Western half of peninsula from Lk. Wales and Lk. Istokpoga, south along the west side of Lk. Okeechobee to Belle Glade

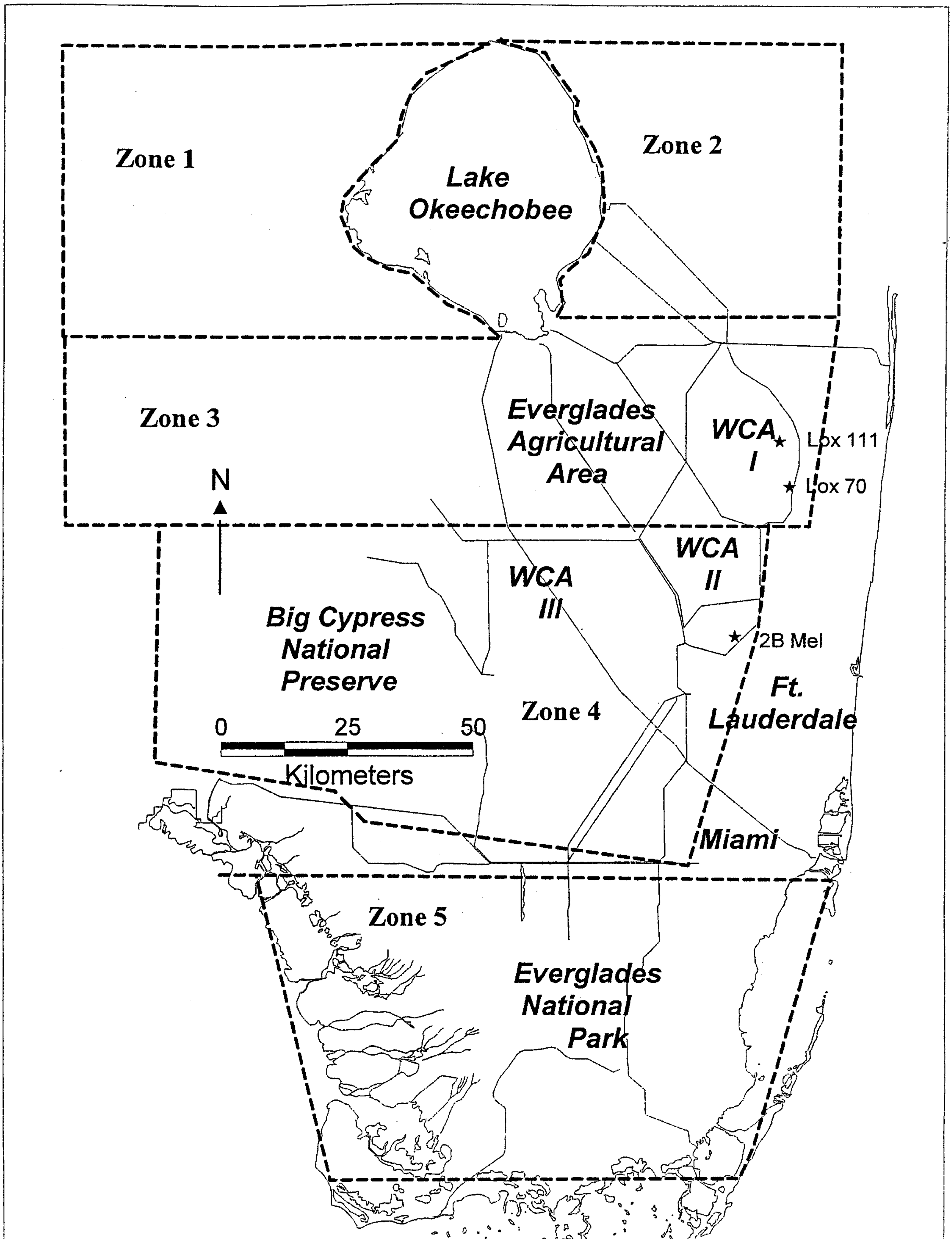

Figure 3.18. Map of south Florida flight zone areas covered in different aerial telemetry flights in 2001.

in Water Conservation Areas 2B and 3A, Everglades National Park, and Arthur R. Marshall Loxahatchee National Wildlife Refuge (Table 3.4). Our monitoring effort represents approximately 4% of the total nests estimated thru aerial survey (no bias correction) from all six colonies. The number of active nests in each marked colony over the season is represented in Figure 3.19.

Table 3.4. Number of nests marked and marking date for each colony monitored in 2001. Date marked is the date any new nests were marked in a colony.

Colony	**Date Marked**	**# of Nests Marked**
Tamiami West (Everglades NP)	2-Mar	24
Lox 111A	23-Mar	163
Lox 111B	28-Mar	40
Lox 70	24-Mar	150
2B Melaleuca	28-Apr	45
2B Melaleuca	25-May	28
Big Pond	11-May	42
L-67	28-May	78
	Total	**570**

Reproductive success

We were able to monitor the overall reproductive success of both early and late nesting birds. In 2001, White Ibises in our six study colonies (combined) had clutch sizes (Mean = 2.50, S.E. = 0.601) comparable to previous years for this ecosystem and in the middle of the range for the species (Table 3.5). Early (Mean = 2.52, S.E. = 0.603) and late nest (Mean = 2.59, S.E. = 0..574) clutch sizes were not significantly different (Wilcoxon-Mann-Whitney, P = 0.329), and individual colony mean clutch sizes ranged from 2.39 to 2.70 (Table 3.6).

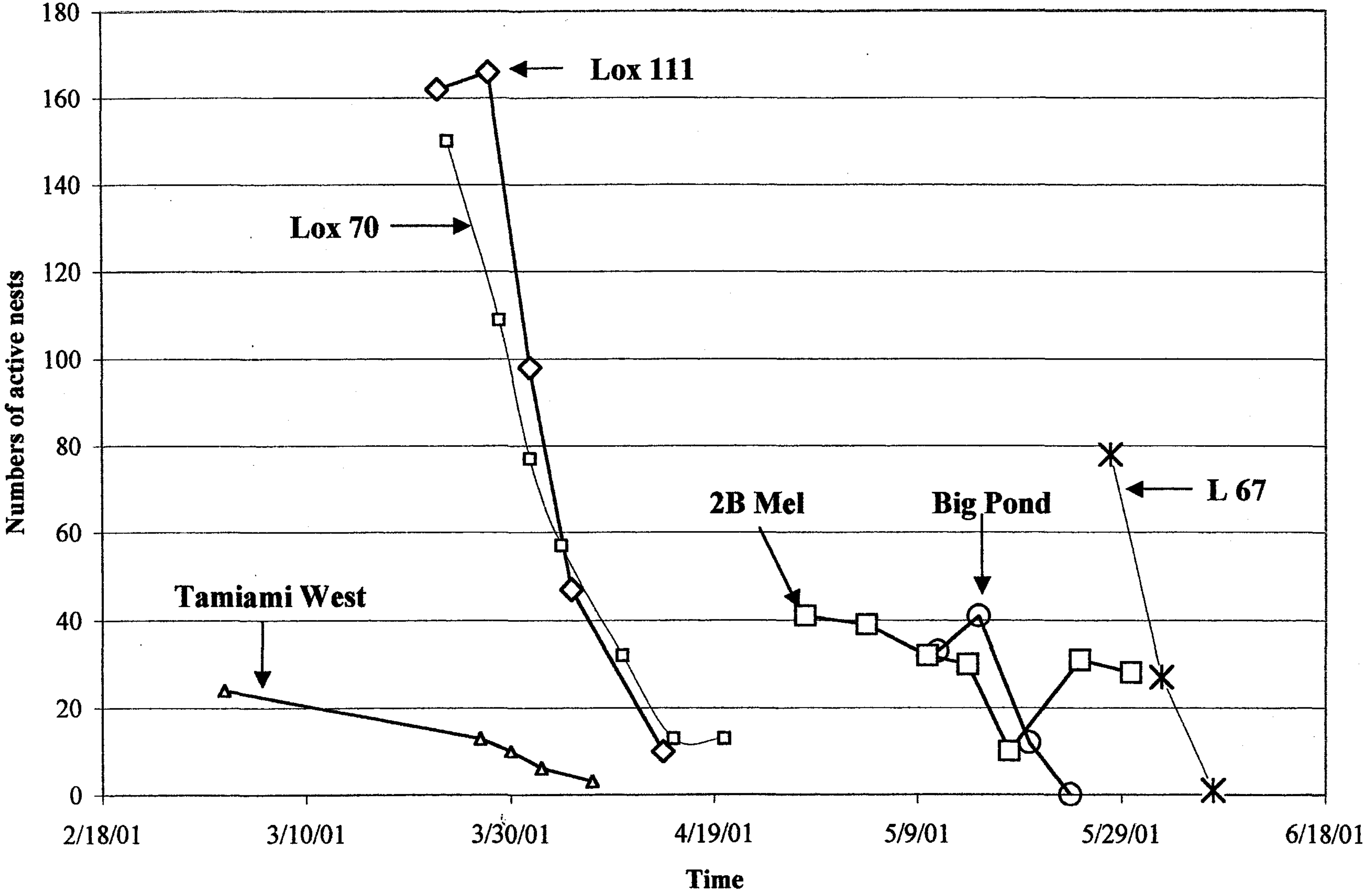

Figure 3.19 Number of active marked White Ibis nests over time for each study colony in 2001.

Table 3.5. Comparison of White Ibis clutch sizes and nest success in this study with those from studies in other years and locations.

			Clutch Size			**Nest Success (%)**	
Study	**Location**	**Year**	**Mean**	**S.D.**	**N**	**Mayfield**	**Traditional**
Hammat 1981	Coastal Lousiana	1977	1.97	0.070	100	10.1	n.a.
Rudegeair 1975	Coastal Everglades	1971-74	2.07	n.a.	208		
Frederick 1993	Loxahatchee NWR	1992	2.20	n.a.	n.a.		
Kushlan 1977	Coastal Everglades	1972-73	2.20	0.640	290		
Allen-Grimes 1982	Coastal North Carolin	1981	2.23	n.a.	312	59	n.a.
Frederick 1993	WCA 3	1992	2.24	0.572	68	16	33.7
Frederick 1995	WCA 3	1995	2.36	0.771	11	12.6	5
Girard and Taylor 1979	Coastal Central Florid	1975	2.40	0.570	77		
Kushlan 1977	Interior Everglades	1972-73	2.45	0.670	51		
Shields 1985	Coastal North Carolin	1984	2.46	n.a.	493		
Kushlan 1977	South Florida Lakes	1972-73	2.49	0.560	202		
This study	**Interior Everglades**	**2001**	**2.50**	**0.601**	**274**	**4.6**	**24.6**
Smith 1994	Lake Okeechobee	1991	2.50	0.570	96	34	39.6
Frederick and Collopy 1988	Interior Everglades	1987	2.53	0.527	162	48.9	60.4
Rudegeair 1975	Interior Central Florid	1973-74	2.53	n.a.	74		
Frederick 1987	Coastal South Carolin	1984	2.55	n.a.	380		
Smith 1994	Lake Okeechobee	1990	2.60	0.620	85	47.8	52.9
Smith 1994	Lake Okeechobee	1992	2.60	n.a.	116	n.a.	35.3-48.3
Shields 1985	Coastal North Carolin	1983	2.64	n.a.	262	57	n.a.
Smith 1994	Lake Okeechobee	1989	2.70	0.480	46	40.5	51
Frederick and Collopy 1988	Interior Everglades	1986	2.72	0.534	94	20.4	30.6
Rudegeair 1975	"Inland Florida"	1926-29	3.08	n.a.	49		

Table 3.6. Clutch sizes of White Ibis nests marked for study in 2001.

Nesting Period	**Location**	**Mean**	**S.D.**	**N**
Early	Loxahatchee 111	2.56	0.612	112
Early	Loxahatchee 70	2.48	0.573	81
Early and Late*	2B Melaleuca	2.39	0.614	46
Late	Big Pond	2.70	0.635	23
Late	L-67	2.08	0.289	12
	All colonies combined*	2.50	0.601	274
	All early nesting	2.52	0.603	197
	All late nesting	2.59	0.574	49

*Includes nests censored from the early vs. late comparisons (N = 28).

Hatchability (percent of eggs that hatched that were available to hatch at the time of hatching) of eggs from marked nests (all clutch sizes combined) was not significantly different for early and late nesting birds (t-test, P = 0.207) (Table 3.7).

Table 3.7. Hatchability (number of eggs hatching/number of eggs surviving to hatch) of eggs in nests marked for study in 2001 (all colonies).

Nesting Period	**Clutch size**	**Mean**	**S.D.**	**N (Nests)**
Overall*	1,2,3 combined	0.854	0.215	86
Early	1,2,3 combined	0.821	0.238	52
Late	1,2,3 combined	0.900	0.161	10
Overall*	2	0.957	0.142	35
Early	2	0.969	0.125	16
Late	2	1.000	0.000	2
Overall*	3	0.770	0.232	47
Early	3	0.740	0.247	34
Late	3	0.833	0.075	6

*Includes 2B Melaleuca nests censored from the early vs. late comparisons.

The 2001 overall hatchability (85.4%) for White Ibises in the Everglades system was the lowest recorded since 1986 (88.8%) (Table 3.8).

Table 3.8. Comparison of White Ibis hatchability* from marked nests in 2001 with marked nests. from WCA 3 in select previous years.

Year	Hatchability
2001	**0.854**
1986	0.888
1992	0.916
1995	0.931
1987	0.972

*Number of eggs hatching/number of eggs surviving to hatch.
Previous years data from Frederick and Collopy 1988.

We are uncertain as to the cause of this low hatchability in 2001. Female birds may be able to dump certain toxins, such as mercury, into their eggs (Lewis et al. 1993) and if this is the case, egg mercury levels may be high enough to affect embryo development (Bryan et al. 2001). Embryonic deformities and mortalities in piscivorous birds have been associated with varying levels of mercury contamination (Heinz 1979). However, while mercury contamination is a possible explanation for low hatchability, it appears unlikely since mercury levels in the Everglades have steadily decreased since 1994 and recent hatchability rates have not been as low as this year (Chapter X).

Overall combined (early and late period nests) nest success was extremely poor (Mayfield's = 4.6%, S.D. = 0.9%) for 2001. Overall early nesting success (Mayfield's = 4.6%, S.D. = 0.9%) was not significantly higher than overall late nesting success (Mayfield's = 2.9%, S.D. = 0.9%) ($Z = 1.44$, $P = 0.075$) (Table 3.9). Early and late nesting differences were evident when nest success was broken down into the incubation and nestling periods. Early nests showed higher success during the incubation ($Z = 6.87$, $P < 0.0002$) period than late nests, while late nests showed higher success than early nests

Table 3.9. Mayfield and traditional nest success of White Ibises from nests marked in the study for 2001. Same letters indicate these values were significantly different.

		Early nesting	**Late nesting**	**Combined**
	Nests	372	152	491
	Nest days	3490	819	4090
	Successful nests	99	30	103
INCUBATION				
	Daily nest success	0.9218	0.851	0.9051
	S.D.	0.0045	0.0124	0.0046
	Incubation period nest success	0.1808^{A}	0.0338^{A}	0.1233
	S.D.	0.0187	0.0104	0.0131
	Nests	100	23	123
	Nest days	707	182	889
	Successful nests	34	21	55
NESTLING				
	Daily nest success	0.9066	0.989	0.9235
	S.D.	0.0109	0.0077	0.0089
	Nestling period nest success	0.2536^{B}	0.8567^{B}	0.3282
	S.D.	0.0428	0.0937	0.0444
OVERALL	**Overall nest success***	0.0458	0.029	0.0405
	S.D.	0.0091	0.0094	0.007

*Probability of a White Ibis nest in 2001 producing at least one chick to fledging (14 days).

Traditional nest success	
Early	0.2661
Late	0.1974
Combined	0.2462

during the nestling period (Z = -5.85, P < 0.0002). When compared to nesting success from previous years, 2001 was at the extreme low end of the scale for the species (Table 3.5).

We estimated the total number of successful White Ibis nests for the six study colonies by multiplying the number of nest starts in a colony by the overall Mayfield nests success probability and then adding across colonies. This yielded an estimated 650 successful nests from 14,155 nest starts for all six study colonies. When compared to actual field observations of the number of juvenile White Ibises from the ground inside and outside of the four colonies that produced chicks in 2001, our estimation of the number of successful nests appears to be low. In addition, the traditional nest success for the study colonies was 24.6% larger than Mayfield's. Previous studies have shown traditional nest success to consistently overestimate nest success relative to the Mayfield method (Frederick and Collopy 1988, Erwin and Custer 1982).

We observed some degree of nest abandonment on all the tree islands visited across all six study colonies, apparently in spite of an island's structure, density of nesting ibises, or frequency of visits to that island. We observed 42.6% abandonment of marked nests in Lox 111 colony by the first day chicks were observed in the colony compared to 72.5% at the same stage in Lox 70 and ~ 45.8% (approximate due to a longer period between colony visits) for Tamiami West. Unmarked nests 10-35m from the marked nest area in Lox 70 were found to have ~53.2% (range 33.3 – 85.7%, N = 78) abandonment at the same stage of nesting. Since all marked nests in 2B Melaleuca were already in the nestling stage (or very near to hatching) when we initially marked the nests, this colony could not be used for comparison with the early nesting colonies because most abandonment occurred during incubation. Overall nest abandonment ranged from 18.3% (2B Melaleuca) to 100% (Big Pond and L-67) (Table 3.10). We observed significant scavenging events in two colonies, Lox 70 and Big Pond.

Table 3.10. Overall abandoment of marked White Ibis nests per colony through the end of the nestling period (nestlings >14 d).

Nesting Period	**Colony**	**% Abandonment**
Early	Tamiami West	*
Early	Loxahatchee 111	66.5
Early	Loxahatchee 70	88.6
Early	2B Melaleuca	25.0
Late	2B Melaleuca	6.5
Combined**	2B Melaleuca	18.3
Late	Big Pond	100.0
Late	L-67	100.0

*Abandoment could not be established for this colony due to the infrequency of visits during the incubation period.

**Includes censored nests not used in the early vs. late comparisons (N = 33).

Due to the nature of the damage to the eggs in these colonies we suspect grackles of scavenging the eggs post-abandonment in Lox 70 and a terrestrial mammal was suspected in Big Pond colony.

Large scale nest abandonments and subsequent low nesting success have been attributed to fast rises in the water level surrounding colonies of White Ibises (Frederick and Collopy 1989, Frederick and Spalding 1994), which can disperse concentrations of prey making them both less available and more difficult to obtain. In mid-April 2000, a strong pulse of rain is believed to have caused the widespread abandonment observed in Loxahatchee NWR that year, and low initial hydrological levels were believed to be the cause in WCA 3. In 1999, we observed some abandonment of late nesting White Ibises after the onset of the rainy season; however, the majority of White Ibises were successful. There were no complete failures of White Ibises in any colonies in 2000, compared with the complete abandonment of two of six marked colonies in 2001. Through aerial surveys in 2001, we observed repeated large scale nesting events followed by complete or nearly compete abandonment in several colonies (see earlier this chapter). From these observations, it does not appear that White Ibis abandonments from marked colonies were associated with a fast rise in water levels in WCA 3 and Loxahatchee NWR in 2001. In addition, it seems unlikely that the extreme drying pattern observed around most of these colonies caused the observed pulses of abandonment.

Human disturbance, via entering colonies, can affect nesting success, with certain periods (ie. courtship and egg-laying) more sensitive to disturbance than others (Tremblay and Ellison 1979). In a study of Tricolored Herons (*Egretta tricolor*), Frederick and Collopy (1989) found no difference in the affect of the frequency of visits on five different measures of reproductive success. In this study, we entered colonies on a regular basis only after the majority of nests were near the completion of egg-laying and the frequency of our visits was less frequent than other studies of reproductive success (Frederick and Collopy 1989, Erwin et al. 1999, Sydeman et al. 1991). We therefore do not believe that our efforts were particularly disturbing, and certainly were within the limits of disturbance enacted in most other studies of nest success. We did observe significant scavenging in Lox 70 and human disturbance has been associated with increased predation and scavenging of nest contents (Frederick and Spalding 1994). However, the increase in nest content scavenging usually occurs while researchers are in the colony and we did not observe any scavenging or predation events in any colonies where we were actively working.

Non-statistical analysis of growth measurements of first-hatched chicks in the nest suggests that late hatched chicks may have been in better condition at any given age than early hatched chicks when comparing size corrected mass (mass / tarsus length^3) to age (Figure 3.20). However, we feel that this conclusion is tentative because our sample sizes were low, our measurements were often not repeated over time more than once per bird, and small miscalculations in the age of nestlings can strongly bias results.

Juvenile success

We radio-tagged a total of 53 juvenile White Ibises (29 early hatched and 24 late hatched birds) from three colonies in order to study first–year survival of fledglings (Table 3.11). Juveniles could not be tagged from the latest nesting colonies we monitored (Big Pond and L-67) since neither colony produced any young. Two additional late-nesting colonies in the Water Conservation Areas (Cypress City and Pocket) were large enough to monitor nesting success, but we could not initially get to either colony to mark nests or chicks due to dry conditions.

Table 3.11. Location, tag date, and number of juvenile White Ibises radio-tagged in 2001.

Nesting Period	Colony	Marking Date	# of juveniles
Early	Lox 111	21-Apr	13
Early	Lox 70	1-May	11
Early	Lox 70	3-May	5
Late	2B Melaleuca	18-May	3
Late	2B Melaleuca	21-May	10
Late	2B Melaleuca	25-May	6
Late	2B Melaleuca	9-Jun	5
		Total tagged =	53

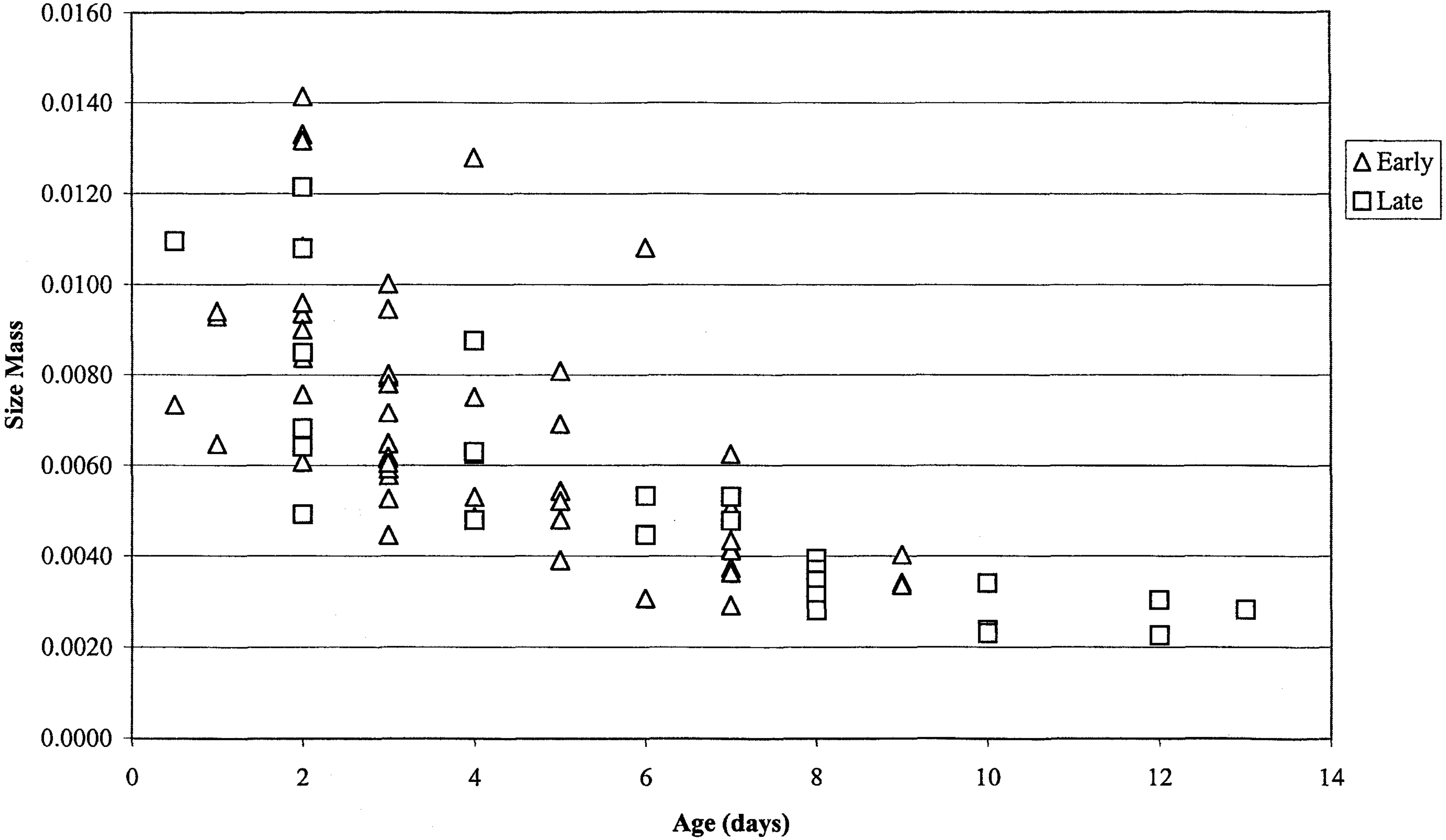

Figure 3.20. Size mass (mass / tarsus^3) ratio to age for Early and Late nesting period first-hatched chicks from marked nests in 2001.

Bi-weekly relocation flights began on 4 June 2001, when birds started leaving the first colony with tagged juveniles, and ended on 10 July 2001. Six additional flights were made, three in both May and August. As of 20 November 2001, we logged 62 hours of aerial tracking and an additional 7 hours of tracking from the ground. We located and recovered the transmitters of three dead radio-tagged birds, one in Loxahatchee 70 and two in 2B Melaleuca. A fourth radio was recovered from inside 2B Melaleuca colony. In the absence of evidence suggesting mortality (juvenile ibis feathers, bones, etc.), we considered this fourth transmitter as having become detached from the bird, and so the fate of this bird remains unknown.

Through aerial telemetry tracking we determined the age marked birds began leaving the colony (independence). To obtain independence age, we considered each tagged chick to be 20 days of age when marked in the colony, and then added to this age the additional number of days until that particular bird was not found on a telemetry flight over its respective colony (evidence of colony independence date was when a bird was missing from a colony on two successive aerial flights, we then used the first date missing as the fledge date). We did the same for the last bird to fledge the colony, using the last date a bird was not found on a flight (see above for evidence of independence date selection). Mean independence age for marked birds was 62.5 ± 6.9 days of age (range 48-87 days) and a majority fledged by 59.4 ± 3.8 days of age. Anecdotal observations showed that while some juveniles fly only a short distance (<5 km) upon first leaving a colony, there was the potential for rapid long distance emigration (>120 km) within the first week after fledging. To date we have located 14 of the 49 (28.6%) marked birds that are assumed to have successfully fledged from their colony (Table

3.12). We considered a bird fledged from a colony if we did not locate its signal (alive or dead) within a given colony on two successive tracking trials.

The majority of relocations of radio-tagged birds to date were in agricultural fields southwest, south, and east of Lake Okeechobee (Table 3.12, Figure 3.21). At two locations, south of La Belle and in southeastern Martin County, the focal birds were located within a mixed group of foraging juvenile and adult White Ibises. A newly cleared field south of La Belle consistently hosted three radio-tagged birds (from two different natal colonies) and at one point the number of adult and juvenile ibises foraging here increased to over 1,500 birds. The small number of relocations of radio-tagged birds in any coastal or inland wetland areas (30.0%, when only considering relocations >5km from natal colony) is interesting as it suggests that juveniles are not using these locations as post-fledgling habitat. Aerial observations through August confirmed low numbers of foraging ibises in south and central Florida in general, with the exception of scattered groups across agricultural fields. Due to repeated aerial surveys over the most-likely areas of occupation, it seems that most of the birds we have failed to locate left the south Florida area entirely. One probable reason for this large-scale departure is the dispersal of prey through increased water levels from the rainy season.

We plan to continue aerial tracking flights over the aforementioned locations in December 2001 and January 2002 when we suspect White Ibis numbers will begin to increase again in Florida due to colder weather farther north. We intend to focus on wetlands, agricultural areas, and large roosts.

Table 3.12. Location of all radio-tagged juvenile White Ibises found outside their colony of origin in 2001.

Location Date	Natal Colony	Bird ID	Dispersal distance (km)	Location
4-Jun	Lox 111	Y11	60	Big Cypress Seminole Indian Reservation
4-Jun	Lox 111	Y5	60	Big Cypress Seminole Indian Reservation
8-Jun	Lox 70	G412	5	SE corner of Loxahatchee NWR
11-Jun	Lox 70	G404	25	NE corner of Loxahatchee NWR
11-Jun	Lox 70	G419	5	SE corner of Loxahatchee NWR
12-Jun	Lox 70	G410	5	SE corner of Loxahatchee NWR
12-Jun	Lox 70	G419	20	WCA 2B
18-Jun	Lox 70	G406	120	Hendry County
22-Jun	Lox 70	G422	120	Belle Glade
25-Jun	Lox 70	G405	15	Housing development just S of Lox NWR
25-Jun	Lox 70	G406	115	Hendry/Collier County line
2-Jul	2B Melaleuca	B282	100	Moonshine Bay, Lake Okeechobee
2-Jul	2B Melaleuca	B292	115	South of La Belle in Hendry County
2-Jul	Lox 70	G412	120	South of La Belle in Hendry County
3-Jul	Lox 70	G406	120	South of La Belle in Hendry County
3-Jul	Lox 70	G412	120	South of La Belle in Hendry County
3-Jul	2B Melaleuca	B292	115	South of La Belle in Hendry County
3-Jul	2B Melaleuca	B286	65	Belle Glade
9-Jul	Lox 70	G406	120	South of La Belle in Hendry County
9-Jul	Lox 70	G412	120	South of La Belle in Hendry County
9-Jul	2B Melaleuca	B292	115	South of La Belle in Hendry County
10-Jul	Lox 70	G421	75	Ag field west of 711 in Martin County
14-Aug	Lox 111	Y8	375	Withlacoochee Bay near Yankeetown

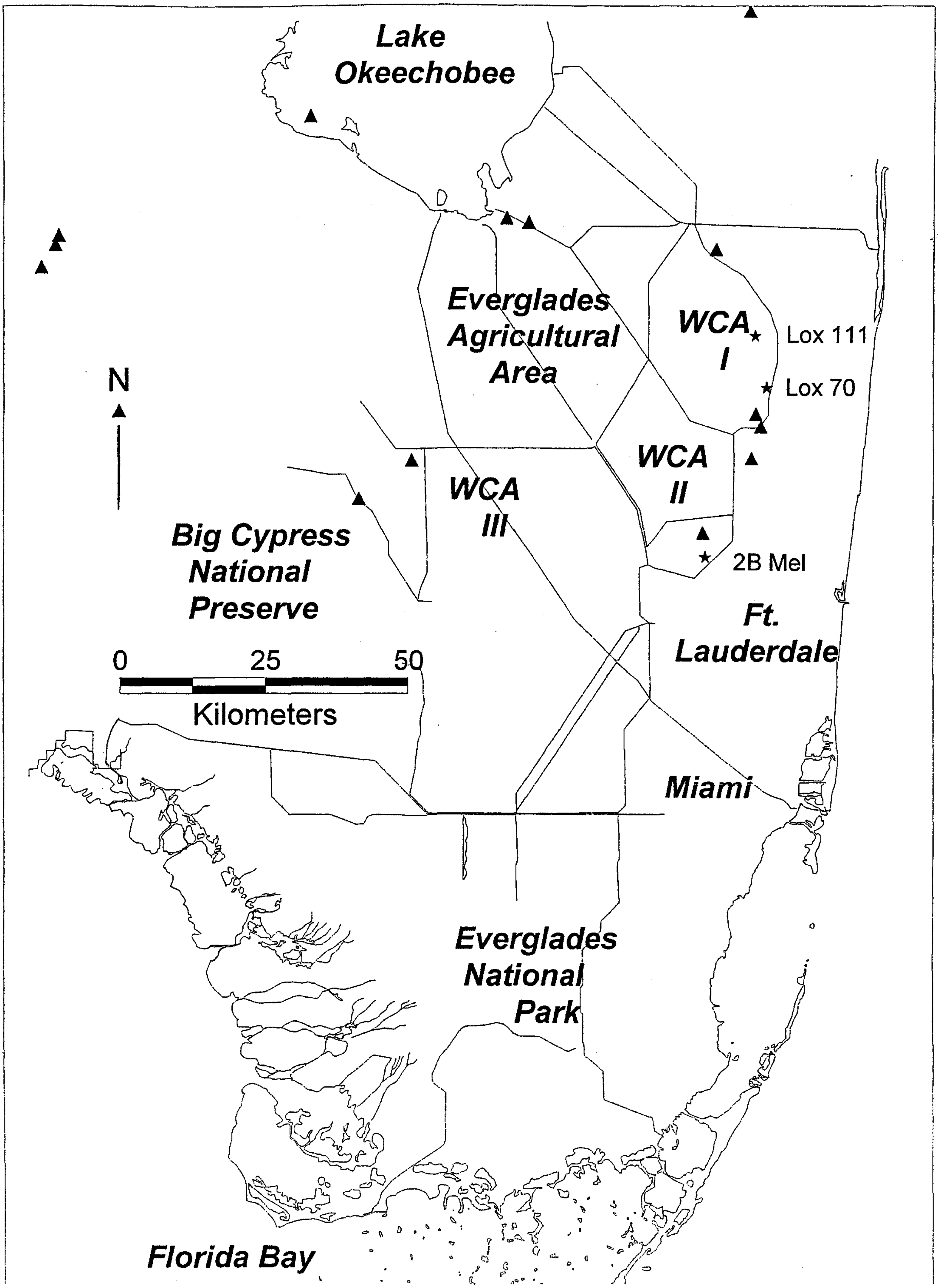

Figure 3.21. Map showing location of all radio-tagged juvenile White Ibises found outside their colony of origin in 2001.

Section C. Degradation of colony substrate

In past reports, we have noted considerable degradation of active or former colony substrate in WCAs 2 and 3. This is a continuing trend that appears to pose some limits on available nesting substrate for wading birds. The process seems to be characterized by prolonged hydroperiods (>4 yr continuous surface water) in the moderate to deeper elevational depths of the WCAs, leading to increased mortality of vegetation. Although willow is highly tolerant of flooded conditions, it will die if its roots are not dried with some frequency. The prolonged high water of the seven years of the 1990's (1993 – 1999) has apparently resulted in mass mortality of willow in several colonies (see Table 3.2).

Table 3.2. Current condition of large willow heads in WCAs 2 and 3, as estimated from aerial surveys.

Colony or former colony name	Estimated percentage of Former willow left
Big Melaleuca	< 1/3
L-67	<1/8
False L-67	<1/8
Andytown	0
Cyress City	<1/8
Alley North	<2/3
Pocket	<1/2

For example, both Andytown and Cypress City (immediately south of Alligator Alley in NE WCA 3, See Figure 3.5) are virtually gone, and all nesting at Andytown has ceased L-67 in central WCA 3 was, up until the mid 1990s, a very large willow tree island (>0.5 km in length) and a large, active colony. With the exception of a tiny battery island at the north end, the willow and buttonbush vegetation has now been killed entirely, and nesting has all but ceased at this location. To a lesser extent, the same process has occurred at Big Melaleuca colony, to the extent that we had some trouble finding the colony from the air for the first time in 1999. The Alley North colony has had considerable die-back of willow in the central part of the colony, and willow coverage has been reduced by at least one third. With the possible exception of the Pocket site, these colonies are the only very large willow heads left in WCA 3. These large willow heads are also important roost and nesting sites for the endangered Snail Kite.

Section D. Effects of fires on foraging and breeding wading birds in the Everglades

Many studies have documented the relationships between habitat, fire and avian abundance (Howard et al. 1959, Vogl 1973, VantHul et al. 1997, Reynolds and Krausman 1998). However, the direct effects of fire on bird survival are rarely reported (Bigham et al. 1964, William and Stasiak 1979). Birds directly affected by fire are usually ground nesters whose eggs and/or chicks are vulnerable to ground-fires (William and Stasiak 1979), or waterfowl which are flightless during wing molt (Hohman et al. 1992). Flighted, adult birds seem well equipped to escape dangers from fire and smoke. Here we report on the effects of Everglades fires on large breeding colonies of wading birds and on the fire-related death of approximately 50 adult White Ibises found away from colonies.

We studied the effects of fires on wading birds in northern WCA 3A of the central Everglades . This area is a seasonally inundated grassland dominated by extensive stands of sawgrass (*Cladium jamaicense*) and cattail (*Typha angustifolia).* The extremely flat, open habitat is occasionally broken by cypress heads and tree islands. Lower elevation islands are vegetated with either willow (*Salix caroliniana*) and buttonbush *(Cephalanthus occidentalis*), cypress, or introduced melaleuca trees (*Melaleuca quinquinerva*). A mix of tropical hardwoods is found on islands of higher elevation (Craighead 1971, Gunderson 1994).

Effects of fire on wading bird breeding colonies

On May 2, 1994, we observed the lightning ignition of a ground fire north of Alligator Alley (Interstate Highway 75) and immediately west of Florida SR 27 in northeastern WCA 3. This fire burned over 2,833 hectares over one week. The burned area consisted of contiguous stands of sawgrass and cattail, with widely dispersed tree islands. The study island was large (cf 2 km greatest dimension), dominated by willow and buttonbush, and embedded in a matrix of cattail and sawgrass. This tree island, (variously referred to as "Alley North" and "Rescue Strand"), is the site of one of the largest wading bird colonies in the WCAs (26.11.910 N; 080.31.330W). At the time of the 1994 fire, the colony contained approximately 2,100 wading bird nests (including White Ibises, Glossy Ibises, Black-crowned Night Herons, Great Egrets, Great Blue Herons, Snowy Egrets, Roseate Spoonbills, Anhingas, Tri-colored Herons), and Little Blue Herons). On 8 May 1994, we found that most of the grassy vegetation surrounding the colony was burned although the lower stems and roots of grasses had been protected by shallow surface water (c.f. 2 – 10 cm). The shrubby vegetation within the colony showed no evidence of fire, even though the grassland vegetation on the immediate borders had obviously burned. Walking through the colony, we found no evidence of nest abandonment or of dead or moribund chicks of any species, despite the thick smoke that drifted into the colony during the fire.

On 16 April, 1999, a larger fire began in the same area, apparently from anthropogenic ignition. The fire burned 70,010 hectares north of Alligator Alley before ending on 30 April. During 1999, the Alley North colony contained approximately 8,000 nests of the same species as used the colony during 1994. As in 1994, the sawgrass and cattail surrounding the Alley North colony was burned to the ground, but the roots were protected by 2 – 5 cm of water or saturated soil. The vegetation within the colony did not burn. The 1999 fires also burned around the Mud Canal colony (26.00.60N, 080.32.50W) south of Alligator Alley, but the colony vegetation, and the nesting birds were similarly unaffected.

We conclude from these examples that under moderately dry conditions (eg. soil still moist or some surface water) green willow and buttonbush are unlikely to burn, and that fire poses little risk under these conditions to nesting wading birds in the Everglades. Unlike tree islands dominated by tropical hardwoods, the substrate of willow tree-islands is either lower than, or at the same level as the surrounding marsh. Therefore, the willow and buttonbrush colonies are likely to be as wet or in some cases in deeper water than surrounding areas. Further, willow and buttonbush do not tend to accumulate dead aboveground biomass. Instead, theycreate a moist, poorly flammable humus (Craighead

1971) which provides relatively little fuel to initiate or sustain fires, especially when water is at or is close to the soil surface. Large wading bird colonies are located almost exclusively in willow and buttonbrush tree islands in the central Everglades (90% of colonies in 1994, see Frederick 1995). Although this preference for nesting in wet or deep water areas may arise primarily because of the nesting birds' need for a water barrier beneath or surrounding the colonies for protection from mammalian predators (Rodgers 1987, Frederick and Collopy 1989), we suggest that nesting in willow colonies also provides a degree of protection from fires in wetland habitat.

Fire-related mortality away from colonies

As part of a study of White Ibis reproductive physiology, on 1 April 1999 we trapped and radio-tagged a female White Ibis near the Alley North colony in northern WCA 3A. Subsequently, this bird was identified through her activities as a breeder in the colony. On 21 April, this bird's transmitter gave a mortality signal, located approximately 7.6 km northeast of the colony. Upon reaching the site on 24 April, we found the carcass of the marked bird as well as approximately 50 other dead adult White Ibises. The birds were found within a 15 X 15 m space in the northwest corner of a stand of dense cattail (75 X 50 m), with a few dead birds scattered up to 150 m from this concentration. The cattail was dessicated and brown, but not burned to the same extent as the surrounding sawgrass. All birds were found ventral side down. The carcasses were badly decomposed, and the feathers were charred and blackened. We concluded from the vegetation and the condition of the birds that the fire had passed across the cattail area relatively quickly.

Direct effects of the fire seem to be a plausible explanation for the death of the birds. The birds may have been debilitated by smoke inhalation, or trapped at the cattail island with dense, low smoke overhead from the burning surroundings. The birds may have gone to the cattail stand to take refuge from the fire. The birds may also have been purposely foraging in close proximity to the fire line, as a result of insects or other prey being driven by the smoke and flame (Smallwood et al. 1982). The birds may have been unable to fly because of low, thick smoke, which could happen with a rapid wind shift. Although the birds could also have been killed by lightning strike, the association of nearly all the birds with the only unburned patch of vegetation would be surprising from a spatially random process such as lightning. Indeed, the concentration of birds in this relatively unburnt area suggests strongly that they were seeking refuge from fire and smoke.

Previous work has shown that nests and eggs located on the ground are the most susceptible to fire, with an assumption that flighted birds could easily escape fire. Our report suggests two exceptions to these general rules. First, we found apparent selection of the least flammable vegetation by nesting ciconiiform birds, as well as little damage to nests during a fire, even to those of ground-nesting species. Second, we found a group of dead adult birds whose death was most easily interpretable as being caused by fire, suggesting that there may be costs to foraging or flying in and around fires, even for active, flighted adult birds.

CHAPTER IV: BIASES IN MEASURING SIZE OF WADING BIRD BREEDING POPULATIONS

Part 1. Observer variation and accuracy in estimating large numbers of nesting birds: a controlled simulation

Introduction

Nearly all counts or estimates of wildlife are subject to various biases, including the ability to detect animals that are present, and the ability to count animals that are visible (LeResche and Rausch 1974, Caughley et al. 1976, Prater 1979, Gibbs et al. 1988). These biases can significantly affect estimates of the size of aggregation, density and population. Estimates are known to be affected by various factors, including vegetation density, size, shape and dispersion of aggregation (Erwin 1982). The most common error for observers is to undercount (Erwin 1982, Kadlec and Drury 1968, Dodd and Murphy 1995). Training and experience have generally been found to be associated with a decreased tendency to undercount, but there is little evidence that age, prior experience or feedback training have any effect on the accuracy of estimates (Erwin 1982, Kemp 1984).

Visual estimation of large numbers of colonially nesting or aggregated birds has frequently been used to monitor the size of populations, to use waterbird reproductive responses as biological indicators (Ogden 1994, Custer and Osborn 1975, Erwin and Custer 2000), and for many kinds of research. Such estimates must contend with several sources of variation in estimates, including vegetative occlusion of some nests, variations in density and size of aggregations, and differences in the visibility of species. In addition, large colonies may be more difficult to estimate than smaller colonies. Colony sizes may range from tens to hundreds of thousands of birds.

The use of visual estimation for these situations has met with considerable variation in success. McCrimmon (1982) found that aerial visual estimates were quite comparable to ground counts for nesting Great Blue Herons. In the same species, Gibbs et al. (1988) found that aerial visual estimates averaged 87% of ground counts. Dodd and Murphy (1995) found that variation of visual estimates of Great Blue Heron colonies in South Carolina was greater than 20% of the true value (determined by ground counts), but suggested that aerial estimates were acceptable for detection of a 15% annual change in numbers for a statewide survey. Erwin (1982) asked observers to estimate aggregations of Canvasbacks (*Aythya valisneria*) on a uniform background from photographs. Although there was relatively poor accuracy for daily estimates, "population estimates" of a total of 50 photographs over a period of 5 days were with one exception within ten percent of the total.

Other studies suggest that visual estimation techniques have much poorer accuracy. Rodgers et al. (1995) compared aerial visual and ground counts of Wood Stork colonies. Although degree of vegetative cover had no effect on accuracy of estimates, the 95% confidence intervals of aerial estimates were large (–75 to 206% of ground counts), with variance of aerial estimates proportional to the square of the ground count. There was a significant tendency for observers to confuse Wood Stork nests with those of Great Egrets, another large white-colored species that nests in the tops of trees. Rodgers et al. recommended caution when using raw estimates from aerial surveys, as there was a tendency to bias for colonies with a large proportion of white-plumaged species. Aerial counts estimates of seven ciconiiform species nesting in a single mixed-species colony in Florida had between 32 and 100% error by comparison with ground counts (Kushlan 1979). Kadlec and Drury (1968) found that the variance of aerial counts of Herring Gulls (*Larus argentatus*) were proportional to the square of ground counts, and suggested that aerial counts were "not adequate" for obtaining population estimates of nesting gulls. Similarly, Hutchinson (1979) found that 95% confidence intervals of aerial surveys were ± 140% of ground counts for gulls, and ± 56% for Double-crested Cormorants (*Phalacrocorax auritus*).

With the exception of the study by Erwin, these studies have used ground counts as the "true" number of birds, with the assumption that there is little or no bias in those counts. While this may be true for some situations, it is especially unlikely in vegetated colonies.

This information collectively suggests that aerial visual estimates of large aggregations of birds may sometimes be associated with high variances and poor accuracy. Many of the historical and current large-scale surveys of colonially nesting ciconiiform birds in the U.S. have relied heavily on aerial survey techniques (e.g. Custer and Osborn 1975, Portnoy et al. 1977, Ogden 1976, 1994, Texas Colonial Waterbird Survey 1990, Frederick et al. 1991, Runde et al. 1992), and the interpretation of these surveys depends heavily on the measurement of biases.

We examined accuracy and observer variation in counts of large numbers (200 - 6000) of densely nesting birds in vegetated situations. We placed known numbers of scaled model birds on a physical scaled model of a wading bird colony. Trained biologists repeatedly estimated the numbers of birds in a series of trials. We also compared true numbers with photographic counts of the same trials. The model ensured that the numbers of actual birds were known and that the numbers of birds could be changed rapidly for multiple counts in any testing session. These advantages effectively allow the vegetation to remain a constant in all tests, and dramatically reduce any potential bias in the "true" counts.

Methods

We constructed a scaled model of a large mixed-species wading bird colony, modeled after a representative colony in south Florida. We covered a 122 X 144 cm sheet of 19mm thick plywood with plastic "grass" carpet, painted with flat green paint, and occasional hobby modeler's shrubs and trees. Grasses were denuded in some areas using a small handheld torch to mimic the pockets of low-growing vegetation typical of many colonies. All aspects of the model (vegetation heights and densities, size of colony, size of birds) were 0.0063 times normal size. At this scale, the eye of a standing observer above the model placed on the ground would be equivalent to an observer looking at the colony from an altitude of between 240 and 320 m, which are typical aerial survey altitudes.

"Birds" were represented by alfalfa seeds painted white, corresponding to the size and rough shape of an adult White Ibis. We pre-counted seeds using an agricultural seed counter. The measured accuracy of this method averaged over 98% (10 trials, actual seed number between 30 and 800).

We tested the abilities of biologists to estimate randomly picked numbers of targets spread on this colony model. We contacted biologists in private, state and federal natural resource agencies who had some prior experience counting animals (not necessarily birds); participation in the study was by informed consent only and anonymity was guaranteed through procedures (below). We located 18 biologists who had some previous experience estimating numbers of wildlife, not just birds. Since our model could not support 18 viewers at once, we conducted the experiment over three sessions, between 17 November 2000 and 10 August 2001. All sessions were identical and did not offer different treatments. Each session consisted of 20 trials each, presenting a different number of seeds to estimate for each trial. Seeds were scattered in a fairly uniform density by laying a grid over the model that was divided into 10 cm^2 sections. Approximately 100 seeds were scattered in each section. The numbers of seeds were randomly predetermined from each of 14 categories. The order of presentation of trials was randomly determined, but all sessions had the same order of presentation. One trial was omitted in Session 1 due to spillage of seeds, while the last four trials were omitted from Session 3 due to deteriorating lighting conditions.

Prior to each trial, observers were allowed to view randomly spaced groups of dots on white paper representing 50, 100, 500 and 1,000 targets. All observers (range: 5-9 per session) viewed the model by slowly walking together around the model for 60 seconds (1 bout). Each trial consisted of three of these 60-second bouts, and observers wrote down their estimates after each bout on a standardized data sheet. Following the third bout, observers then wrote down a final, "best guess" estimate for the trial, with instructions that the final number did not need to have any relationship with the preceding three bout estimates. During the walking, we asked observers to keep moving, and observers were allowed to alter their "altitude" by adjusting their posture.

Following the entire session (range: 1.75 – 2.50 hours), all observers were asked to fill out a brief questionnaire, with details about prior experience, age, use of corrective previously surveyed was classified as small (1-999 individuals), medium (1000-9999 individuals), and large (more than 1 million individuals). We also classified our trial colony sizes as small (1-2000 birds), medium (2001-4000), and large (4001-6000). We analyzed the effects of these factors and education level and corrective eyewear with a repeated measures analyses of variance. Age effects and fatigue effects were analyzed with correlation analyses with average individual error as the covariate. If variables did not meet test assumptions (normality and homoscedasticity) we used equivalent nonparametric tests. Analyses were preformed on SAS software.

Results

Estimation of error among observers.

The overall tendency among observers was to undercount (81% of all estimates). The mean underestimate (N=255) varied from the true value by –48.61% (SE = 1.41%). The mean overestimate (N=59) varied from the true value by 54.92% (SE = 7.15%). When total overestimates and underestimates were combined, the mean error for all estimates by all observers was –29.16% (SE = 0.57%, Figure 4.2). This value demonstrates that the average tendency by observers is to underestimate. Because overestimates canceled out underestimates, we examined the absolute value of total observer error (mean = 49.80%, SE = 7.54%, Figure 4.3). This value illustrates that the

Figure 4.1. Questionnaire for observers participating in colony estimation experiment.

Questionnaire: Your number__________

Please answer the following questions. We will match this questionnaire with your counts but the person doing the analyses does not know who participated in the counts. Likewise, Peter and Becky never see the questionnaire, so they cannot match the counts with the counter.

1) How old are you? (Please circle number of years) 20-25 26-30 31-35 36-40
41-45 46-50 51-55 56-60 61-65 66-70

2) Have you ever counted animals before in a survey or census? Yes No
If yes, please circle all that apply:
<u>Animals counted were</u>: Small Birds (passerines), Large Birds, Small Mammals (rodents), Large Mammals (deer), Reptiles, Amphibians, Fish

<u>State of animals:</u> Animals were moving Animals were stationary Mixed

If you have done numerous types please describe: (e.g. migrating raptors = moving large birds, and stationary amphibians = lifting rocks in a stream).____

3). What is the largest number of animals you have attempted to count prior to this exercise?

4) How long ago was the last time you conducted a survey?________________

5) Approximately how many surveys have you done?_______________

6) Do you wear corrective lenses?______________

7) What is your level of education?_____________

8) How do you think you did?

Well estimates within 0-15% error
Good estimates within 16-30% error
Fair estimates within 30-55% error
Poor estimates within 55% or more error

9) Do you think this exercise is a good mimic of real life situations? Yes No

demonstrates that the average tendency by observers is to underestimate. Because overestimates canceled out underestimates, we examined the absolute value of total observer error (mean = 49.80%, SE = 7.54%, Figure 4.3). This value illustrates that the average estimation of colony size was off by approximately 50%, as either an overestimate or an underestimate of the true number. For all trials, there was great variation among observers, as well as within a single observer (Figures 4.2-4.3)

We expected that estimation ability would decrease as "colony" size increased, but Table 4.1 shows that this did not have a significant effect, at least within the range of 250 – 6000 seeds that we experimented with (ANOVA, F = 0.21, df = 2 and 262, P=0.8076). We also used a Spearman rank correlation to determine if fatigue had a significant effect on estimation ability. Estimation ability did not significantly decrease as the trial number increased within sessions (F=0.97, df = 19, 296, P=0.4992).

We found no significant effects of total number of surveys previously conducted, date when the observer last conducted a survey, largest number of animals previously surveyed, highest education level, or the use of corrective lens on estimation error (Table 4.1).

Error from photographic counts of seeds on the model.

Counts of photographs taken of each trial during the first two sessions resulted in a mean aggregate error (both over and underestimates combined) of –13.17% (SE = 3.65%). Approximately 51% of the photo counts were underestimates. The absolute value of the mean error in photographic counts was 20.98% (SE = 3.94%). Using a Spearman rank correlation test, we found a negative correlation between total number of

Table 4.1. Effects of various factors on ability to estimate large

numbers of birds.

Factor	Categories	d.f.	F	P
Size of Colony	<2000 2000 - 4000 >4000	2, 262	0.21	0.8076
Total # of Surveys previously conducted	0 - 50 100 - 500 >500	2,15	0.1	0.9063
Last survey conducted	<6 months 1 - 2 years > 2 years	2,15	0.22	0.8047
Largest # of Animals previously conducted	100's 1,000's 1,000,000's	2,14	1.16	0.3432
Highest Education Level	Bachelor Master Ph.D.	2,15	3.17	0.0711
Use of corrective lens	Yes No	1,16	0.98	0.3376
Fatigue*		r_s=-0.393		0.0780
Age*		r_s=-0.005		0.9835

* Spearman rank correlation test

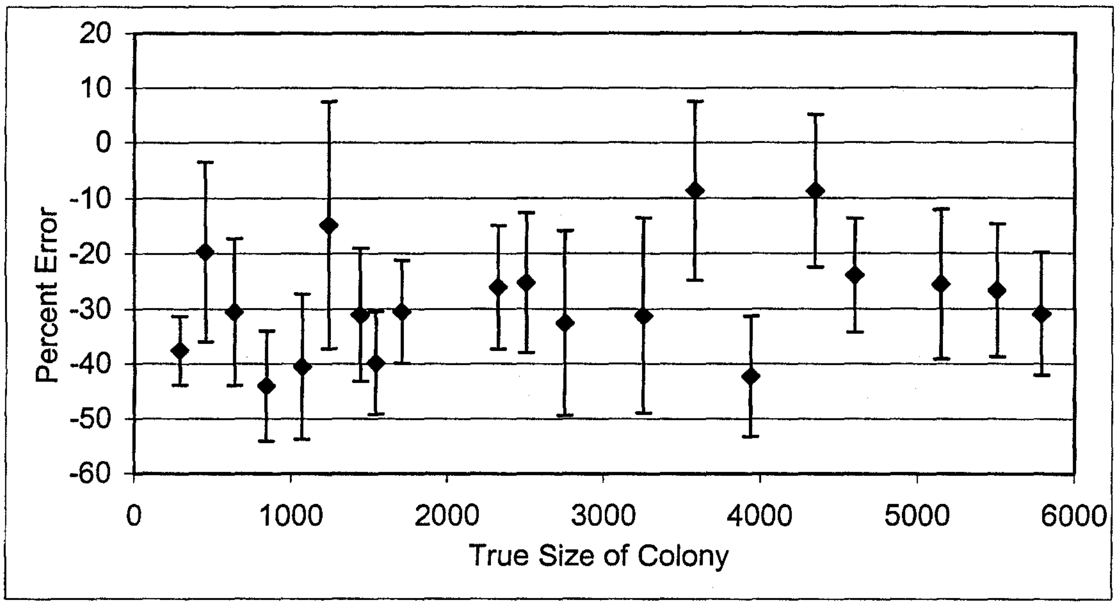

Figure 4.2. Estimation ability among observers (mean percent per colony size ± 1 SE).

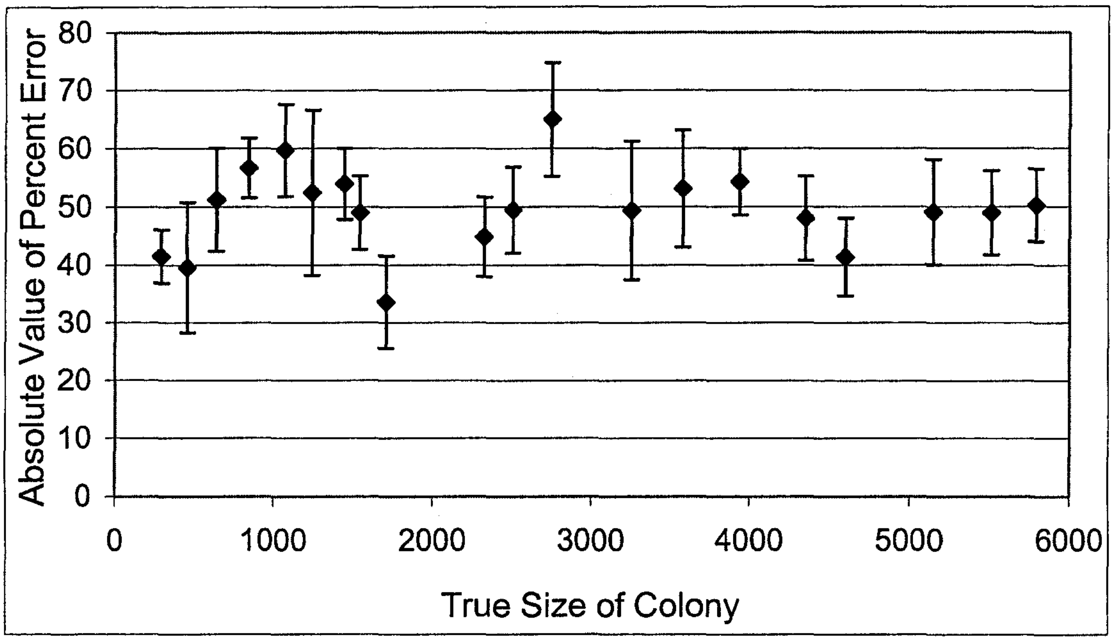

Figure 4.3. Estimation ability among observers based on the combined absolute value of estimation error (mean percent ± 1 SE).

seeds per trial and the seed counts from photographs (r_s=-0.55, P=0.0002). As the colony size increased, the underestimates also increased. Absolute values of mean photographic counts had a lower mean error (20.98%) in estimating colony size compared to absolute values of mean observer estimates (49.80%) ($F_{1,18}$ = 5.66; P = 0.0287, Figure 4.4).

Discussion

These results indicate that there is considerable variation among observers in estimation error, and that this variation is unpredictable if observers change regularly. Our results indicate that undercounts were by far the most common error, and estimates of birds in vegetated habitats from both aerial or photographic surveys should therefore be treated as underestimates. The absolute value of the mean error among trials demonstrates that in general, even experienced observers are miscounting by 50% on

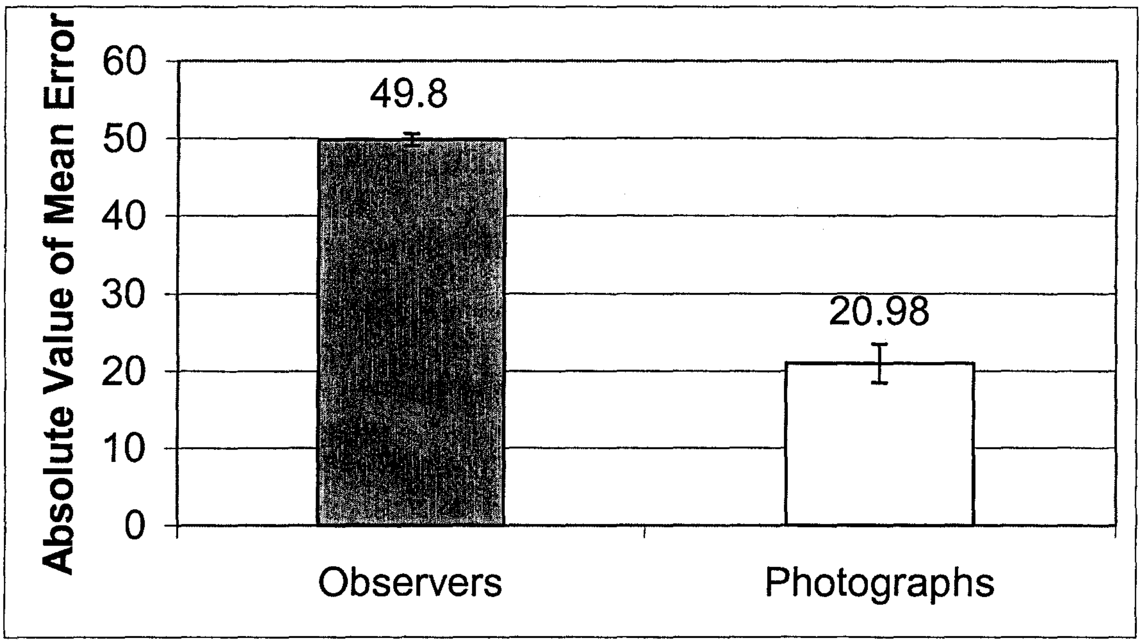

Figure 4.4. Comparison between mean absolute value of estimation methods: observers (SE=0.75); photographs (SE=2.51).

average. Although multiple observations of the same colony by separate people may result in a decreased total error due to canceling effects from over- and underestimates, our results were based on an experiment where observers did not communicate with one another during the trials. We do not currently understand what consistent biases would be introduced into the overall mean via discussion of estimates among observers.

Based on these findings, we recommend that caution be used in interpreting estimates of large numbers of birds in a vegetated landscape. Photographs were shown to decrease error when estimating colony sizes, however these estimates still showed an overall error of approximately –13%. Similar to observer estimations, the absolute value of the mean error in counting photographs was found to be larger at 21%, because of canceling effects from over- and underestimates. The error associated with photographs was significantly lower than the error of observers however, so we recommend their use in obtaining more accurate colony estimates. In general, recall that photographs and aerial estimations of colonies work best for species that can be easily distinguished from their background, such as white species of wading birds.

The use of past aerial surveys may be useful for identifying trends in population fluctuations. We recommend caution, however, when attempting to use these surveys to derive absolute population sizes. Based on our experiment, we have determined that accurate correction factors would be virtually impossible due to the large variability within a single observer as well as among observers. If an individual's error in estimating large numbers of birds can be determined, then applying a correction factor for those data may be appropriate. Remember however, that when examining overall trends in populations, it is best to maintain a consistent methodology for comparison purposes. Even though certain methods may contain biases, these biases should remain constant among years.

Part 2: Effects of nesting asynchrony on accuracy of "snapshot" counts of breeding wading birds.

Introduction

"Snapshot" counts are any type of survey or count that is performed at a single point in time. Examples include most kinds of surveys, whether they are conducted weekly, monthly, or annually, and at some time scale ultimately encompasses most animal monitoring programs. Continuous counts are those that would be able to track any changes in the parameter of interest on an almost continuous basis. Examples of continuous counts include intensive studies of animal behavior and real-time weather recording. The obvious advantages of snapshot counts are that they are relatively rapid to conduct and usually cost considerably less than continuous monitoring. In many cases involving animals, snapshot counts are the only possible option due to logistical constraints.

The standard method for monitoring breeding wading bird reproduction in the Everglades has become monthly aerial surveys during the breeding period (see Chapter III), followed up by either ground checks soon after the surveys, or by comprehensive one-time ground surveys throughout the WCAs during March through May. Generally, peak counts at any given colony are summed across colonies to derive an estimate of the total breeding pairs during the season. Although this represents one of the most advanced monitoring schemes in use anywhere in the world for waterbirds, there is the possibility of significant bias in resulting estimates, based on the problem of asynchronous nesting, and nest failure between surveys.

The basic problem is that many nests may begin and fail prior to the initial survey, or between consecutive survey dates. In these cases, the failed nests would not be counted in any survey, and the survey estimate would therefore be an underestimate of the true number of breeding pairs. In addition, it is impossible to tell nests that are "new" in any survey unless the total number is different from the previous survey, or the nesting is clearly in a new part of the colony. Usually, some "peak" count during the breeding season is taken as the total number of breeding pairs in the colony. T the degree to which these problems affect estimates has not been investigated to date, either for the Everglades situation, or for nesting birds in general.

In order to estimate the magnitude of this error, we used a large sample of start and end dates for individually marked nests studied in the Everglades and simulated whether each nest would have been detected through monthly surveys. In this simulation, we assumed no visibility or counting biases – as though all nests active on a given date were actually seen and counted. The estimates of bias resulting from this exercise are therefore due to the effects of asynchrony and nest failure only.

Methods

We assumed that all monthly surveys would occur on the 15th of each month, from February through July of any year. We compared these dates of survey with known activity periods of individual nests monitored during 1986 – 1995, for the purpose of measuring nest success. Colonies where nests were studied were selected based on several criteria. We tried to include a mix of large colonies with multi-species composition, as well as small colonies that were typical of particular species or regions not otherwise represented. Colonies were visited once every 5-8 d, subject to inclement weather and equipment failure. With the exception of Tamiami East colony (which was accessible from a road on foot), all colonies were approached to within 20 m by airboat, were only visited in early morning hours (0630-0900) to avoid thermal stress on eggs and chicks, and visits were limited to a maximum of one hour. If the colony was small, all nests were marked with numbered strips of pink or red surveyor's flagging. If the colony was large, all nests were marked within approximately two meters of a trail within the colony. Trails were oriented towards the densest nesting sections, but included both edge and central nests. The total number of nests marked or rechecked on subsequent visits was determined by a one-hour limit on visitation. Thus, nests were probably selected via a process that was close to random

Colonies were first visited once clutches were determined to be complete or nearly complete. On each visit, nest contents were recorded, often with the aid of a bicycle mirror affixed to an extendable aluminum pole. A nest was considered active with the laying of the first egg, and inactive at the loss, destruction, or abandonment of the contents. Following complete loss of nest contents, new clutches in the same nests were counted as new nest starts, since we could not determine whether the same pair had produced the second clutch. Since egg laying was often completed by the time of the first visit to any nest, laying dates were frequently inferred by back-counting from the hatching date of the first chick. Incubation periods used were from first egg laid to hatching of the first egg, derived from the literature and from earlier studies in the Everglades (Frederick and Collopy 1988); we used 28 days for Black-crowned Night

Herons, Great Blue Herons and Great Egrets, 22 days for Little Blue Herons, Tricolored Herons, and Snowy Egrets, and 21 days for White Ibises. Unless some evidence at the nest suggested a date for the actual failure, the date of failure was assigned to the midpoint between the penultimate and the ultimate . This assignment determined the number of days each failed nest was estimated to have survived.

Young ciconiiform birds typically spend the last several weeks prior to fledging at the nesting site out of the nest and walking around the treetops. At this stage, they are extremely difficult to reliably locate without the use of radio telemetry (Frederick et al. 1993). Nests in this study were followed either until they failed, or until young were of an age beyond which their mobility impaired our ability to find them.. This age was predetermined by a combination of experience and empirical determination . We routinely followed nestlings until they were 14 days of age for all species except Great Egrets and Black-crowned Night Herons (21 days).

For the purposes of this exercise, we assumed a nest would be active, visible, and countable for a minimum of 5 d prior to the laying of the first egg. During this time, all species studied were in the process of nest building and courtship, and one member of the pair is nearly always present at the nest site. In addition, we also assumed that a nest with large young would be visible and countable for some time following the artificial end of the nestling period. This is justifiable since nestlings of all species studied are confined to the colony and often in the immediate vicinity of the nest for a period of at least two weeks past the 14 and 21-d periods we originally used for estimating nest success. In addition, it is reasonable to assume that the probability of a nest surviving increases dramatically once the chicks have passed the 14 and 21-day periods (Frederick et al.

1993). For the purposes of this study, we assumed that if a nest survived the 14 or 21-day chick period, it would be visible and active for another ten days on average.

We performed species-specific analyses for Great Egrets, White Ibises, and small day-herons. The small day-herons (Tricolored Herons, Snowy Egrets, Little Blue Herons) were lumped together because their nests and eggs are indistinguishable prior to hatching. Thus if a day-heron nest failed during the incubation stage, it would not otherwise be assigned to species. The only solution was to lump these three species into one group, so that early failures would be mixed with more successful nests.

We used an Excel spreadsheet to determine whether individual nests would have been counted in monthly surveys. The nest was considered "counted" if the start date occurred prior to the survey date, and the end date occurred after a given survey date. Some of the longer-lived nests were counted in more than one survey. We made no assumptions about whether new nesting attempts were renests or new pairs attempting for the first time. We also created a hypothetical "best-timing" survey by assuming the survey would occur at the averaged date of nest initiation plus ten days.

Results

Table 4.2 shows the proportions of total nests in the sample that would have been counted by monthly snapshot surveys, and by the "best-timing" survey. As expected, very early and late survey dates picked up almost none of the nests. However, the counts done during "peak" periods of activity were surprisingly poor estimators of the total numbers of nests initiated, ranging between 36 and 76% of the total for any given species-year combination. This suggests initially that peak snapshot surveys are undercounting the true population by 24 – 64% .

Table 4.2. Summary of probabilities associated with finding the correct number of nests in any month using monthly snapshot surveys. Effects are due to asynchrony alone: estimation and visibility biases are not includ

	n Nests	February	March	April	May	June	July	mean plus 10[1]	Highest monthly
GE 1986	248	0.388	0.414	0.190	0.069	0.000	0.000	0.500	0.414
GE 1987	89	0.270	0.348	0.427	0.247	0.000	0.000	0.348	0.427
GE 94	371	0.005	0.143	0.765	0.375	0.000	0.000	0.375	0.765
GE 1995	186	0.000	0.419	0.677	0.005	0.000	0.000	0.785	0.677
WI 1986	245	0.000	0.000	0.000	0.245	0.416	0.000	0.592	0.416
WI 1987	227	0.000	0.000	0.000	0.330	0.374	0.040	0.264	0.374
SH 1986	248	0.000	0.036	0.369	0.277	0.112	0.000	0.450	0.369
SH 1987	344	0.000	0.009	0.535	0.561	0.044	0.000	0.651	0.561
SH 1995	97	0.000	0.062	0.722	0.124	0.000	0.000	0.691	0.722

1. Count occurring on mean nesting date plus 10 days.

The proportion counted of any species also varied considerably among years of study, as expressed by standard deviations of the interannual means (Figure 4.5).

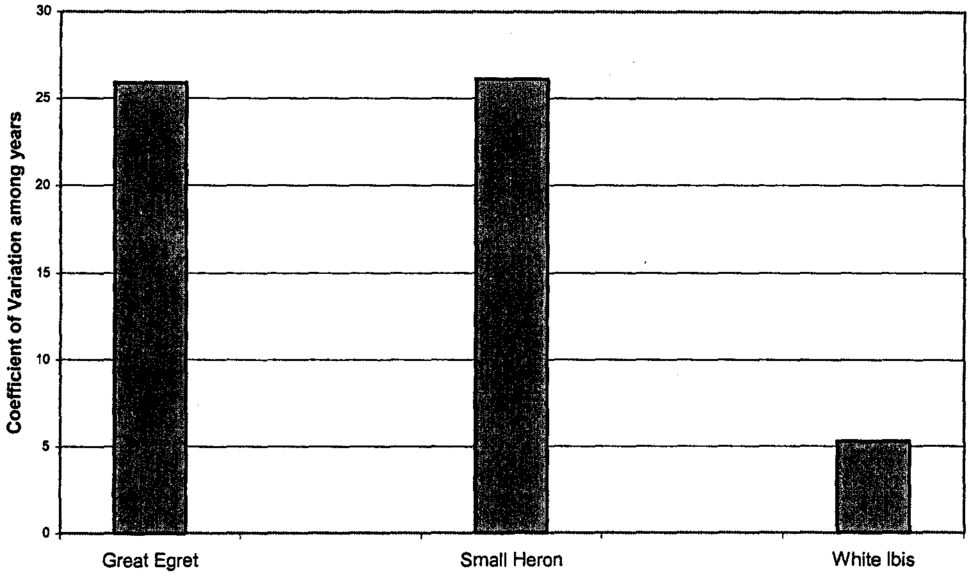

Figure 4.5. Coefficients of variation (Standard deviation /mean) in modeled annual proportions of nests detected by monthly aerial surveys.

Standard deviations were 16%, 14%, and 2% errors among years, for Great Egrets, small herons, and White Ibises, respectively. The high interannual variation associated with Great Egrets and small herons suggests that it would be difficult to apply a universal correction factor to account for the bias, and that correction factors would have to be derived on an annual basis instead. The very small variation associated with the bias in estimating White Ibises is likely an artifact of the small sample size (2 years) over which the interannual variation was estimated. The degree of interannual variation increased with the number of years studied.

Discussion

These results illustrate that there is the potential for a large error in estimating nesting populations using monthly snapshot surveys, and that there is considerable variation in the degree of bias from year to year. It is safe to conclude that snapshot surveys are likely to yield underestimates of the true value, and that the degree of underestimation will be larger in years and species where nest success is low and degree of asynchrony high.

The interpretation of these results is not straightforward, and several caveats must be considered. First, it should be recognized that aerial snapshot surveys are not the only method by which wading bird nests are estimated in the Everglades. For example, this technique is not used at all for estimating numbers of dark-colored species which cannot be seen well from the air, such as Great Blue Herons, Tricolored Herons, Little Blue Herons, and Glossy Ibises. Dark-colored species are estimated using ground counts, which are performed perhaps once or at most twice per season at any given colony. These one-time surveys are not randomly planned, and are timed to hit peak nesting. Nonetheless, the effects of asynchrony and nesting failure on estimates of these dark-colored species are likely to be more severe than for the lighter-colored species, which are estimated on a monthly basis.

The types of bias revealed by this exercise would be most pronounced in cases where a colony or group of birds begins nesting, and then fails catastrophically prior to a survey date. Although this situation could well occur, it should be recognized that there may be other methods of detecting such a failure. Through other, non-survey activities, our field crew is often in the air or on the marsh for a large proportion of the days within the nesting season, and through nesting success studies, roost counts, capture attempts, mercury sample collection, and other activities, we often note the status of colonies that might not be detected via monthly surveys. Since these other activities are rarely regular and are often geographically biased, it is not possible to estimate the probability of detection using these methods.

Summary

The net effect of both counting error (see Part 1 in this chapter) and bias due to asynchrony and nest failure between survey dates (collectively called snapshot survey error – Part 2) result in estimates that are biased lower than the true values. Both types of error are essentially independent processes – one is a counting error, and the other is a timing error. For this reason, the resulting correction factors for these two errors in no way cancel or interact, and they should be multiplied together when attempting to correct raw survey counts.

However, both types of error also result in biases that are unpredictable in magnitude. The counting error depends strongly on the individual doing the counting, and even the direction of the counting error is in question (over- or underestimating), depending on individual. For this reason, the use of correction factors should rely on applying the known biases of individuals to the data that those individuals have collected. One unknown in this process is whether biases of individuals are stable over time. Similarly, the bias in snapshot survey error also is not predictable, and varies from year to year, apparently in response to the degree and timing of nest failure. Since this is difficult to predict without direct measurement of nest success, the use of a correction factor for snapshot survey bias also includes a lot of uncertainty.

As with any type of biased survey information, it is unwise to use the raw or corrected information as a true measure of absolute value. However, if the survey methodology and the bias remain similar from year to year, it may be possible to use the measure (in this case numbers of nesting birds) as an index of population trends. Unfortunately, in our case although the survey methodology that we have used since 1986 has changed very little in protocol, the two variables that are likely to influence the degree of bias from year to year (variation in individuals counting and variation in nest success) have changed. This suggests that the annual numbers of breeding pairs cannot even be used as an accurate indicator of population trends.

Thus we are certain that our survey methodologies produce estimates that are biased considerably lower than true values, and that our ability to apply correction factors is hampered by the unpredictable variation in individual counting and annual nest success. Until we have evaluated the relative impact of these two types of error upon the sensitivity of the measure, all but the most extreme comparisons with past survey data should be undertaken with caution.

We suggest that bias in future surveys can be reduced considerably through the use of aerial photographs of large aggregations, and through measurement of the counting biases of individuals doing the counting in each season. The problem with adopting these two refinements is that the resulting estimates of population size will be all the more incomparable with past surveys simply because of the removal of biases.

CHAPTER V. ESTIMATING NUMBERS OF BREEDING AND NON-BREEDING WADING BIRDS IN THE EVERGLADES.

During the mid – late 1990's we gathered evidence that suggested large numbers of adult wading birds were not coming into reproductive condition. Our initial estimates were that on average over 70% of white-colored species did not breed during the period 1988 – 1998 (see annual reports for this project from 1999, 2000). Understanding why the majority of adult birds were not apparently coming into reproductive condition therefore seemed to be of key importance in restoring populations of wading birds to the south Florida ecosystem, especially since the apparent rates of nonbreeding were predicted to lead to a declining population. Four main hypotheses were proposed to explain the large proportion of nonbreeding birds (Chapter I). Of these, two suggested that the observation is simply an artifact of error in measuring numbers of breeding birds. The potential for uncertainty in measurement was large enough that we felt we needed to measure and model the effects of two forms of estimation error: counting error by observers, and the potential for missing birds whose nests failed either before, or in between, monthly surveys (see Chapter IV).

In this chapter, we describe the potential sources of error in estimating numbers of both breeding and nonbreeding wading birds in the Everglades using breeding and SRF survey information, and attempt to model the effect of those errors on bias in estimating the proportion of the wading bird population that was breeding within years (hereafter "survey models"). We also evaluate the agreement and differences of these models with the direct measurement of breeding proportions resulting from our studies of marked White Ibises (Chapter IX).

Methods

We compared numbers of nesting birds we had estimated through colony counts (Chapter III and previous reports in this study series) with total number of birds on the Everglades marsh. This latter information was obtained by SRF surveys (information supplied by Tom Bancroft, now of The Wilderness Society, and Craig Theriot and Dave Nelson of U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg MS). The SRF surveys derive density estimates from systematic aerial transects of known area constituting 15% of the total area. This survey program was pioneered in Everglades National Park in 1985, and after initial testing, has been conducted in the WCAs of the Everglades every year since. Typically, surveys of the entire WCAs are flown monthly during January through June of each year.

During any month of the breeding season, these SRF estimates are likely to include nonbreeding birds of adult age, breeding birds not actively attending nests, nonbreeding juveniles, and birds that will migrate out of the ecosystem and perhaps breed elsewhere ("nonbreeding migrants"). We used several assumptions in order to estimate the number of nonbreeding birds from the SRF totals. First, we only used estimates of total numbers of birds taken from the May SRF survey flight. We reasoned that by May, breeding by wading birds at even the most northerly locations in North America is well underway. The remaining birds in the Everglades are therefore quite unlikely to be migrant birds overwintering in the Everglades.

We also assumed that a portion of total birds on the marsh would be juvenile birds, and we used two different methods to estimate the proportion that should be juvenile. First, we used a demographic model to estimate the proportion of a hypothetical stable population that would be juvenile, given typical demographic parameters (survival, mortality, fecundity, and age at first reproduction), for White Ibises, Wood Storks, and Great Egrets. Since many of the demographic parameters for these species are poorly known, there is uncertainty in estimating the juvenile proportions using models. For this reason, we designed these models to be biased in the direction of overestimating juvenile proportions. To do this, we used the higher end of the range of possible fecundity values, the lower end of the range of possible adult survival values and the upper end of the range of possible juvenile survival values. Further, despite some evidence that wading birds may breed in their first year (Hafner 1998), we assumed for all three species that the age at first reproduction was two years of life. All these assumptions bias the resulting models to produce proportions of juveniles that are liberal, not conservative. Since juveniles are subtracted from the total SRF population in our manipulations, a too-liberal proportion of juveniles would bias the estimation of nonbreeding birds downwards, and lead to a liberal estimation of the proportion of birds that are breeding (and conservative estimation of the proportion nonbreeding). Our estimates of juvenile proportion ranged from 2 – 10%, depending on species.

We also attempted to estimate the numbers of juveniles directly. To do this, we used White Ibises, in which first-year juveniles are clearly distinguished from adults by their dark plumage, and second year birds are variably white with dark patches. We asked Craig Theriot to record the numbers of juvenile ibises in SRF surveys beginning in

2000. The numbers of juveniles amounted to less than 1% of total ibises in that year. However, we assumed that there is probably some unknown visibility bias for juveniles, which are dark, by comparison with the white-colored adults. This assumption leads us only to the conclusion that the proportion of juveniles is some number greater than 1%. Although this is a very inaccurate estimate, we believe it would be surprising if the visibility bias were so strong that the true proportion of juvenile ibises exceeded 10%. Because this conclusion derived from direct counts was so ambiguous, we decided to use the upper end of the estimates derived from modeling (10%).

We used the following formula to derive the proportion of the adult population that was breeding (P_b):

$$P_b = \frac{N_b}{[SRF - (0.5 * N_b) - (0.1 * SRF)] + N_b}$$

Where N_b = Number of breeding birds counted

SRF = Number of birds estimated on the marsh surface through SRF surveys in May

Note that this model assumes that half of the breeding birds are out foraging at any time and are so counted in the SRF estimates, and that 10% of the SRF population is composed of juvenile birds

We used the above model with its assumptions as a starting point to derive estimates, by species and year, of the proportion of the entire adult population that was breeding during the period 1986 – 2001. We then considered the potential effects of several uncertainties in our counts of both breeding and nonbreeding birds:

1. *Effect of Inaccuracy of observers counting birds.* This bias is outlined in Chapter IV, and includes biases resulting from counting inaccuracy, and from vegetative occlusion of birds in colonies (collectively called counting biases). Although we found that there were very large differences among individual observers, we did not have enough information on the biases of specific observers during the years examined to apply individual-specific correction factors. Since bias did not increase with size of nesting aggregation estimated, there seemed to be no basis for applying different correction factors based on size of colony. We therefore assumed a constant error across all individuals and colony sizes, and used the aggregate average error of –29.2% (SE = 0.57%).
2. *Effect of undercounting breeding birds through monthly snapshot surveys, due to asynchronous nesting, and nest failure.* Colony estimates during aerial surveys are derived by counting the total number of adult birds attending nests. Using nest records of three species, we estimated that an annual average of 52.5 % of nests would not have been detected by monthly aerial surveys, had begun and failed prior to the first survey, or because nests had begun and failed between the dates of successive monthly surveys. Since these biases varied unpredictably among years, we were unable to derive year-specific correction factors for this kind of bias. Instead, we corrected annual numbers of breeding birds using a random value that could vary during any year between the annual maximum monthly detection rates we measured for each species (Chapter IV). For ibises, we estimated that we had detected between 37 and 41% of nests, and for Great Egrets between 41 and 76%; in the absence of other information for Wood Storks,

we used the same detection rates as for Great Egrets. Since this bias from timing of surveys, and the bias from observer counting error (#1 above) are essentially independent effects, we felt justified in multiplying both factors together to get a single correction factor, that we applied to the raw counts of breeding birds for any year. We then used the corrected numbers of breeding birds in the formula (above) with the same assumptions.

3. *Effect of undercounting birds on SRF surveys.* During the development phases of the SRF surveys, the bias of observers counting birds in belt transects on either side of the aircraft were measured for both dark and light-colored species (note I need to talk to Portier here about exactly how those were measured, and whether there are species specific biases). Since we used data for White Ibises, Wood Storks, and Great Egrets in our models, we applied only the undercount bias for light colored species. The results suggested that observers were counting only 70% of the light-colored species that were actually present on the marsh. We therefore estimated that 30% of the birds on the marsh were not included in the raw SRF counts, and corrected the total numbers of birds on the marsh surface accordingly in Model #3. The corrected numbers of birds in SRF counts were then used in the formula above.

Results

Table 5.1 shows the uncorrected estimates of the proportion of birds breeding by comparing numbers of breeding birds with SRF estimates of total birds in the ecosystem. This method of estimation suggested that large portions of the birds in the

Everglades during May were not found in breeding colonies (means ranged from 60 – 80%) Since we are aware of strong biases in aerial estimations that result in undercounts, we consider the data in Table 5.1 as an incorrect, straw-man model.

Table 5.1. Proportions of birds on the marsh surface in May that are estimated to have bred during the annual season. No corrections for observer bias or undercount for either breeding or SRF surveys were applied in this model.

	GREG	**WHIB**	**WOST**
1986	0.139	0.105	0.009
1987	0.168	0.224	0.000
1988	0.184	0.416	0.000
1989	0.149	0.076	0.256
1990	0.088	0.228	0.408
1991	0.096	0.036	0.000
1992	0.345	0.357	0.229
1993	0.458	0.052	0.000
1994	0.309	0.271	0.000
1995	0.521	0.658	0.000
1996	0.245	0.120	0.387
1997	0.220	0.207	0.154
1998	0.434	0.151	0.000
1999	0.390	0.331	0.269
2000	1.001	0.333	0.705
2001	0.292	0.640	0.480
mean	**0.317**	**0.238**	**0.161**

In Table 5.2, we present the results of the model that included estimates of undercounts of breeding birds (both counting error and errors due to snapshot monthly surveys) but with no correction for counting error in SRF surveys.

Table 5.2. Proportions of birds on the marsh surface in May that are estimated to have bred during the annual season. Note that this model includes corrections for the underestimation of breeding birds, but no correction for the underestimation of SRF survey counts.

	GREG	WHIB	WOST
1986	0.341	0.315	0.027
1987	0.403	0.572	0.000
1988	0.420	0.828	0.000
1989	0.252	0.249	0.408
1990	0.257	0.587	0.797
1991	0.200	0.119	0.000
1992	0.542	0.744	0.386
1993	0.720	0.177	0.000
1994	0.664	0.624	0.000
1995	0.772	1.027	0.000
1996	0.394	0.365	0.575
1997	0.428	0.551	0.317
1998	0.640	0.415	0.000
1999	0.718	0.744	0.555
2000	1.216	0.712	1.059
2001	0.51023	1.02605	0.73808
mean	**0.530**	**0.566**	**0.304**

By comparison with no corrections for underestimation of numbers of breeding birds (Table 5.1), the model with corrections predicts an increase in the average annual proportion breeding of between 13% (Wood Storks) and 34% (White Ibises). Since the estimated numbers of breeding birds have been increased in this model, the direction of the result is not surprising.

Table 5.3 presents the estimates of breeding proportion when we included corrections for underestimates of breeding birds and corrections for underestimates of SRF survey counts. This model results in estimates intermediate between the two previous models –

Table 5.3. Proportions of birds on the marsh surface in May that are estimated to have bred during the annual season. This model includes corrections for the underestimation of breeding birds, as well as corrections for the underestimation of birds on SRF surveys.

	GREG	WHIB	WOST
1986	0.243	0.309	0.017
1987	0.315	0.572	0.000
1988	0.336	0.845	0.000
1989	0.297	0.244	0.468
1990	0.231	0.554	0.753
1991	0.248	0.117	0.000
1992	0.602	0.744	0.438
1993	0.710	0.169	0.000
1994	0.641	0.649	0.000
1995	0.730	1.027	0.000
1996	0.409	0.345	0.593
1997	0.423	0.551	0.313
1998	0.811	0.415	0.000
1999	0.652	0.718	0.492
2000	1.216	0.729	1.059
2001	0.642	1.112	0.867
mean	**0.531**	**0.569**	**0.313**

there is an average increase in the annual proportion breeding of between 7.3% (Wood Storks) and 23% (White Ibises) as compared to the model with no corrections for estimation bias.

Discussion

The results presented above suggest a number of possible interpretations, most of which must be viewed according to the uncertainty inherent in the data. Of the three models presented, we have the least confidence in the one using raw numbers of breeding birds and SRF counts. Given the large errors in estimation of breeding birds demonstrated in Chapter IV, we are confident that the numbers of breeding birds must be considerably larger than our raw estimates, and that we should at minimum correct for this bias to the extent possible. The correction factors we used, however, are relatively crude in that they do not take into account the large individual variation in observer error, nor the large interannual variation in bias of snapshot surveys.

The last of the survey-data models also did not take into account the large variation associated with SRF estimates of total population size. The confidence limits associated with the SRF estimates are typically larger than the estimates themselves.

Although we believe that the two models that include correction factors for SRF and/or breeding counts are probably more accurate than the model without corrections, we believe that there is still considerable uncertainty surrounding any of the predictions of the corrected models.

We have also searched for evidence of nonbreeding birds by following marked adult White Ibises (Chapter IX). Many of the adult ibises we marked with radio tags were never found in breeding colonies (see Table 9.3), including 29% of birds marked during 1999, 32% in 2000, and 61% in 2001. However, all of these ibises emigrated from the Everglades by the end of March, indicating that these animals were migrants and should not be included when determining proportion of breeding birds in the Everglades system. Of the birds that remained in the Everglades past 21 March, we found 100% associated with a colony on at least one occasion, which we believe is strong evidence that they were breeding. This suggests that in each of the years, few or none of the adult ibises in the ecosystem during the post-March period were nonbreeding.

For 2001, this result is in apparent agreement with the level of nonbreeding suggested by models that used corrected survey data – both models predicted 100% or more of the adult ibises in the ecosystem were breeding in 2001. However, for 2000, the survey models predicted between 27 and 29% of the ibis population would not be breeding – yet we found 100% of our marked birds were breeding in that year.

There are several possible explanations for the disagreements between modeled results and field measurements. First, it is clear that there is a large inherent uncertainty in any of the models derived from survey data. For this reason, these models are at best useful for predicting large fluctuations in breeding proportion, and are probably not accurate for detecting small annual changes or for predicting actual breeding proportion only within wide confidence limits. For this reason, we might never expect there to be a very close agreement between field information from individuals, and breeding proportions derived from survey models.

Second, the telemetry data, while qualitatively accurate, have the tradeoff of having relatively small sample sizes (total N = 37 birds over three years). It is therefore difficult to assume that the marked individuals were representative of all birds in the ecosystem, particularly when considering individual years (n = 7, 22, and 8 birds in 1999, 2000 and 2001 respectively). For this reason, we can expect some error in using the sample of marked birds as surrogate indicators of the entire population in the ecosystem. The small sample sizes and the absence of other information make it difficult to predict the power of our ability to discern small changes in the proportion of the adult population that is breeding annually.

We suggest that the information from field-marked birds provides the more reliable of the two types of information. One problem is that we have data from field-marked birds for only three of the 16 breeding seasons that we have examined, and all three of those seasons have been either considerably better than average in terms of stimulating nesting (1999), or supernormal (2000 and 2001). Thus we have no years with small numbers of breeding starts in which we also had radio-marked birds, making it difficult to assay the accuracy of survey model results in those years.

However, there is evidence that the breeding proportions derived from some of the more extreme years are likely to have been accurate. For example, during 7 of the years between 1986 and 2001, there were no Wood Storks recorded breeding in the central Everglades. Yet the average number of storks recorded in the system during May SRF surveys of those years was 828 (uncorrected for SRF counting error). Since we did not record any storks on nests during these years, counting errors and snapshot survey error are unlikely to account for the small proportion breeding.

Similarly, in 1991, uncorrected SRF estimates indicated over 47,000 ibises in the central Everglades during May, and only 218 nests were recorded. Even if the 218 nests are corrected for counting error and snapshot survey bias, only 769 birds were estimated to have bred, a small proportion of the 47,000 birds supposedly on the marsh. This difference seems too large to be accountable to survey and counting error. Similarly, very large differences were apparent in 1993 and 1996 for this species. These extreme examples suggest that there were a number of years in which a very low proportion of the ibises or storks in the Everglades were actively nesting. In these years, the numbers of birds nesting in any one place were apparently small. Although one might expect a similar percent observer error in small colonies as in large ones (Chapter IV), and perhaps a larger than average snapshot survey error due to increased nesting failure in these years with poor nesting conditions, the absolute value of both errors is still likely to be small in comparison with the large numbers of birds estimated on the marsh surface.

The next question, however, is whether the nesting proportions in the Everglades are on average high enough to sustain stable populations of breeding wading birds. Because the inherent inaccuracies of the survey-model method, and the limited number of years of the direct field-measurement method, we do not feel confident that this question can be answered with the available analyses. This does not indicate, however, that we believe that breeding proportions present either a substantial or a nonexistent problem for the demography of Everglades wading birds – only that our current tools do not allow us to fully explore the potential of nonbreeding as a demographic process.

CHAPTER VI. PHYSIOLOGY, NUTRITION AND REPRODUCTION IN A LARGE COLONY OF CAPTIVE SCARLET IBISES

Introduction

Breeding wading bird populations in the Everglades have declined dramatically since some point since the late 1940's. Comparison of aerial and ground survey of breeding colonies to aerial strip transect counts of wading birds on the marsh surface suggests there is an alarmingly high proportion of adult wading birds (70%) present during the breeding season that do not breed (See Chapter I.). A majority of the wading birds in the Everglades are and have historically been White Ibises. A high proportion of non-breeding adult birds during the nesting season could be explained by several potentially inter-related human induced problems in the Everglades. These include both water management and contaminants, and their possible effects upon ibis prey populations, or direct effects upon the ibises themselves (see Chapter I).

One hypothesis to explain the high proportion of non-breeders is that many birds are not obtaining enough food prior to or during the nesting season in order to justify a nesting attempt. Comparison of pre-season body condition and hormonal profile of breeding and non-breeding ibises in the Everglades could prove useful in testing this hypothesis, by separating environmental problems affecting ibis food supply from those involving potential contaminants that may be interrupting breeding cycles. The ability to distinguish breeding and non-breeding White Ibises in the field is a necessary tool in order to further investigate this problem. The development of reliable field marks of breeders and nonbreeders in a study of a captive population of ibises has been one of the goals of this study.

It is also unclear whether ibis reproduction is energetically limited by prebreeding body reserves, or alternatively, by the rate of nutrient intake at the time of nesting. The degree to which reproductive decision is limited by reserves (fat or lipid stores) varies widely among bird species. Drent and Daan (1980) introduced two models, the "capital" model and the "income" model. In capital breeders (such as geese, Anserinae), females use body condition relative to a changing threshold in deciding when and where to breed. In income breeders (e.g. grouse, Tetraoninae), females use the rate of change in body condition relative to fixed thresholds in making a reproductive decision. Thomas (1988) suggested there is a continuum between capital and income strategies. Currently, we do not know to what extent ibises rely upon endogenous versus exogenous nutrient resources to initiate and maintain reproduction, or how variable this is among individual ibises. This distinction has management implications for wading birds, since it determines the relative importance of pre-breeding feeding resources vs. resources available at the time of nesting, and so may dictate the timing of hydrological management actions. It is also unclear whether fat or lipid accumulation through hyperphagia is a response rather than a limiting factor to the onset of reproduction. The ability to measure and even experiment with the role of food and body condition for initiation of breeding is more easily separated by study of captive, marked individuals whose diet is well known than in free-ranging birds.

The Scarlet Ibis (*Eudocimus ruber*), considered by many (eg, Hancock et al. 1992) to be a color-morph of the White Ibis , is common in North American zoos and exhibits high individual variation in reproductive response in captivity. This feature suggested to us that there commonly exists in captivity, variation in some parameter of physiology upon which reproduction depends. By understanding variable reproduction in captivity, we might be led to understand physiology or energetics of reproduction in these birds. We studied reproduction and its association with body condition and endocrine events in a captive colony of over 400 Scarlet Ibises at Disney's Discovery Island, a bird park in Orlando, Florida. We attempted to manipulate body condition in some birds and to determine whether this affected the propensity of individuals to breed. The use of a marked population of captive birds enabled us to control food type and amount, and to measure body condition in a large number of individuals prior to breeding. We realize that the mechanisms that result in nonbreeding in captivity may be different from those in operation in free-ranging populations. However, we assume that the role of body condition in affecting reproductive status is likely to be the same in both situations. Because reproductive decision can also be influenced by other factors such as age, experience, social facilitation, time of season, abiotic factors and mate quality, we also attempted to monitor or control as many of these factors as we could.

Methods

In 1998 and 1999, we studied the reproduction of over 400 individually color-banded Scarlet Ibises in a 3,082 m^2 aviary. Built over 20 years ago, the aviary is nearly 20m high at some points and encloses some mature trees. The flock is composed of birds predominantly under 6 years of age, with a few individuals as old as early twenties. The sex ratio is roughly 60/40 male to female.

The birds were fed free choice on a commercial flamingo diet, supplemented daily with 33lbs of smelt or silversides. Although they were fed free choice, the ibises would not feed singly but only in small groups. This behavior caused feeding intake to be limited by dominance to a large degree. Typical feeding bouts involved subordinate birds approaching the feeders initially, feeding rapidly for a few seconds, then being supplanted by successively more dominant birds until the whole group left. During these feedings, many birds fed for only a few seconds.

Nearly all ibises were trapped, weighed and measured once between mid-February and mid-March. During both years, measurements included mass, bill chord, bill length, bill depth at the base of the nares and tarsometatarsal length. In 1999 we also measured curved wing chord. Body condition was estimated as a size-corrected mass, determined as the difference between observed mass and an expected mass. Expected mass was predicted through a linear regression of body mass upon a body size factor score. The size factor score was an attempt to express a composite measurement of relative body size. It was derived from a principle components analysis of all of the skeletal measurements. We determined pre-nesting body conditions for 226 birds in 1998 and 378 birds in 1999 during the two months prior to the nesting season.

Nesting pairs were observed at close range from March through July during both years. We compared pre-season body conditions of both sexes in different groups that ultimately reached different nesting stages. In 1998, nesting stages were ranked as "no attempt to breed", "courting or nest building with no egg production", "nesting with egg production" and "successful hatching". In 1999, the nesting stage categories were the same except for the second category, in which three new distinctions were made. These were birds that were observed courting and copulating over several days but were not observed nest building, birds that were observed nest building, and birds that were observed copulating but never courting or nest building. We compared pre-season body condition across all these groups using one-way ANOVA.

In order to determine how responsive and variable body conditions were among individuals during the reproductive cycle, we weighed individuals repeatedly throughout the 1999 nesting season using several feeding stations fitted with electronic balances that could be read from a remote read-out. Ibises were weighed as they fed from a dish.

To assess the roles of other potential factors that might contribute to reproductive status and success, we compared breeding and nonbreeding birds in their age, nest density controlled for date (as a possible indicator of social facilitation) and male bill length and size factor score. Nest density was determined as the ratio of the number of other nests present when a pair started nest building to the ground area covered by the whole colony during its maximum size. In 1999, we also looked for any birds re-nesting with the same mate from the previous season in order to determine if experience with previous mates increased the likelihood of nesting success.

We attempted to manipulate breeding success and/or timing of breeding by altering pre-nesting body condition of a random sample of birds from the aviary. We anticipated that the randomness of the sample would control for possible existing confounding factors, such as dominance status and parasite load, for which we were unable to obtain direct measurements. Prior to the 1999 season, two groups of 30 birds were trapped and held for 54 days in large cages separated from the main aviary group. We could not fast birds to decrease their body condition, but we did supplementally feed one group to increase body condition. We altered body condition in one group of birds through supplemental feeding while keeping a control group on the normal aviary diet. The experimental group was fed to satiation once a day on lipid-rich fish to increase deposition of fat in these individuals. Individuals in these two groups were then observed during the nesting season in order to determine if increased fat or feeding prior to the breeding had increased the likelihood, timing, or success of nesting attempts.

In 1999, we monitored testosterone, estradiol and progesterone levels in the feces of known individuals throughout the nesting season in order to compare hormonal changes in breeding and non-breeding birds. Hormone levels were measured from fecal samples through a double ether extraction followed by radioimmunoassay performed in the lab of Dr. Timothy Gross at the USDA Caribbean Science Center in Gainesville, FL. Fecal samples were collected opportunistically from known individuals of both sex throughout the breeding season, stored on ice for up to 7 hours, and stored thereafter at –30°C until analysis.

Results

Body Condition and Reproduction

The proportion of all birds in the aviary that successfully produced eggs or young did not differ significantly between 1998 and 1999 (males, $\chi2 = 1.26$, $p = 0.15$; females $\chi2 = 0.329$, $p = 0.64$). 43.3% of the males and 34.4% of the females in the aviary produced eggs or young in 1998 and 33.9% of males and 29.8% of females did so in 1999. In 1998, we found lower pre-breeding body condition of both sexes who did not attempt to nest or whose nests did not produce eggs, compared to those whose nests did produce eggs (Figure 4.1). This difference was only significant for females (t = -2.551, p=0.023). The courtship of birds was not followed in 1998, so during that year, birds that did not progress beyond the courtship phase were categorized either as attempting to nest but not producing eggs, or as making no attempt to nest. In 1999, we distinguished between courting and nest building birds. In 1999, we found a significantly lower pre-breeding season body condition in both males and females observed only courting or never attempting to nest, compared to those that were later observed building nests or producing eggs (males, t = -2.239, p = 0.026; females, t = -2.34, p = 0.021, see Figure 6.2). Mean differences in body weight in these contrasts between successful and non-successful breeding groups were 18.92 grams for males and 31.42 grams for females in 1998, and 16.81 grams for males and 16.88 grams for females in 1999.

In 1999, 22 males and 20 females were observed copulating with each other but were not observed courting together for any length of time as is typical when a social partnership is formed. Within this group, the males were on average 16.95 grams below their expected mass while the females were on average 14.83 grams above their expected mass.

Non-breeding males were in significantly better body condition than non-breeding females (t = 2.363, df = 100, p = 0.02). This result is likely due to the skewed sex ratio in favor of males, and suggests that some males may have not been able to nest despite having high body condition.

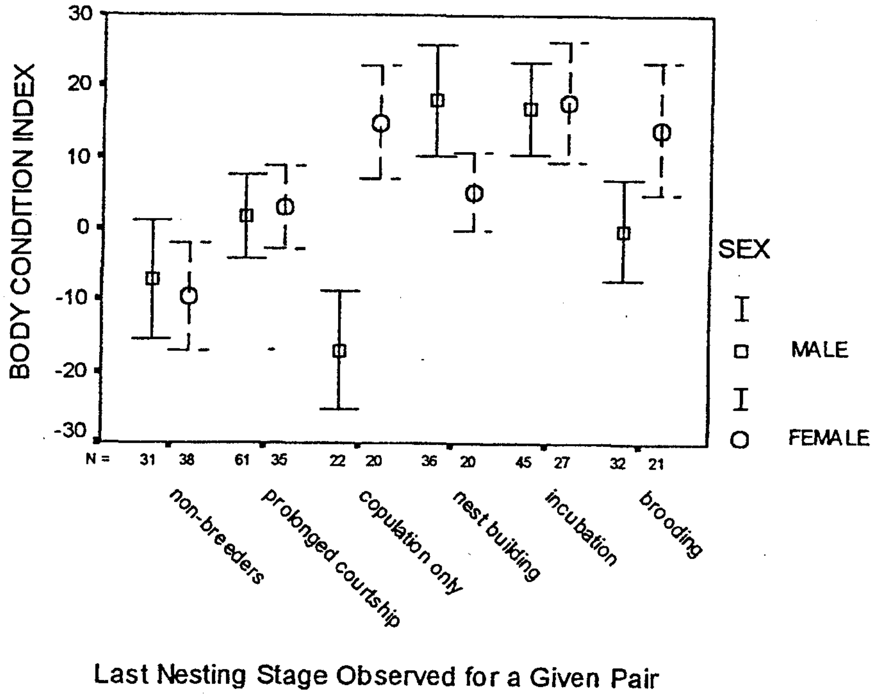

Figure 6.1. Pre-breeding body condition (mean, 1 SE) for last observed nesting stage in 378 captive Scarlet Ibises during the 1999 breeding season.

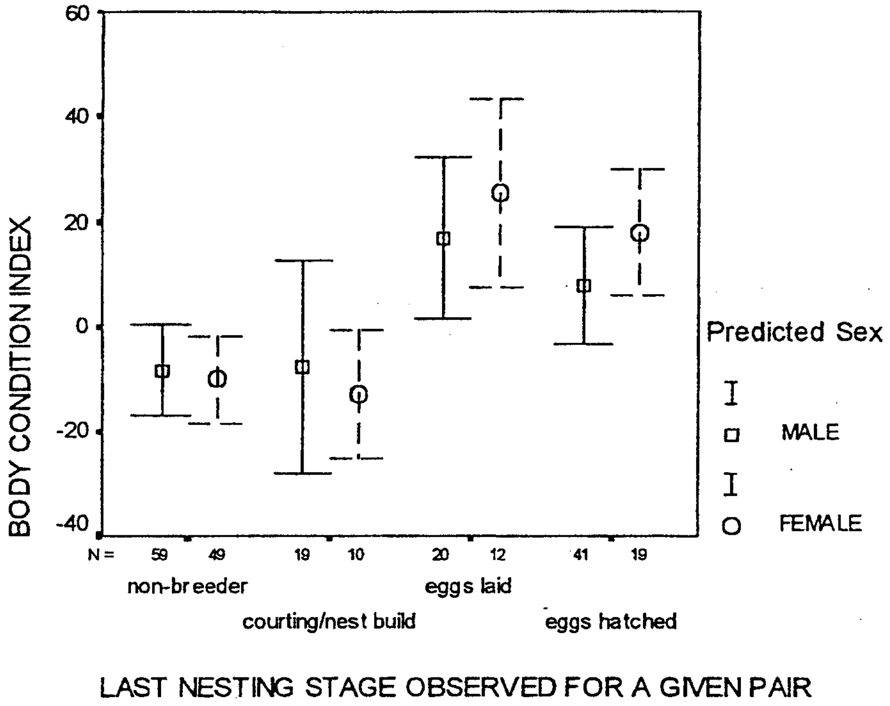

Figure 6.2. Pre-breeding season body condition (mean, 1 SE) for last observed nesting stage in a group of 229 captive Scarlet Ibises during the 1998 breeding season.

Changes in Body Condition Associated with Reproduction

Our feeding stations indicated that body masses of males and females increased an average of 107 grams prior to nesting with no significant differences in the amount of increase between successful and non-successful individuals. Both sexes lost weight during the incubation period. Males lost on average 43.21 grams ($n = 14$) while females lost on average 21.67 grams ($n = 3$). Females tended to start breeding in high body condition, decreasing throughout the nesting stage ($F = 6.78$, $p<0.001$) while male condition remained more stable from start to finish (Figure 6.3).

Other Correlates to Reproductive Success

There were no significant differences in mean male or female age that were related to nesting success, although failure to progress beyond the courtship stage was associated most frequently when old males were paired with young females (Figures 6.4 and 6.5).

There were no obvious male morphologic traits, such as size, that were significantly associated with nesting success. However, male bill length (both years) (1998: $r = -0.395$, $p = 0.036$; 1999: $r = -0.485$, $p = 0.049$) was significantly correlated with hatch date, with longer-billed males nesting earlier. Successfully nesting females had significantly larger body size factor scores ($t = -2.868$, $p = 0.005$ in 1999 and $t = -2.321$ $p = 0.027$) than unsuccessful females. However, this may have resulted largely from the fact that smaller females tended to nest in the densest parts of the colony (r = -

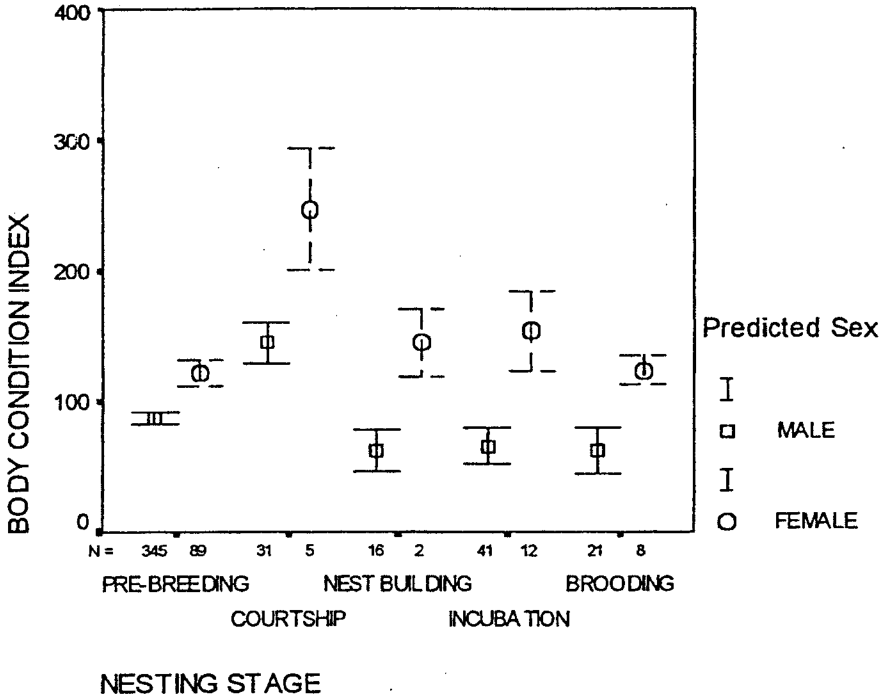

Figure 6.3. Body condition of 332 captive Scarlet Ibises during subsequent nesting stages.

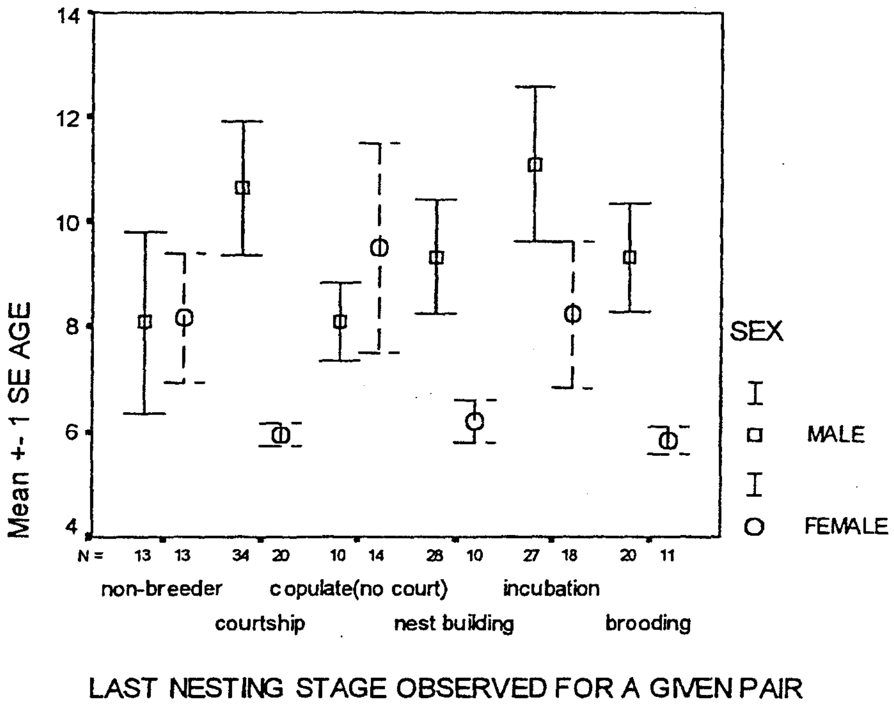

Figure 6.4. Mean ages for last observed nesting stage in a group of 378 captive Scarlet Ibises during the 1999 breeding season.

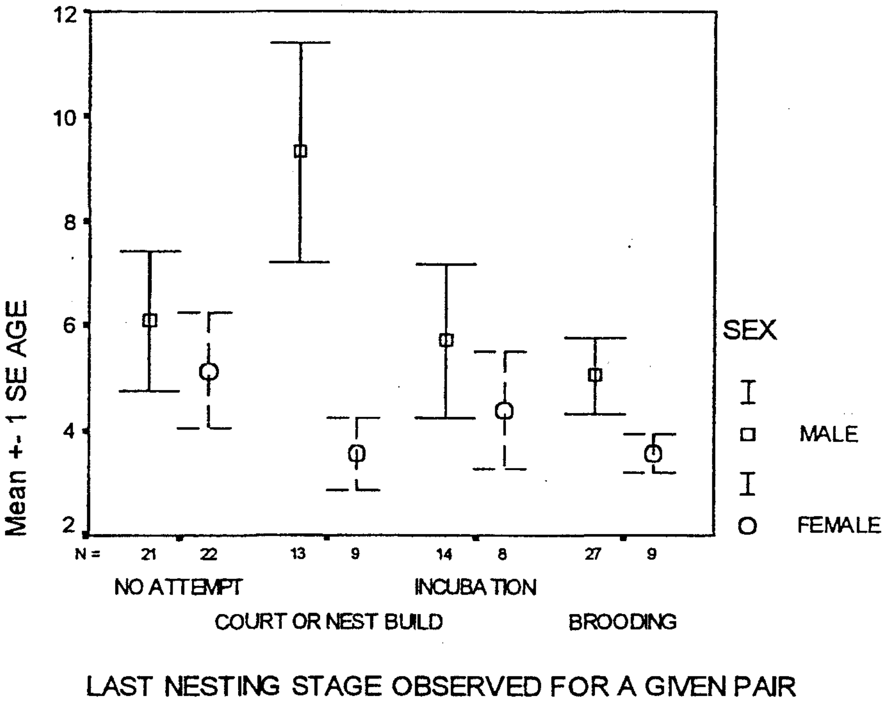

Figure 6.5. Mean ages for last observed nesting stage in a group of 229 captive Scarlet Ibises during the 1998 breeding season.

.370, $p = 0.022$) where egg loss to conspecifics was highest. We found no birds that re-nested in 1999 with the mate they had in 1998. Previous nesting experience with particular individuals therefore is not likely to be an important factor contributing to nesting success.

Supplemental Feeding Experiment

Before their release back into the aviary, the supplementally fed group gained significantly more mass (mean = 108 grams) than the control group (mean = -39 grams) ($t = -11.5$, $p<0.001$). However, we found no significant differences between supplementally fed birds and controls in either the last nesting stage in which they were observed, or in their timing of breeding.

Hormone profiles of breeding and non-breeding ibises

In males, estradiol and progesterone levels were correlated with testosterone levels (E; $n = 74$, $r = 0.456$, $p < 0.001$and P; $n = 74$ $r = 0.319$, $p = 0.006$) but were not correlated with each other (Figure 6.6). In females, only progesterone levels correlated to testosterone levels ($n = 60$, $r = 0.435$ $p = 0.001$). In both sexes, testosterone levels decreased significantly across time ($r = -0.232$, $p = 0.045$ for males and $r = -0.35$, $p=0.006$ for females) and nesting stage (male; $p = 0.013$; females, $p = 0.049$) (see Figure 6.7). Female progesterone levels decreased significantly across time ($r = -0.633$, $p < 0.001$) but not nesting stage. Male progesterone levels did not significantly change over time or nesting stage (see Figure 6.8). Males and females exhibited contrasting trends in fecal estradiol levels across nesting stage but not across time (See Figure 6.6).

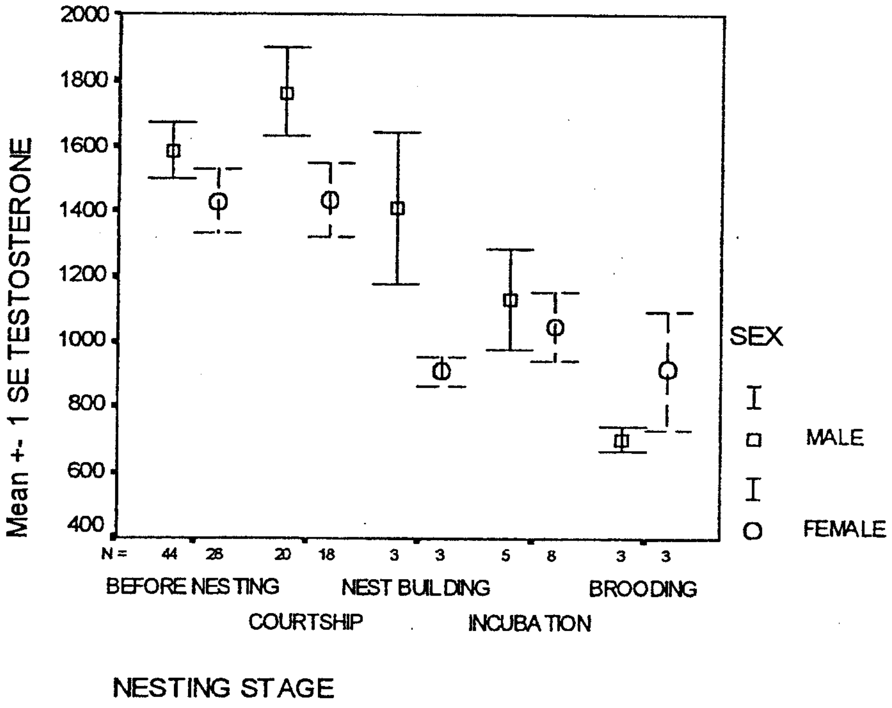

Figure 6.6. Mean testosterone concentration for various nesting stages in a group of captive breeding Scarlet Ibises.

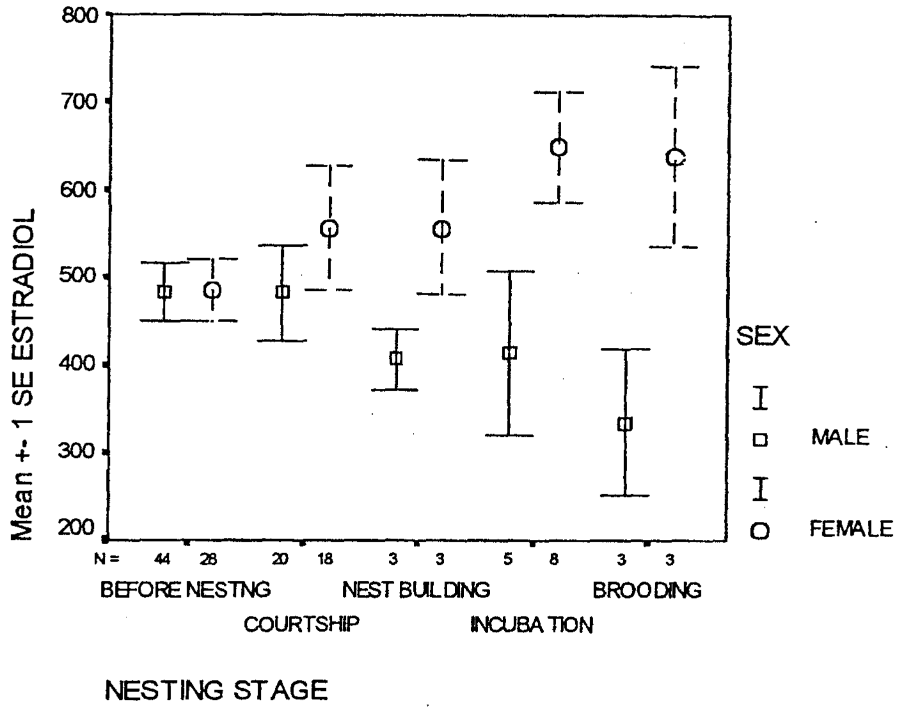

Figure 6.7. Mean estradiol levels for various nesting stages in a group of captive breeding Scarlet Ibises.

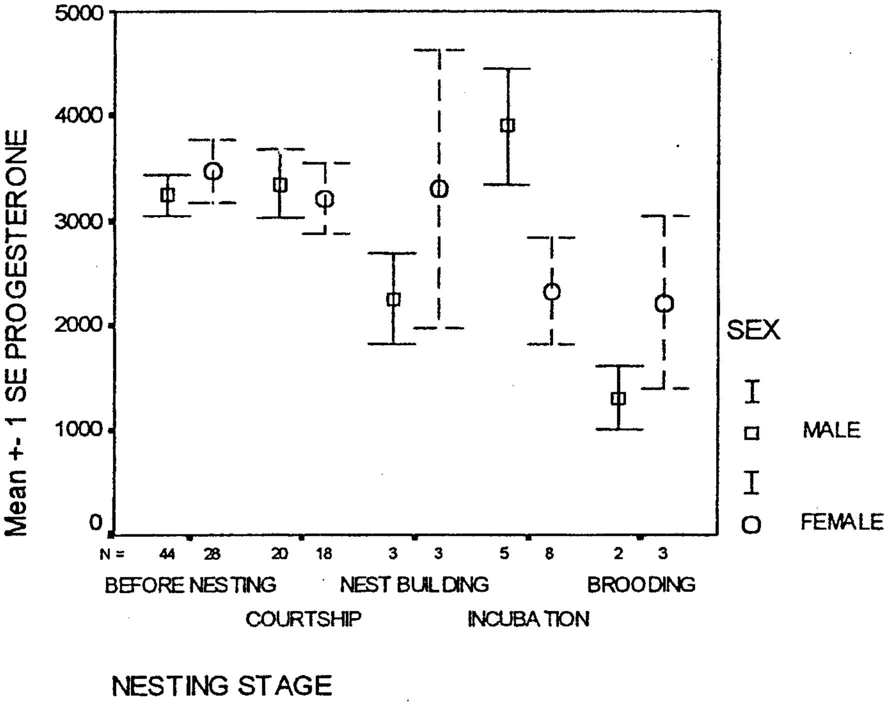

Figure 6.8. Mean progesterone concentrations for various nesting stages in a group of captive breeding Scarlet Ibises.

These divergent profiles for the sexes may allow for the detection of breeding vs non-breeding birds through the T/E ratio. Males that became breeders showed significantly higher levels of testosterone, estradiol and progesterone in the pre-breeding period than did non-breeding males at any point during the nesting season (df =41 // T; t = 2.039,p = 0.048, mean difference = 334.6 picogram/gram fecal weight // E; t = 2.149, p = 0.038 mean diff = 138.5 // P; t = 2.196, p = 0.034, mean diff = 826.4). We found no such differences in the hormone levels of females.

Discussion

In both years of the study, we demonstrated a significant and repeated association between pre-breeding body condition and the stage of reproduction achieved. This average difference in mass in both males and females was about 20 to 30 grams of fat. The biological significance of an average difference of this magnitude is hard to judge. While a 30g difference represents less than 4% of an 800g bird, it does represent 22% of the maximum individual variation in mass observed in our study for an average sized male and 27% observed for an average sized female. We observed variation in size corrected mass on the order of 30% above and below expected mass for males and females of a given size. During the course of the study, we found one nearly starved female at 69% of her expected mass. If we make a conservative estimate that roughly half of an individuals variation in mass is due to variation in body condition and not gut content or measurement error (birds were capable of varying by as much as 50 grams in the course of one day), we can estimate that the average maximum fat store is 138.06g for males and 112.82g for females.

This estimate of fat store becomes more relevant when one considers its possible energetic use. If we consider the cost of flight as 0.12g/km (males) and 0.094g/km (females) and foraging flights averaging 8km early in the season to 25 km late in the season (Pennycuick,1989), then these values of maximum body storage that we estimate represent almost all of the foraging trips taken in a typical breeding season (about 25-75). Males and females were on average observed to lose 43.21g (n=14) and 21.67g(n=3) body mass respectively during incubation. Using the equation from Calder (1986), our body store estimates for Scarlet Ibises represent a total fasting endurance of nearly 8.95 days for males and 7.32 days for females. As a male's reproductive fitness is probably greatly affected by his ability to fast while mate guarding during his partner's fertile period and seeking extra–pair copulations while other males are away foraging, this may explain why we observed differences in pre-breeding season body condition between non-breeding and successfully breeding males. To the female, the cost of producing an average brood of three 35 gram neonates is equivalent to the energy content of 66.28g of body fat (Calder,1986). This added to the 20g lost during incubation represents a significant energetic cost in terms of stored fat or exogenous sources.

Based upon Pennycuick's calculations, the energetic cost of flying for carrying one gram of fat is 0.000142 gfat/km for a bird of a female ibises size. If a female were to carry all of the energy she needed for producing and incubating a three-egg clutch stored as fat, the cost during flight would be 0.0125gfat/km. This is rather small, since an ibis would burn only one extra gram of fat in 80 km of flight by carrying this extra weight. The flight itself would cost an energetic equivalent of 7.52gfat. A female carrying the amount of difference in mass we observed when comparing breeding and non-breeding females, would only incur roughly a third of this cost. So it seems that not only does 30 grams of fat potentially represent many days worth of energy gain obtained during foraging, it is also not very costly to carry around for birds of this size.

We were unable to influence breeding status or success by supplementally increasing body condition. At first glance, this result suggests that body condition prior to breeding is relatively unimportant for breeding, and contradicts the differences in body condition found between successful and unsuccessful breeders. However, there are several lines of evidence that suggest that the contradiction is more apparent than real. First, in both years we have shown that pre-breeding body condition is strongly associated to reproductive success. Second, body condition within the aviary increased overall in both males and females just prior to nesting despite no change in the free-choice feeding regime. This suggests that it was possible for all animals in the aviary (controls and supplemented birds) to increased body condition on the flamingo chow diet alone. It also suggests that prebreeding hyperphagia is at least a precursor to breeding. Whether this prebreeding fattening is a cause or a consequence of breeding is much harder to judge. The fact that we observed a high degree of dominance interactions over food leads us to believe that some individuals were unable to gain access to food on enough occasions to increase body condition. Conversely, this suggests that the dominant individuals of both control and supplemented groups were able to fatten during the period between their release back into the aviary, and initiation of breeding. This period averaged 43.14 (s.d. 18.32, range 18 – 71, n = 7 males) days for males, and 31.3 (s.d. 18.11, range 13 – 49, n = 4 females) days for females. This is an obvious confounding factor in the experimental design, and would be expected to lead to a finding of no differences in reproductive success between experimental groups. The failure of supplemental feeding to affect reproductive outcome or timing might also be the result of sampling (only one replicate of the entire experiment). Alternatively, reproduction might have been limited by some other nutritive component of the diet than fat.

We therefore conclude that the experimental effort to alter reproductive success by altering prebreeding body condition was confounded by one or more factors. On the basis of our nonexperimental work relating body condition to reproductive success, we believe that prebreeding body condition is an important determinant of breeding initiation and breeding success. This parameter will probably also be a useful indicator by which we may distinguish breeding from non-breeding female ibises in the field. We conclude also that hormone levels can be useful in distinguishing non-breeders, particularly males. Testosterone level does appear useful in determining breeding stage of both sexes. And, the breeding stage of females may be distinguished upon the basis of testosterone / estrogen ratio alone.

Our results also suggest strongly that the month or two prior to breeding is a period that is essential to determining the propensity to breed. During this period, ibises evidently need to fatten up, and are probably strongly dependent upon readily available food sources to accomplish this goal. From this information, it seems quite likely that in the wild, the proportion of adults which breed, and the success of breeding are both influenced strongly by prebreeding foraging conditions.

CHAPTER VII. TECHNIQUES FOR STUDYING WHITE IBISES IN THE EVERGLADES: DEVELOPMENT OF TRAPPING METHODS AND A MODEL FOR PREDICTING INDIVIDUAL REPRODUCTIVE STAGE.

Part A. Trapping White Ibises: evaluation of techniques and factors that affect success

Introduction

Most techniques to trap adult long-legged wading birds involved capturing them on the nest (Frederick 1986, Jewell and Bancroft 1991, DeSanto et al. 1997). Although nest sites are often a dry and reliable place to find adult birds, trapping on the nest and repeated visits to wading bird colonies may have adverse effects on nesting success (Jewell and Bancroft 1991) and consequently may bias reproductive and population studies. Additionally, nest-trapping techniques would have limited our research to capturing only incubating or brooding birds.

Capturing wading birds away from their nest (e.g. in a grassy, inundated wetland) can be difficult because it is hard to predict where a bird will be and when it will be there. In the past, rocket nets have been used to capture Ciconiiformes such as Great Blue Herons (*Ardea herodias*) (Parris 1977) and Wood Storks (*Mycteria americana*) (Bryant pers. com.). Bateman (1970) placed mist nets at watering sites near breeding colonies to capture White Ibises and Cattle Egrets (*Bubulcus ibis*). However, neither of these techniques have been reliable because of the difficulty of repeatedly attracting birds to a specific site (Bateman 1970) and the wariness of the birds to approach mist nets (Bateman 1970, Parris 1977).

We captured ibises to examine their reproductive physiology on an individual basis and tracked birds with radio telemetry to record behavior. To conduct this research we developed a reliable, portable and safe method of capturing White Ibises away from nests. In this section, we describe the lure arrangement and the water and vegetation variables that affected our trap success, and compare the safety, efficiency, expense, and ease of use of rocket nets and mist nets.

Methods

Study Area and Trap Site Selection

From January through June of 1999, 2000, and 2001, we captured White Ibises in Everglades Water Conservation Areas (WCAs) 1, 3A and 3B (Broward, Dade, and Palm Beach Cos., FL). These areas are flat, seasonally inundated freshwater marshes dominated by extensive stands of sawgrass (*Cladium jamaicense*) and cattail (*Typha angustifolia)*. The sawgrass marsh landscape is interrupted by tree islands and sloughs (Gunderson 1994). Peat depths in these areas range from 10 cm to greater than 2 m.

We surveyed WCA's by aircraft and airboat to identify potential White Ibis foraging areas (i.e. water depth less than female ibis bill length), areas where ibis were seen foraging, and roost or colony sites. At roost and colony sites we observed the primary departure direction and then selected a trap site one to three km away from the roost in that direction. We attempted to trap birds from sunrise to 1000 hrs. Trapping in the early morning hours avoided heat stress to the birds and birds seemed to respond best to the decoys in low light conditions. We processed captured birds on an airboat parked approximately 25 m from the trap area.

Factors Affecting Trapping Success

Ibises were lured to trap sites with white plastic flamingos supported by 1-m long steel wire legs (Union Products, Leominster, MA; Cat. No. 77280 Snomingos, 1 decoy =1 m x 0.75 m x 0.5 m, 300 g). Typically, we placed 30-40 decoys in the trap site for at least one day before any trap attempt. We recorded the number of days the decoys were at the site, how many decoys we used, area covered by decoys, water depth, vegetation height, time of first White Ibis arrival, species of birds that landed with the decoys, and length of stay. To calculate decoy density we estimated the area as the distance between the two decoys at the end of the longest axis of the decoy set (length, mean = 6.1 m ± 1.7) multiplied by the distance between the two most distant decoys along the axis perpendicular to the length measurement (width, mean = 4.3 m ± 1.6) and then divided the number of decoys by the area.

Trapping Techniques

We attempted to capture adult White Ibises lured to the decoy site with one of four traps: noose carpets, bow net, rocket net, or mist nets.

Noose Carpets and Bow Nets

Noose carpets consisted of approximately 75 monofilament nooses fastened to chicken wire with a knot and super-glue, and placed on a 1 x 1 m steel rod frame. We submerged 5-noose carpets approximately 4 cm under the water surface in the center of the decoy arrangement. We tied 1 m elastic cord to each carpet and anchored them to a rebar sunken into the muck.

We constructed a 5 m x 4 m rectangle bow net from conduit rods (3 cm diameter) attached to a gate hinge on either side with a 10 cm transverse spring. Volleyball nets were attached to the rods to entangle the birds. This technique required that birds landed within a specific area that can be covered once the trap is sprung.

Rocket Net

The rocket net was a 17.4 m x 12.9 m, 3 cm mesh waterfowl-pigeon-dove net (Wildlife Materials, Carbondale, IL). During our first attempts to rocket-net ibises we deployed the net from a wooden box. A similar design has been used by biologists who capture Wild Turkeys (*Meleagris gallopavo*) in snow (Eriksen et al. 1993) and American White Pelicans (*Pelecanus erythrorhynchos*) in water (King et al. 1998). The box contained the net and held it above the marsh surface so that the net did not get wet. This box was constructed with 1.9 cm (.75 inch) thick plywood. The top and bottom were trapezoids with the widest edge (95.5 cm) facing the open side of the box and the narrow end (26 cm) in the rear. The sides were 70 cm in length. The box was 61 cm tall. All edges were reinforced with aluminum angle bar. Three rockets deployed the net after firing from angle iron launchers attached to the top of the box (Eriksen et al. 1993). We constructed multiple boxes with similar dimensions using thinner wood in attempts to decrease box weight. All of these boxes suffered extensive damage (came apart from force of the explosion) after just one use.

To anchor the net we tied 15 m nylon rope at each corner and the center of the net. These ropes were held outside of the box while packing the net. Half cinder blocks (13 kg) were tied to the end of each rope. The center anchor was placed next to the box and each corner line was dragged at a 45 degree angle from its' respective corner. Three weight-forward rockets (Wildlife Materials. Carbondale, IL) were loaded with black powder charges (Winn Star Co., Marion, IL) and each was attached with a 60 cm metal link chain and U-bolt to a corner or the center of the net.

We fired the charges via a 12-volt motorcycle battery connected to a toggle switch and a 35 m insulated copper electrical line (Wildlife Materials, Carbondale, IL). The charges were wired in parallel. The rocket box was placed approximately 8 m from the center of the decoys.

After four attempts to capture ibises with the rocket net deployed from the box we noticed that many birds escaped while the net unfolded, and that birds would escape by running underneath the net that was supported by tall vegetation. We therefore flattened any vegetation around the decoys either with our feet or by driving the airboat over the area, and used a supporting platform (Cox and Afton 1994) that allowed the net to be partially extended before it was fired over the birds. We placed 7 corrugated plastic roofing panels (1 m x 3 m, Home Depot, Miami, FL) on marsh vegetation so that they overlapped about 1 m on each end. Their total length was approximately 19 m. The net was stored accordion style folded onto the anchored edge in about .75 m widths and then rolled from left to right. To set the net we simply placed it on the plastic sheets and unrolled. The density of vegetation and surface area of the plastic sheets were enough to support the net and keep it above water. By folding the net in this manner the leading edge, or firing line was on top and the rockets could be easily attached to the net.

The rockets were placed in 3 launchers constructed from 180 cm 3-angle fence post with two 15 cm steel pipes welded perpendicular to the post at 100 cm and 135 cm from the bottom. The launchers were placed into the ground at varying depths depending on the substrate. The different pipe heights allowed us to adjust the rocket height accordingly. The middle post was placed behind the middle point of the plastic sheets and angled slightly back. The corner posts were placed half way from the middle post to the end of the plastic sheets on each side. These posts were angled slightly above horizontal and aimed at the estimated top corner of the extended net. For this set the charges were wired in series.

We used nylon ropes and cinder blocks for anchors. For this set all lines were taut and placed directly behind their point of attachment on the net. The insulated firing line was spliced in series for attachment of the rockets. We wound the firing line once around each post to prevent it from being carried with the net upon deployment. The rockets were fired only after the birds landed at the decoys and there were no birds circling in the area. After firing the net, we ran from the boat to the net with at least two fire extinguishers (to put out any fires started in vegetation) and bird bags.

We were able to reset the rocket net the same day if we used the platform technique. To do this we would refold the net on to the panel platform and insert fresh charges into the rockets. We were not able to reset the net if we were using the box technique because the wet net was to heavy to deploy properly from the more tightly folded arrangement in the launching box.

Mist Nets

We placed two 3 m x 12 m 100 mm gauge mist nets (Avinet Inc.) in a V shape around the plastic decoys. We were careful that the bottom edge of the net was at least 30 cm above the water to ensure that caught birds did not get wet. For this reason, at sites where the poles sank into deep muck, we did not always use the lower trammel on the net. The nets were supported by three aluminum poles (height = 3.06 m). At the crux of the V the net tiers were interlaced on a common pole. Each pole was anchored by two guy lines and concrete weights (8 kg), and inserted into a 1.5 m length of conduit placed into the muck for added support. The middle pole was placed at the edge of the decoys (less than 1 m from decoys) and the nets ran along the edges of the decoy cluster. After we retrieved birds from the mist net we collapsed the nets to ensure that no birds would be captured while we were processing birds on the boat.

Analyses

We categorized trapping attempts as either successful or unsuccessful (i.e. a success attempt is one or more trapped birds). We combined results from mist net and rocket net attempts because trapping success was not significantly affected by trap type (all interaction terms $P > 0.05$). We used a multivariate analysis of variance (Manly 1994) to compare lure characteristics (number of decoys, density of decoy set) and environmental conditions (water depth, and vegetation height) between successful and unsuccessful sites. To avoid problems of non-independent samples we used only the first trapping event at any one location for analysis.

To examine differences between trap types we used a t-test, or nonparametric Wilcoxon Sign Rank test, depending on the nature of the data. All descriptive statistics are reported as mean ± standard error. Statistical analyses were done on SAS software.

Results

Factors affecting trap success

The decoys were successful in attracting seven species of wading birds on one or more visits (White Ibis, Snowy Egret (*Egretta thula*), Cattle Egret, Glossy Ibis (*Plegadis*

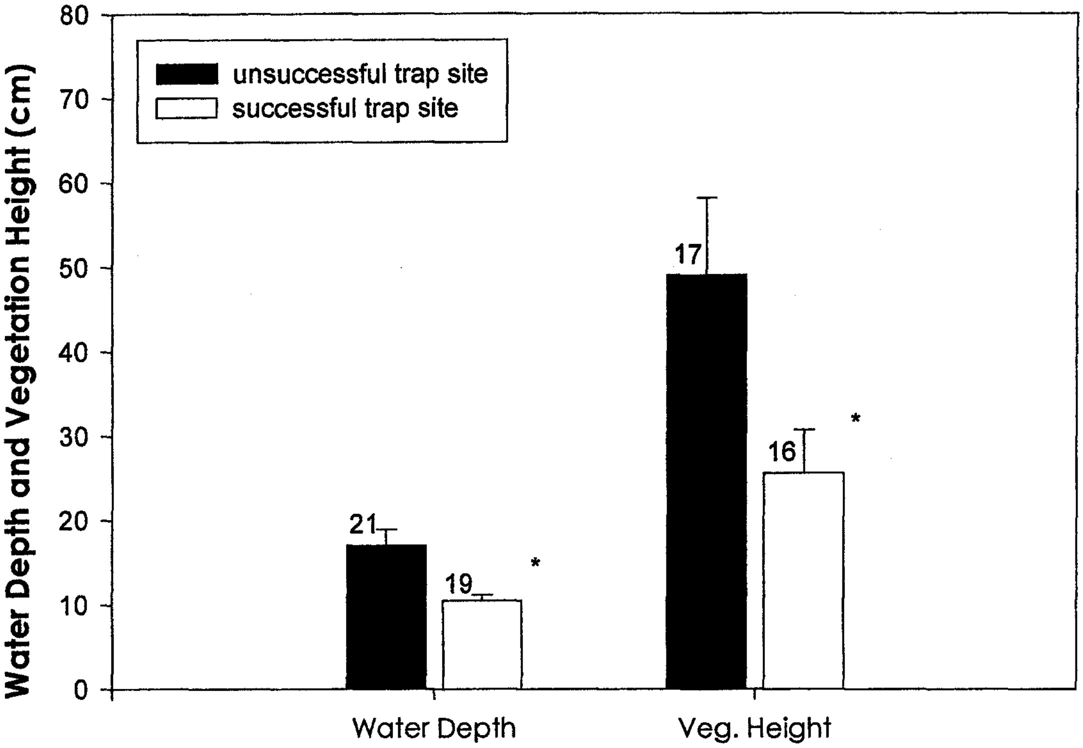

Figure 7.1 Environmental factors that affected trap success for White Ibises in the Everglades (years 1999-2001) include water depth (MANOVA: P = 0.037), and vegetation height (MANOVA; P = 0.036). '*' indicates a significant difference between successful and unsuccessful sites. Sample sizes are denoted at the upper left corner of bar

Table 7.2. Descriptive statistics of three capture methods used to trap White Ibises in the Everglades (mean ± 1 s.e.).

Trap	**# of days**	**# of sets**	**set/day**	**Time to prep 1st set (min)**[a]	**Time to prep other sets (min)**	**Total prep time (min)**	**Total clean time (min)**	**Total set time (min)**	**# WHIB trapped**	**WHIB trapped / day**[b]	**cost**
Rocket net (box launch)	4	4	1	30.25 ± 2.72	---	30.25 ± 2.72	28.75 ± 3.56	122 ± 27.36	3	0.75 ±0.74	$2500
Rocket net (platform)	19	29	1.52 ±0.14	35.11 ±2.04	27.00 ±1.19	56.15 ±5.70	35.17 ±3.44	79.47 ±17.86	34	1.78 [c] ±0.66	$2000
Mist net	78	174	2.24 ±0.14	26.96 ±1.06	8.75 ±0.46	40.76 ±2.34	21.88 ±0.80	130.02 ±6.26	97	1.25 ±0.1	$500
Total	101	207	2.05 ±0.12	28.03 ±1.00	10.72 ±0.72	43.27 ±2.19	24.60 ±1.01	120.2 ±6.25	134	1.33 ±0.17	

a: for descriptions of Time to prep first set; Time to prep other sets; Total clean time and Total set time, see text.

b: ± 1 standard deviation

c: mean changes to 1.16 ± 0.25 if remove day caught 13 birds *falcinellus*), Great Egret (*Ardea albus*), Tri-colored Heron (*Egretta tricolor*), and Little Blue Heron (*Egretta caerulea*)) for an average length of stay of 3.41 (± 2.87) minutes. After our first season in 1999, we vocally discouraged all birds that were not White Ibises to prevent them from hitting mist nets.

We captured 134 White Ibises. The number of decoys and the density of their arrangement had no significant effect on trap success ($F_{1,31} = 0.01$, $P = 0.984$; $F_{1,31} = 0.66$, $P = 0.4230$, respectively). Both water depth and vegetation height affected trap success ($F_{1,31} = 4.74$, $P = 0.0372$; $F_{1,31} = 4.78$, $P = 0.0365$ respectively; Table 7.1). Birds were more likely to be trapped in shallow water with low vegetation height (Figure 7.1). Additionally, birds arrived (time from nets set) more quickly to shallow trap sites (Spearman correlation $r_s = 0.423$, $P = 0.0175$).

Trapping Techniques

We did not trap any ibises with the noose carpets (N = 7) or the bow net (N = 15). However, both the rocket net and the mist nets were successful methods for capturing ibises. The maximum number of birds we captured with one rocket net set (or day) was 13. The maximum number of birds we caught with one mist net *set* was three and in one day of mist netting was five (4 sets). However, on average we caught a similar number of birds per day using either method (1.78 ± 0.7 rocket net; 1.27 ± 0.1 mist nets; Wilcoxon 2-sample S = 948.0, $P > 0.8$). Though means were similar between techniques, trapping

Table 7.1. MANOVA table for variables that affect White Ibis trap success. '*' indicates a significant effect ($\alpha = 0.05$). An insignificant Wilk's λ indicates that α will not be adjusted to correct for multivariate effects.

Source	df	SS	F	MANOVA *P*
ANOVA: Water Depth				
Trap success	1	111.385	4.74	0.0372*
Error	31	728.814		
ANOVA: Vegetation Height				
Trap success	1	4514.214	4.75	0.0365*
Error	31	29294.801		
ANOVA: Number of Decoys				
Trap success	1	0.018	0.00	0.9838
Error	31	1397.496		
ANOVA: Density of Decoys				
Trap success	1	0.522	0.66	0.4230
Error	31	24.546		

MANOVA: water depth, vegetation height, number of decoys, and density of decoys

Source	wilk's λ	F	Num df	Denom df	*P*
Trap success	0.75695631	2.2476	4	28	0.0893

success using rocket nets (1 - 18 bird / set) was more variable than using mist nets (1 – 3 bird / set).

Preparing a rocket net trap took significantly more time than preparing a mist net trap (Table 7.2). The average amount of time to set up the rocket net was 1.09 person-hours. Each subsequent set of the rocket net on the same day required an additional 0.9

person-hours. The average time to set the mist nets was 0.45 person-hours and just 0.15 person hours (9 minutes) to reset the nets. Thus, we were able to set many more mist net traps per day than rocket net traps (2.24 ± 0.1 vs. 1.52 ± 0.1, respectively). Rocket net traps also took more time to clean up than mist nets (Table 7.2).

On five occasions using the rocket net we had a misfire when the net did not deploy correctly or did not deploy at all. One was the result of a twisted lead line; four others were the result of a broken circuit. Additionally, we had one misfire when we forgot to unplug the battery from the firing line and the net fired while we were setting the trap. No one was permanently injured, but we did experience temporary hearing loss because we were so close to the rockets when they fired. It may also be important to consider potential adverse effects of the rocket noise on the birds.

Ibises rarely escaped the mist net once they contacted the net (6 of 103 escaped). More often, ibises seemed to see and avoid the net prior to contact. Of the 347 birds that approached the nets, 97 were captured (28%). Most birds (68%) were trapped on the outside of the 'V' set. Even with a large mesh net, ibises were often not entangled but instead became 'bagged' in the trammel lines. Thus, it was important to set appropriate distances between tiers in the mist nets and maintain tight trammel lines. Once a bird was caught in the mist net no other birds approached the area until the captured bird was removed.

Five captured ibises (3 with a rocket net, 2 with mist nets) were entangled and struggled in surface water. These birds were too wet to fly after processing, but did fly after being isolated for approximately 45 minutes in a recovery box. To avoid this problem while using the rocket net we attempted to trap in areas that had vegetation to support the net. However, birds could escape from underneath the net if vegetation provided enough room for the birds to lower their head and run to the edge of the net. To avoid the problem of birds getting wet in the lower tiers of the mist nets we trapped in areas with little surface water, and did not walk directly underneath the nets while we set them. Repeatedly treading on the marsh vegetation would create troughs of muddy water under the nets. No birds sustained permanent injuries or died by either method.

Discussion

Factors affecting trap success

As far as we know, only one other worker has used decoys to lure wading birds to a trap site. Bateman (1970) placed wading bird silhouettes in watering areas near colonies to lure White Ibises and Cattle Egrets into mist nets. He found that at each site the effectiveness of the decoys declined over time. Birds became wary and difficult to catch. In contrast, we found that if environmental variables were favorable, birds responded to decoys irrespective of how long they had been in place. Indeed, the number of decoys, decoy density and the number of days left at a site had no effect on capture success. We captured birds at the same site up to 17 days after the decoys had been set. Other workers have used decoys to lure wading birds to foraging areas to conduct experiments on environmental and social factors that affect foraging success and behavior (D. Gawlik in press, and E. Stolen pers com.).

Ibises arrived sooner and were more likely to be captured at sites with lower water levels and shorter vegetation. At these sites prey items may be more concentrated and easier to capture (Gawlik in press). These results are consistent with the idea that shallow, open wetlands with sparse vegetation provide the best foraging areas for White Ibises (Surdick 1996).

Trapping techniques

Although we were certain some ibises landed on the noose carpets, we trapped no birds with this technique. This is a passive trapping technique and unless the bird spends a considerable amount of time on the carpet, or hits a noose with force, the bird is unlikely to become tangled. A bow net trap requires that birds land within a specific area that can be covered once the trap is sprung. Unfortunately, in a large open landscape with few physical obstacles (e.g. the Everglades) it is hard to achieve this accuracy, even with the use of decoys.

Rocket net equipment was heavy compared to mist nets. In addition, mist nets were safer to transport and use. Although there were no differences in trap success, the mist nets took less time to prepare for use, less time to reset, and less time to clean up (Table 7.2). Because reset times were consistently shorter for mist nets, this trap method may be better for multiple captures of a few birds in a given day.

Mist nets were less effective than the rocket net at one rocky, shallow area near a deep canal. Birds foraged at this site for approximately one month before the breeding season. This was our only site that birds returned to predictably for many days whether or not decoys were in place. Many species of birds foraged here and the birds were usually concentrated in a small area by natural obstacles. Here it was difficult to anchor mist net poles and the nets were very visible. Additionally, we lost trap time by removing the constant by-catch (22 individuals of 8 species) from the mist nets. By comparison, the rocket net set was easy to camouflage and leave in place and we could select the appropriate time to fire the net, resulting in decreased by-catch.

We had no permanent injuries or mortalities of birds using either method. Other researchers who have used rocket nets report drowning (Cox and Afton 1994) or collision with the net or rocket (King et al. 1998) as causes of injury or death. In addition, indirect factors such as the possible number of birds captured at one time with a rocket net may have adverse effects. Studies of ducks trapped by the hundreds show that prolonged entanglement in the net and handling times may cause muscle myopathy (Dabbert and Powell 1993) or decreased survival (Cox and Afton 1998).

We found that luring White Ibises with white plastic flamingo decoys and using either capture technique was efficient and reliable. Mist nets were easier to use, cheaper, weighed less, took less time to set and clean up, and can be safer than rocket nets. However, we could capture more birds at one time with a rocket net. These methods may also be useful for capturing other species of wading birds as evidenced by the individuals from seven other species of water birds that landed within the decoys.

Part B. White Ibis integument color changes during the breeding season: description, hormonal correlates and classification model.

Introduction

In many bird species, the color of the cere, bill and legs becomes more vivid during the breeding season (Eens et al. 2000; Negro et al. 1998; Burley et al. 1992). Typically, bill and leg colors are strongest early in the breeding season (e.g. courtship) and subside by chick fledging stage (Burley et al. 1992). Vivid colors may serve as a signal to potential mates of readiness to breed or indicate an individual's quality as a mate (Keyser and Hill 2000; Hill 1996).

Birds cannot synthesize the color pigments (carotenoids) responsible for these colors, and changes must therefore be the result of diet shifts, including content and quantity, and/or metabolic changes (Negro et al. 2000). The mechanisms responsible for color changes are poorly understood (Bortolotti et al. 1996). However, many other reproductive changes (behavioral and physiological) are associated with increases in hormone levels. Hormone levels may influence color changes through changes in metabolism or allocation of nutrients.

Because the colors of bill and legs change through the season, these changes may serve as an empirical tool for studying the reproductive biology of birds that are difficult to otherwise study intensively. In many cases this may allow researchers to avoid using invasive techniques, such as capturing adult birds on (or near) their nest which has been associated with temporary or permanent nest abandonment (Jewell and Bancroft 1991). Integument color changes may be used to model the reproductive stage of birds for which little other reproductive information exists. The development and use of such a model would allow us to identify birds that have become reproductively active (see Chapter VIII).

Male and female White Ibises display dramatic changes in bill and leg color during the breeding season. Birds develop red bills and legs and, during the display stage, large gular sacs (Kushlan and Bildstein 1992). In this section we will 1) describe the color changes of White Ibis bills and legs during the breeding season, 2) investigate the hormonal correlates of color changes, and 3) present a model based on bill and leg color changes to classify the reproductive stage of White Ibises captured away from their nest.

Methods

We categorized the breeding season of White Ibises into five distinct stages: pre-breeding, display, copulation and egg production, incubation and chick rearing. Pre-breeding birds were those captured prior to any nesting activity within the study area or birds captured in early spring that showed no external signs of reproduction. Display birds were ibises that have begun to show breeding colors, or attend colonies (monitored through radio telemetry, see Chapter IX), and/or females who had distended gular pouches. The display stage usually lasts 10 days (Kushlan and Bildstein 1992). Nest building probably takes place during the end of the display stage and the beginning of the copulation and egg production stage. Copulation and egg production takes place over approximately 10 days (Kushlan and Bildstein 1992). We identified female ibises in egg production by palpating the abdomen and noting the presence of an egg. This method was later validated by laparoscopy (Chapter VIII). Male ibises stay at the colony at this time and do not make regular foraging trips (see Chapter VII). Male and female ibises incubate the eggs beginning with the laying of the last egg. Incubation lasts about 3 weeks, and both sexes contribute to chick rearing by brooding and feeding the chicks. Chick rearing lasts approximately 6 weeks. Although these reproductive stages may be discrete physiological and behavioral events, we expected many characteristics to be highly variable across individuals, and estimates may overlap especially among sequential events. For example, a bird captured during late incubation may have more in common with chick rearing adults than birds in the first week of incubation. Therefore, we consider our analyses of physiological characteristics to be conservative estimates of differences among reproductive stages.

Sampling birds

We sampled tree and shrub nesting ibises of known nesting stage at colonies in central Florida (Lake, Polk, and Orange Co.). The colony on Discovery Island at Disney World (Orange Co. FL) was located on an island that housed a small zoo. Ibises in this colony were free-living but habituated to humans. At Discovery Island and at a colony on Lake Griffin (Lake Co. FL) we trapped adult ibises on the nest using a cylinder-wire-mesh nest trap designed by Frederick (1985). We recorded the stage of the nesting bird as incubation (eggs in nest) or chick rearing (chicks in nest).

We also captured birds in pre-breeding, display and copulation/egg laying stages at foraging sites in the Everglades (see above Chapter VII). Pre-breeding birds were those that were captured before any nesting had begun in the Everglades area, and display birds were those with large, pronounced gular pouches. To identify birds that were laying eggs we palpated female ibises' abdomens. In one case we were also able to follow a male back to his nest via radio-telemetry 25 days after he was captured. At his nest were three chicks less than 5 days old and identify that he was in copulation stage when trapped. Once adults were trapped (either on the nest or with a mist net) we collected blood from the jugular vein (3 ml), marked the bird with a USFWS aluminum band, and measured mass and other morphological measurements (see Chapter VIII). We scored bill and leg colors by holding a paint swatch (Wal-Mart stores brand numbers 0071-1111) up to the body part and recording the color that most closely resembled the bill or leg. We attempted to score colors in consistent light conditions. A similar method using the Munsell color system has proven successful for scoring bird plumage conspicuousness (De Repentigny et al. 1997). Hormone levels were determined by radioimmunoassay (see Chapter VIII).

Analyses

To analyze changes in integument color we scanned the standard color swatches (Hewlett Packard ScanJet 6100C) and scored them for red, blue and green content using *PhotoStudio 2.0* (Arcsoft). Color content values were entered into a principal components analysis based on a covariance matrix. The first principal component accounted for variations in brightness (light to dark) and the second principal component accounted for variation in hue (ratio of green content to blue content) (Table 7.3). A low score on the first principal component indicates a darker color than a high score. A low score on the second principal component indicates more blue color than green. Each bird was given a score from the first two principal components of its bill color and leg color. To investigate how colors change during the breeding season we performed a MANOVA on color scores collected from known stage birds. We used reproductive

Table 7.3. Eigenvalues and Eigenvectors (below) for principal components created from the variables red, blue and green measured in White Ibis leg and bill color (N = 72).

Principal Component	Eigenvalue	Difference	Proportion	Cumulative
PRIN 1	5852.83	5251.58	0.89	0.89
PRIN 2	601.25	448.74	0.09	0.98
PRIN 3	152.51	.	0.02	1.00

Eigenvectors

Color	PRIN 1	PRIN 2	PRIN 3
Red	0.162	0.501	0.850
Green	0.687	0.561	-0.462
Blue	0.708	-0.659	0.253

stage as the predictor variable and scores on the principal components for bill and leg color and the length of bill that is colored black (mm) on the bill ("bill black") as the response variables. To compare means between groups we performed an *a posteriori* Tukey's mean comparison test (Zar 1999). Before conducting the MANOVA we checked for gender effects. There were no differences between male and female ibis color changes (all interaction term P's ≥ 0.25).

To control for gender variation in endocrinological processes, we performed a canonical correlation analysis for data collected from male and female ibises separately. Canonical correlation evaluates the relationship between two groups of (continuous) variables (James and McCulloch 1990). This test attempts to maximize correlations between canonical variables from each set of groups, in this case color scores and hormone levels. We chose this test in part because it does not imply causation (only correlation). In addition, physiological responses are often the result of interactions among different hormones, and this test allowed simultaneous examination of correlations among all hormones, with the potential for interactive effects.

To develop the classification model for reproductive stage we chose the variables with the lowest P-values calculated in the MANOVA (the first two principal component scores for leg color, the first principal component score for bill color and the variable 'bill black'). We then conducted a discriminant function analysis to classify reproductive stage. All data met the assumptions of discriminant analysis (homogeneity of covariance matrices and normality; Manley 1994).

All analyses were performed using SAS 6.12 statistical software. Descriptive statistics are reported as mean ± standard error.

Results

Reproductive changes

All ibis integument colors changed shades during reproduction (Table 7.4). The first principal component score for leg color was significantly lower during the display and copulation phase, and the second principal component scores were low during the display stage. In other words, leg color was darkest red with a blue tint during the display phase. Ibis legs became paler with more of a green tint as the nesting season progressed (Figure 7.2). The first principal component for bill color was lowest during the display and copulation stages. Scores for the second principal component were low during the display, copulation, and incubation stages. Ibis bills were a dark shade of pink during the display stage and then faded to a light salmon color during chick rearing (Figure 7.3). As ibis bill colors faded, the black tip extended from the distal to the proximal portion of the bill. Ibis bills did not have a significant amount of black until the breeding season had started (Figure 7.4).

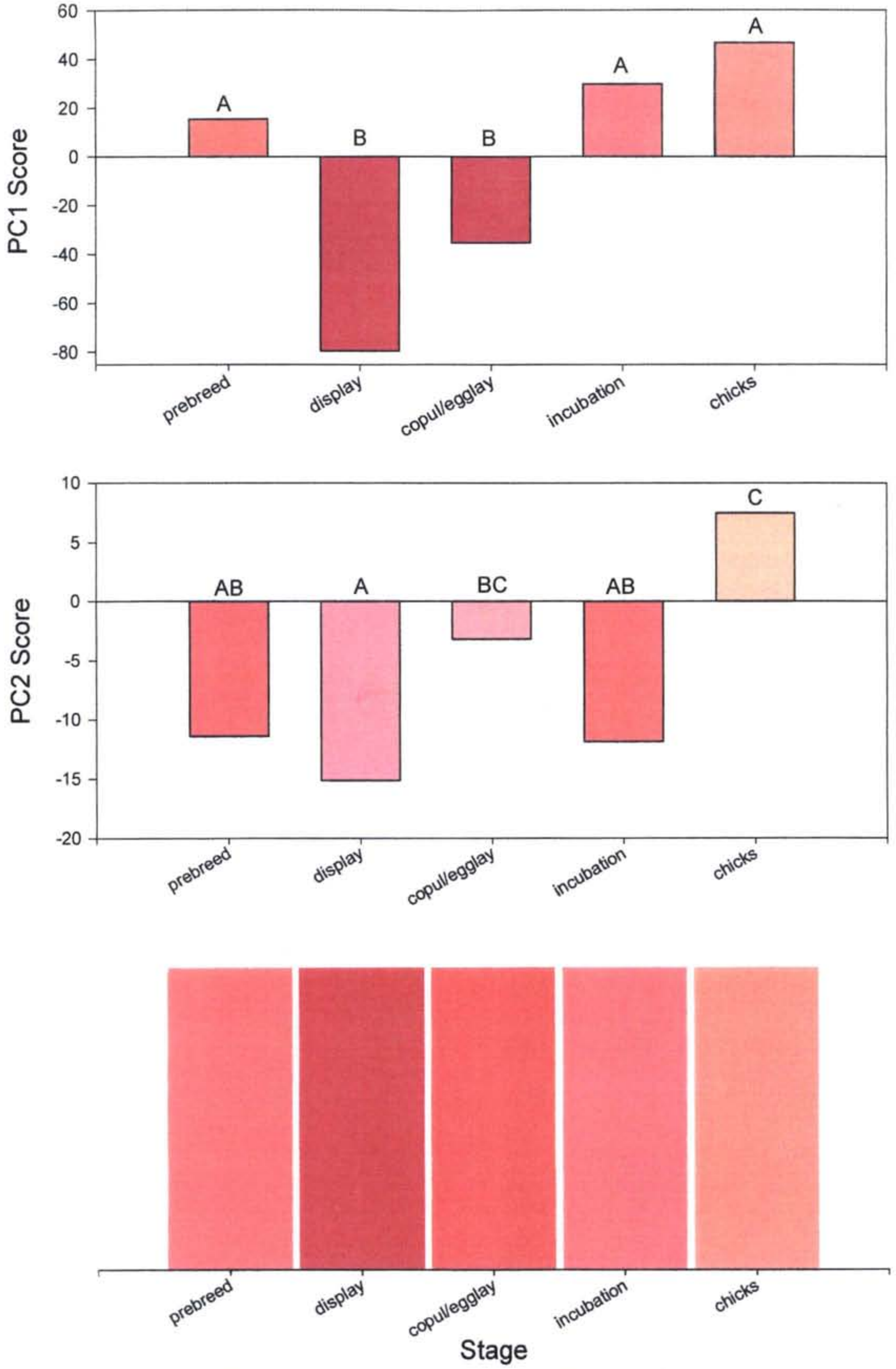

Figure 7.2. Changes in ibis leg color during the breeding season. Top: changes in principal component 1 score. Fill colors are the "average" score for each breeding stage. Middle: changes in the principal component 2 score. Fill colors are the "average" score for each stage. Means with the same letter are not significantly different. Bottom: 'true' ibis leg colors. During the display stage the legs are darkest with a blue tint.

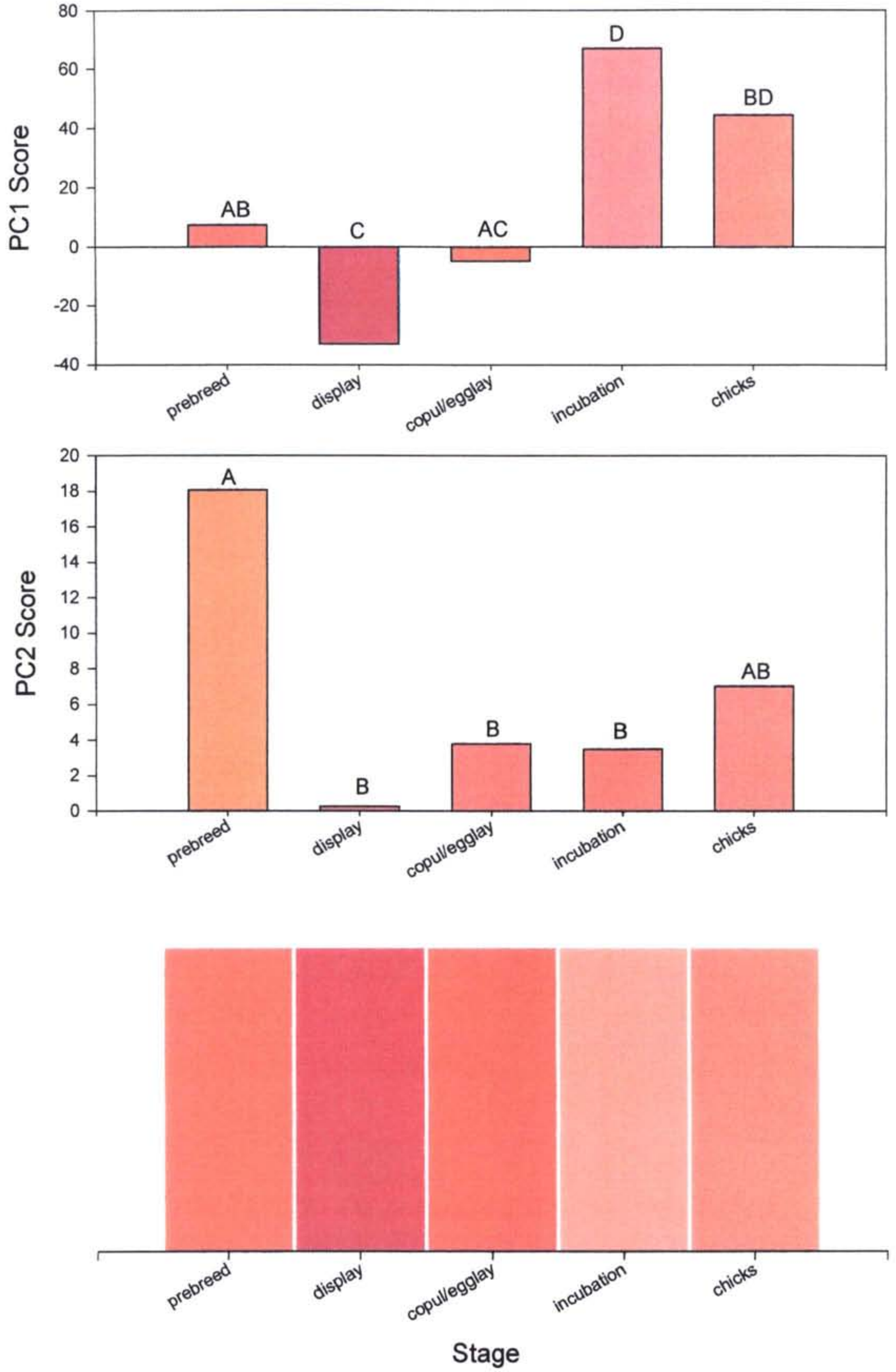

Figure 7.3 . Changes in ibis bill color during the breeding season. Top: changes in principal component 1 score. Fill colors are the "average" score for each breeding stage. Middle: changes in the principal component 2 score. Fill colors are the "average" score for each stage. Means with the same letter are not significantly different. Bottom: 'true' ibis leg colors. During the display stage the bills are darkest.

Table 7.4. MANOVA table for effect of White Ibis reproductive stage on principal component scores for leg and bill colors and amount of black on the bill. A significant Wilk's λ indicates that α will be adjusted to correct for multivariate effects. Bonferroni adjusted α = 0.01.

Source	df	SS	F	MANOVA *P*
ANOVA: Leg PC1				
Stage	4	125560.862	15.71	0.0001
Error	54	107865.404		
ANOVA: Leg PC2				
Stage	4	3408.501	10.77	0.0001
Error	54	4273.103		
ANOVA: Bill PC1				
Stage	4	72449.466	13.12	0.0001
Error	54	74590.946		
ANOVA: Bill PC2				
Stage	4	2679.447	5.84	0.0006
Error	54	6196.956		
ANOVA: Black on bill				
Stage	4	91881.824	24.06	0.0001
Error	54	51624.684		

MANOVA: Leg PC1, Leg PC2, Bill PC1, Bill PC2 and black on bill

Source	Wilk's λ	F	Num df	Denom df	*P*
Diet	0.0626	10.89	20	167	0.0001

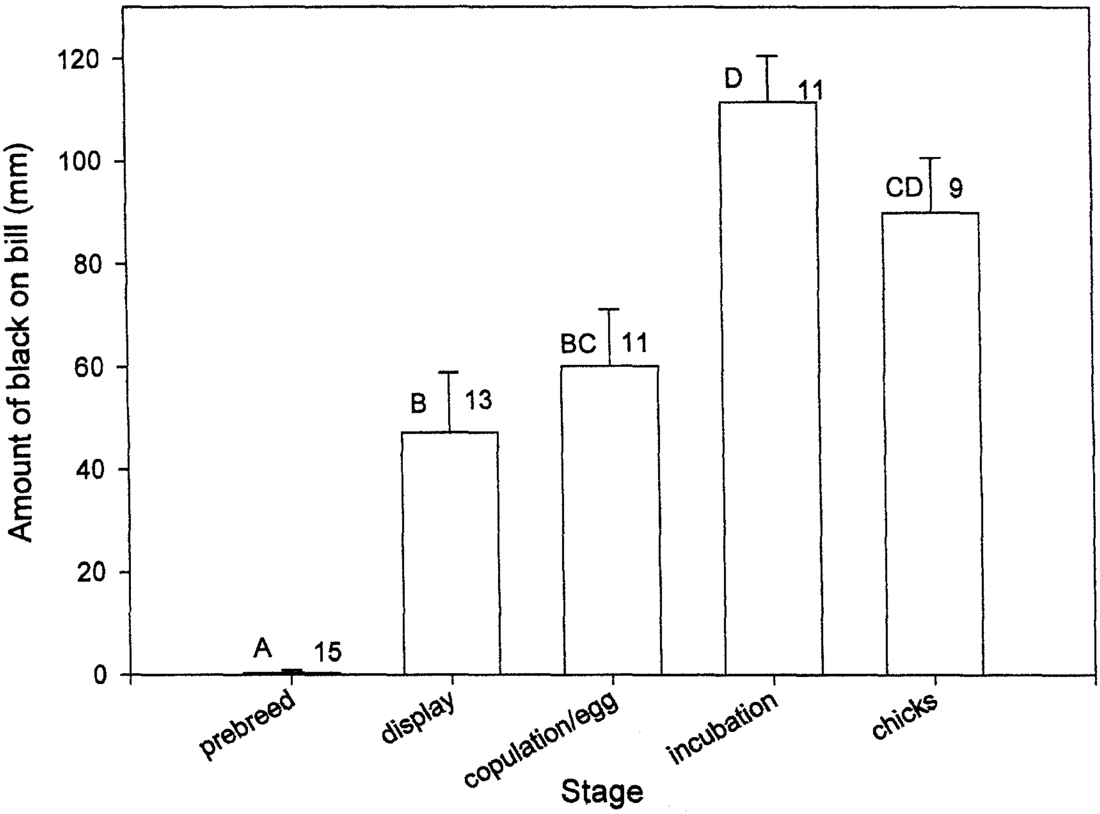

Figure 7.4. Changes in the amount of black on the bill over the course of the breeding season (mean ± s.e.). Samples sizes are indicated by a number on the upper right of the bar. Bills are most black during the incuabtion stage as face and bill areas lose their strong red color. Means with the same letter are not signifcantly different.

Hormone levels and color changes

Female ibis color changes correlated with testosterone levels (Wilk's λ $F_{12,85} = 2.78$, $P = 0.0030$) (Table 7.5). The first canonical correlation indicated a relationship between testosterone and the first principal component score for of leg color and the second principal component score for bill color (Table 7.6).

Table 7.5. Eigenvalues for the canonical correlation between hormone levels and color scores for female White Ibis. '*' indicates significant at $P < 0.05$.

Canonical Correlation	Eigenvalue	Difference	Proportion	Cumulative
1	0.8645	0.6159	0.7540	0.7540*
2	0.2486	0.2152	0.2168	0.9709
3	0.0334	.	0.0291	1.0000

Table 7.6. Squared multiple correlations between hormone levels and color scores for female White Ibis. Numbers in bold indicate large contribution to canonical variable.

Hormone	Color Canonical Variable 1	Color Canonical Variable 2
Estradiol	0.0884	0.2455
Testosterone	**0.4531**	0.4558
Progesterone	0.0251	0.0251

Squared multiple correlations between female White Ibis color scores and the first two canonical variables of the hormone variables

Color Score	Hormone Canonical Variable 1	Hormone Canonical Variable 2
Leg PC1	**0.3610**	0.3612
Leg PC2	0.0005	0.0369
Bill PC1	0.0587	0.1262
Bill PC2	**0.2446**	0.2629

This relationship was not as clear for male ibises. None of the canonical correlations approached significance (Table 7.7; all P's ≥ 0.49). Further, none of the canonical variables explained much variation among any of the variables (Table 7.8).

Table 7.7. Eigenvalues for the canonical correlation between hormone levels and color scores for male White Ibis.

Canonical Correlation	Eigenvalue	Difference	Proportion	Cumulative
1	0.2831	0.1984	0.6559	0.6559
2	0.0847	0.0209	0.1963	0.8522
3	0.0638	.	0.1478	1.000

Table 7.8. Squared multiple correlations between male White Ibis hormone levels and the first two canonical variables of the color variables

Hormone	Color Canonical Variable 1	Color Canonical Variable 2
Estradiol	0.0335	0.0335
Testosterone	0.1697	0.1865
Progesterone	0.1051	0.1383

Squared multiple correlations between male White Ibis color scores and the first two canonical variables of the hormone variables

Color Score	Hormone Canonical Variable 1	Hormone Canonical Variable 2
Leg PC1	0.0601	0.0847
Leg PC2	0.0155	0.0372
Bill PC1	0.0123	0.0550
Bill PC2	0.0019	0.0035

Classification model

Six birds were captured on their nest, an additional 53 were captured away from the nest but had distinctive characteristics that indicated their stage of reproduction (i.e. large gular pouch or egg in oviduct). We used data collected from these 59 birds to create a discriminate function analysis. Four variables contributed significantly to the model (Tables 7.9 and 7.10). The model correctly identified stage of reproduction 96.4% of the time (resubstitution validation).

Table 7.9. Eigenvalues for the canonical variables used to classify reproductive stage of White Ibis. '*' indicates significant at the 0.0001 level.

Canonical Variable	Eigenvalue	Difference	Proportion	Cumulative
1	2.880	1.69	0.62	0.62*
2	1.185	0.57	0.25	0.87*
3	0.613	0.61	0.13	0.99*
4	0.002	.	0.00	1.00

Table 7.10. Pooled within canonical structure for variables Leg PC1, Leg PC2, Bill PC1, and amount of black on bill on the first 3 Canonical Variables.

Measured Variable	Canonical Variable 1	Canonical Variable 2	Canonical Variable 3
Leg PC1	0.4683	0.5117	0.6011
Leg PC2	0.3308	0.4325	0.6511
Bill PC1	0.5258	0.0575	-0.5271
Black on bill	0.6505	-0.6450	0.3331

Discussion

Reproductive changes

Male and female White Ibises exhibited dramatic color changes during the breeding season that appeared to be consistent with nesting stage. Ibises developed extended gular pouches, dark pink bills, and scarlet legs during the display stage. As ibis bills faded from dark pink they developed black tips. The amount of black on the bill was greatest during incubation. This blackening of the bill may be the result of changes in epidermal generation and sloughing associated with the preceding color change; however, this process is poorly understood.

Color changes probably depend on the consumption of carotenoids from crayfish (Negro and Garrido-Fernandez 2000) or other animals in the ibis diet. Thus, changes in soft tissue color could be the result of increased food intake, changes in metabolism, changes in the distribution of the metabolites, or a combination of these (and other) factors. Ibises do increase in body mass before courtship and egg production (see Chapters VI and VIII). Whether brightly colored skin areas are the result of changes in diet and hormone levels, and whether or not these relationships have a function in communication among ibises remains poorly understood.

It is important to point out that this study did not evaluate how the ibises perception of color of ibis bills and legs changed (Cuthill et al. 1999; Rojas et al. 1999). Unlike humans, birds see UV light and are more adept at distinguishing between colors (Siitari et al. 1999). Indeed, the colors we see as more conspicuous during courtship and display may not be more conspicuous to ibises. However, increased surface area of vividly colored regions via formation of an enlarged gular pouch indicates that the birds may be communicating by display of exposed skin areas.

Hormone levels and color changes

Female ibis color changes correlated with changes in testosterone. Several other studies have found a relationship between secondary sexual traits and androgens (Eens et al. 2000; Evans et al. 2000). The 'immunocompetence handicap hypothesis' predicts that color changes are related to testosterone, but that testosterone causes immunosuppression (Evans et al. 2000). Thus, it may be costly to be colorful and vivid traits that are stimulated by testosterone are considered an indicator of mate quality because individuals are able to display large sexual characteristics despite the potentially adverse effects upon their immune system (Eens et al. 2000).

The relationships among testosterone, sexual traits, and signal function may depend upon the species and the type of secondary trait or ornament (Bortolotti et al. 1996). Many birds exhibit sexually dimorphic feather coloration or undergo a prenuptial molt so that breeding plumage is more colorful than non-breeding plumage. The selection factors affecting the exhibition of vivid colors during the breeding season may differ between species that undergo a prenuptial molt versus species that change integument color, such as ibises. Feather pigmentation depends on the diet and metabolism of the bird while molting, usually preceding the breeding season, and growth and development of feathers may take several days. Integument color changes depend on changes in diet, metabolism and hormone levels during the breeding season and can occur quickly. Thus, changes in skin color are faster and less permanent than changes in feather color. Consequently, changes in skin color may be more indicative of readiness to breed than quality of mate, or social ranking.

Male ibises did not show a correlation among any of the hormone levels and skin colors. This is interesting in light of the fact that, for many birds that display secondary sexual characteristics, males and females respond similarly to testosterone (Eens et al. 2000). Further, male and female ibises displayed very similar color patterns. One possible explanation is that males may have a different physiological mechanism that promotes color changes than females. Alternatively, it should be remembered that a significant correlation between testosterone and color change in female ibises does not imply causation and this relationship may be the result of concurrent changes in female physiology and behavior. For example, female ibises may begin to increase the amount of food they consume at the same time testosterone levels that stimulate courtship behavior are increasing.

Classification model

Our work has demonstrated that White Ibis bill and leg color changes can be scored and used to classify the reproductive stage of birds. A model based on integument color changes (bill and leg) to classify the reproductive stage of birds captured and sampled away from their nest was useful for our study of White Ibis reproductive physiology. This technique allowed us to identify birds that underwent physiological changes associated with reproduction and address our questions concerning non-breeding behavior and abandonment. This technique may also be useful for studying other species that show stage specific coloration. Other researchers may use similar color change models to identify reproductive stage or other individual information (e.g. age or social status) that may be conveyed through plumage and integument color differences.

CHAPTER VIII. REPRODUCTIVE PHYSIOLOGY OF FREE-LIVING WHITE IBISES

Introduction

Over the past 13 years the number of ibises in breeding colonies has appeared to be considerably lower than the number of ibises present within the Everglades system (see Chapters I and V). Three of the four non-exclusive hypotheses that may explain this observation suggest that variability in ibis reproductive effort (number of breeding pairs) accounts for this difference. Indeed, it is difficult to estimate nesting effort because of asynchronous breeding, nest abandonment, and second nesting attempts and, unfortunately, these phenomena are difficult to quantify (Chapter IV, V). Though several studies have attempted to correlate environmental conditions with reproductive effort and abandonment rates, these studies have looked at large scale patterns of colony formation and nest numbers (Frederick and Collopy 1989, Kushlan and White 1977). No studies have examined individual behavior or the physiological factors that may affect nesting attempts, abandonment rates, or non-breeding behavior. To better understand nest initiation and abandonment we conducted a study to describe the physiological and environmental factors that correlate with White Ibis reproductive patterns.

White Ibises are the most abundant (in number and biomass) wading bird in the Everglades system. Ibises are similar to other wading birds in the Everglades in that they nest colonially on tree islands with other wading birds. In addition, their population decline over the past 40 years is representative of population declines of most wading bird species in the Everglades system. We believe understanding environmental and physiological factors that affect ibis reproduction may have larger implications for successfully managing all wading birds in the Everglades system.

White Ibises in the Everglades display an unusual breeding pattern compared to most temperate species in that they have a flexible breeding schedule (nest initiation ranges from February to September) (Kushlan and White 1977). Although most avian species show a distinct seasonal pattern in reproductive behavior, many species exhibit flexibility in their reproductive schedule. Flexibility in the timing of reproduction is the result of unique relationships among reproductive physiology, external conditions and behavior. This flexible breeding schedule, like nomadic movements, allows ibises to exploit favorable environmental conditions (Frederick and Ogden 1997).

To examine individual physiology and behavior we asked the following three questions: 1) Are there non-breeding birds in the Everglades system throughout the breeding season? By modeling ibises' external changes during the breeding season and examining gonadal changes we were able to identify the proportion of a random sample of adult birds that were reproductively active (Chapters VIII and IX). 2) Do White Ibises skip years between breeding efforts? Many birds skip years between breeding efforts because they are physiologically or energetically limited (Hector et al. 1985). Thus, if ibis reproduction is very costly it may be a natural part of ibis life history for the birds to skip years between nesting attempts. Alternatively, if the birds were adversely affected by a toxin (such as mercury) then they may be unable to reproduce. To answer this question we captured birds and examined the potential physiological constraints of ibis reproduction (i.e. body condition changes and gonad growth patterns) (Chapter VIII), and observed their reproductive behavior between years with radio telemetry (Chapter IX).

And 3) is White Ibis reproductive physiology affected by mercury levels? Mercury, a known neurotoxin, is a common toxin in the Everglades (Chapter X). However, little is known of mercury's effect on hormonal pathways that control reproduction. We measured mercury levels in male and female ibises and examined how breeding behavior, hormone levels and mercury may be related (Chapter X). In this Chapter we describe White Ibis reproductive physiology and identify potential constraints on reproduction (see also Chapter X on mercury).

Methods

Trapping Adult White Ibis

We trapped adult ibises with rocket nets, mist nets and nest traps (Chapter VII). We set all of our traps by sunrise and we stopped trapping by 1000 hrs. We trapped during the early morning hours to avoid heat stress to the birds and control for variation in hormone levels in the birds that might be caused by diel hormone patterns.

Measuring and sampling of birds

Once birds were trapped, we immediately collected a 3 ml blood sample from the jugular vein with a 22-gauge needle and 5 cc syringe (mean time from bird captured to completion of blood collection: 10.4 ± 0.7 mins.). If we captured more than one bird at a time, we placed birds in cloth sacks until they could be processed. While birds were being processed we placed a leather hood on their head to cover their eyes. Birds typically responded by appearing to 'sleep' (i.e. droop head and become docile). We marked each bird with a U.S. Fish and Wildlife Service Band placed on the leg above the carpel joint.

Ibises males are larger than females. Thus, we could usually estimate the gender of a bird from its bill and body size. We later we compared our subjective assessment to a more objective one using discriminant function analysis of body measurements (see below). We palpated female birds for egg presence. If a female did not have an egg or if the bird was male we examined their gonads through a laparoscopic procedure. Birds were anesthetized with isoflurane gas administered via a portable respirator and oxygen tank. A hose attached to a plastic cone (20 cm x 7 cm) that covered ibis bills and nasal openings delivered the mixture to the bird. Within 3-4 minutes ibises were unresponsive to touch. To view the gonads we made a small (5 mm) incision through the skin near the posterior rib on the left side of the bird. We slid the incision over the musculature between the ribs and made another incision into the abdominal cavity, so that the two incisions would not overlap when the skin was slid back into place. We then inserted an otoscope to view the gonads. Gonad length and width were estimated using a scale on the otoscope and we described color and, for ovaries, stage of oogenesis. Later, we used equations for calculating volumes of cylinders (testes) and spheres (ovary follicles) to estimate gonad size. Once the exam was complete, we discontinued isoflurane treatment and sealed the incision with veterinary quality super-glue. Ibises recovered quickly from the anesthesia, usually less than 2 minutes.

We measured mass to the nearest gram, straight and curved bill length, bill depth, wing chord, and tarsus length to the nearest mm and color of the captured birds. Colors were measured by holding a paint swatch up to the body part and recording the color that most closely resembled the leg or face (see Chapter VII). We also visually scored furcular fat stores and pectoralis size and examined birds for brood patches. Three scapular feathers were collected for mercury analysis (see Chapter X). Blood samples were stored on ice until the plasma could be separated (3-5 hours after collection). Plasma was stored at -20°C until analyzed for steroid hormone levels by radioimmunoassay (Guillette et al. 1993).

Determining gender and stage of reproduction

As mentioned above White Ibises are sexually dimorphic, with males up to a third larger than females and relatively little overlap in characters like bill length and curvature. However, there is overlap in size and morphometrics. We therefore verified our initial estimates of gender with statistical methods of classification.

To determine gender by classification with a discriminant function analysis we used body measurements of birds whose sex was determined through laparoscopy or genetic sexing (total N = 58, F = 32 and M = 26; genetic sexing by Zoogen see Frederick et al. 1998). Stage of reproduction was determined by a classification model based on leg and bill color (see Chapter VII).

Analyses

There were no significant differences in any morphological measurement among years (all MANOVA P's>0.05). Therefore, we pooled data collected in all years of this study (1998, 1999, 2000, and 2001). All descriptive statistics are reported as mean ± standard error. Statistical analyses were done on SAS software. All data were examined to make sure they fit the assumptions of the tests (e.g. normality). The most common assumption violated was homoscedasticity. Log transformed variables usually met this assumption, but did not change analysis interpretation (Sokal and Rohlf 1995).

Therefore, all hormone parameters and mercury levels were log-transformed for analysis. If parametric requirements could not be met then the appropriate non-parametric test was used (Hollander and Wolfe 1999).

Results

Gender classification

Overall accuracy of the gender discriminant function model was 99% with 100% of males being correctly identified and 99.95% of females correctly identified. Bill length straight, bill depth, and tarsus length best discriminated between the males and females. Keel length and wing length did not significantly contribute to the model. We did not use mass because we found that the inclusion of gravid females significantly affected this variable's ability to predict sex.

Table 8.1. Eigenvalues for the canonical variable used to classify gender of White Ibis. '*' indicates significant at the 0.0001 level.

Canonical Variable	Eigenvalue	Difference	Proportion	Cumulative
1	8.8040	.	1.00	1.00*

Table 8.2. Pooled within canonical structure for variables bill straight, bill depth, and tarsus length on the first Canonical Variable.

Measured Variable	Canonical Variable 1
Bill Straight	0.8315
Bill Depth	0.3959
Tarsus Length	0.6454

Responses to Anesthesia and handling

White Ibises responded well to anesthesia with isoflurane. Birds were exposed to high flow anesthesia (level:5) for 4-6 minutes, after which we decreased the flow of isoflurane (level:1) to keep birds anesthetized. The procedure of anesthetizing the bird, making an incision, examining the gonads and resealing the skin took 16 minutes on average (± 0.7 min; N = 45). After completion of other morphology measures we placed birds in a recovery box for approximately 10 minutes. All birds flew well upon release.

Gonad Changes

We attempted to visually examine the gonad condition of 21 female and 16 male adult White Ibises. We successfully scored the largest ovarian follicle on 81% of the female birds. If a bird had an egg in the oviduct it was difficult to view the ovaries. Subsequently, if we felt the presence of an egg through physical exam then we did not attempt to perform a laparoscopy on the birds. Ovaries were largest during copulation and egg production (Figure 8.1). Yolk began to deposit in follicles during the display stage. Ovary sizes seem to correlate with increases in daylength, though the brevity of egg production and the variation in nesting attempts makes this relationship difficult to interpret (Figure 8.2). No steroid levels correlated with ovary size (all P's > 0.18).

We successfully viewed the testes of 100% of male birds we laproscopied. Testis size also showed changes during the breeding cycle. Testes were largest during display, egg production and incubation (Figure 8.3). Enlarged testes were a yellowish white color, but smaller testes were bluish green. Testes size increased with increasing

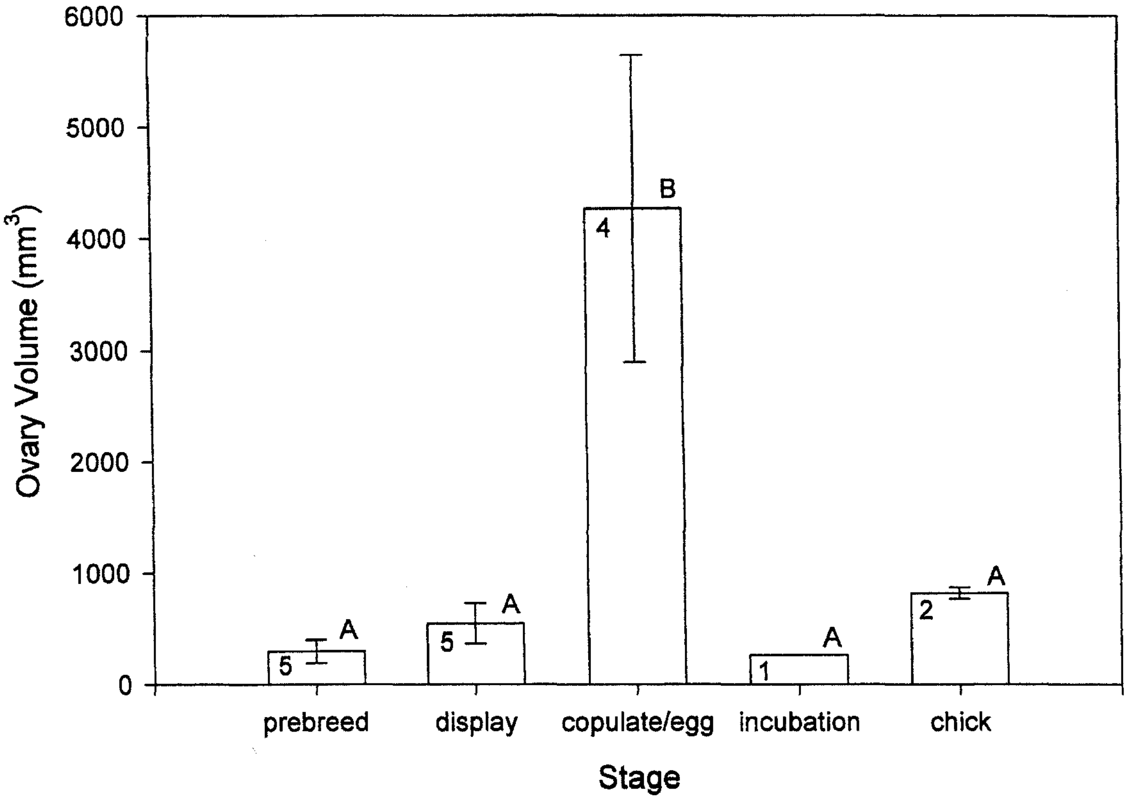

Figure 8.1. White Ibis ovary changes during the 2000 and 2001 Everglades breeding season (mean ± s.e.; Kruskal-Wallis $X^2 = 10.81$; $P = 0.0287$).Sample sizes are shown in upper left corner of bar. Means with different letters are significantly different.

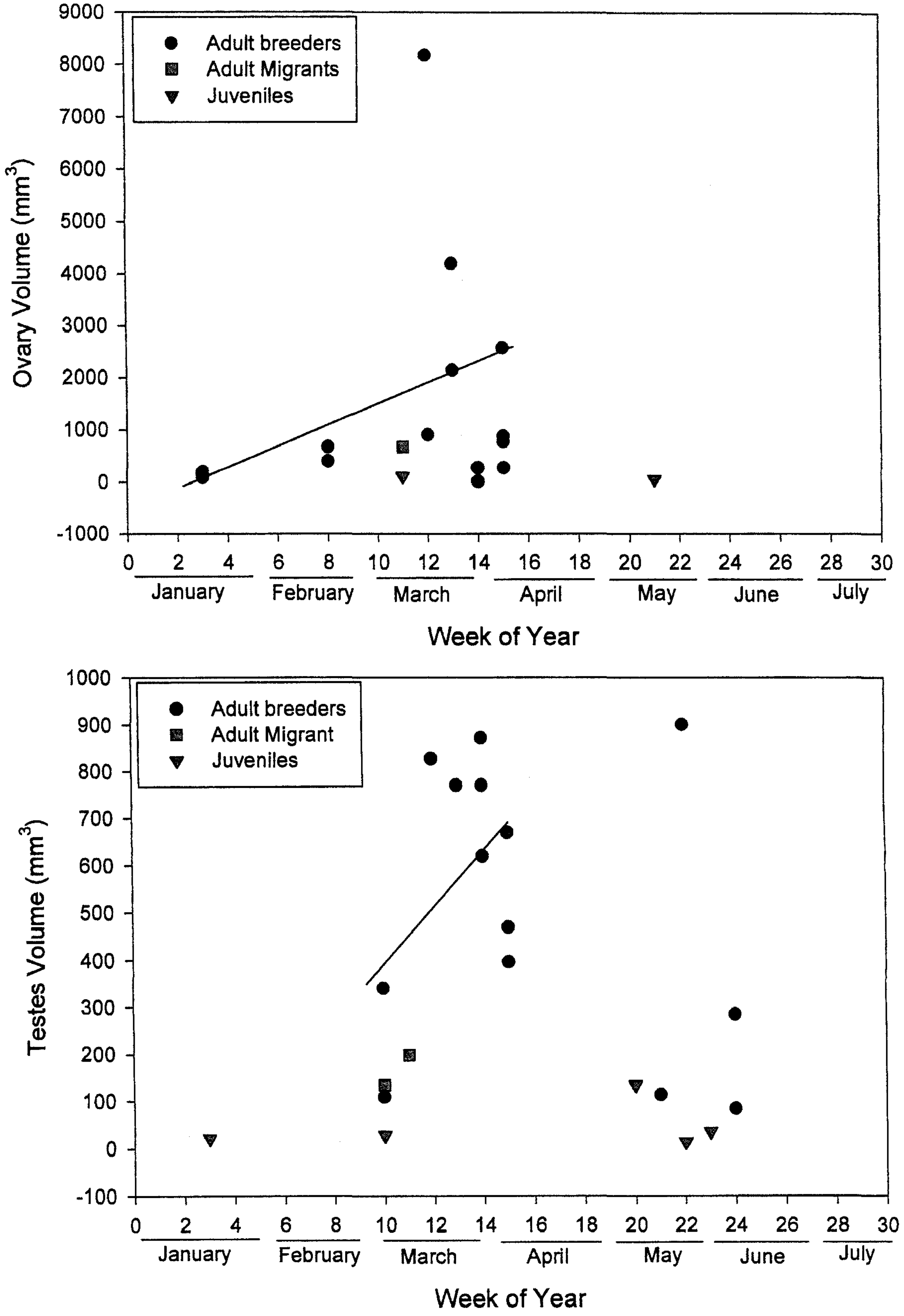

Figure 8.2. The relationship between date and White Ibis gonad changes. Adult female and male ibises reponded to increasing photoperiod with growth of ovaries or testes, respectively. Juvenile gonads showed no response to day length. Gonad development in early May represents late breeders or double brood efforts. Adult migrants show similar gonadal growth as adult breeders. Black lines are best fit for breeding adults in early Spring to illustrate gonadal growth.

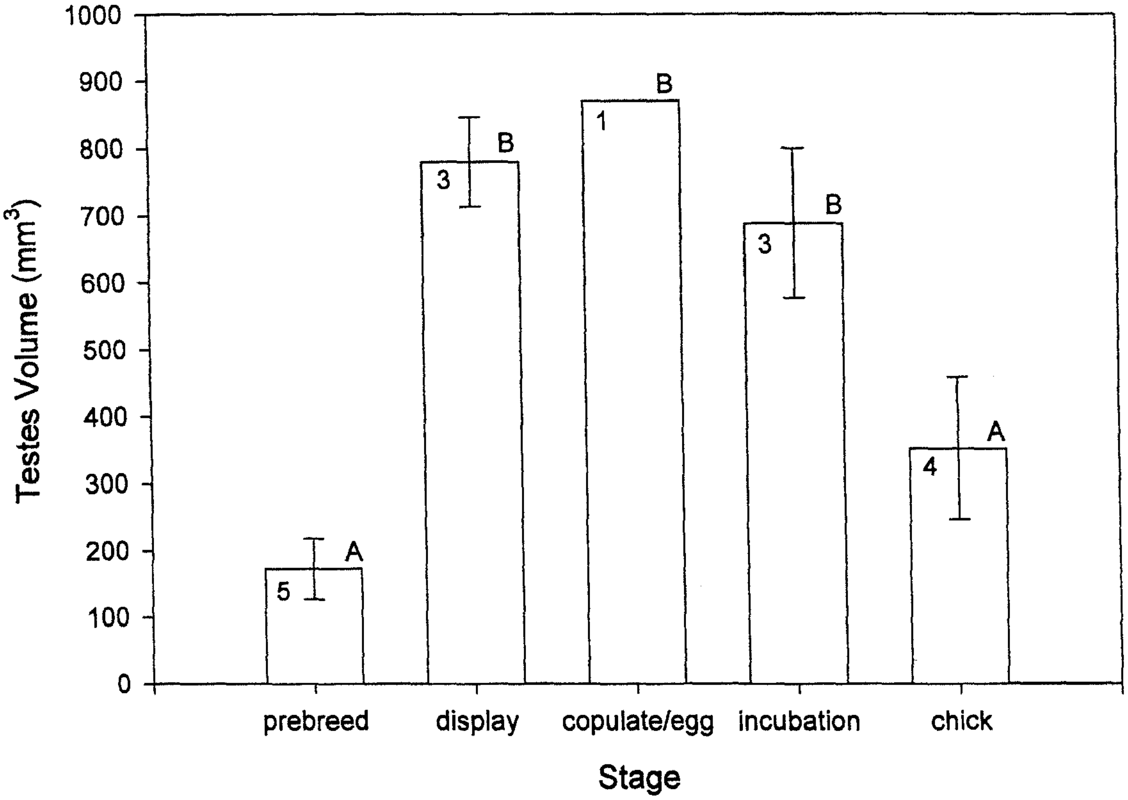

Figure 8.3. White Ibis teste changes during the breeding season (mean ± s.e. $F_{4,11} = 10.79$; P = 0.0008) in the Everglades (2000-2001). Sample sizes are shown inside upper left corner of bar. Means with different letters are significantly different.

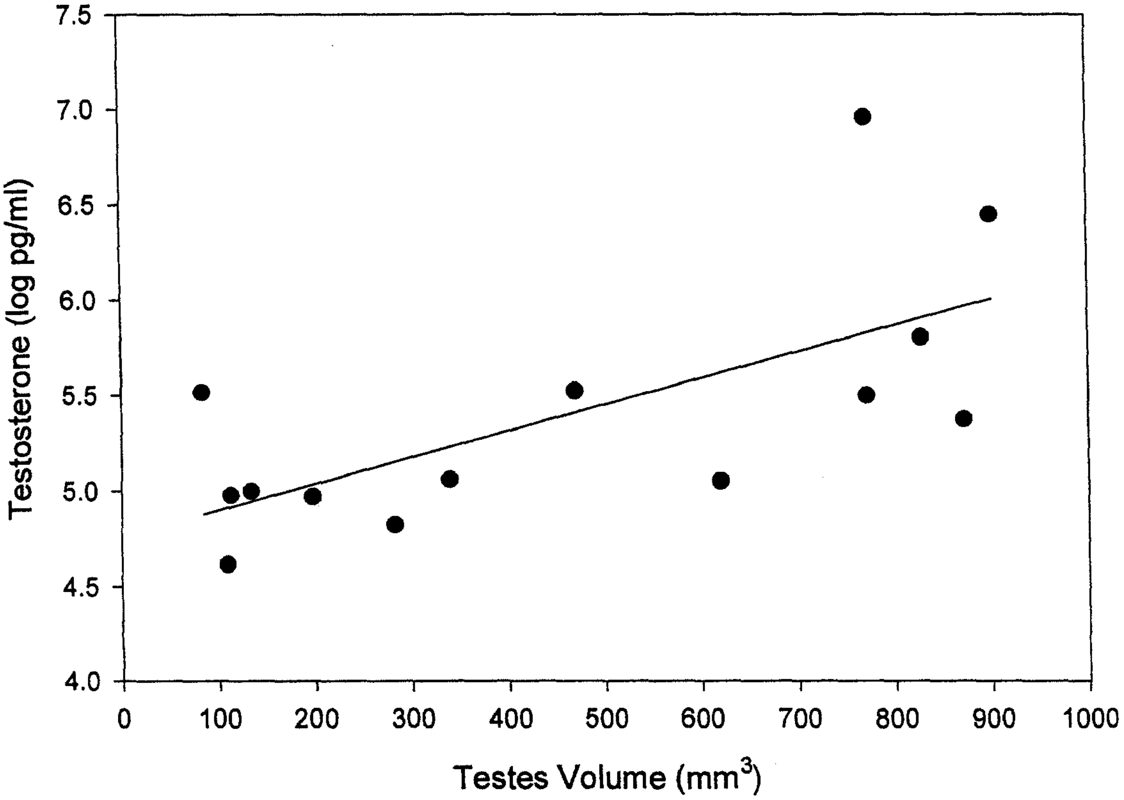

Figure 8.4. The relationship between testes size and testosterone levels (Pearsons $r_s = 0.68$; P = 0.0075) of White Ibises breeding in the Everglades during the Springs of 2000 and 2001.

daylength (Figure 8.2). Birds with large testes in late spring may be late breeders or attempting a second breeding effort. Testes are the main producer of testosterone and testis size correlated with male ibis testosterone levels ($r_s = 0.68$; Figure 8.4). Progesterone and estradiol did not correlate with testis size (P's > 0.19).

We also examined the gonads of 7 juvenile birds (birds with brown body and head feathers) to observe relative size and color. Juvenile female ovaries (N = 2) were small (76 mm^3) and pale white. Hatch year and after-hatch year male testes were small (46 mm^3 ± 22; N = 5) and bluish green. Third year male ibis testes were relatively small (25 mm^3 ± 0.7; N = 2) but yellowish-white indicating that third year birds may have a functional reproductive system (Figure 8.2).

External Changes

To evaluate changes in body condition we calculated a condition score that corrected for size variation (e.g., larger birds are likely to weigh more, all other things being equal). The first factor of a principal components analysis accounted for variation in size of morphological measurements such as bill and wing length; we used this principal component as a size factor score. We then created an expected relationship (linear regression) between mass and the size factor for each sex. The residual from each individual was then treated as its' body condition 'score'. In other words, a negative score means that a bird had a lower mass/size ratio than expected (poor condition).

Female ibises went through significant body condition changes over the course of the breeding season (Figures 8.5). Female body condition scores increased from the prebreed to display stage, and then decreased through the chick stage. Concomitantly, changes in pectoralis scores also changed during the breeding season. Female pectoralis

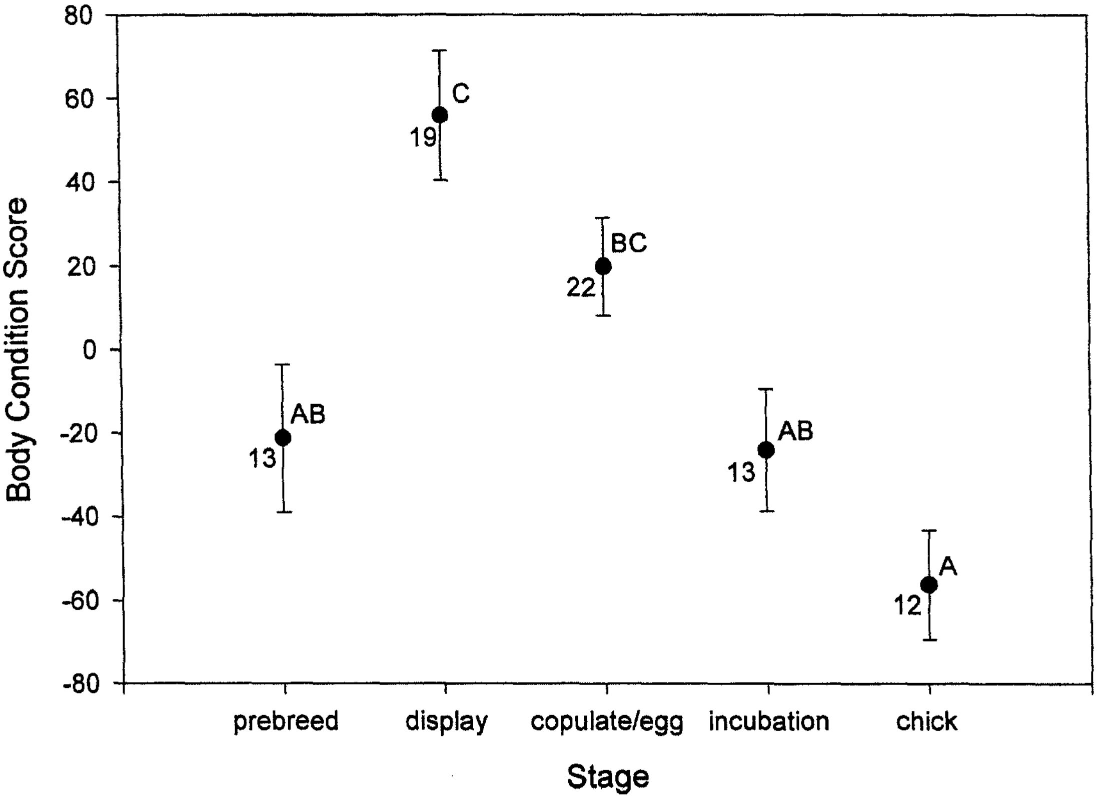

Figure 8.5. Female White Ibis body condition changes during the breeding season (means ± s.e.; $F_{4,74} = 8.85$; $P = 0.0001$) in the Everglades (1999-2001). Means with different letters are significantly different. Sample sizes noted to left below mean.

scores during the chick rearing stage were significantly lower than pre-breeding female pectoralis scores (i.e., did the proportion of females with each pectoralis score change depending on reproductive stage? Kruskal Wallis $X^2 = 11.024$, $P = 0.0263$; Figure 8.6). Female fat scores, however, did not show significant changes during the breeding season (Kruskal Wallis $X^2 = 1.346$, $P = 0.8534$, Figure 8.7).

Male ibises also lost mass during the breeding season (Figure 8.8). Male birds showed more variation in condition scores in each stage than females. Their condition scores were highest early in the season and lower later in the season. Male pectoralis scores tended to be highest during the display stage and then decrease during copulation but this change was not significant (Kruskal Wallis $X^2 = 7.511$, $P = 0.1112$, Figure 8.6). Male fat scores did change significantly during the breeding season. Males had the highest fat scores during the display stage (Kruskal Wallis $X^2 = 10.231$, $P = 0.0367$, Figure 8.7).

Male and female ibises developed brood patches during the breeding season. Birds (50% of birds captured during display, N= 15) began to develop brood patches during the display stage and by the egg production and incubation stages the majority of birds showed bare, vascularized brood patches (90%, N = 26). After incubation brood patches were less vascularized and birds tended to groom feathers over the bare area. Some birds captured in the chick brooding stages showed down growth in the brood patch region (12%, N = 17).

White Ibises molted body feathers throughout the breeding season. We recorded birds as molting if more than 4% of their body feathers were in sheaths. Most birds molted during the pre-breeding stage (85%; N = 27) but 33% of birds in display (N = 18),

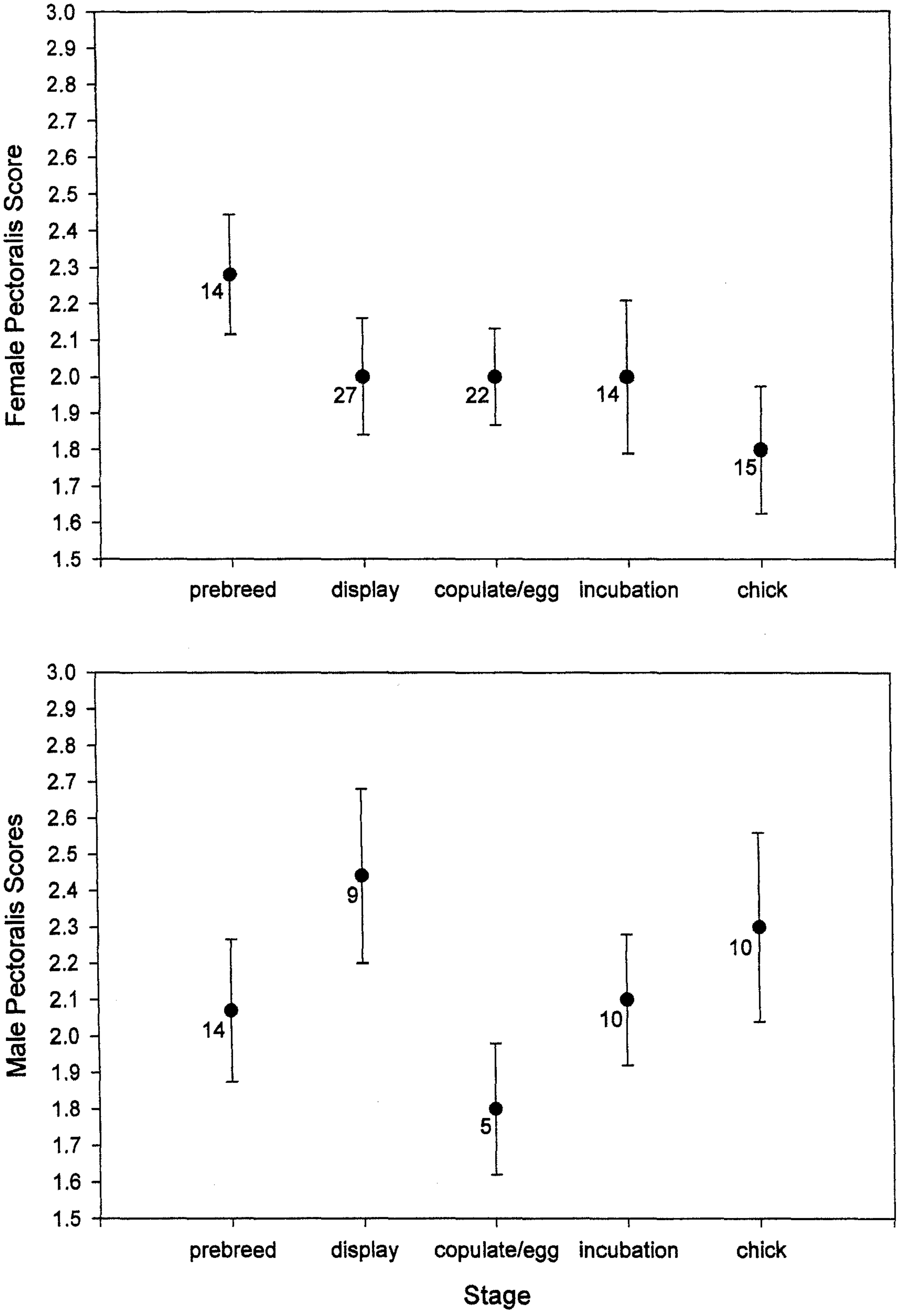

Figure 8.6. The relationship between pectoralis score and stage of reporduction in feamle (top) and male (bottom) White Ibises in the Everglades (years 1998-2001). Females had lower scores in the chick rearing period than in the prebreeding stage (P = 0.02). Males showed no signifcant patterns in pectoralis development (P = 0.11).

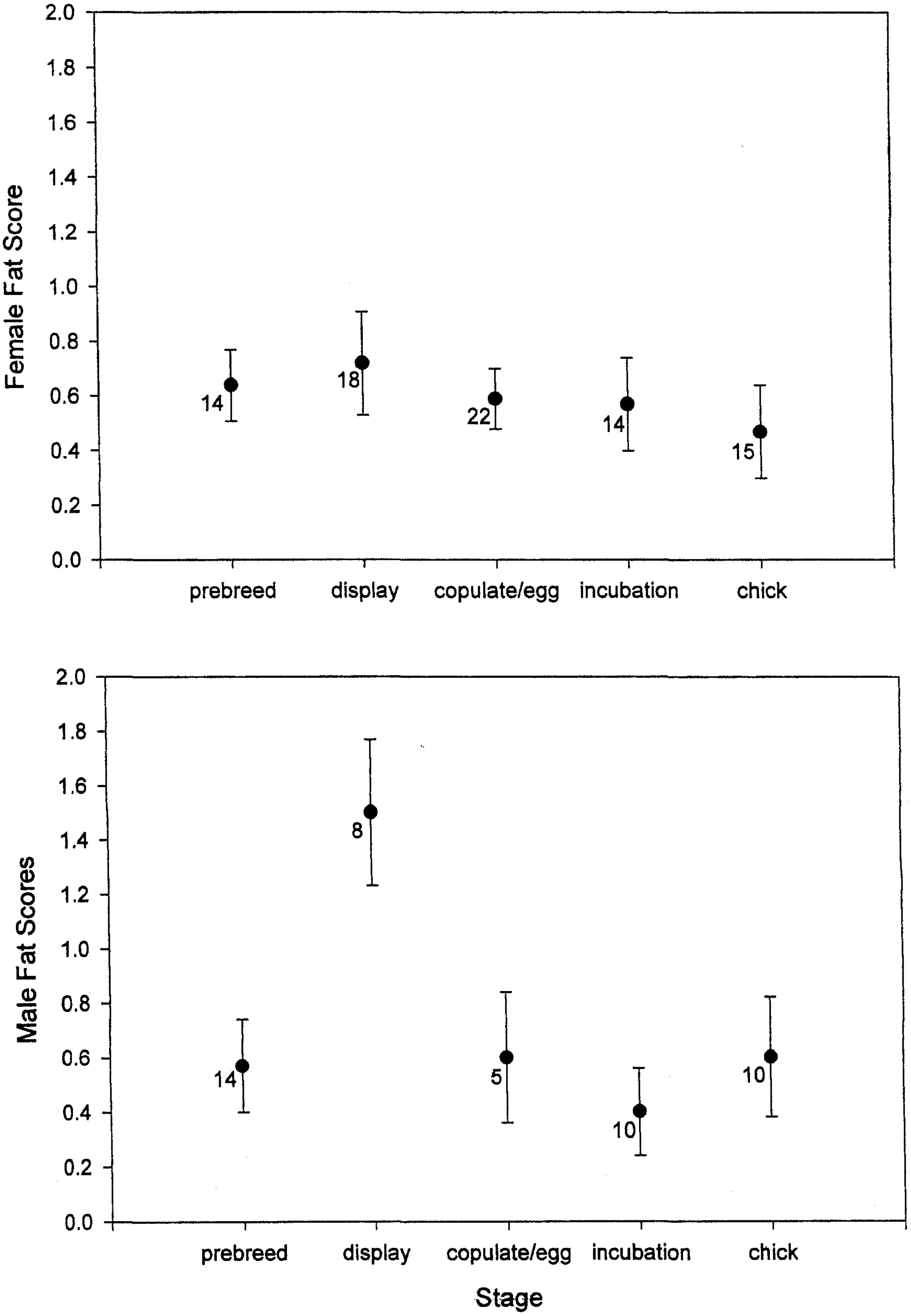

Figure 8.7. The relationship between fat score and stage of reporduction in feamle (top) and male (bottom) White Ibises in the Everglades (years 1998-2001). Females showed no significant patterns in fat stores (P = 0.85). Males had highest fat stores during the display stage (P = 0.03).

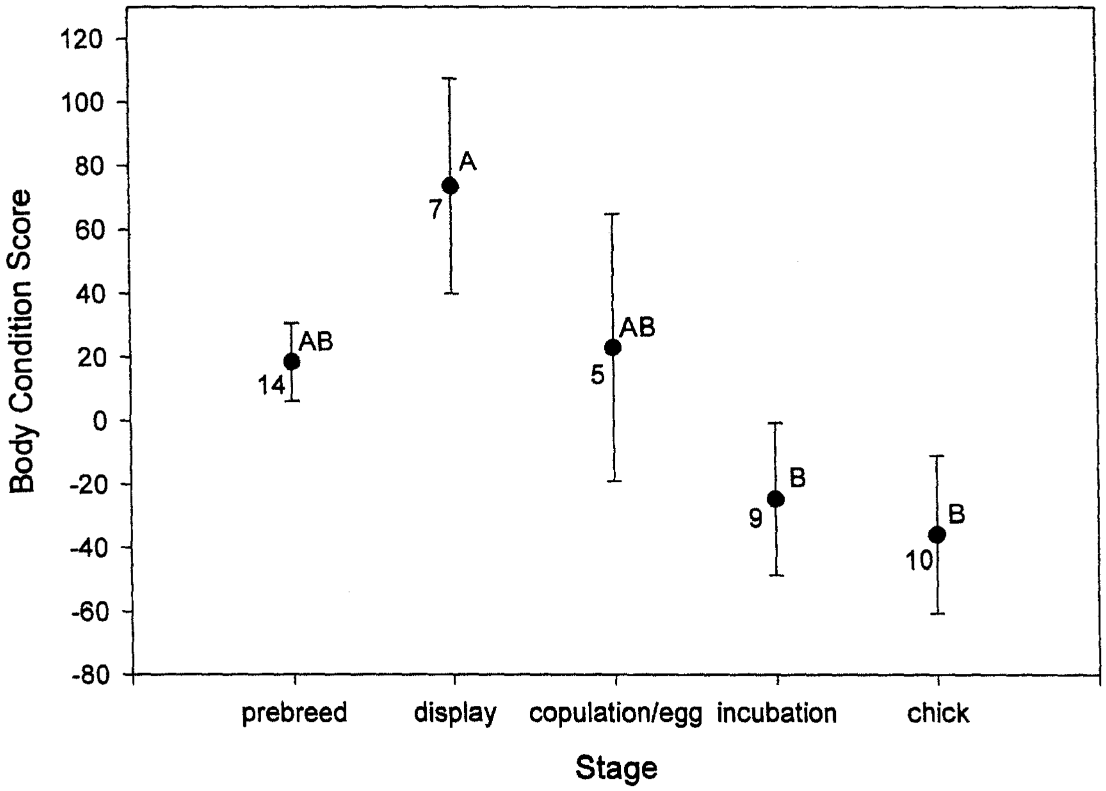

Figure 8.8. Male White Ibis body condition changes during the breeding season (means ± s.e.; $F_{4,40} = 2.98$, $P = 0.0305$) in the Everglades (1999-2001). Means with different letters are significantly different. Sample sizes noted to the left, below mean.

16% of birds in egg production (N = 19), 14% of incubating birds (N = 14), and 15% of chick rearing birds (N = 20) were also molting.

Hormone Changes

Hormonal stress response

Corticosterone (commonly referred to by the label "B") is a steroid hormone released from the adrenal glands during stressful situations. Many birds respond to capture and handling by increasing circulating corticosterone levels. We examined the relationship between corticosterone and handling time (time from capture to completion of blood collection). Corticosterone levels increased as handling time increased ($P = 0.0001$). For further analyses, we estimated baseline B levels from a regression equation (corrected level = corticosterone – ((collection time * 1.64)-517)) to control for the effects of handling time. Further analyses of corticosterone results are based on these corrected levels.

We also found a relationship between progesterone (P) levels and handling time ($P = 0.0002$). We corrected for the effects of handling time on P levels with the regression equation: corrected level = progesterone – ((collection time * 1.50)-518)). We used corrected progesterone levels for further analyses.

Corticosterone

In addition to corticosterone's role in acute stress responses, this hormone may also play a role in reproduction by facilitating metabolism and fat deposition. For these analyses we examined changes in corrected (see above) corticosterone levels during the breeding season. Female corticosterone levels changed during the breeding season ($F_{4,56} = 2.97$, $P = 0.0272$, Figure 8.9). Female ibises had the lowest B levels during pre-breed,

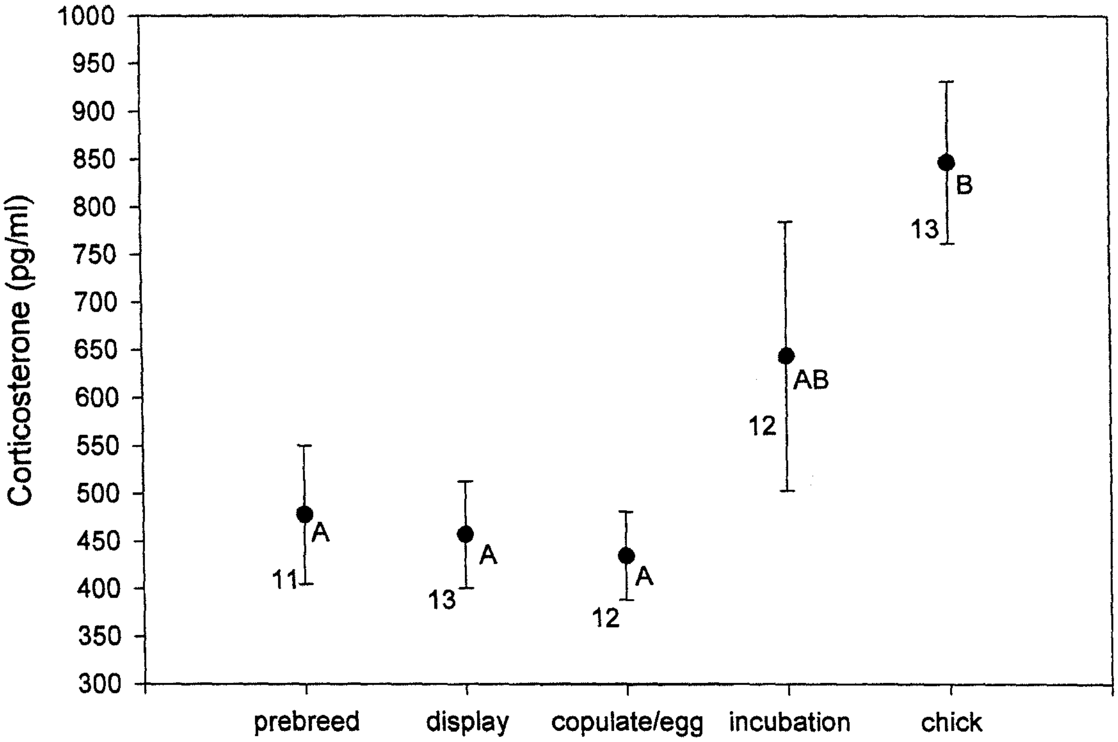

Figure 8.9. Female White Ibis corticosterone changes during the breeding season (mean ± s.e.; $F_{4,56} = 2.97$; $P = 0.0272$) in the Everglades (1999-2001). Means with different letters are sigificantly different. Sample sizes noted to left, below mean symbol.

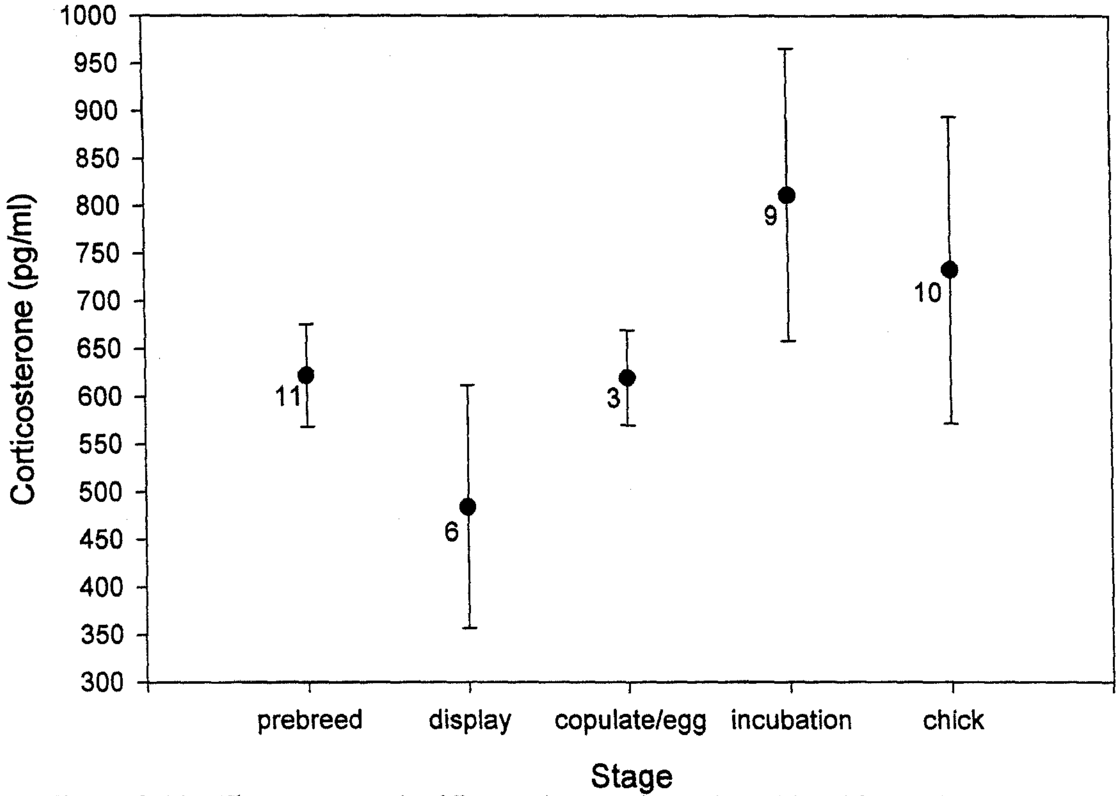

Figure 8.10. There are no significant changes in male White Ibis corticosterone levels during the breeding season (mean ± s.e.; $F_{4,34} = 0.82$; $P = 0.5203$) in the Everglades (1999-2001). Sample sizes are noted left, below mean symbol.

display and egg production stages. Corticosterone levels began to get more variable during incubation and were significantly higher than earlier stages during the chick stage.

Male ibises had no significant changes in corticosterone levels during the breeding season ($F_{4,34} = 0.82$, $P = 0.5203$, Figure 8.10; although see Chapter X). However, male ibis B levels were more variable than females.

Progesterone

As female ibises began reproductive activity their progesterone levels increased ($F_{4,50} = 2.91$, $P = 0.0307$, Figure 8.11). Progesterone levels increased from the pre-breed to display stage and then were maintained at intermediate levels throughout egg production, incubation and chick rearing. Male ibises showed no significant changes in P levels during the breeding season ($F_{4,31} = 0.61$, $P = 0.6558$, Figure 8.12, although see Chapter X). Like corticosterone levels, male progesterone levels were more variable female corticosterone levels.

Testosterone

Female testosterone (T) levels were highest during the display stage and then decreased successively during egg production, incubation and chick rearing ($F_{4,52} = 4.92$, $P = 0.0019$, Figure 8.13). Male ibises showed a similar pattern of high T during the display stage ($F_{4,22} = 4.93$, $P = 0.0033$, Figure 8.14). These levels then decreased during the later breeding stages, with the exception of one outlier during the copulation and egg production stage that had one of the highest T levels recorded (3728 pg/ml).

Estradiol

Female ibises showed seasonal changes in estradiol levels ($F_{4,60} = 2.94$, $P = 0.0274$, Figure 8.15). Estradiol levels showed no significant differences among pre-

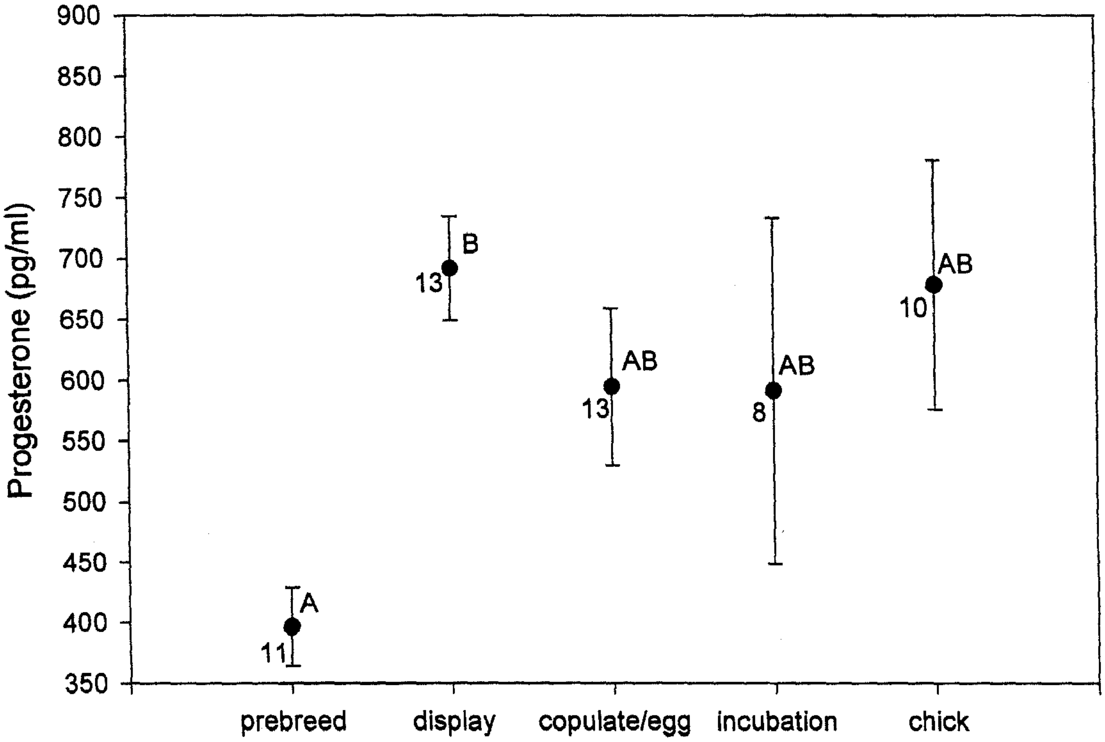

Figure 8.11. Female White Ibis progesterone changes during the breeding season (mean ± s.e.; $F_{4,50} = 2.91$; P = 0.0307) in the Everglades (1999-2001). Means with different letters are sigificantly different. Sample sizes noted to left, below mean symbol.

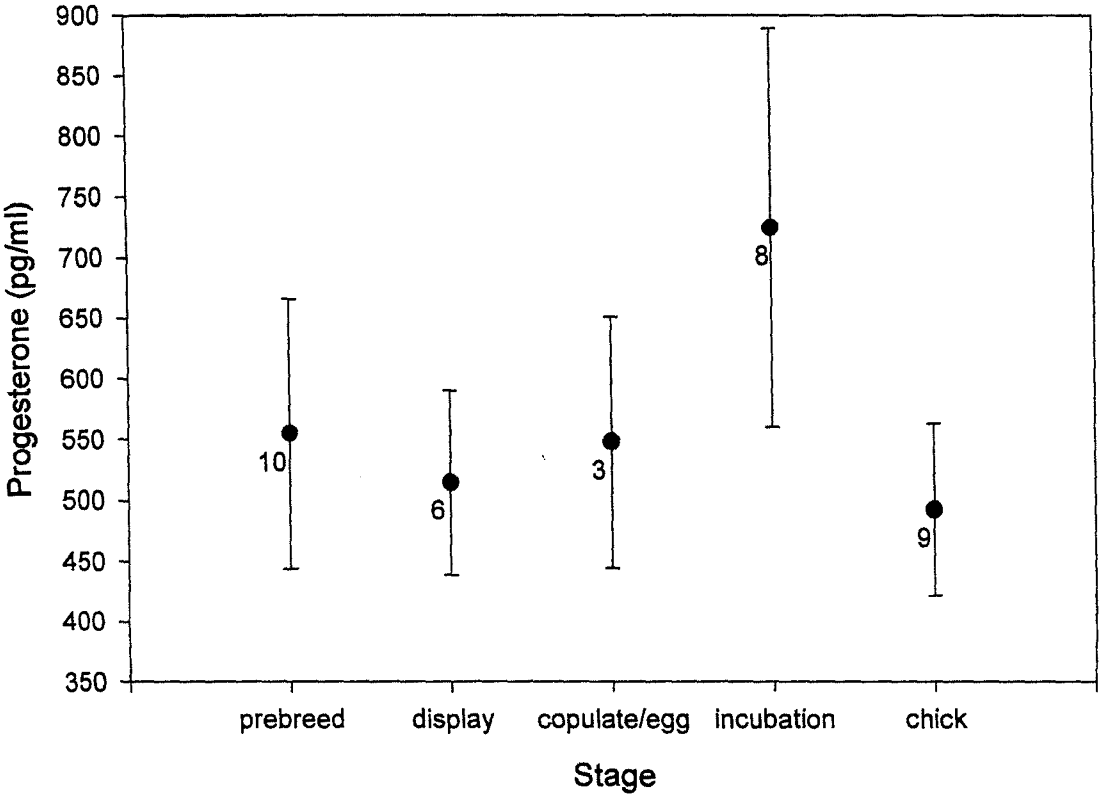

Figure 8.12. There are no significant changes in male White Ibis progesterone levels during the breeding season (mean ± s.e.; $F_{4,31} = 0.61$; P = 0.6558). In the Everglades (1999-2001). Sample sizes noted to left, below mean symbol.

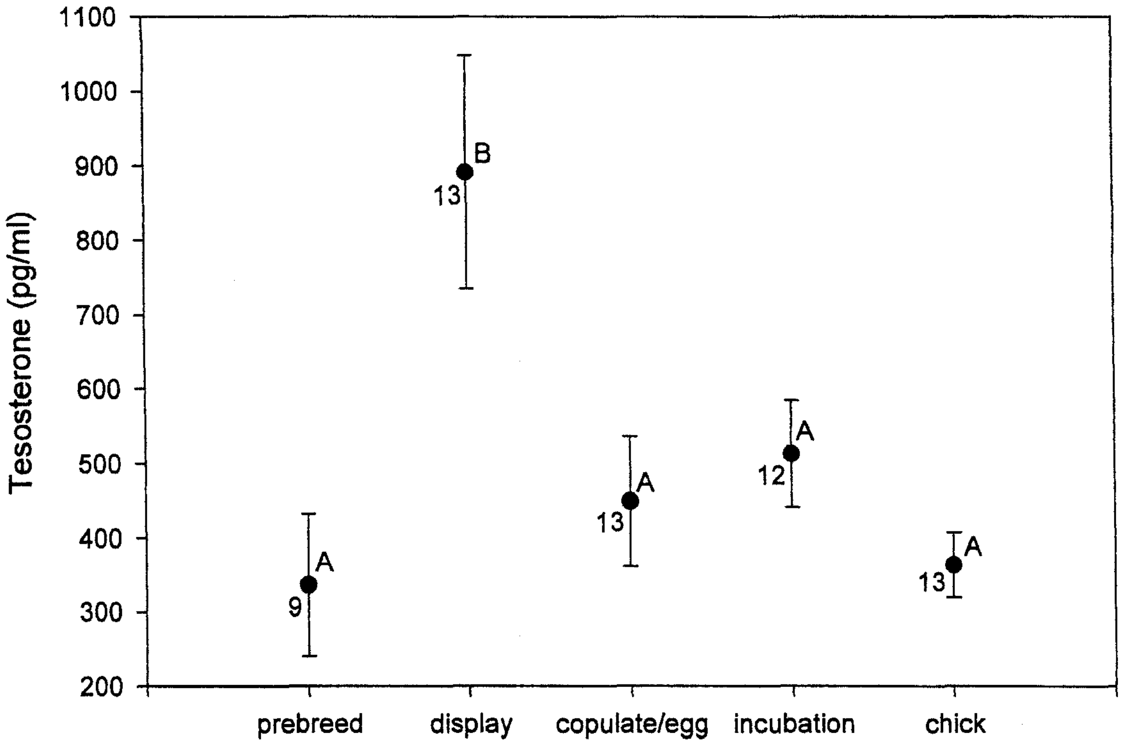

Figure 8.13. Female White Ibis testosterone levels during the breeding season (mean ± s.e.; $F_{4,52} = 4.92$; $P = 0.0019$) in the Everglades (1999-2001).

Means with different letters are significantly different. Sample sizes are noted to left, below mean. (note: F value with year block)

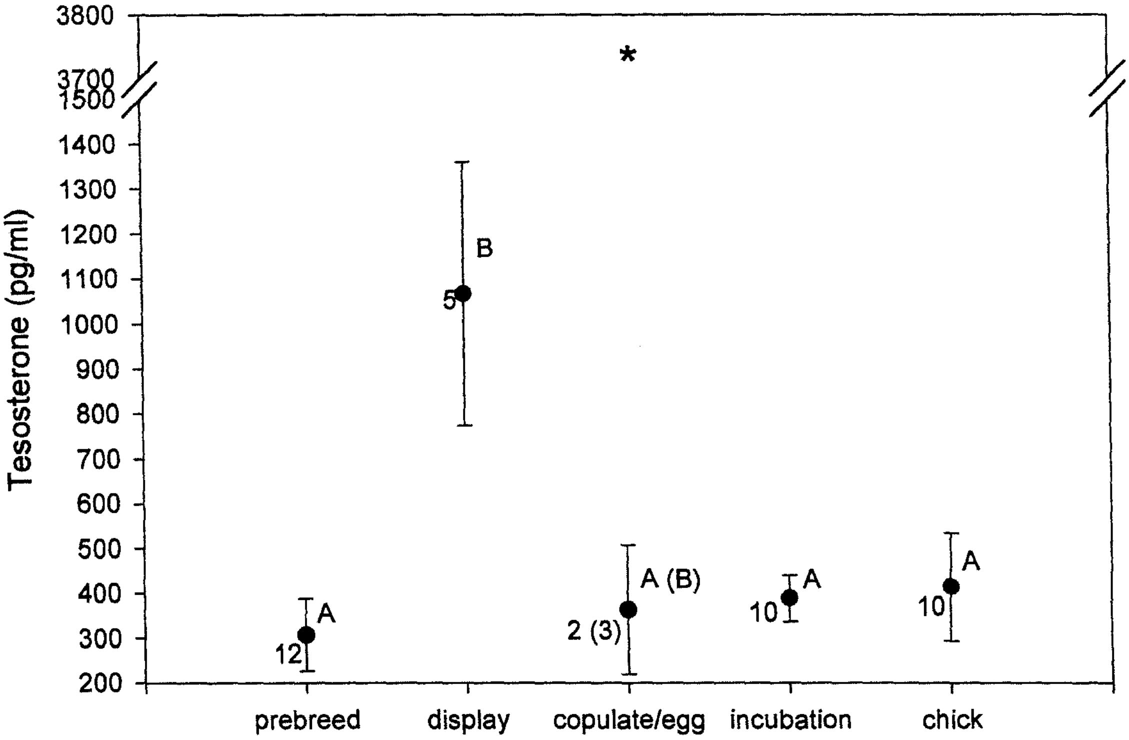

Figure 8.14. Male White Ibis testosterone levels during the breeding season (mean ± s.e.; $F_{4,22} = 4.93$; $P = 0.0033$) in the Everglades (1999-2001). Means with different letters are significantly different. Sample sizes are noted to left, below mean. '*' denotes an outlier during the copulate/egg stage. Numbers in ( ) are results that include outlier in calculations. (note: F value with year block)

breeding birds, display, egg production and incubation stages. However, estradiol levels increased from the incubation to chick rearing stage. Male ibises also showed seasonal changes in estradiol levels ($F_{4,25} = 2.86$, $P = 0.0441$, Figure 8.16). Estradiol levels were lowest during copulation stages and then increased during incubation and chick rearing.

Discussion

This is the first study to describe the reproductive physiology of a free-living wading bird. White Ibises are an interesting species because they are a colonially nesting, sub-tropical bird that depends on appropriate environmental conditions for successful nesting (Bildstein 1993). White Ibises in the Everglades have a long window of nest initiation (compared to most temperate species), which leads to high variation in the timing of nesting attempts. White Ibises showed gonadal recrudescence as daylength increases similar to other seasonal species.

In 2001 many of the White Ibises we captured in did not attempt to breed in the Everglades system and showed no external signs of reproduction (Chapter IX). However, these same birds were physiologically responding to day length changes by developing functional testes and ovaries. For most bird species increasing day-length stimulates gonad growth, the first physiological change leading to breeding. Subsequent hormone and behavior changes following gonadal increase typically depend on local conditions (e.g. food and nest site availability; Wingfield et al. 1992). In 2001 environmental conditions in the Everglades may not have stimulated the magnitude of reproductive effort seen in 1999 and 2000 (Chapters IX and III).

Ibis gonadal growth patterns were similar to other seasonally opportunistic species. During the early spring as days get longer ibis gonads develop, but the onset of

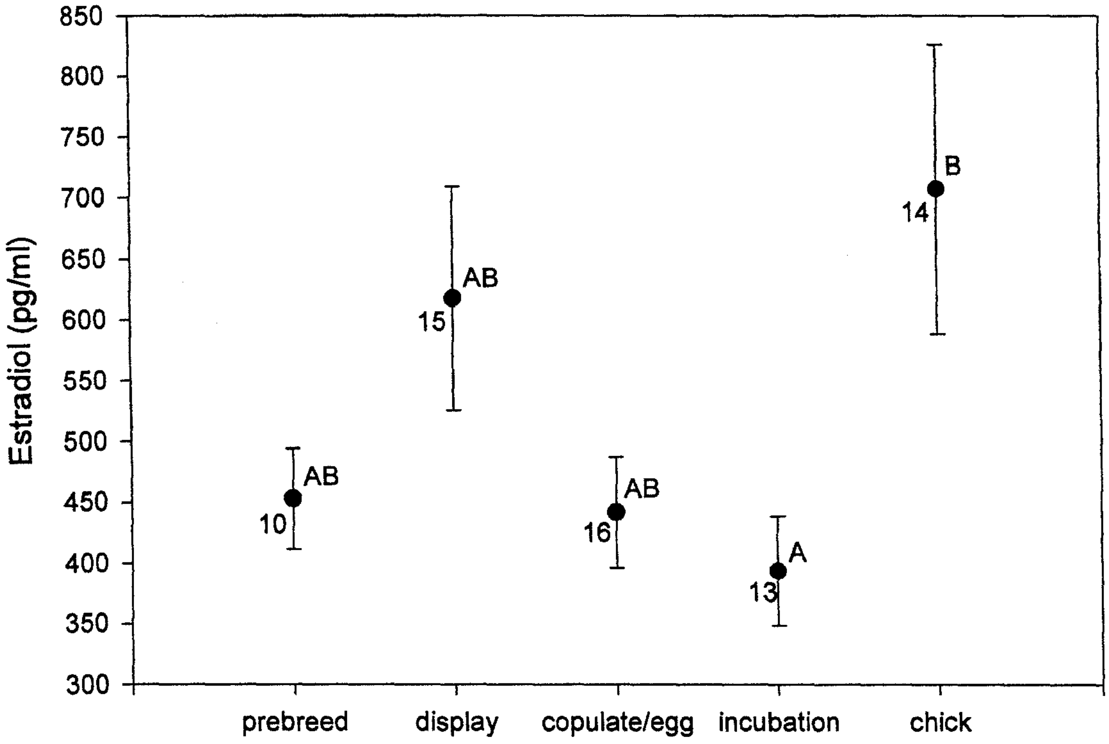

Figure 8.15. Female White Ibis estradiol levels during the breeding season (mean ± s.e.; $F_{4,60} = 2.94$; $P = 0.0274$) in the Everglades (1999-2001) (note: F value with year block).

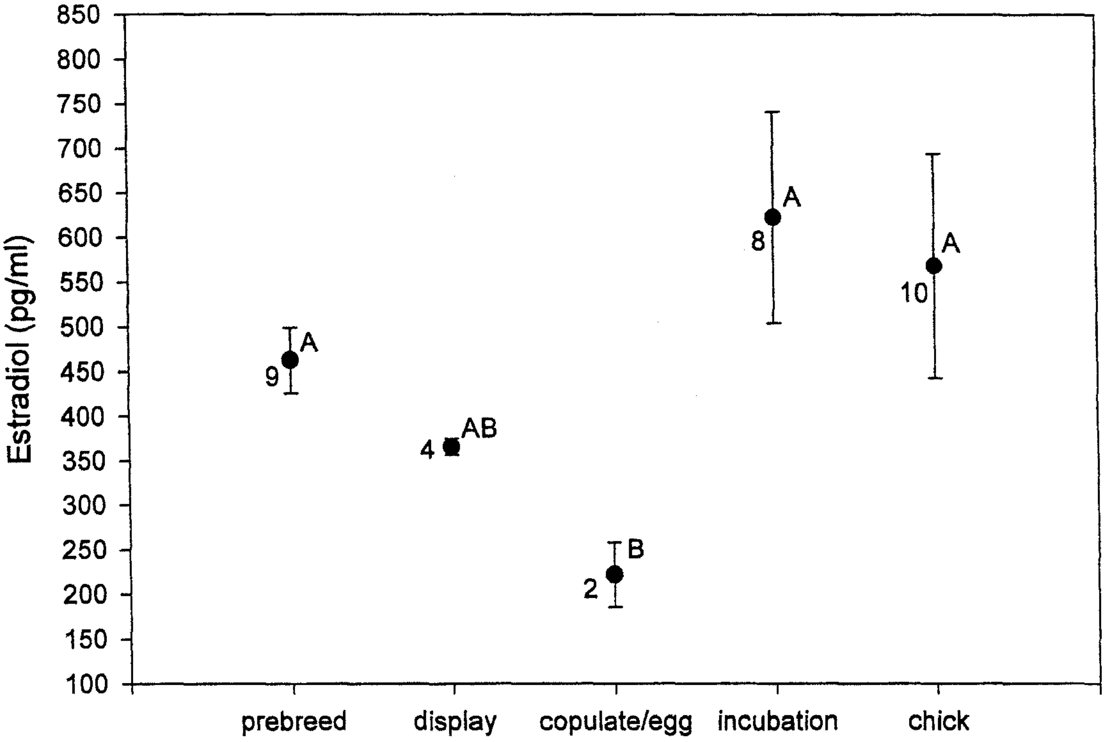

Figure 8.16. Male White Ibis estradiol levels during the breeding season (mean ± s.e.; $F_{4,25} = 2.86$; P = 0.0441) in the Everglades. Means with different letters are significantly different. Sample sizes noted to the left and below mean symbol. (note: F value with year block).

nesting is probably affected by local conditions such as food availability. Thus, ibises are particularly receptive to good environmental conditions part of the year. However, if conditions were appropriate in other parts of the year, ibises were able to develop functional gonads to take advantage of these conditions (Kushlan and Bildstein 1992). This seasonal pattern mixed with the potential to opportunistically reproduce has been described for other species with predictable environmental seasons but unpredictable prey patterns, such as red crossbills (*Loxia curvirostra*; Hahn 1998).

Hormonal Changes

Female and male ibises experienced many hormonal changes during the course of the breeding season. These changes began as gonads developed and environmental conditions were favorable for reproduction. During the display stage, testosterone levels increased for both sexes. This T increase may facilitate integument color changes (Chapter VII) and courtship behaviors. The subsequent decrease of T during incubation and chick rearing is consistent with other studies (reviewed in Norris 1997). In species that provide parental care high T levels may inhibit incubation and brooding behavior (Norris 1997). The success of White Ibis nesting efforts depends on both sexes attending the eggs and chicks (Kushlan and Bildstein 1992).

The similar increase of female progesterone levels during the display stage probably contributed to yolk deposition in the ovaries and the physiological preparations for egg production (Norris 1997). Changes in estradiol levels were more difficult to interpret. Male and female birds showed high levels of estradiol during chick rearing. Unfortunately, the role of estradiol during reproduction (in stages other than egg production) is poorly understood (Norris 1997). Estradiol may facilitate chick feeding and/or estradiol may work with other hormones (e.g. corticosterone) to stimulate mass gain.

In female ibises corticosterone levels were low in early breeding stages and then increased through incubation and were highest in chick rearing. Other studies have shown that birds may modulate B secretion during reproduction because of its potential effects at disrupting breeding behavior. The increase in corticosterone during chick rearing likely coincided with the significant loss of mass and decrease in body condition. Corticosterone promotes feeding activity in hungry birds and stimulates gluconeogenesis in birds that are unable to feed (such as an incubating bird).

CHAPTER IX. ANNUAL EFFECTS ON COLONY ATTENDANCE BY RADIO-MARKED WHITE IBISES

Introduction

There is very little known about ibis life history, despite intensive studies of reproductive behavior and feeding ecology. Few studies have followed the fate of individuals within a season (although see De Santo et al. 1997) and no studies have followed the fates of individuals between breeding seasons. Therefore, philopatry estimates are based on continous colony use, though it is not known if it is the same individuals attending the colony between years. Studies of individual behavior could lend insight on breeding dispersal, survival between breeding seasons and the environmental factors associated with nest site selection.

White Ibis reproductive patterns in the Everglades are highly variable within years and between years. This variation may be the result of differences in survival and recruitment to the breeding population, breeding dispersal, or variation in factors (such as water levels) that affect timing and location of reproduction. We marked individual White Ibises with radio transmitters and followed them throughout the breeding season to: 1) identify breeding birds, 2) monitor breeding dispersal, and 3) study breeding behavior within and between years.

Methods

White Ibises were captured and marked with bands and radio tags as described in Chapters VII and VIII. Forty-nine adult birds (ATY) and 2 after-second year (ASY) bird received a 6-Volt or 4-Volt radio-transmitter (American Enterprises; Tallahassee, FL) we estimate that radios had an 18-24 month life span and a range of 3-4 km. Radios were equipped with a motion sensitive switch (mortality switch) that would double the frequency of beeps when the radio had not moved for 36 hours. Eight birds carried the radio-transmitters via a backpack style harness consisting of leather breast patch and Teflon ribbon stitched with cotton thread. In an attempt to reduce handling time we developed a harness styled after an elastic figure-8 harness. Forty-three radio-transmitters were attached using Teflon ribbon figure-8 harnesses that looped around the top of each leg and across the back. This harness was fitted and then stitched together with cotton thread above the radio. The harnesses were made to come off the bird in 1 –3 years via deterioration of the cotton stitch. We did not mark female birds that were gravid with a late stage egg because our main goal in marking birds was to determine if they were breeding birds. We assumed gravid females were breeding.

We attempted to locate the birds using fixed-wing aircraft and radio-telemetry receivers. Two 'H' style radio antennas were attached to the plane with wing strut brackets (Telonics). Each antenna's coaxial cable attached to a switch box that allowed listeners to receive signals from both antennas at the same time or from only one antenna at a time. This allowed researchers to determine direction of the signal. The switch box was attached to a splitter box that allowed for dual receiver hook up. Thus, two workers could scan per flight. We used a Telonics receiver (TR-2 Receiver and a TR-1 Scanner/Programmer) and ATS receiver (R2000 Receiver/Scanner). On each flight we visited all known ibis nesting colonies and flew transects (7 km apart; 300 m high) over Water Conservation Areas 1, 3A, 3B, 2A, and 2B. If we located a bird we recorded the location and description of the location as seen from the air (e.g. in a colony, with a group of feeding birds). We also monitored birds in colonies through regular visits to known breeding colonies in an airboat. To listen for signals from the boat we elevated the yagi-radio antenna at least 3 m above the airboat with a telescoping pole and scanned continuously for long periods (5 hours) for signals from marked bird. If a bird was relocated in a colony during daylight hours it was considered a breeding bird. In 2000 and 2001 we listened for signals from birds marked in previous years as well as birds marked that spring. When we did not detect a signal from a bird marked in a previous year, we recorded 'no information', and these birds were not used in analyses. Birds that we did not detect a second year may have dropped their radio harness, had a radio with a dead battery, died, not been present in the Everglades, or not detected by our surveys. We identified birds as emigrants if we repeatedly relocated a bird in early spring (early March), but then no longer detected a signal. Loss of signals in March was usually episodic with many birds leaving the Everglades system in a short period. Loss of these signals are unlikely to be the result of concomitant radio failure as loss of signals did not correlate with length of time the radio had been turned on. Thus, the most probably explanation is that many birds left the Everglades system in a mass movement (migration)

Results

We opportunistically observed nest attendance exchanges between unmarked breeding adults whenever possible while listening at colonies. On 14 occasions we were able to quantify the time a previously attending bird spent in the colony after its mate arrived at the nest. In all of these cases we observed the arrival of the mate from outside the colony, watched the adult birds exchange nest care positions, and the relieved bird depart from the colony. Males on average spent 35.5 seconds (± 7.4 sec, N = 4) in the colony before departing. Females spent a little over a minute before departing (64.6 sec ± 13.6, N = 10). These departure times were not affected by whether or not the pair had eggs or chicks, though we would assume that early in the season (during egg-production) males may remain at the nest considerably longer to guard their mate from extra-pair copulations (Frederick 1987). Thus, we are confident that later stage breeding birds leave the colony promptly upon the return of their mates. This indicates that radio signals from within the colony are a good indicator of the presence of a breeding bird attending a nest.

In 1999, 2000, and 2001 we marked 51 White Ibises with radio transmitters (Table 9.1). We relocated 84% (N = 43) of the marked birds at least once. We retrieved one marked bird that died (Epanchin et al. in review) and one radio (attached with backpack-style harness) that had prematurely dropped from the bird.

Table 9.1. The sex, year, and stage of reproduction of Everglades White Ibises marked with a radio-transmitter. Figures in bold represent number of birds found in colonies the year they were marked.

	1999		2000		2001		
Stage	Female	Male	Female	Male	Female	Male	Total
Pre-breed			1	1	3 **(2)**	2	7
Display	1		6 **(4)**	**2**	**1**	1	11
Copulate/egg	**1**		6 **(4)**	**3**			10
Incubation	**2**	3 **(2)**		3 **(2)**		1	9
Chick	3 **(2)**	3 **(1)**	**1**	1	2	2	12
ASY*		1				1	2
Total	7	7	14	10	6	7	51

* ASY represents 'after-hatch year' bird, these birds have just completed the molt into adult plumage. They may not be reproductively active.

Thirty of the 43 birds were relocated in colonies in at least one year. The majority of the radio-marked birds (20 of 30, 67%) were located as breeding birds (in a least one year) at Alley North, a large colony in northern WCA 3A (see Appendix 1 - 4 for coordinates). We also located birds in Hidden Colony in southwestern WCA 3A (N = 1), Heron Alley in WCA 3B (N = 3), Shark Valley in Everglades National Park (N = 1), and Loxahatchee 111 (N = 5) in Loxahatchee NWR.

We relocated thirteen birds on the marsh, away from colonies. Two of these birds were juvenile birds, marked in their third year. Two birds died or lost their radio harness. We detected mortality signals of these two radios during aerial surveys, but could not retrieve these radios because we could not get to their location on the marsh. Four other birds were marked late in the breeding season, most likely during chick rearing. We did not relocate these birds in colonies during the year they were marked, but we did relocate them the following winter (Jan.-March). However, after winter we no longer detected their signals. This was also the case for five other birds, marked early in the season, which we regularly relocated until the third week of March. These nine birds may have wintered in the Everglades and then departed by the end of March (Tables 9.2 and 9.3).

Breeding vs. migrant

In 2000 and 2001, we relocated 22 birds (61%) that we had marked during one of the previous seasons (Tables 9.2 and 9.3). In 2000 we relocated seven birds marked in 1999 (58%). Six of these '1999 birds'(86%) were located in colonies during the 2000 season. Five of the six breeding birds were located in the same colony where they bred in 1999 (Alley North). One female that had bred at Hidden colony in 1999 bred at Alley North in 2000.

In 2001, we relocated 15 birds marked in 2000 (N = 14; 63%) and 1999 (N = 1). Six of the previously marked birds (40%) were located in colonies. One of the six (17%) stayed at the same colony (Loxahatchee 111) where it bred in 2000. The other five birds

Table 9.2. Breeding status and site fidelity of White Ibises marked with a radio transmitter in the springs of 1999 and relocated in springs (Jan.-June) of 2000. Status and Dates in bold indicate birds that probably emigrated from the Everglades before the third week of March in each respective year.

			1999				**2000**			
Bird ID Number	**Sex**	**Year Marked**	**Status**	**Number of Relocations**	**Location**	**Last Day Located**	**Status**[a]	**Number of Relocations**	**Location**	**Last Day Located**
1092	F	1999	Unknown*	0	WCA 3A	23 Apr	**Unknown**	1	BCNP	**5 Mar**
1541	F	1999	Unknown*	1	WCA 3A	11 May	Breeder	12	Alley North	20 Apr
1571	M	1999	Unknown*	1	WCA 3A	16 Jun	Breeder	8	Alley North	19 Apr
896	F	1999	Breeder	10	Alley North	16 Jun	Breeder	9	Alley North	9 Apr
1079	F	1999	Breeder	4	Alley North	11 May	Breeder	6	Alley North	27 Apr
1929	F	1999	Breeder	4	Hidden	5 Jun	Breeder	9	Alley North	3 Apr
1431	M	1999	Breeder	2	Alley North	9 Jun	Breeder	9	Alley North	7 Jun
1034	M	1999	Unknown*	2	WCA 3A	8 May	Unknown	0		
1458	F	1999	Breeder	3	Alley North	11 Jun	Unknown	0		
1042	M	1999	Breeder	8	Alley North	16 Jun	Unknown	0		

* Birds that were captured after 21 March 1999. These birds had signs of brood patch and gular sac development suggesting that they had attempted to breed earlier in the season.

Table 9.3. Breeding status and site fidelity of White Ibises marked with a radio transmitter in the springs of 2000 or 1999 and relocated in springs (Jan.-June) of 2000 and 2001. Status and Dates in bold indicate birds that probably emigrated from the Everglades before the third week of March in each respective year.

Bird ID Number	**Sex**	**Year Marked**	**2000**				**2001**			
			Status	**Number of Relocations**	**Location**	**Last Day Located**	**Status**[a]	**Number of Relocations**	**Location**	**Last Day Located**
1473	F	2000	**Unknown**	3	WCA 3A	**8 Mar**	**Unknown**	4	WCA 3A	**14 Feb**
985	M	2000	**Unknown**	4	3A Roost	**6 Mar**	**Unknown**	6	3A Roost	**19 Mar**
579	M	2000	Unknown*	1	WCA 3A	8 Jun	**Unknown**	13	3A Roost	**16 Mar**
1681	F	2000	Unknown*	1	ENP	6 Apr	**Unknown**	1	3A Roost	**19 Mar**
1710	F	2000	Unknown*	1	WCA 3A	7 Apr	Breed/Fail	1	L-67	28 May
1431	M	1999	Breeder	9	Alley North	7 Jun	**Unknown**	6	3A Roost	**16 Mar**
1650	M	2000	Breeder	12	Heron Alley	8 Jun	**Unknown**	1	WCA 3A	**14 Feb**
1272	F	2000	Breeder	3	Lox 111	7 Apr	**Unknown**	2	3A Roost	**19 Jan**
1226	F	2000	Breeder	5	Alley North	20 Apr	**Unknown**	1	WCA 1	**13 Feb**
1555	F	2000	Breeder	18	Alley North	16 May	**Unknown**	8	3A Roost	**5 Mar**
1197	M	2000	Breeder	1	Lox 111	7 Jun	Breeder	5	Lox 111	23 Apr
1244	M	2000	Breeder	6	Alley North	8 Jun	Breed/Fail	1	L-67	28 May
1256	F	2000	Breeder	10	Alley North	1 May	Breed/Fail	20	Big Pond	9 May
1015	F	2000	Breeder	1	Alley North	8 Jun	Breeder	1	Lox 70	18 Apr
1587	F	2000	Breeder	2	Alley North	7 Jun	Breeder	3	Lox 70	1 Apr
1526	F	2000	Breeder	6	Alley North	20 Apr	Unknown	0		
1213	F	2000	Breeder	9	Alley North	8 Jun	Unknown	0		
924	F	2000	Breeder	5	Alley North	9 Apr	Unknown	0		
912	M	2000	Breeder	9	Heron Alley	8 Jun	Unknown	0		
944	M	2000	Breeder	3	Heron Alley	9 Apr	Unknown	0		
974	M	2000	Breeder	10	Alley North	8 Jun	Unknown	0		

* Birds that were captured after 21 March 2000. These birds had signs of brood patch and gular sac development suggesting that they had attempted to breed earlier in the season.

[a] Breed/Fail birds nested in a colony where all ibis nests were abandoned.

had bred at Alley North in 2000. This colony had no successful ibis nests in 2001. Instead, these birds attempted to bred at Loxahatchee 70 (N = 2), L-67 (N = 2), and Big Pond (N = 1). Unfortunately, all breeding ibises at the L-67 and Big Pond colonies failed (Chapter III).

A higher proportion of previously radio-marked birds bred in the Everglades in 2000 than in 2001 (Fishers exact one-tailed test, P = 0.05). In 2001, birds were more likely to emigrate from the Everglades (60%) versus 14% in 2000.

Discussion

Nesting by adult ibises in the Everglades in consecutive years indicates that these birds are not energetically or physiologically limited from breeding every year. One of the objectives of our study was to address this phenomenon. Many species that skip years between reproductive efforts do so because they are limited energetically (Hector et al. 1985). For example, biennially breeding Wandering Albatross (*Diomedea exulans*) have a prolonged period of fledgling dependence on the adults. In theory the adults are energetically taxed by this prolonged dependency period and therefore can not successfully reproduce every year (Hector et al. 1985). The ability of ibises to breed in sequential years that we have demonstrated suggests that if a proportion of birds are not breeding it is unlikely that it is a natural part of ibis life history. Further, our research on the body conditions changes that occur during the breeding season showed that birds can quickly gain mass and are able to withstand significant mass loss (Chapters VI and VIII).

Our ability to track birds over consecutive years has allowed insight into their philopatric behavior. During 2000, we were able to relocate over half the birds (58%)

that were marked with transmitters in 1999. The majority of these birds (71%) returned to the same colony to breed in 2000. This suggests that ibises can be philopatric, at least in some years. However, in 2001 the Alley North tree island had no nesting White Ibises, thus none of the thousands of birds that had bred there the previous year returned. This impression of erratic philopatry is consistent with data we have collected over the past 15 years, that suggests that colony size can be extremely dynamic (Kushlan and Bildstein 1992). However, as is the case with many other bird species, ibises probably use a mixed strategy approach for deciding where to breed. Perhaps birds visit and evaluate areas where they have been successful before but do not always choose to nest at that site (i.e. if conditions seem unfavorable as in the 2001 drought conditions).

In 2001, only 40% of relocated radio-marked ibises (70% in 2000) were found in colonies (Table 9.3), suggesting that many birds were not nesting. In contrast, 100% of the birds we captured after the third week in March of 2001 showed signs of reproduction. For example, all of the birds captured after 21 March 2001 had a black bill. This usually indicates that a bird has gone through the soft tissue color changes (i.e. bright red color on bill and legs) associated with breeding (Chapter VII). In addition, every radio-marked ibis relocated in the Everglades Ecosystem during 2001 (i.e. WCA's 1, 2A, 2B, 3A, 3B, ENP, BCNP, and Florida Bay) past 21 March attempted to breed.

Ten birds (N = 9 in 2001, N = 1 in 2000) that had been regularly relocated (but never in a breeding colony) did not remain in the Everglades Ecosystem after the third week in March (Table 9.3). These birds may have been wintering in the Everglades and emigrated to different breeding areas. White Ibises are a nomadic bird that may abruptly migrate to different breeding areas. Favorable environmental conditions in February and early March (as seen in 1999 and 2000) may recruit birds that had wintered in the Everglades (or discourage emigration from the Everglades).

CHAPTER X. WADING BIRDS AS BIOINDICATORS OF MERCURY CONTAMINATION IN THE EVERGLADES: ANNUAL AND GEOGRAPHIC VARIATION

Introduction

Populations of wild animals have often been used as bioindicators of environmental contaminants, and many studies suggest that levels of contamination in animals can serve to track fluctuations in contaminants in the environment (Erwin and Custer 2000). Birds have been used as indicators of environmental contaminants, and bird feathers have been widely used for the indication of heavy metal contamination (Thompson and Furness 1989, Burger et al. 1993, Burger and Gochfeld 2000). Mercury (Hg) has been shown to bind well with growing feather tissue, providing a history of contamination at the time that the feather has been grown (Thompson and Furness 1989). Previously we have demonstrated a direct and predictable relationship between cumulative Hg exposure in food and feathers of Great Egret (*Ardea albus*) young raised in captivity (Spalding et al. 2000a). This work provides a firm link between Hg concentrations in growing feathers and Hg in fish.

Many aquatic ecosystems in Florida are known to be contaminated with Hg, to the extent that fish consumption advisories for humans have been issued for approximately 74% of the freshwater lakes and streams so far tested (T. Lange, Florida Fish and Wildlife Conservation Commission, pers. comm.). The Everglades in particular has shown very high contamination levels during the past decade, with potential effects on fish and wildlife populations, and risk to human fishers (Frederick 2000). Yet predicting temporal and geographic differences in Hg contamination is difficult since Hg is known to be dynamic in the various biotic and abiotic pools of wetland systems, and particularly so in the shallow depression wetlands typical of the southeastern U.S. (Frederick 2000, Snodgrass et al. 2000).

Piscivorous wetland birds can be important monitors of changes in Hg contamination for several reasons. First, many species are tertiary consumers, and contamination levels are therefore representative of the contamination levels in the some part of the aquatic wetland food web (Custer 2000). Second, the extremely high bioaccumulation of Hg in these animals may represent an important risk to the reproduction and health of these bird populations. Hg contamination in piscivorous birds has been associated at various contamination levels with embryonic mortality and deformities (Heinz 1979, Fimreite 1971) abnormal chick behavior (Heinz 1975, 1979), altered parental behavior (Heinz 1979, Nocera and Taylor 1998), decreases in reproductive success (Barr 1986, Meyer et al. 1998), decreases in survival of adults and juveniles (Van der Molen et al. 1982), and decreased health of young and adults (Thompson 1986, Wolfe et al. 1996, Scheuhammer 1987). At very high exposure levels, Hg may result in neuronal degeneration, convulsions, and death (Wolfe et al. 1996, Scheuhammer 1987, Spalding et al. 2000b). In herons (Ciconiiformes: Ardeidae), contamination levels similar to those measured in the Everglades have been associated with decreased health parameters (Spalding et al. 1994), decreased fledging mass (Spalding et al. 2000a), decreased appetite and blood cell volume (Spalding et al. 2000b), and altered maintenance behavior and hunting behavior (Bouton et al. 1999). These sublethal effects are suggested to lead to decreased juvenile survival (Spalding et al. 2000a, Frederick 2000).

In this chapter, we present the results of a seven-year study of Hg in growing feathers of piscivorous birds in Florida. We examine geographic variation in Hg exposure within the Everglades wetland ecosystem as reflected by growing feathers of nestling Great Egrets and in one year, White Ibises. Using established relationships between Hg consumption and contamination levels, we also were able to use the feather Hg contamination levels to estimate changes in fish contamination with Hg.

We chose Great Egrets as our main study animal because this species is a tertiary consumer in many wetland food webs (consume medium to large fish, see Frederick et al. 1999, Jurczyk 1993), has a nearly worldwide distribution, and is known to exhibit high levels of Hg contamination in the Everglades wetlands of southern Florida, USA (Sepulveda et al. 1999). At several colonies in 1998, we also collected feathers from young White Ibises, which feed somewhat lower on the food chain (crustaceans and small fish, Kushlan and Bildstein 1992). We used nestling birds for tissue collection because we were confident that while in the nest, their food came from a defined area around the nesting colony (cf 25 km radius, see Bancroft et al. 1994, Frederick 2001).

Finally, we describe the interactions among mercury levels and reproductive hormones in adult White Ibises. The effect of mercury on the endocrine systems of birds remains poorly understood (Askew et al. 1997). However, it is likely that endocrine disruption via mercury contamination may explain changes in behavior and breeding parameters such as decreased reproductive success (Meyer et al. 1998).

Methods

During April and May of each year of study (1994 – 2000, excepting 1996), we collected feathers from wading bird chicks of between 20 and 30 d of age (Great Egrets) and 14 – 20 d of age (White Ibises); after that age, the chicks became too mobile to catch. Since Hg may accumulate in feathers with age of chick (Spalding et al. 2000a), we later standardized feather concentrations for age of chick. Since rates of bill growth are relatively invariant among individuals of a given age in ciconiiform birds (Werschkul 1979, Williams 1997), we used bill length (culmen, in mm) as an indicator of age. Using least-square means, we then adjusted mean Hg concentrations for individual colony locations, to a 7 or 8-cm culmen measurement in White Ibises and Great Egrets, respectively (corresponding to approximately 16 and 28 d of age, respectively).

From each bird, we collected 3 – 8 growing feathers (still erupting from sheaths, or had vascularized tissue or "pulp" visible on the shaft end) from the scapular region. Within any nesting colony, we collected feathers from the largest chick in each of up to 29 nests between April and June of each year. During air-conditioned storage in paper envelopes (>3 weeks in all cases), the pulp part of the feathers dried to a large extent. Although we did not dry feathers to constant mass, we have for this reason chosen to express concentrations as "dry weight" since it is a more accurate term than "fresh weight".

Mercury levels of adult White Ibises

Adult White Ibises were captured with mist nets and rocket nets (Chapter VII) and processed as discussed in Chapter VIII. Three scapular feathers were collected and stored as described above.

Determination of mercury concentrations in samples

Individual feather samples were analyzed for total Hg concentrations by the Florida Department of Environmental Protection Chemistry Section in Tallahassee, FL. Feather samples were digested with trace metal grade sulfuric acid and nitric acid, followed by 5% potassium permanganate. Samples were analyzed using a cold vapor atomic absorption spectrometer (Varian 30/40, Palo Alto California USA, with deuterium background correction, fitted with cold vapor/hydride generator using stannous chloride reductant and automated with an SPS5 autosampler). A five-point calibration curve was created each day, and quality control samples for all runs included triplicate samples (rejection if agreement <10%), digestion blanks of deionized water, high (4 ug/l), low (1 ug/ml) methylmercury chloride sample matrix spikes, fish tissue standards (DORM –1, 0.15 – 0.2g), and a practical quantification level (PQL) standard inorganic Hg solution (0.25 ug/l). All Hg concentrations reported in this paper are for total Hg concentrations.

Using the predictive relationship between Hg consumption and growing feather tissue established by Spalding et al. (2000a) we used feather Hg concentrations to back-estimate the average Hg/body mass consumed by nestling birds in different colonies (cumulative Hg consumed/body mass = $^{1.1456}$ growing feather Hg in mg/kg dw/ 8.0588). We then used colony and year-specific averaged body masses of chicks sampled, and body size-specific food consumption rates measured in the field (Williams 1997, Frederick et al 1999) to estimate average concentrations of Hg in food items eaten by nestling Great Egrets.

We used analysis of covariance (SAS Institute) to estimate least-squares (LS) mean Hg concentrations within any colony or year. To adjust for the effect of age (bill length) in expressing the means, we examined colony, year, and bill length as potential sources of variation in the models. We used the same technique to assay for potential effects of colony and year. We also used *t*-tests in pairwise comparisons of LS mean feather Hg concentrations in colonies within years.

Results

Mercury in Great Egret chicks

We collected feathers from a total of 529 Great Egret chicks in a total of 7 colonies in the Everglades between 1994 and 2000 (Table 10.1).

Within the Everglades, mean concentrations of total Hg in colonies from all years ranged from 3.2 to 26.9 mg/kg dw (Table 10.1), with extreme values for individual birds ranging from 1.4 to 59 mg/kg dw. We found significant effects of colony (F = 17.86, P <.0001), year (F = 72.97, P <0.0001) and colony X year interaction (F = 7.77, P <0.001) on feather Hg concentrations from individual Great Egrets. We found no significant effect of bill length on Hg concentrations. Colony least-square means were consistently different from each other within years (Table 10.1), suggesting local differences in exposure rate. JW1 colony consistently showed the highest levels of Hg contamination in young birds in nearly all years, and was located in an area that also showed high (cf 0.4 ppm ww) Hg concentrations in whole mosquitofish (*Gambusia holbrooki*, see Stober et al. 1996) relative to other Everglades locations. Despite the consistent geographic

Table 10.1. Least-squared mean total mercury concentrations in feathers of nestling Great Egrets in the Water Conservation Areas of the Everglades, 1994 – 2000. LS means were standardized to an 8-cm bill size. Missing values indicate data were not collected for that year and location, and LS means of colonies with different letters within a year are significantly different (t-test, $p<0.05$)

Colony		1994	1995	1997	1998	1999	2000
L- 67	LS mean	16.28^{B}	15.86^{B}		13.90^{B}	5.50^{BC}	3.28^{AB}
	S.E.	0.889	1.178		0.863	1.01	1.077
	N	25	14		26	20	17
Tamiami	LS mean		12.14^{C}		6.30^{A}	7.64^{AB}	
	S.E.		1.10		0.863	1.038	
	N		16		26	18	
Mud Canal	LS mean	9.65^{A}	6.96^{A}				5.93^{AB}
	S.E.	1.671	1.969				2.887
	N	7	5				21.00
3b mud	LS mean			29.20^{B}		9.03^{A}	
	S.E.			1.97		1.22	
	N			12		13	
JW1	LS mean	26.87^{C}	16.81^{B}	25.18^{B}	13.21^{B}	3.97^{C}	3.96^{A}
	S.E.	1.563	1.18	1.33	0.90	1.230	1.184
	N	8	14	11	24	13	14
Hidden	LS mean	12.33^{A}	7.67^{A}	15.23^{A}	6.06^{A}	3.93^{C}	3.80^{B}
	S.E.	0.924	0.880	1.665	0.863	0.941	3.130
	N	23	25	7	26	22	16
Alley North	LS mean	13.31^{AB}	7.11^{A}	12.30^{A}	5.93^{A}	8.15^{AB}	5.56^{AB}
	S.E.	1.392	1.221	0.889	0.818	0.985	3.340
	N	10	13	25	29	20	21
Annual CV		42.6	41.3	45.6	41.7	40.9	25.9
Annual n		73	87	43	131	106	89

variation in feather Hg concentration in nestlings, there was also a significant effect of year on Hg concentration, with a 73% decline in mean feather Hg concentrations in Everglades colonies between 1994 and 2000. From feather Hg, we estimated that Hg in the diet of young birds declined between 1994 and 2000 by 67% (Table 10.2, averaged over all colonies) and by as much as 87% in one colony (Hidden colony, 2.27 mg/kg ww in 1994, 0.09 mg/kg ww in 2000).

Table 10.2. Estimated concentration of mercury (mg/kg food, ww) in aggregate diet of nestling Great Egrets in Everglades nesting colonies, as estimated from feather mercury concentrations (see methods for derivation procedure).

Colony	1994	1995	1997	1998	1999	2000
L-67	0.3368	0.4021		0.3017	0.1274	0.0872
TTE		0.2950		0.1441	0.2049	
Mud Canal	0.2325	0.1270				0.1290
3b mud			0.4935		0.2250	
JW1	0.5464	0.3313	0.5255	0.2844	0.1044	0.0990
Hidden	0.2650	0.1683	0.3354	0.1300	0.1078	0.0950
Alley North	0.3082	0.1579	0.2613	0.1927	0.1899	0.1458

Mercury levels of adult White Ibises

We collected 99 feather samples from adult White Ibises in the Everglades during the springs of 1999, 2000, and 2001. The interaction between year and gender significantly explained mercury levels ($F_{2,93} = 5.50$, $P = 0.0055$, Figure 10.1). Female mercury levels did not change significantly among years, but male ibis mercury levels did. Male mercury levels were highest in 2001. In 1999 and 2001 male mercury levels were significantly higher than female mercury levels, but in 2000 they were similar.

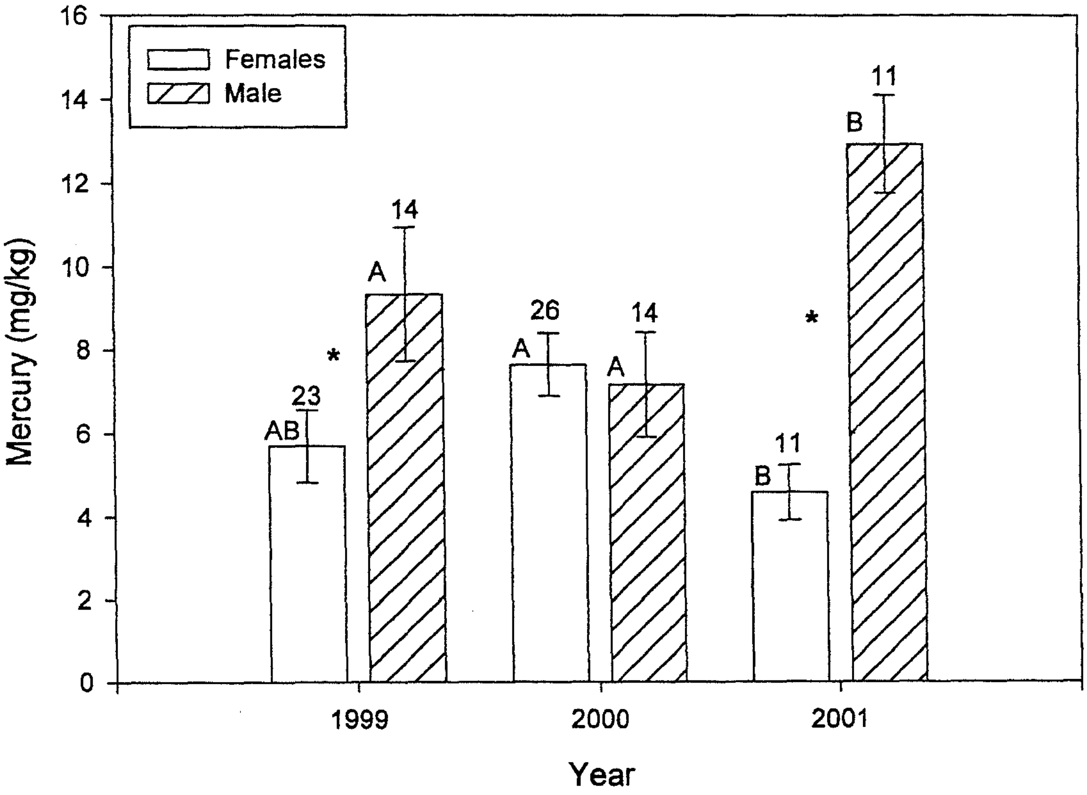

Figure 10.1. mercury levels of adult White Ibises during the 1999, 2000 and 2001 breeding seasons in the Everglades (year*sex ineraction $F_{2,101} = 5.50$, $P = 0.0055$). Letters above bars indicate significant differences within gender between years. '*' indicates a significant difference within years between genders. Numbers above error bars are sample sizes.

We found no interactions between mercury levels and female hormone levels (estradiol, testosterone and corticosterone), or stage of reproduction (ANCOVA all P's > 0.32). There was a trend (ANCOVA $F_{4,37} = 2.24$, $P = 0.0834$) for incubating females with high mercury levels to have high progesterone levels ($r_s = 0.64$). Mercury did not correlate with female body condition (Pearson $r_s = 0.182$, $P = 0.139$).

Although male ibises showed significantly higher mercury levels in 2001 than in 2000 we grouped results from all years for our analysis of mercury effects on physiology. We found no significant interactions between mercury and male testosterone and estradiol levels, or stage of reproduction (ANCOVA all P's > 0.3). There was a significant interaction between progesterone levels of incubating males and mercury levels and a significant interaction between corticosterone and mercury levels in males during the display and chick rearing phases. Indeed, if mercury levels were included as a covariate in P and B analyses we saw significant hormone changes (similar to female birds; Chapter VIII) through the breeding season. As with female ibises, mercury did not correlate with male body condition scores ($r_s = 0.148$, $P = 0.362$).

Discussion

The main source of Hg exposure for Great Egrets in the Everglades is dietary (Jurczk 1993), and very little of the total body burden of Hg in chicks is likely to come from the egg components (Day et al. 1996). Since a strong relationship has also been established between dietary Hg exposure and Hg in growing feathers of nestling Great Egrets, we feel confident that the Hg concentrations we measured in the field were a reflection of Hg in the diet of young wild birds.

Our annual samplings in the Everglades indicated that Hg exposure varied significantly with geographic location of colony. In the Everglades, the geographic differences probably reflected the considerable geographic variation in Hg concentrations in soil (Hurley et al. 1998), methylation rates (Gilmour et al. 1998), mosquitofish (Stober et al. 1996) and other aquatic animals (Cleckner et a. 1998). In 1995, the geographic differences in mean colony feather Hg corresponded in a relative way to geographic differences in whole-body Hg found in mosquitofish (see Stober et al. 1996)). An interesting feature of the Great Egret feather Hg concentrations in the Everglades was that the relative geographic differences were stable over time, with few changes in position of ranked colony Hg concentrations over the years. This suggests that geographic differences in concentrations of feather Hg in the Everglades are stable over time, at least when considering the scale at which Great Egrets are foraging from colonies (cf 25 km radius). However, this information by itself indicates only that relative magnitude of Hg exposure by location did not change over time and does not imply that Hg concentrations did not change over time. The period of study (1994 – 2001) in the Everglades was long enough to encompass considerable hydrological variation, including a period of long inundation (1994 – 1998), of extremely deep water (1994 – 1995), and two years in which much of the marsh surface was exposed by drying, followed by reflooding (1999, 2000). Thus it is unlikely that the stability of geographic differences in Hg exposure for the birds was due to any particular water regime, at least at the large scale at which the birds forage.

The marked decline in average Hg levels in the Everglades between 1994 and 2000 (average of 73%) was consistent in trend across the majority of colonies, suggesting that a real decline in Hg exposure in diet of Great Egrets had occurred across the ecosystem. Further, this decline occurred during a variety of water conditions (as above), suggesting that the trend in exposure was not the result of water conditions alone. By extrapolating from the feather Hg dynamics, we estimated a 67% decline in Hg content of the Great Egret prey items during the study. Contemporaneously, Lange et al. (1999, and unpublished data) found a steady decline in concentrations of age-standardized fillets of Largemouth Bass in the Everglades, from 2.3 mg/kg ww in 1992 to 0.4 mg/kg ww in 2000 (82% reduction). It should be realized that the bass were sampled in canals rather than marsh where the birds feed, and that Great Egrets rarely eat fish as large as bass (Frederick et al. 1999). Nonetheless, the Hg concentrations in a piscivorous bird and a piscivorous fish from the same ecosystem both declined by roughly the same percentage over the same time period, suggesting that there was some general reduction in Hg concentrations in the aquatic food web.

The mechanism by which Hg concentrations declined is difficult to pinpoint. One of the most important sources of Hg deposition in the Everglades may be municipal and medical waste incineration in the metropolitan areas of Dade and Broward counties, though there is some debate about sources and mass transport (Dvonch et al. 1999, Frederick 2000). Hg emissions from municipal waste incineration have declined nationally since 1990 as a result of decreased Hg in waste. In Florida, state regulations phased in during the early 1990s mandated the use of scrubbing systems on incineration stacks, which may also have reduced Hg emissions. We suggest that these decreases in local emissions are two likely explanations for the decreases in Hg concentrations in Everglades biota.

The potential effects of this reduction in Hg for Great Egrets may be biologically important. The peak exposure levels recorded in feathers in 1994 (12 – 26 mg/kg dw, depending on colony) often exceeded the feather tissue values (5 – 40 mg/kg) suggested by Scheuhammer (1987) to be associated with impaired reproduction. This is a necessarily conservative comparison, since the Everglades birds were measured while still in the nest, and would have likely accumulated considerably more Hg over the two years it may take to become reproductive. Adult feather values during the same period regularly exceeded the 20 mg/kg suggested by Scheuhammer to result in "substantial risk" to the birds (Beyer et al. 1997). The average feather concentrations in 1994 were in the range of values associated with reduced packed-cell volume and loss of appetite of Great Egrets in a laboratory setting (Spalding et al. 2000 a, b). However, we have presented evidence elsewhere to suggest that effects in the field are likely to be considerably underestimated by LOAELs measured in stress-free captive environments (Spalding et al. 2000b). By comparison, the feather concentrations we measured in 2000 (0.45 – 0.77 mg/kg dw) are well below any hepatic or feather tissue threshold so far suggested for impairment (Thompson 1996, Wolfe et al. 1996, Scheuhammer 1987, Spalding et al. 1994, Spalding et al. 2000 a, b, Heinz 1975).

We believe that the evidence presented here supports the use of feather tissue in piscivorous birds for assaying Hg contamination in the upper end of the food web of wetlands, especially at large geographic scales. The successful use of this method and its adaptation to other ecological situations rests heavily upon three things: 1) the use of young birds which can accumulate Hg only from their immediate surroundings, 2) an empirically measured relationship between Hg ingested and Hg concentrations in the tissue sampled, and 3) an understanding of the distance from the nest at which food is generally obtained by parents.

Adult male ibises showed different exposure trends to mercury than did female ibises. Male ibises are larger than female birds and may consume more contaminated prey than female birds. However, if this hypothesis was true then we would have expected to see a correlation within sex between body condition and mercury levels. A better explanation may be that female birds were able to dispose of mercury into eggs (Lewis et al. 1993). Indeed the yolk protein is produced in the liver, which is the main site of toxic chemical metabolism. If female birds were dumping mercury into the eggs there may be levels at which mercury may affect embryo or chick development (Bryan et al. 2001). We did not measure concentrations of mercury in ibis eggs, however.

High mercury levels in male ibises resulted in interactions with progesterone and corticosterone. However, these effects were stage dependent. This may indicate that mercury only influenced endocrinology during certain points at which hormonal changes were necessary to influence the subsequent physiological or behavioral change. Increases in hormone level may be the result of increased hormone secretion or decreased receptor sites and hormone metabolism. Laboratory research has shown that high mercury levels block progesterone receptors in oviducts (Lundholm 1991). Progesterone's role in male reproduction remains poorly understood, although some studies suggest that progesterone may initiate and maintain nest attendance (Hirschenhauser et al. 1999). Indeed our study showed an interaction between mercury levels and progesterone only in incubating birds. Unfortunately, the consequent physiological or behavioral changes that may have been affected remain a mystery, since our evidence is entirely based on correlation, not causation. Similarly, we saw an interaction between mercury levels and corticosterone in display and chick-rearing males. Corticosterone is generally associated with stress responses and mass gain (Heath and Dufty 1998). Female ibises show an increase in corticosterone levels during chick stage, probably to gain back mass lost during reproduction. Male birds may depend on these same interactions but it is unclear how mercury may affect the relationships among mass gain, corticosterone and breeding stage. Further studies that investigate the sex specific interactions among mercury, hormone levels and breeding behavior would be useful in understanding this relationship.

CHAPTER XI. SYNTHESIS AND CONCLUSIONS.

In this chapter we attempt to pull together many of the results and themes from the preceding chapters, in an effort to capture as much new understanding as possible from the diverse results of this monitoring and research project.

What environmental conditions make wading birds initiate nesting?

The period of study demonstrated a large and very significant increase in nesting numbers in the ecosystem, by comparison with almost any benchmark of the previous two decades. Although there were increases in most species, the most pronounced increase was among those species that forage tactilely (Wood Storks, White Ibises, Glossy Ibises) and those that forage in tight social flocks (Snowy Egrets). By comparison, the birds capable of foraging in deeper water and that typically forage by stealth and vision (Great Egrets, Great Blue Herons) did not have as strong increases, and in at least one year (2001) did very poorly.

The hydrological conditions in 1999, 2000 and 2001 were those that have been associated with large numbers of nesting birds in the past – relatively high initial stages, falling rapidly and with little interruption between November and April. However, the large number of nesting birds cannot be explained by these conditions alone, since similar conditions prevailed in at least two years during the mid-1990's and nesting numbers were comparatively paltry. This suggests that there were other factors involved in the attraction of large numbers of birds in 1999 – 2001. We have suggested that an extensive and in some places severe drought in other parts of the southeastern US may have made the Everglades one of the few places that were suitable for nesting for a large number of birds. It is also possible that the marked decline in mercury contamination was related to the increase in nesting numbers. Finally, there is the possibility that some combination of hydrological conditions may have resulted in extremely dense prey populations. However, our results are largely based on association, and we are unable to isolate the combined or individual effect of these events, especially with the small sample sizes available for any given set of conditions. The basic problem is that we are attempting to understand the effects of at least five variables that may each have independent actions(hydrology, weather, prey population fluctuations, contamination, and conditions outside the ecosystem), and we have no ability to vary these effects in an experimental way. These effects are likely to be isolated either through a very large number of years monitored, or through some combination of experiments with captive animals.

However, the present study has also demonstrated conclusively that while antecedent severe drought in the Everglades ecosystem may often lead to large nesting events in the years following droughts, these droughts are not the only events that can lead to large nestings. Although we maintain that droughts play an important role in the ecology of wading bird populations and the Everglades ecosystem, we believe that research should also be focused on identifying other mechanisms by which prey are made abundant and available over large areas of the marsh.

Our experimental work with captive Scarlet Ibises was inconclusive on the question of whether food during the prebreeding period is limiting for the initiation of breeding in ibises. However, as a by-product of the experiment, we learned that ibises do put on considerable mass prior to breeding, and can fatten up to these levels in a very short time (as little as two weeks). This suggests that at least in ibises, a long period of hyperphagy prior to breeding may not be required, if foraging conditions are good. The relative importance of prebreeding body condition, and the rapidity of fattening in other species remains unknown.

Management of breeding colony substrate

Our observations on the degradation of nesting substrate, particularly in large willow colonies, suggests strongly that long periods of high water in the Everglades should be avoided if large willow heads are to be maintained. Since longer hydroperiods and deeper water are projected over much of the central Everglades under restored conditions, this is an important consideration for planners and vegetation modelers. Similarly, our observations on the effects of fire on colonies suggests that under even moderately dry conditions, large willow-dominated colonies are not particularly flammable, and in many cases fire protection of colonies may not be warranted.

How should we count birds?

Our attempts to measure error in counting and estimating numbers of birds by using monthly aerial surveys present a new dilemma in the monitoring of waterbird populations. First, it seems clear that most past aerial counts are likely to have been undercounts, perhaps by large amounts (e.g., 29 – 50% were likely to have been missed by observers counting, and an additional 24 – 63% were missed by spacing surveys one month apart). Second, our simulations suggest that both sources of error are likely to vary in an unpredictable way over time, indicating that correction factors are unlikely to be reliable for deriving probable true absolute numbers of birds. Perhaps more importantly, the lack of consistent sources of variation means that past counts are probably not reliable even as indices of abundance.

Of course, the accuracy of indices depends on the level of inference that is desired. If the difference in numbers of nesting pairs in two years or two epochs is large enough, the potential sources of error may be overwhelmed as sources of variation. For example, the apparently very large nestings of 1992, 2000 and 2001 seem to clearly be much larger than other nestings during the 1990's. And the very large nestings of the 1930's (>100,000 pairs) were almost certainly larger than the nestings of the 1990's. However, the confidence in inference declines rapidly as the comparisons become less extreme.

Some of these sources of error can probably be reduced. First, our work suggests that counting error can be reduced considerably through the use of photographic counts (reduced from 29% aggregate error with observers to 13% error with photos). However, we caution that our experiment had relatively low tree density, which resulted in near-optimal conditions for the use of photographs. We also suggest that if individual variation in observer counting error can be measured, then annual counts could presumably be corrected. However, it is unknown whether observer-counting error remains stable over time, especially if observers have received training in counting. Investigation of this dynamic is therefore an essential first step in coming up with annual observer correction factors.

Error resulting from monthly spacings between surveys are less amenable to correction. In this case, the main error results both from the fact that nests are spread out over a four-month nesting season, and from the problem of nests starting and failing between surveys. One way to get at the latter problem would be to measure nest failure rates in a variety of colonies in each year – that way the proportion missed through monthly surveys could be estimated. However, this work would be extremely time consuming and costly, and would also result in some unknown level of disturbance to the birds. The problem of asynchronous nesting is really intractable, and is unlikely to be solved by surveys spaced more closely in time if nesting is very spread out.

During the consideration of estimation problems, we also have repeatedly identified the problem of renesting, and its effect on estimating the breeding population size. Breeding population has always been counted as numbers of nesting attempts, which skirts the issue of renesting completely. However, if most pairs that fail at their nesting attempt later renest, it might make a very large difference in the estimation of the size of the breeding population. Very little is known about the propensity of ciconiiform birds to renest following failure. Unlike many high latitude breeders, the breeding season in south Florida is up to five months long (nearly year-round in some coastal locations), and renesting one or more times is theoretically possible. However, no measurements have been made of this phenomenon for the simple reason that it is very difficult to track individual birds that fail at nesting. Although we can offer no ready means for measurement, we believe strongly that a study of renesting is important for understanding the demography of wading birds in south Florida.

Are there appreciable numbers of nonbreeding adult wading birds in the Everglades?

We do not feel confident about almost any statements concerning nonbreeding in Everglades wading birds, especially with the large uncertainty in estimating numbers of breeding and nonbreeding birds revealed by our studies (above). Further, our considerations of potential migrants, animals that might have bred earlier in the year at other locations, and movements of Caribbean birds into south Florida, all suggest that our abilities to detect nonbreeding in the Everglades through surveys are quite poor.

We believe it safe to say that we found no evidence for large numbers of nonbreeding ibises through our studies of radio-marked birds, and our studies of physical and physiological signs of breeding suggested that nearly all adult birds we caught were breeding. However, its also clear that we studied this phenomenon most intensively during three years when breeding numbers were considerably above normal, when nonbreeding might be expected to be at a minimum. In this light, it seems impossible to say at present whether nonbreeding occurs, or if it does, whether it occurs at high enough proportions to affect the population trajectory of any species in the south Florida ecosystem.

What physiological mechanisms result in initiation of breeding in ibises?

Our work has filled some important gaps in understanding the physiology of reproduction in ibises. First, our work has confirmed that ibises do develop brood patches, and that many ibises molt during the breeding cycle. Second, we have described the color and physical changes that breeding ibises go through, to the extent that breeding birds can be identified from these color changes, and sexes can be reliably discriminated on the basis of physical attributes.

The full significance of the description of hormonal changes is difficult to evaluate. Like many birds, the control of gonadal growth in ibises appears to be related to day length and age. However, it is likely that the development of other attributes (hormonal changes, color changes, body mass changes) are more influenced by local conditions; we suspect that social and feeding conditions are primary among these influences. Beyond this, however, we run out of comparative models – most endocrine models of birds are from temperate or domestic species. The White Ibis is instead subtropical and tropical in distribution, and seems to be adapted to a rapid reproductive response when conditions are attractive, over a long breeding season.

Our radio-marking studies were instrumental in leading us to several conclusions. First, we have demonstrated that adults can breed in successive years, and that they are not limited by energy or other constraints to breeding at some longer interval. Second, our results indicate that ibises may be quite philopatric – 71% of adults marked in 1999 and relocated in 2000 bred in the same colony. This finding is interesting since this species has considerable reputation as a non-philopatric bird (Frederick and Ogden 1997).

Body condition changes of breeding ibises

Scarlet Ibises and White Ibises show similar patterns in body condition changes during the breeding season. Birds increase mass during courtship and display and then subsequently loss mass throughout reproduction. To examine how these mass changes may affect breeding success, we experimentally manipulated the mass of captive birds via supplemental feeding of an experimental group. However, we found that the control group could quickly reach a mass equivalent to the experimental groups if given access to adequate (non-supplemented, although ad libitum) food supply. We saw no differences in nesting behavior between the fed and control groups. Although this experiment did not yield the expected results, it demonstrated that ibises that are in poorer condition (than fed group) could quickly gain mass. Mass gain associated with the onset of breeding was likely the result of increased food intake and changes in metabolism.

Increased energy stores may be important for fasting in male birds that do not eat during the nest building and copulation stages and important for egg production in female birds.

Birds that use endogenous energy stores for egg production are called ‘capital breeders’. Birds that eat (use acquired energy) during egg production are considered ‘income breeders’ (Stearns 1992). The body condition changes of ibises suggest that they more closely fit the capital breeder predictions. However, our studies of free-living White Ibises suggest interesting sex specific differences. Male ibises showed highest fat scores during the display stage. Males also tended (though not significant) to lose pectoralis mass through the display and copulation stages. Therefore, the endogenous stores of fat and protein (pectoralis) may be used during the copulation and nest building stages when male ibises fast. This use of endogenous stores would be consistent with the ‘capital breeder’ model.

Female White Ibises also showed body condition changes during the breeding season but what caused these mass changes is less clear than male ibises. Female ibises showed no significant changes in fat stores and an incongruous loss of pectoralis mass (compared to body condition changes). It is not evident how female ibises may be storing energy reserves for egg production. In contrast to male ibises, female White Ibises forage throughout the breeding season. Thus, ibises may not depend on endogenous energy stores for egg production. This would be consistent with our findings that females do not store fat or protein during the breeding season and consistent with the predictions of an ‘income breeder’. Conversely, female ibis body condition changes show a pattern consistent with ‘capital breeder’. Some female mass changes may be attributable to development of the ovary and oviduct; however, it is unlikely that ovaries account for all body condition changes. Sex-specific energy storage and metabolism is an interesting and relatively unstudied theme in biology. Most studies of avian reproduction energetics focus on female requirements because egg production is likely the mostly costly stage of reproduction (per unit time). Ibises present an interesting model of energy use because male mate guarding depends on the individual's ability to fast. Further, understanding complex relationships among food availability, ability to gain mass, and nesting effort may show that ibises can respond quickly to favorable environmental conditions. However, conditions must remain favorable throughout the egg production stage so that females can satisfy egg production requirements

Could mercury contamination affect breeding by Everglades wading birds?

We found a positive relationship between mercury in adult male ibises and both progesterone and corticosterone levels during incubation. The apparently stronger relationship in males may be due to the fact that males had higher circulating levels of mercury than did females, probably because females were able to excrete significant amounts of mercury through egglaying. We are aware that at higher physiological levels of mercury, progesterone receptors may be blocked. This would fit with the positive relationship between mercury and progesterone. If receptors are blocked, then the negative feedback loop would be inhibited and progesterone production would continue. What little is known about progesterone's role in avian reproduction suggests that decreased progesterone might lead to poorer nest attendance or even abandonment of nesting. In the case of the male ibis, the higher progesterone in mercury contaminated birds is thought to be indicative of blockage of progesterone reception sites, which would effectively amount to the same thing as low progesterone levels in other studies. High abandonment rates of wading birds has been noted as a characteristic of the Everglades nesting populations in the past (Frederick and Spalding 1994). However, any potential connection between nesting and mercury contamination is extremely tenuous.

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APPENDICES

Appendix 1. Locations and species composition of colonies and single nests found in WCA 3 and 2 during aerial and ground surveys conducted from January through July of 1998.

	Latitude	**Longitude**															
COLONY	**decimal**	**degrees**	**WOST**	**WHIB**	**GREG**	**SNEG**	**TRIC**	**LBHE**	**GRBH**	**GLIB**	**CAEG**	**BCNH**	**DCCO**	**GBHE**	**ANHI**	**RoSP**	**Total**
Hidden	25.7988	80.8430		5	360	111	663	2							30		**1,171**
Alley North	26.1892	80.5258		500	475	60					40	15		6		10	**1,106**
2Bse-20	26.1467	80.3783			60		15	90			300			1	150		**616**
TTW	25.7586	80.5459			250							6			200		**456**
Mud Canal	26.0100	80.4608		30	95	17		20			275			3			**440**
TTE	25.7586	80.5084			57				1				5		250		**313**
CypressCity	26.1242	80.5429			120									1	12		**133**
Starter Mel.	25.9408	80.6224			40										80		**120**
Big Mel.	26.0467	80.6250			105										2		**107**
Unknown	26.1457	80.7447			105												**105**
3BEMud	25.7970	80.4945			100												**100**
Unknown	26.1443	80.7502											100				**100**
Unknown	25.9623	80.5720			40								12	1	40		**93**
Unknown	26.1443	80.7502			85												**85**
Heron alley3	25.7976	80.5346				28	42	3	1						9		**83**
Crossover	25.9400	80.8317			80												**80**
Unknown	25.7983	80.7627			80												**80**
Unknown	26.0490	80.6167			75												**75**
L-67	25.9555	80.5653			62									4			**66**
North 3A	26.1224	80.7819			60										3		**63**
Unknown	26.1010	80.4540			50									2	10		**62**
JW2	26.1253	80.7323			30	10	10	10							1		**61**
Unknown	26.1435	80.7493			60									1			**61**
Unknown	26.3300	80.5012			60												**60**

COLONY	Latitude decimal	Longitude degrees	WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	Total
Unknown	25.9652	80.8207					15	40									**55**
Andytown	26.1250	80.5046			13									3	35		**51**
Unknown	25.9168	80.5987							1					2	45		**48**
Unknown	25.8383	80.5255			47												**47**
unknown	25.9225	80.8300			40												**40**
AGCanEa	25.7982	80.4834													38		**38**
3B-NAGCA	25.8275	80.5200											35	1			**36**
North 3A	26.0341	80.6747					5	30							1		**36**
Unknown	26.0158	80.6590			36												**36**
Unknown	26.1233	80.7282			35												**35**
Unknown	26.1150	80.6598			35												**35**
3B-NAGCA	25.8399	80.5315			10		3	2						2	15		**32**
Unknown	25.8497	80.5317			32												**32**
JWnew	26.1088	80.7527			25									4			**29**
Unknown	26.1393	80.3892											29				**29**
Unknown	26.1300	80.7008			28												**28**
Unknown	26.1343	80.7025			25												**25**
3A	25.8190	80.6775			7										16		**23**
Unknown	26.1093	80.7850			23												**23**
Unknown	25.8150	80.6043			22												**22**
Unknown	26.1300	80.7035			20									1			**21**
Unknown	26.2913	80.5832			20												**20**
unknown	25.9662	80.5727			20												**20**
Unknown	26.2095	80.8220			19												**19**
AGCanEa	25.7977	80.4942													16		**16**
2A	26.2585	80.3668			15												**15**
west3A	25.9797	80.7419												4	10		**14**

	Latitude	Longitude															
COLONY	**decimal**	**degrees**	**WOST**	**WHIB**	**GREG**	**SNEG**	**TRIC**	**LBHE**	**GRBH**	**GLIB**	**CAEG**	**BCNH**	**DCCO**	**GBHE**	**ANHI**	**RoSP**	**Total**
3A	25.8515	80.6725												1	5		**6**
3BNAg Ca	25.8946	80.5142			1									3	2		**6**
North 3A	26.1122	80.7447			4		2										**6**
Unknown	25.8190	80.6775					4							2			**6**
Unknown	26.0145	80.6310												3	3		**6**
west3A	25.8308	80.7536													6		**6**
3A	25.9425	80.7317												2	3		**5**
3BNAg Ca	25.8334	80.5036					2							1	2		**5**
3B-NAGCA	25.8403	80.5275													5		**5**
Unknown	26.1097	80.7533			5												**5**
Unknown	25.9543	80.6844												5			**5**
Unknown	26.0054	80.6428			3									1	1		**5**
Unknown	25.8548	80.6407												1	4		**5**
3A	25.8634	80.7062													4		**4**
3A	25.9543	80.6844												4			**4**
3A	25.9518	80.6784													4		**4**
3BCell2	25.7898	80.5753												3	1		**4**
N3A	26.1286	80.7154			1		1					1		1			**4**
Unknown	26.1128	80.7446			3									1			**4**
Unknown	25.8333	80.6573												2	2		**4**
Unknown	26.0148	80.6313													4		**4**
Unknown	26.3272	80.4398			4												**4**
west3A	25.8587	80.7438													4		**4**
3A	25.9405	80.8130												1	2		**3**
3A	25.7777	80.7326												1	2		**3**
3A	25.5988	80.7130													3		**3**
3A	25.8778	80.7089												3			**3**

COLONY	Latitude decimal degrees	Longitude	WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	**Total**
3A	25.8644	80.7061													3		**3**
3A	25.9336	80.7033													3		**3**
3A	25.9406	80.6805													3		**3**
3BCell2	25.7868	80.5705													3		**3**
3BNAg Ca	25.8656	80.5160												2	1		**3**
3B-NAGCA	25.8205	80.5012												1	2		**3**
3bNWAG	25.8190	80.6126							3								**3**
North 3A	26.1249	80.7770												3			**3**
Unknown	25.9897	80.6726													3		**3**
Unknown	25.9790	80.6553													3		**3**
Unknown	25.8989	80.6293												1	2		**3**
Unknown	26.0244	80.5407			3												**3**
west3A	25.8873	80.7703													3		**3**
west3A	25.8316	80.7575													3		**3**
west3A	25.9291	80.7553												3			**3**
west3A	25.9109	80.7316												1	2		**3**
3A	25.7971	80.7312												1	1		**2**
3A	25.9122	80.7252												1	1		**2**
3A	25.9102	80.7206												1	1		**2**
3A	25.8781	80.7056												2			**2**
3A	25.8440	80.7046												1	1		**2**
3A	25.8462	80.7033												1	1		**2**
3A	25.7810	80.6890												1	1		**2**
3A	25.9302	80.6879													2		**2**
3A	25.8356	80.6855													2		**2**
3A	25.8356	80.6845													2		**2**
3A	25.9296	80.6797												1	1		**2**

COLONY	Latitude decimal	Longitude degrees	WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	Total
3A	25.9453	80.6756												1	1		2
3A	25.9456	80.6752												1	1		2
3A	25.8193	80.6712													2		2
3A	25.9039	80.6695													2		2
3A	25.8172	80.6687												1	1		2
3BCell2	25.7802	80.5755												1	1		2
Unknown	25.8432	80.6454													2		2
Unknown	26.0845	80.6267												2			2
Unknown	25.9755	80.6257													2		2
Unknown	25.9149	80.6073												1	1		2
west3A	25.8026	80.8086											1		1		2
west3A	25.9807	80.7962												2			2
west3A	25.8663	80.7642													2		2
west3A	25.9805	80.7605												2			2
west3A	25.9478	80.7587												1	1		2
west3A	25.9562	80.7530												2			2
west3A	25.9940	80.7470												2			2
west3A	25.9377	80.7365												2			2
west3A	25.9132	80.7325												1	1		2
west3A	25.9377	80.7321												2			2
west3A	25.8588	80.7306												2			2
west3A	25.8748	80.7286													2		2
3A	25.7840	80.7317												1			1
3A	25.7865	80.7314												1			1
3A	25.7790	80.7287												1			1
3A	25.9746	80.7239												1			1
3A	25.7220	80.7095													1		1

	Latitude	Longitude															
COLONY	decimal degrees		WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	Total
3A	25.8505	80.7049													1		1
3A	25.8634	80.7044													1		1
3A	25.8445	80.7013													1		1
3A	25.8811	80.6942													1		1
3A	25.8124	80.6932												1			1
3A	25.7940	80.6896												1			1
3A	25.9286	80.6876													1		1
3A	25.8356	80.6865													1		1
3A	25.9767	80.6859													1		1
3A	25.8361	80.6855													1		1
3A	25.8256	80.6834												1			1
3A	25.8852	80.6831												1			1
3A	25.8819	80.6831												1			1
3A	25.9714	80.6808													1		1
3A	25.8090	80.6786													1		1
3A	25.8464	80.6780													1		1
3A	25.8145	80.6758												1			1
3A	25.9325	80.6757													1		1
3A	25.8277	80.6757												1			1
3A	25.8321	80.6736												1			1
3A	25.9178	80.6674													1		1
3A	25.8952	80.6626													1		1
3B gbhsur	25.8997	80.5309												1			1
3BNAg Ca	25.9026	80.5442												1			1
3BNAg Ca	25.9105	80.5306												1			1
3BNAg Ca	25.8794	80.5299												1			1
3BNAg Ca	25.8946	80.5099												1			1

COLONY	Latitude decimal	Longitude degrees	WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	Total
3BNAg Ca	25.8194	80.5036												1			**1**
3BNAg Ca	25.9301	80.4677												1			**1**
3B-NAGCA	25.8369	80.5534												1			**1**
3B-NAGCA	25.8240	80.5200												1			**1**
North 3A	26.0693	80.7722					1										**1**
North 3A	26.0746	80.7298												1			**1**
Unknown	26.0203	80.8093												1			**1**
Unknown	26.0031	80.6644												1			**1**
Unknown	25.9701	80.6586													1		**1**
Unknown	25.9134	80.6377													1		**1**
Unknown	26.0766	80.6304												1			**1**
Unknown	25.8776	80.6280							1								**1**
Unknown	26.1441	80.3916											1				**1**
west3A	25.9572	80.8156												1			**1**
west3A	25.7949	80.8101												1			**1**
west3A	25.8338	80.8082													1		**1**
west3A	25.9062	80.7982					1										**1**
west3A	25.7744	80.7974												1			**1**
west3A	25.7984	80.7946												1			**1**
west3A	25.7928	80.7935												1			**1**
west3A	25.9317	80.7892												1			**1**
west3A	25.7966	80.7836												1			**1**
west3A	25.9053	80.7763													1		**1**
west3A	25.8917	80.7688													1		**1**
west3A	25.8497	80.7615													1		**1**
west3A	25.7978	80.7596												1			**1**
west3A	25.9937	80.7468												1			**1**

COLONY	Latitude decimal	Longitude degrees	WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	Total
west3A	25.9938	80.7465												1			**1**
west3A	25.9140	80.7363												1			**1**
west3A	25.9178	80.7331													1		**1**
west3A	25.9130	80.7325													1		**1**
west3A	25.9100	80.7312													1		**1**
west3A	25.9092	80.7308												1			**1**
west3A	25.9682	80.7293												1			**1**
west3A	25.8738	80.7282												1			**1**
west3A	25.8560	80.7272													1		**1**
west3A	25.9104	80.7230													1		**1**
Totals:			**WOST**	**WHIB**	**GREG**	**SNEG**	**TRIC**	**LBHE**	**GRBH**	**GLIB**	**CAEG**	**BCNH**	**DCCO**	**GBHE**	**ANHI**	**RoSP**	**Total**
			0	535	2,979	226	803	209	8	0	615	22	193	179	1,240	10	**7,019**

Appendix 2. Size, composition and location of wading bird colonies located in WCAs 2 and 3 during January - June, 1999. Counts of all species are in numbers of nests. Species codes are: WOST = Wood Stork, GREG = Great Egret, WHIB = White Ibis, SNEG = Snowy Egret, TRHE = Tricolored Heron, GBHE = Great Blue Heron, ANHI = Anhinga, LBHE = Little Blue Heron, YCNH = Yellow-crowned Night Heron, BCNH = Black-crowned Night Heron, CAEG = Cattle Egret, GRHE = Green Heron, ROSP = Roseate Spoonbill, DCCO = Double-crested Cormorant.

	Decimal Degrees		Species													Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
N-S canal 3B	25.79727	80.52833		20			5	8	33	1	24		20				111
Hidden	25.75862	80.54593		300	97	246	427		18	3						598	1,689
	25.85323	80.83872		45	1		4		10	3	4						67
West Ag Canal	25.79727	80.62928		4	4		10	2	25	4	28		10				87
West Cent. Ag	25.79727	80.61803			13		11		24	4	13		9				74
Anhinga alley	25.79727	80.49832		35	4		25	4	300	5	24		16				413
	26.11643	80.65973		50			5		2	5							62
1-67 canal	25.97622	80.53853					18	7	10	5			14				54
TTW	25.75862	80.54593	60	400	150	15	8			6	10	35	5				689
	25.98755	80.70667				5	15	1	15	8							44
East Central Ag	25.79720	80.50520		5	25		12	3	20	9	25		7				106
	26.04087	80.80177		7			13		2	15	4						41
Heron alley	25.79732	80.55930		3	180	20	50	1	70	17	10		16				367
Mud Canal	26.01000	80.46167		85			50	3	76	20	16	300					550
2B-20	26.14458	80.37980		80		30	25	5	80	20	4	190					434
	26.09195	80.71212				20	10			22							52
	26.05398	80.75617		25		10	10	1	1	25	1						73
	26.07105	80.80747				62	20			40							122
	25.96732	80.80855				20	27		2	45							94
	26.01552	80.79425					27	1		65							93
	25.96563	80.82068				10	10	1		65							86
Alley North	26.18917	80.52583		750	4000	300	150	6			20			35			5,261
JW new	26.14352	80.74763		560				4									564
Crossover	25.94000	80.83250	180	260													440
Big Mel	26.04710	80.62670		125	150				3		1						279
2B stork	26.16338	80.34770	70	55				2	15					12			154
Starter Mel.	25.94072	80.62443		70				32	45						4		151
3B MUD East	80.49450	25.79700		130				6	10								146

	Decimal Degrees						Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	26.04000	80.62167		140													140
buffer Zone	26.10228	80.45448		80												50	130
Cypress City	26.12500	80.54167		120				4									124
	26.13628	80.70842		110													110
N-S canal 3B	25.79727	80.56482					3	2	60		19		25				109
	26.13162	80.70212		80					20								100
L-67	25.96140	80.57283		70				2	25								97
	26.03253	80.69203		75			2	5	12								94
	25.93500	80.62500		80													80
	26.01807	80.69217		75													75
2B 2nd colony	26.19167	80.30833	10	60													70
2B	26.17890	80.32265		65													65
	26.11167	80.66167		58													58
	25.85022	80.67305		1				2	50								53
	25.77180	80.69293		12				2	30								44
	26.14693	80.74308		44													44
	25.91687	80.59850		5				3	25						10		43
	25.91535	80.63137						4	38								42
	26.10810	80.79742		20			1	1	18				2				42
TTE	25.75862	80.50843		41													41
JW1	26.11088	80.75247		35				4	1								40
	26.03638	80.79008					15			20			1				36
	25.75500	80.68667		25					9								34
	25.96952	80.70602		33				1									34
	26.17892	80.33175		31													31
3B deer island	25.80833	80.60350		31													31
	25.81847	80.67747		18				1	12								31
	25.98663	80.82052					18			5	5		3				31
	25.98345	80.81245					10			20							30
	26.04315	80.72285					12	2		12	1						27
	26.13447	80.73778					7			20							27
	26.05337	80.74155		18			4				3						25

	Decimal Degrees							Species								Unidentified	Colony
Colony name	**Latitude**	**Longitude**	**WOST**	**GREG**	**WHIB**	**SNEG**	**TRHE**	**GBHE**	**ANHI**	**LBHE**	**BCNH**	**CAEG**	**GRHE**	**ROSP**	**DCCO**	**small herons**	**Totals**
	26.00017	80.54167		24													24
	25.91448	80.77408						3	21								24
	26.09612	80.79638		15			5				2		2				24
	26.04012	80.82900		18				5	1								24
	25.98523	80.45443		20				3									23
Holiday Trail S	26.02607	80.53910		17				4	2								23
	25.87573	80.64495						1	22								23
	25.83178	80.67382						1	22								23
	25.77727	80.69903						1	22								23
	25.93968	80.70728						2	20				1				23
	26.05842	80.55195						2	20								22
	25.00950	80.70333		22													22
	25.85032	80.83637						2	20								22
	25.82800	80.67577						1	20								21
	25.97323	80.69878		21													21
	25.97128	80.70125		20				1									21
	25.77905	80.70195						4	17								21
	25.90107	80.73907						1	20								21
	25.79688	80.80763						3	18								21
	26.12000	80.50833		20													20
	25.84638	80.70292							20								20
	25.86375	80.70570						1	18						1		20
	25.97773	80.74195		4			9	3	3				1				20
	25.97788	80.80493					18						2				20
Canals NE 3A	80.58818	26.08628		8			1	6	2		1		1				19
	26.26245	80.49672		18				1									19
	25.85560	80.64300						1	18								19
	25.95082	80.72992						1	16						2		19
	26.03373	80.76063					15	2					2				19
	26.03435	80.76078					16	2		1							19
blue shanty can	25.79727	80.62650							2		6		10				18
	25.86423	80.66352						2	16								18

	Decimal Degrees							Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	26.13277	80.70840		18													18
	25.81653	80.77282							18								18
	26.09667	80.49500		17													17
	25.89482	80.50407		15				1					1				17
	25.95203	80.69423						2	15								17
	26.08255	80.76415					15						2				17
	26.03892	80.80990					10			7							17
2A	26.26667	80.37667		12				4									16
	25.83558	80.68528						1	15								16
	25.83532	80.69317						1	15								16
	26.12270	80.73285		16													16
	25.77613	80.79603						1	15								16
	26.10595	80.79678					5	2	4		1		4				16
	25.92610	80.68600							14				1				15
	26.03470	80.69197		5			4	2	4								15
	25.89270	80.77440					1	3	11								15
	26.10757	80.78378					10			5							15
	25.97503	80.80967					9			4	2						15
Mud Canal So.	25.98312	80.45775		12				2									14
	26.10883	80.49900		14													14
	25.91298	80.63787						1	13								14
	25.89363	80.67688						2	12								14
	25.81047	80.49152							4		3		6				13
	25.82253	80.49408		1					4		8						13
	25.86265	80.50608		13													13
	25.89420	80.51425		5				4	3		1						13
3B deer island	25.83667	80.53000		13													13
	25.87372	80.65815							13								13
3B deer island	25.81333	80.68167		13													13
	25.91007	80.72068						1	11						1		13
	26.09983	80.79647					4		3	2	2		2				13
	25.82155	80.48547							4				8				12

	Decimal Degrees							Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.81050	80.49137							4		2		6				12
	25.86563	80.50625		11					1								12
	26.01398	80.63102						3	9								12
	26.09433	80.66083		10				2									12
	25.90383	80.67017						1	11								12
	26.02857	80.69127		12													12
	25.97927	80.69553		2					9				1				12
	25.88623	80.70187						2	5						5		12
	25.90643	80.79723					12										12
	26.11375	80.65163					4			7							11
	25.86375	80.66187						1	10								11
	25.95140	80.66737						1	10								11
	25.89532	80.73823						1	10								11
	26.05985	80.80395					5			6							11
	25.86468	80.51623		7				3									10
	26.06452	80.66723					4			6							10
	25.82320	80.72180							10								10
	25.81312	80.72865							10								10
	25.91330	80.73455						4	6								10
	26.02242	80.73482		5				2	1				2				10
	25.93678	80.73700						4	6								10
	25.89373	80.50035		2				1					6				9
	26.00063	80.59688						2	7								9
	25.97185	80.63355							9								9
	26.12205	80.65328		7					1				1				9
	25.91317	80.66588							9								9
	25.88553	80.66690						1	8								9
	25.89405	80.66820						1	8								9
	25.81877	80.67180						2	7								9
	25.76503	80.67735							9								9
	25.97183	80.68115					2	2	3		2						9
	25.86090	80.72478						1	8								9

	Decimal Degrees							Species								Unidentified	Colony
Colony name	**Latitude**	**Longitude**	**WOST**	**GREG**	**WHIB**	**SNEG**	**TRHE**	**GBHE**	**ANHI**	**LBHE**	**BCNH**	**CAEG**	**GRHE**	**ROSP**	**DCCO**	**small herons**	**Totals**
	25.94918	80.73328						2	7								9
	26.04193	80.76077		4				5									9
	25.96355	80.77018		1			1	3	4								9
	25.88788	80.77073					1		6	1			1				9
	26.09152	80.79378		4			2	1	2								9
	25.86855	80.80685					7	2									9
	25.89167	80.50380		8													8
	25.89257	80.52800		6				1			1						8
	26.20922	80.66585		8													8
	25.84608	80.67747							8								8
	25.93033	80.67950						1	6				1				8
	25.94047	80.68102						1	7								8
	25.89783	80.70490						1	6				1				8
	25.77767	80.71015						3	5								8
	25.93340	80.71363						1	5				2				8
	25.91458	80.71942						1	5						2		8
	25.77248	80.72803						4	4								8
	25.88907	80.80448					5						3				8
	26.20853	80.39307						7									7
	25.81157	80.49735									7						7
	25.82005	80.50158						2	3		1		1				7
	25.87092	80.50468						5	2								7
	26.04525	80.61588					6		1								7
	25.88382	80.63800						3	4								7
	25.90820	80.65010							7								7
	26.03462	80.65188					6			1							7
	25.87410	80.66058							7								7
	25.82515	80.68283						1	6								7
	26.07483	80.69265					5			2							7
	25.90803	80.70377						1	6								7
	25.90403	80.70792						1	6								7
	25.81023	80.70843						1	6								7

	Decimal Degrees		Species													Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	26.07153	80.71605					7										7
	25.79627	80.73162						1	6								7
	25.96505	80.73737						2	4				1				7
	25.96560	80.74203						1	6								7
	25.98132	80.81663				2	5										7
	25.86338	80.49368		2			3						1				6
	25.84273	80.64568							6								6
	26.13633	80.64723		5			1										6
	25.97817	80.65642						2	3				1				6
	25.91373	80.66165							6								6
	25.81590	80.67295							6								6
	26.10977	80.70037								3			3				6
	25.89243	80.70228						1	5								6
	25.80795	80.70258									1		5				6
	25.80735	80.70497						1	4				1				6
	25.85047	80.70500						2	4								6
	25.80598	80.70835						1	5								6
	25.96628	80.74097							5				1				6
	25.77712	80.74490						1	4				1				6
	25.83037	80.75677						1	5								6
	25.95783	80.77220						2	4								6
	25.93187	80.78075							3				2				5
	25.79053	80.79033					4	2									6
	25.77250	80.79262						6									6
	25.91988	80.79877					6										6
	26.02088	80.85292						4			1		1				6
Canal NE 3A g	80.46128	26.06160							3		1		1				5
	25.87852	80.52897		3				2									5
	25.95742	80.64708						1	4								5
	25.87550	80.66140						1	4								5
	25.89495	80.66263						1	4								5
	25.92865	80.68785						1	4								5

	Decimal Degrees							Species									
Colony name	**Latitude**	**Longitude**	**WOST**	**GREG**	**WHIB**	**SNEG**	**TRHE**	**GBHE**	**ANHI**	**LBHE**	**BCNH**	**CAEG**	**GRHE**	**ROSP**	**DCCO**	**Unidentified small herons**	**Colony Totals**
	25.83118	80.68882						1	4								5
	25.85792	80.71002							4				1				5
	25.77987	80.72870						3	2								5
	25.99545	80.73195					1	2	2								5
	26.05435	80.73372					5										5
	25.90798	80.74155							5								5
	25.94202	80.74753						1	4								5
	25.94367	80.74953						1	4								5
	25.90562	80.76697						1	4								5
	25.95492	80.77285						1	4								5
	25.91765	80.77390					5										5
	25.95787	80.77490						1	4								5
	25.81420	80.77597						1	4								5
	25.77665	80.79333						2	3								5
	25.97847	80.79387		5													5
	25.80653	80.79600						1	4								5
	26.03965	80.80463									5						5
	25.87488	80.50125						2					2				4
	25.89938	80.62970						1	3								4
	26.07695	80.63082						3					1				4
	25.87463	80.66163						2	2								4
	25.83022	80.66215							4								4
	26.00283	80.66757							2				2				4
	25.91350	80.67043							4								4
	25.80850	80.67862						1	3								4
	25.95485	80.68467						3	1								4
	25.99172	80.68468						1					3				4
	25.84703	80.68537							3				1				4
	25.89418	80.68707							4								4
	25.78890	80.69707							4								4
	25.82898	80.69897						1					3				4
	25.78228	80.70032							4								4

	Decimal Degrees		Species													Unidentified small herons	Colony Totals
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO		
	25.93338	80.70318							4								4
	25.86302	80.70407							4								4
	25.78722	80.72413						1	3								4
	25.82827	80.72650											4				4
	25.80173	80.72975											4				4
	25.77795	80.73262						2	2								4
	26.03797	80.73640		1				1			1		1				4
	25.86635	80.73848							4								4
	25.93897	80.74552							4								4
	26.11670	80.75240					4										4
	25.83603	80.75583						1	3								4
	25.85270	80.75745							4								4
	25.86578	80.76467							4								4
	25.90693	80.79410						2	2								4
	25.93760	80.79573							1		1		2				4
	25.84325	80.79823						3	1								4
	25.98090	80.80012						1	1				2				4
	25.97140	80.81353						3					1				4
	25.78973	80.83588						1	2				1				4
	26.02562	80.84500							3		1						4
	26.21150	80.39133						3									3
	25.82448	80.48852									1		2				3
	25.82417	80.48897									1		2				3
	25.81690	80.50558						1	2								3
	25.87442	80.52407		2				1									3
	25.88522	80.52847		1				1	1								3
	26.10847	80.63105						2					1				3
	25.93668	80.64997						1	2								3
	25.79287	80.68137						2	1								3
	25.77338	80.69993							3								3
	25.80457	80.70390							1				2				3
	25.84388	80.70423						1	2								3

	Decimal Degrees							Species+I352								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.87813	80.70903						2	1								3
	25.77665	80.71215						1	2								3
	25.85923	80.71343						1	2								3
	25.77768	80.71632						2	1								3
	26.03875	80.72248						3									3
	25.82302	80.72448						1	1				1				3
	25.78140	80.72475						1	2								3
	26.02398	80.73290						1	1		1						3
	25.96015	80.73395							1				2				3
	25.99358	80.74648						2					1				3
	26.08837	80.75423						2					1				3
	26.13368	80.75960					2						1				3
	25.89832	80.76955						1	2								3
	25.79348	80.77103							3								3
	25.91485	80.77900							2		1						3
	25.79820	80.78215						1	2								3
	25.77442	80.78957						3									3
	25.86378	80.80770					2						1				3
	26.03853	80.83287		3													3
	25.78985	80.83643							2				1				3
	26.05472	80.46523						2									2
	25.89433	80.50993						1					1				2
	26.06662	80.63825						2									2
	26.03892	80.63977							1				1				2
	26.05392	80.64193											2				2
	25.96497	80.64957						2									2
	25.83332	80.64992							2								2
	25.87433	80.65375						2									2
	25.97942	80.65440							2								2
	25.94903	80.65512						2									2
	25.96790	80.65603											2				2
	25.83520	80.65653						1	1								2

	Decimal Degrees							Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.94382	80.65795						1					1				2
	25.82788	80.66317							2								2
	25.83592	80.66372							2								2
	26.00773	80.66408											2				2
	25.82487	80.67103						1	1								2
	25.82197	80.67213						1	1								2
	26.06908	80.67258						2									2
	26.00958	80.67575						2									2
	25.97417	80.69760											2				2
	25.95225	80.70122							1				1				2
	25.79462	80.70165							2								2
	25.85430	80.70253							2								2
	25.88787	80.70593							2								2
	25.80642	80.71002							2								2
	25.79587	80.71030						1	1								2
	25.80448	80.71275						1	1								2
	25.80565	80.72002											2				2
	25.87853	80.72045							2								2
	25.91953	80.72382						1	1								2
	26.12730	80.72395					2										2
	25.89298	80.72533						1	1								2
	25.96272	80.72567						1	1								2
	25.99328	80.72600						2									2
	25.79358	80.72933						1	1								2
	25.78350	80.73165						1	1								2
	25.76893	80.73220						1	1								2
	26.00062	80.73290						1	1								2
	25.90713	80.73685							2								2
	25.99607	80.73950											2				2
	26.02292	80.74093						1			1						2
	26.03392	80.76120											2				2
	25.88425	80.76657						2									2

	Decimal Degrees							Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.91280	80.77362						2									2
	25.91387	80.77925							2								2
	25.90972	80.78090						1					1				2
	25.88713	80.78183						1	1								2
	25.79975	80.78333							1				1				2
	25.97398	80.78548									2						2
	25.80687	80.79062						1	1								2
	25.85870	80.79325						1	1								2
	25.76847	80.79915						2									2
	25.88728	80.80420						2									2
	25.87583	80.80657						1					1				2
	25.93108	80.80737						1					1				2
	25.78550	80.80817						2									2
	25.83807	80.81353						2									2
	25.87935	80.83055						2									2
	26.01013	80.83837						1			1						2
	26.06307	80.83873						1					1				2
	26.03413	80.85575						2									2
	26.20958	80.40165						1									1
	25.82788	80.49305							1								1
	26.01127	80.58238							1								1
	25.95222	80.62753											1				1
	25.91347	80.63803						1									1
	25.85492	80.64125						1									1
	26.09557	80.64132						1									1
	25.87550	80.64527						1									1
	25.93003	80.64648							1								1
	25.91175	80.65552						1									1
	25.98637	80.65562											1				1
	25.83208	80.65797							1								1
	26.03478	80.65845											1				1
	25.87140	80.65947						1									1

	Decimal Degrees							Species								Unidentified	Colony
Colony name	**Latitude**	**Longitude**	**WOST**	**GREG**	**WHIB**	**SNEG**	**TRHE**	**GBHE**	**ANHI**	**LBHE**	**BCNH**	**CAEG**	**GRHE**	**ROSP**	**DCCO**	**small herons**	**Totals**
	25.87350	80.66048						1									1
	25.97635	80.66230											1				1
	25.90652	80.66402											1				1
	25.94080	80.66417							1								1
	25.99340	80.66575						1									1
	25.98428	80.66618						1									1
	25.81733	80.66818						1									1
	25.91217	80.66952						1									1
	25.82567	80.67132						1									1
	25.82262	80.67195						1									1
	25.98548	80.67618						1									1
	25.81222	80.67668						1									1
	25.80205	80.67758		1													1
	25.81332	80.67895						1									1
	25.96517	80.68005						1									1
	25.79310	80.68085						1									1
	25.89643	80.68148						1									1
	25.85177	80.68447							1								1
	26.00495	80.68468											1				1
	25.83390	80.68638						1									1
	25.79562	80.68913						1									1
	26.00642	80.69027											1				1
	25.82648	80.69048						1									1
	25.82822	80.69075						1									1
	26.06148	80.69292						1									1
	25.77690	80.69340						1									1
	25.92940	80.69388							1								1
	25.77102	80.69453							1								1
	25.85483	80.69532											1				1
	25.78358	80.69533							1								1
	25.79668	80.69822						1									1
	25.99915	80.69972						1									1

	Decimal Degrees							Species							Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.77355	80.69997							1								1
	25.98943	80.70068											1				1
	25.82413	80.70090							1								1
	25.99745	80.70122						1									1
	25.89118	80.70190							1								1
	25.78112	80.70205							1								1
	25.80908	80.70247											1				1
	26.05937	80.70252						1									1
	25.81747	80.70402							1								1
	25.87882	80.70605											1				1
	25.81043	80.70638						1									1
	25.81043	80.70638						1									1
	25.80413	80.70882							1								1
	25.80757	80.70885							1								1
	25.85748	80.70915							1								1
	25.80887	80.71072						1									1
	25.80805	80.71138							1								1
	25.84377	80.71162							1								1
	25.77343	80.71247						1									1
	25.82303	80.71363						1									1
	25.88610	80.71420							1								1
	25.78360	80.71527						1									1
	25.79407	80.71818						1									1
	25.85763	80.72015							1								1
	25.99667	80.72022						1									1
	25.84153	80.72152							1								1
	25.85768	80.72170							1								1
	25.92003	80.72278						1									1
	25.83060	80.72283											1				1
	25.92112	80.72370						1									1
	25.79258	80.72407						1									1
	25.91250	80.72443							1								1

	Decimal Degrees							Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.88168	80.72475						1									1
	25.95392	80.72912						1									1
	25.79198	80.73133						1									1
	25.79053	80.73153						1									1
	25.79282	80.73247							1								1
	25.77957	80.73510															0
	26.03828	80.73613									1						1
	25.77897	80.74092						1									1
	25.93315	80.74302							1								1
	25.90727	80.74305							1								1
	25.80430	80.74455						1									1
	25.96852	80.74548						1									1
	25.80202	80.74617							1								1
	25.99425	80.74845						1									1
	25.96383	80.74883						1									1
	26.12402	80.75500					1										1
	25.86792	80.76182							1								1
	25.84895	80.76400						1									1
	26.05320	80.76427						1									1
	25.82825	80.76602						1									1
	25.86613	80.76630							1								1
	25.81850	80.77025							1								1
	25.94013	80.77080							1								1
	25.78783	80.77098						1									1
	25.79302	80.77192						1									1
	25.94912	80.77760						1									1
	25.91343	80.77927							1								1
	25.81958	80.77977						1									1
	25.96927	80.78092						1									1
	25.95912	80.78095							1								1
	25.85210	80.78173						1									1
	25.84942	80.78202							1								1

	Decimal Degrees							Species								Unidentified	Colony
Colony name	Latitude	Longitude	WOST	GREG	WHIB	SNEG	TRHE	GBHE	ANHI	LBHE	BCNH	CAEG	GRHE	ROSP	DCCO	small herons	Totals
	25.97213	80.78215		1													1
	25.91660	80.78583						1									1
	25.77553	80.79207						1									1
	25.87358	80.79818						1									1
	25.76935	80.79915						1									1
	25.78643	80.80565						1									1
	25.98172	80.80690						1									1
	25.85692	80.80845							1								1
	25.78688	80.82682						1									1
	25.78683	80.82703						1									1
	25.77573	80.83018						1									1
	25.78278	80.83108						1									1
	25.78883	80.83623						1									1
	25.78967	80.83650						1									1
	25.78960	80.83653						1									1
	25.78533	80.83677						1									1
	25.78755	80.83697						1									1
	26.00502	80.83863											1				1
Totals			320	4,808	4,624	740	1,234	520	2,172	509	271	525	293	47	25	648	16,736

Appendix 3. Locations and species composition of colonies and single nests found in WCA 3 and 2 during aerial and ground surveys conducted from January through July of 2000.

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N26 10.77	W80 31.72	Alley North	700	5		300		1,000	100	20,000		15	30			20	**22,150**
3A	N25 46.36	W80 50.24	Hidden	283					1,349	873	142						38	**2,647**
3B	N25 47.65	W80 31.85	Heron Alley				2	22		50	975						10	**1,049**
3A	N25 52.11	W80 50.61	Jetport	25		400											8	**425**
3A	N25 55.51	W80 50.10	Crossover	150		100											15	**250**
3A	N26 00.97	W80 27.61	Mud Canal	105	12			50	15	30					85		80	**212**
3A	N25 48.08	W80 29.40	3B Mud E	177	1			1		9							40	**188**
3A	N26 07.32	W80 32.50	Cypress City	138				9										**147**
3A	N26 02.75	W80 37.10	Big Melaluca	142														**142**
3A	N26 07.72	W80 42.10		140											7			**140**
3A	N26 02.103	W80 41.469		125	1												10	**126**
2B	N26 08.633	W80 22.916		70	1			3		2					90		25	**76**
3A	N26 06.11	W80 27.27	Holiday Park	50					20									**70**
3A	N25 57.880	W80 35.384	Donuthole	56	8												30	**64**
3A	N25 49.37	W80 51.79	Big Cypr col	60														**60**
3A	N26 08.613	W80 44.600		40	1			16									6	**57**
3A	N25 56.449	W80 37.338	Starter Mel.	38	16												20	**54**
3A	N26 01.48	W80 32.36		50	3												2	**53**
3A	N26 07.39	W80 39.29		38	13												2	**51**
3A	N26 07.469	W80 30.216		30	12												18	**42**
2A	N26 15.007	W80 19.611			1			25		15							9	**41**
3A	N26 00.970	W80 47.666						20		20								**40**
3A	N25 57.931	W80 49.222						35		2								**37**
3A	N25 58.186	W80 42.075		31	1					1							2	**33**
3A	N26 07.15	W80 43.98		32														**32**
2B	N26 09.848	W80 20.800		25				2		3					5		20	**30**
3A	N25 49.36	W80 40.72		29														**29**
3B	N25 48.87	W80 35.06		28														**28**
3A	N25 57.88	W80 49.10						26		2								**28**
3A	N26 08.44	W80 45.05		27														**27**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N26 09.58	W80 32.06		26														**26**
3B	N25 57.23	W80 28.46		25														**25**
3A	N25 59.040	W80 48.734						10		15								**25**
3A	N26 01.198	W80 48.546						15		10								**25**
3A	N26 00.92	W80 47.57						25										**25**
3A	N26 01.323	W80 43.947		23						1						1	1	**24**
3A	N26 05.800	W80 47.925		22						1							6	**23**
3A	N26 03.275	W80 45.395		7				10	2	4							2	**23**
3A	N26 07.97	W80 42.39		22														**22**
3A	N26 02.352	W80 48.596						10		12								**22**
3A	N26 02.060	W80 40.517					1	14		7								**22**
3B	N25 48.88	W80 36.14		21														**21**
3A	N25 49.159	W80 40.584		20	1												15	**21**
3B	N25 53.673	W80 30.260		20														**20**
3A	N26 06.84	W80 39.40		20														**20**
3A	N26 04.607	W80 37.867		20														**20**
3A	N25 57.98	W80 48.44						20										**20**
3A	N26 02.649	W80 43.371			1		2	12		4							4	**19**
3A	N26 06.616	W80 45.136	JW1	17	1													**18**
3A	N25 53.337	W80 48.273						10		8								**18**
3A	N26 05.530	W80 42.700						18										**18**
3A	N26 04.027	W80 47.574						2		15								**17**
2B	N26 11.247	W80 18.462		14	3												25	**17**
3B	N25 53.673	W80 30.883		13	3												2	**16**
3A	N25 52.44	W80 39.00		15														**15**
3A	N26 08.41	W80 47.14						15										**15**
3A	N26 08.41	W80 47.14						15										**15**
3A	N26 06.818	W80 39.132						15										**15**
3B	N25 51.895	W80 30.931		11	2					1							3	**14**
3A	N25 54.954	W80 37.832		11	3												12	**14**
3A	N25 52.730	W80 31.777		11	3												1	**14**
[illegible]	[illegible]	W80 47.398						4		10								**14**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3B	N25 50.929	W80 31.373		8	2		1			2							15	**13**
3A	N26 07.96	W80 39.70		13														**13**
3A	N26 06.845	W80 43.661		11			2											**13**
3A	N26 00.99	W80 47.67						13										**13**
3A	N26 06.47	W80 47.96		12														**12**
3A	N26 06.37	W80 29.89		12														**12**
3A	N25 52.486	W80 39.219		9	3												4	**12**
3A	N26 05.752	W80 39.666		8	1					3								**12**
3A	N25 59.175	W80 49.220						10		2								**12**
3A	N26 02.995	W80 46.922			1			8		3								**12**
3A	N26 07.646	W80 43.464								12								**12**
3A	N25 49.37	W80 38.30		11														**11**
3A	N26 02.332	W80 47.137						1		10								**11**
3A	N25 49.512	W80 38.432		2	5			1		1							7	**9**
3A	N26 05.510	W80 47.573		5	1		2					1					2	**9**
3A	N26 06.177	W80 43.226		3	2		3		1							1		**9**
3A	N26 06.765	W80 44.678		2	5			1		1								**9**
3A	N25 59.267	W80 42.402						7		2							2	**9**
3A	N25 46.272	W80 41.609		6	2												15	**8**
3A	N26 07.029	W80 45.146		4	2		2											**8**
3A	N26 02.736	W80 38.924					3	2		3							1	**8**
3A	N26 09.90	W80 32.21		7											9			**7**
3A	N26 02.015	W80 48.300						5		2								**7**
3A	N26 01.040	W80 47.837			2					5								**7**
3A	N26 04.968	W80 45.882								7								**7**
3A	N25 57.894	W80 44.259			1			3		2		1					1	**7**
3B	N25 55.40	W80 31.14		6														**6**
3B	N25 53.992	W80 31.858		5	1													**6**
3A	N26 05.764	W80 39.594		3	2					1							3	**6**
3A	N26 06.769	W80 45.365		2	1		2			1								**6**
3A	N26 06.66	W80 49.91						6										**6**
3A	N26 05.91	W80 46.03						6										**6**
3A	N26 02.070	W80 45.605							1	5								**6**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3B	N25 50.88	W80 34.57		5														5
3B	N25 52.512	W80 30.056			5													5
3A	N25 54.878	W80 47.451			5												8	5
3A	N25 54.855	W80 47.447			5												4	5
3A	N25 58.676	W80 44.514			1			2		2							3	5
3B	N25 46.441	W80 37.021		1	2			1									6	4
3B	N25 52.264	W80 30.284		1	3													4
3B	N25 50.386	W80 31.864			4												4	4
3A	N26 07.195	W80 39.218		1	3													4
3A	N26 03.637	W80 48.218						2		2								4
3A	N25 47.704	W80 41.340			4													4
3A	N25 49.415	W80 39.231					4											4
3B	N25 46.784	W80 36.751			3												1	3
3B	N25 46.644	W80 35.536			3													3
3A	N26 06.845	W80 43.661		1			2											3
3A	N26 01.686	W80 48.757					3											3
3A	N26 05.957	W80 47.819			2		1											3
3A	N25 54.867	W80 46.410			3												8	3
3A	N25 58.833	W80 45.631			3												1	3
3A	N25 49.860	W80 45.216			3													3
3A	N25 57.350	W80 45.157			3												4	3
3A	N26 08.092	W80 44.244						1		2								3
3A	N25 46.764	W80 43.712			3												3	3
3A	N26 07.722	W80 42.952			1		2											3
3A	N25 46.400	W80 42.711			3												2	3
3A	N25 51.788	W80 42.315			3												5	3
3A	N26 04.474	W80 41.545								3								3
3A	N25 58.313	W80 40.867			3												4	3
3A	N25 48.108	W80 40.800			3													3
3A	N26 03.049	W80 40.605			1			2									2	3
3A	N25 49.855	W80 39.689			3													3
[illegible]	[illegible]	W80 30.00		2														2
	[illegible]	[illegible]			[illegible]													[illegible]

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 49.332	W80 46.214															4	**0**
3A	N25 54.677	W80 46.148															1	**0**
3A	N25 49.289	W80 46.081															1	**0**
3A	N25 48.140	W80 46.070														1	3	**0**
3A	N25 59.197	W80 45.734															1	**0**
3A	N25 55.995	W80 45.501														3		**0**
3A	N25 55.084	W80 45.258															1	**0**
3A	N25 48.115	W80 45.136															2	**0**
3A	N25 54.634	W80 44.805															1	**0**
3A	N25 56.387	W80 44.758															1	**0**
3A	N25 51.489	W80 44.629															2	**0**
3A	N25 56.712	W80 44.613															1	**0**
3A	N25 54.413	W80 44.566															1	**0**
3A	N25 56.376	W80 44.514															1	**0**
3A	N25 51.530	W80 44.455															1	**0**
3A	N25 55.901	W80 44.379															1	**0**
3A	N25 51.968	W80 44.326															1	**0**
3A	N25 52.488	W80 44.130															1	**0**
3A	N26 05.394	W80 44.045															1	**0**
3A	N25 47.043	W80 43.882															1	**0**
3A	N25 46.363	W80 43.862															1	**0**
3A	N25 53.821	W80 43.800															2	**0**
3A	N25 54.525	W80 43.772															1	**0**
3A	N25 48.795	W80 43.742															2	**0**
3A	N25 48.861	W80 43.706															1	**0**
3A	N25 57.788	W80 43.548															3	**0**
3A	N25 53.549	W80 43.526															1	**0**
3A	N25 50.577	W80 43.415															1	**0**
3A	N25 54.930	W80 43.389															2	**0**
3A	N25 48.551	W80 43.374															1	**0**
3A	N25 51.361	W80 43.367															1	**0**
3A	N25 49.407	W80 43.333															4	**0**
3A	N25 49.393	W80 43.272															6	**0**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 47.594	W80 43.092															2	0
3A	N25 52.700	W80 42.714															1	0
3A	N25 47.848	W80 42.651															1	0
3A	N25 47.830	W80 42.644															1	0
3A	N25 52.832	W80 42.614															1	0
3A	N25 51.483	W80 42.580															3	0
3A	N25 47.914	W80 42.578															1	0
3A	N25 48.668	W80 42.538															1	0
3A	N25 46.598	W80 42.505															1	0
3A	N25 48.678	W80 42.501															1	0
3A	N25 51.108	W80 42.454															2	0
3A	N25 48.790	W80 42.384															1	0
3A	N25 52.668	W80 42.376															1	0
3A	N25 53.250	W80 42.349															1	0
3A	N25 53.255	W80 42.346															1	0
3A	N25 52.787	W80 42.344															1	0
3A	N25 52.758	W80 42.337															1	0
3A	N25 51.041	W80 42.313															1	0
3A	N25 51.005	W80 42.292															1	0
3A	N25 48.412	W80 42.258															1	0
3A	N25 54.495	W80 42.254															1	0
3A	N25 48.259	W80 42.230															1	0
3A	N25 48.294	W80 42.220															3	0
3A	N25 46.846	W80 42.200															1	0
3A	N25 51.254	W80 42.199															2	0
3A	N25 48.353	W80 42.194															1	0
3A	N25 50.803	W80 42.184															1	0
3A	N25 50.783	W80 42.178															2	0
3A	N25 48.360	W80 42.173															1	0
3A	N25 46.839	W80 42.104															1	0
3A	N25 47.678	W80 42.082															1	0
3A	N25 50.264	W80 42.054															1	0
																	1	0

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 46.511	W80 42.005															1	**0**
3A	N25 46.409	W80 41.998															1	**0**
3A	N25 46.536	W80 41.995															1	**0**
3A	N25 57.110	W80 41.994															1	**0**
3A	N25 46.647	W80 41.936															1	**0**
3A	N25 47.302	W80 41.836															5	**0**
3A	N25 47.340	W80 41.813															5	**0**
3A	N25 58.132	W80 41.750															2	**0**
3A	N25 52.673	W80 41.640															1	**0**
3A	N25 55.770	W80 41.625															1	**0**
3A	N25 55.885	W80 41.365															1	**0**
3A	N25 46.028	W80 41.325															1	**0**
3A	N25 48.691	W80 41.319															1	**0**
3A	N25 49.520	W80 41.288															1	**0**
3A	N25 48.387	W80 41.279															1	**0**
3A	N25 55.824	W80 41.275															1	**0**
3A	N25 48.918	W80 41.258															1	**0**
3A	N25 55.723	W80 41.194															2	**0**
3A	N25 50.136	W80 41.176															1	**0**
3A	N25 49.734	W80 41.136															2	**0**
3A	N25 50.824	W80 41.116															1	**0**
3A	N25 51.108	W80 41.076															1	**0**
3A	N25 53.789	W80 40.880															1	**0**
3A	N25 56.416	W80 40.869															1	**0**
3A	N25 47.489	W80 40.690															1	**0**
3A	N25 50.769	W80 40.681															1	**0**
3A	N25 48.503	W80 40.662															1	**0**
3A	N25 48.268	W80 40.644															2	**0**
3A	N25 49.406	W80 40.632															1	**0**
3A	N25 48.731	W80 40.592															1	**0**
3A	N25 55.920	W80 40.574															2	**0**
3A	N25 48.571	W80 40.54															1	**0**
3A	N25 49.392	W80 40.399															1	**0**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 56.595	W80 40.385															1	**0**
3A	N25 49.000	W80 40.361															3	**0**
3A	N25 49.150	W80 40.318															9	**0**
3A	N25 49.135	W80 40.282															4	**0**
3A	N25 49.135	W80 40.264															1	**0**
3A	N25 54.233	W80 40.203															2	**0**
3A	N25 51.022	W80 40.041															1	**0**
3A	N25 50.135	W80 39.995															1	**0**
3A	N25 54.776	W80 39.962															1	**0**
3A	N25 56.459	W80 39.854															2	**0**
3A	N25 53.897	W80 39.819															1	**0**
3A	N25 49.714	W80 39.801															1	**0**
3A	N25 49.756	W80 39.792															1	**0**
3A	N25 52.136	W80 39.675															2	**0**
3A	N25 54.478	W80 39.655															1	**0**
3A	N25 56.637	W80 39.463															2	**0**
3A	N25 48.708	W80 39.435															2	**0**
3A	N25 59.185	W80 39.334															1	**0**
3A	N25 58.772	W80 39.304															3	**0**
3A	N25 57.900	W80 38.947															3	**0**
3A	N25 57.432	W80 38.840															2	**0**
3A	N25 51.326	W80 38.546															1	**0**
3A	N25 54.665	W80 38.521															1	**0**
3A	N25 53.002	W80 38.233															1	**0**
3A	N26 05.319	W80 29.681															1	**0**
2B	N26 08.344	W80 23.364															8	**0**
2A	N26 18.368	W80 24.827															1	**0**
			TOTALS	**3,059**	**530**	**500**	**339**	**475**	**2,388**	**1,278**	**21,117**	**2**	**15**	**30**	**243**	**7**	**1,092**	**29,733**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL

Appendix 4. Locations and species composition of colonies and single nests found in WCA's 2 and 3 during aerial and ground surveys conducted from January through July of 2001.

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N26 10.77	W80 31.72	Alley North	1,400			100	50	750				4			2,304
Pocket	N25 58.50	W80 31.63	Pocket								2,265					2,265
2B	N26 09.78	W80 20.74	2B Melaleuca	650	5	50	25	53	150	40	800	50	10		35	1,833
3A	N25 46.36	W80 50.24	Hidden	200					600	800					67	1,600
3A	N26 07.32	W80 32.50	Cypress City	200				20		25	800	30		200		1,075
3A	N25 57.88	W80 34.48	L67	180	2			2		50	600	20			9	854
3A	N25 55.51	W80 50.10	Crossover	55		400										455
3A	N25 52.00	W80 48.20	Big Pond	5				40	100	65	55				20	265
3A	N26 01.48	W80 32.36	Donut	150	1			20		15	20	6			50	212
3A	N25 52.14	W80 48.37						140	10	5						155
3A	N26 00.97	W80 27.61	Mud Canal	150												150
3B	N25 48.08	W80 29.40	3B Mud East	150												150
3A	N26 01.83	W80 41.29		110										24		110
3A	N25 55.07	W80 37.93		100	5										35	105
3A	N25 56.70	W80 39.55							80							80
3A	N25 56.41	W80 37.25	Starter Mel	70	10										25	80
3B	N25 53.27	W80 33.67		80												80
3A	N25 52.44	W80 39.00		75	5										40	80
3A	N25 52.26	W80 48.12						30	45	4						79
3A	N26 06.11	W80 27.27	Holiday Park	75												75
3A	N25 49.18	W80 40.66		65	1										20	66
3A	N25 55.48	W80 46.80						50		4						54
3A	N25 52.04	W80 48.10						35	10	7						52
3A	N26 06.37	W80 29.89		50												50
3A	N26 02.75	W80 37.10	Big Mel	50												50
3A	N26 00.43	W80 35.70		45												45
3A	N25 52.22	W80 48.39							45							45
3A	N25 53.34	W80 48.26						22	15	3						40
[illegible]	[illegible]	W80 48.31							35							35

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3B	N25 46.624	W80 35.554			2													2
3B	N25 47.035	W80 35.312			2													2
3B	N25 46.692	W80 33.866			2												2	2
3B	N25 49.984	W80 33.647			2													2
3B	N25 46.504	W80 31.797			2													2
3B	N25 47.186	W80 31.772			2													2
3B	N25 46.908	W80 31.746			2												1	2
3B	N25 49.435	W80 31.194			2													2
3A	N26 07.074	W80 44.591		1	1													2
3A	N25 50.259	W80 49.110			2												4	2
3A	N25 59.162	W80 48.185								2								2
3A	N25 55.838	W80 47.974			2												3	2
3A	N26 07.969	W80 47.929					2										1	2
3A	N25 50.576	W80 47.608			2												3	2
3A	N25 55.600	W80 47.603			2													2
3A	N25 51.505	W80 47.586			2												3	2
3A	N25 46.656	W80 47.047			2													2
3A	N25 59.504	W80 46.463			2												1	2
3A	N25 57.370	W80 46.370			2													2
3A	N26 02.182	W80 45.720			1					1								2
3A	N25 56.654	W80 45.653			2												2	2
3A	N25 46.868	W80 45.623			2													2
3A	N25 46.683	W80 45.247			2													2
3A	N25 46.691	W80 45.237			2													2
3A	N25 56.610	W80 44.924			2													2
3A	N25 59.608	W80 44.727			2													2
3A	N25 54.829	W80 44.059			2												8	2
3A	N25 46.658	W80 43.980			2													2
3A	N25 57.068	W80 43.748			2											1	4	2
3A	N25 55.270	W80 43.446			2												3	2
3A	N25 49.389	W80 43.308			2												8	2
3A	N25 48.597	W80 43.302			1		1											2
3A	N25 48.614	W80 43.257			2													2

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 49.413	W80 42.806			2													2
3A	N25 46.643	W80 42.635			2												5	2
3A	N25 52.679	W80 42.556			2													2
3A	N25 49.207	W80 42.407			2													2
3A	N25 53.160	W80 42.114			2												1	2
3A	N25 53.168	W80 42.081			2												3	2
3A	N25 47.733	W80 41.333			2													2
3A	N25 55.723	W80 41.242			2												4	2
3A	N25 50.123	W80 41.130			2												1	2
3A	N25 57.278	W80 41.115			2												3	2
3A	N25 53.576	W80 40.602			2													2
3A	N25 49.362	W80 40.323			2												4	2
3A	N25 49.376	W80 40.298			2												2	2
3A	N25 59.276	W80 40.292			2													2
3A	N25 51.825	W80 39.811			2												4	2
3A	N25 51.830	W80 39.763			2												3	2
3A	N26 03.329	W80 38.601					1			1								2
3A	N26 02.340	W80 38.371			1		1											2
3A	N26 00.867	W80 37.830			1					1							12	2
3A	N25 53.963	W80 37.780			2													2
3A	N25 58.515	W80 37.573			2													2
3B	N25 52.491	W80 31.441		1														1
3B	N25 47.844	W80 38.757								1								1
3B	N25 46.399	W80 38.587			1													1
3B	N25 47.187	W80 38.246			1													1
3B	N25 46.961	W80 36.540			1													1
3B	N25 47.104	W80 36.261			1													1
3B	N25 46.022	W80 36.172			1													1
3B	N25 46.295	W80 35.415			1													1
3B	N25 47.359	W80 35.184			1												1	1
3B	N25 47.193	W80 35.164			1													1
3B	N25 46.295	W80 35.011			1													1
[illegible]	[illegible]	[illegible]			[illegible]													1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3B	N25 46.748	W80 34.381			1													1
3B	N25 47.198	W80 34.215			1													1
3B	N25 47.096	W80 34.140			1													1
3B	N25 46.665	W80 34.134			1													1
3B	N25 46.635	W80 34.124			1												1	1
3B	N25 50.208	W80 33.025			1													1
3B	N25 49.983	W80 32.994			1													1
3B	N25 46.219	W80 32.525			1												1	1
3B	N25 49.011	W80 32.449			1												1	1
3B	N25 49.003	W80 32.416			1												1	1
3B	N25 54.121	W80 32.084			1													1
3B	N25 46.723	W80 31.789			1													1
3B	N25 46.766	W80 31.781			1													1
3B	N25 47.147	W80 31.766			1												2	1
3B	N25 46.194	W80 31.760			1													1
3B	N25 53.137	W80 31.700			1													1
3B	N25 53.275	W80 31.639			1													1
3B	N25 48.742	W80 31.311			1													1
3B	N25 49.430	W80 31.182			1													1
3B	N25 50.471	W80 31.128			1													1
3B	N25 53.680	W80 30.600			1													1
3B	N25 49.952	W80 30.260			1												6	1
3B	N25 49.202	W80 30.102			1													1
3A	N25 46.529	W80 49.635			1													1
3A	N25 46.219	W80 49.346			1												2	1
3A	N25 53.149	W80 48.685			1													1
3A	N25 57.480	W80 48.593			1													1
3A	N25 46.850	W80 48.513			1													1
3A	N25 58.909	W80 48.416			1													1
3A	N25 52.549	W80 48.387			1													1
3A	N25 47.178	W80 48.358			1													1
3A	N25 53.241	W80 48.270			1													1
3A	N25 53.096	W80 48.200			1													1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 58.360	W80 48.144			1													1
3A	N25 52.270	W80 48.110								1								1
3A	N25 51.367	W80 48.043			1													1
3A	N25 58.820	W80 47.932			1													1
3A	N25 50.597	W80 47.907			1												2	1
3A	N25 46.179	W80 47.899			1													1
3A	N25 53.059	W80 47.844			1													1
3A	N25 52.358	W80 47.829			1													1
3A	N25 46.150	W80 47.801			1													1
3A	N25 45.967	W80 47.797			1													1
3A	N25 46.557	W80 47.774			1												4	1
3A	N25 54.703	W80 47.567			1													1
3A	N25 52.456	W80 47.478			1													1
3A	N25 52.459	W80 47.471			1												1	1
3A	N25 51.895	W80 47.471			1													1
3A	N25 46.307	W80 47.463			1													1
3A	N25 48.437	W80 47.421			1													1
3A	N25 54.669	W80 47.415			1												1	1
3A	N25 55.506	W80 47.398			1													1
3A	N25 54.960	W80 47.157			1													1
3A	N25 50.450	W80 47.134			1													1
3A	N25 46.677	W80 47.010			1													1
3A	N25 47.902	W80 46.968			1												3	1
3A	N25 51.115	W80 46.905			1													1
3A	N25 51.694	W80 46.793			1												2	1
3A	N25 49.163	W80 46.789			1													1
3A	N25 51.210	W80 46.734			1													1
3A	N25 47.442	W80 46.723			1													1
3A	N25 57.475	W80 46.660			1												1	1
3A	N25 56.903	W80 46.658			1													1
3A	N25 51.282	W80 46.654			1													1
3A	N25 57.540	W80 46.636			1													1
																	4	1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 46.945	W80 46.530			1													**1**
3A	N25 54.810	W80 46.402			1													**1**
3A	N25 57.476	W80 46.365			1												6	**1**
3A	N25 47.288	W80 46.332			1													**1**
3A	N25 57.869	W80 46.310			1													**1**
3A	N25 46.558	W80 46.220			1													**1**
3A	N25 47.454	W80 46.217			1													**1**
3A	N25 47.783	W80 46.211			1													**1**
3A	N25 53.941	W80 46.205			1												2	**1**
3A	N25 48.099	W80 46.162			1													**1**
3A	N25 58.438	W80 46.036								1								**1**
3A	N25 54.332	W80 46.003			1													**1**
3A	N25 56.333	W80 45.915			1												1	**1**
3A	N25 51.972	W80 45.852			1												1	**1**
3A	N25 47.615	W80 45.779			1													**1**
3A	N25 46.634	W80 45.737			1													**1**
3A	N25 47.196	W80 45.638			1													**1**
3A	N25 47.673	W80 45.620			1													**1**
3A	N25 46.914	W80 45.540			1												1	**1**
3A	N26 02.086	W80 45.528			1													**1**
3A	N25 56.898	W80 45.507			1												3	**1**
3A	N25 47.172	W80 45.474			1													**1**
3A	N25 49.840	W80 45.393			1												1	**1**
3A	N25 46.626	W80 45.355			1													**1**
3A	N25 55.760	W80 45.349			1													**1**
3A	N25 46.698	W80 45.321			1													**1**
3A	N25 50.147	W80 45.319			1												2	**1**
3A	N25 53.740	W80 45.281			1												2	**1**
3A	N25 54.277	W80 45.279			1													**1**
3A	N25 57.850	W80 45.231			1												1	**1**
3A	N25 47.880	W80 45.148			1													**1**
3A	N26 06.766	W80 45.113			1													**1**
3A	N25 57.175	W80 45.062			1													**1**

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 51.853	W80 44.987			1												2	1
3A	N25 50.837	W80 44.976			1												2	1
3A	N25 56.611	W80 44.918			1													1
3A	N25 52.041	W80 44.869			1												1	1
3A	N25 56.492	W80 44.847			1												2	1
3A	N25 54.866	W80 44.756			1													1
3A	N25 59.610	W80 44.730			1													1
3A	N25 46.652	W80 44.695			1													1
3A	N25 58.141	W80 44.667			1												3	1
3A	N25 46.736	W80 44.527			1												2	1
3A	N25 57.958	W80 44.508			1												4	1
3A	N26 03.184	W80 44.502								1								1
3A	N25 46.749	W80 44.440			1													1
3A	N25 54.060	W80 44.316			1												5	1
3A	N25 53.665	W80 44.261			1												7	1
3A	N26 07.639	W80 44.168								1								1
3A	N26 05.412	W80 44.168			1													1
3A	N26 05.558	W80 44.165			1													1
3A	N26 02.317	W80 44.165			1												2	1
3A	N25 56.265	W80 44.145			1												7	1
3A	N25 55.018	W80 43.971			1												3	1
3A	N25 56.617	W80 43.954			1												6	1
3A	N26 07.165	W80 43.935					1											1
3A	N25 47.790	W80 43.889			1													1
3A	N25 46.287	W80 43.800			1													1
3A	N25 47.602	W80 43.760			1												1	1
3A	N26 04.450	W80 43.756			1												1	1
3A	N25 52.462	W80 43.752			1													1
3A	N26 00.044	W80 43.727			1													1
3A	N26 01.395	W80 43.718			1													1
3A	N25 46.355	W80 43.679			1													1
	[illegible]	W80 43.512			1													1
																	1	1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 47.543	W80 43.438			1													1
3A	N25 55.175	W80 43.434			1												1	1
3A	N25 58.460	W80 43.385			1													1
3A	N26 02.364	W80 43.357			1												1	1
3A	N25 59.731	W80 43.283			1												1	1
3A	N25 52.734	W80 43.271			1												1	1
3A	N25 49.570	W80 43.039			1													1
3A	N25 49.567	W80 43.017			1													1
3A	N25 59.343	W80 43.012			1												2	1
3A	N25 46.653	W80 42.995			1													1
3A	N25 46.635	W80 42.977			1													1
3A	N25 47.007	W80 42.899			1													1
3A	N25 46.143	W80 42.825			1													1
3A	N25 53.763	W80 42.809			1													1
3A	N25 48.901	W80 42.789			1													1
3A	N25 55.911	W80 42.785			1												6	1
3A	N25 48.256	W80 42.770			1													1
3A	N25 46.605	W80 42.708			1													1
3A	N25 47.794	W80 42.657			1												1	1
3A	N25 47.809	W80 42.655			1												1	1
3A	N25 54.222	W80 42.580			1													1
3A	N25 48.312	W80 42.544			1												8	1
3A	N25 48.310	W80 42.531			1												5	1
3A	N25 48.471	W80 42.524			1													1
3A	N25 48.652	W80 42.506			1												3	1
3A	N25 48.614	W80 42.491			1												4	1
3A	N25 54.226	W80 42.487			1												2	1
3A	N25 56.377	W80 42.475			1												2	1
3A	N25 51.575	W80 42.411			1													1
3A	N25 47.858	W80 42.393			1												1	1
3A	N25 51.812	W80 42.332			1												8	1
3A	N25 52.618	W80 42.318			1													1
3A	N25 52.651	W80 42.315			1													1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 54.486	W80 42.257			1												3	1
3A	N25 53.831	W80 42.254			1												1	1
3A	N25 53.823	W80 42.245			1												1	1
3A	N25 46.906	W80 42.141			1													1
3A	N25 46.756	W80 42.128			1												5	1
3A	N25 53.302	W80 42.104			1												2	1
3A	N26 06.582	W80 42.017			1													1
3A	N25 55.954	W80 41.931			1													1
3A	N25 47.804	W80 41.930			1													1
3A	N25 47.812	W80 41.929			1													1
3A	N25 57.082	W80 41.582			1												2	1
3A	N25 49.690	W80 41.448			1													1
3A	N25 48.702	W80 41.313			1													1
3A	N25 47.476	W80 41.311			1													1
3A	N25 48.674	W80 41.233			1												1	1
3A	N25 48.200	W80 41.222			1													1
3A	N25 50.032	W80 41.204			1												1	1
3A	N25 47.750	W80 41.110			1												1	1
3A	N25 57.902	W80 40.798			1												1	1
3A	N25 55.783	W80 40.790			1												1	1
3A	N25 53.581	W80 40.603			1												1	1
3A	N25 48.849	W80 40.578			1													1
3A	N26 04.273	W80 40.572								1								1
3A	N25 49.694	W80 40.539			1												4	1
3A	N26 04.468	W80 40.480					1											1
3A	N25 56.710	W80 40.446			1												2	1
3A	N25 49.483	W80 40.377			1													1
3A	N25 48.817	W80 40.265			1													1
3A	N25 48.836	W80 40.253			1												2	1
3A	N25 49.027	W80 40.140			1												2	1
3A	N25 49.028	W80 40.132			1												3	1
3A	N25 53.613	W80 40.088			1												4	1
					1												3	1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3A	N25 53.547	W80 40.052			1												2	1
3A	N25 55.060	W80 40.045			1												3	1
3A	N25 59.048	W80 39.997			1												1	1
3A	N25 53.110	W80 39.980			1												3	1
3A	N25 49.825	W80 39.974			1												1	1
3A	N25 53.151	W80 39.958			1												2	1
3A	N25 53.701	W80 39.769			1												2	1
3A	N25 51.831	W80 39.758			1													1
3A	N25 51.811	W80 39.725			1													1
3A	N25 54.813	W80 39.680			1												4	1
3A	N25 52.517	W80 39.640			1												2	1
3A	N25 52.089	W80 39.625			1													1
3A	N25 52.528	W80 39.617			1												5	1
3A	N25 52.297	W80 39.578			1													1
3A	N25 52.326	W80 39.558			1													1
3A	N25 58.183	W80 39.478			1													1
3A	N25 52.420	W80 39.478			1													1
3A	N25 58.058	W80 39.384			1												1	1
3A	N25 54.698	W80 39.366			1													1
3A	N25 56.959	W80 39.334			1												1	1
3A	N26 04.191	W80 38.709			1													1
3A	N25 52.521	W80 38.681			1													1
3A	N25 56.291	W80 38.592			1												1	1
3A	N25 56.296	W80 38.572			1												1	1
3A	N25 51.306	W80 38.464			1												1	1
3A	N26 05.685	W80 38.445			1													1
3A	N25 54.792	W80 38.295			1												1	1
3A	N26 05.596	W80 37.615			1													1
3A	N26 05.596	W80 37.580			1													1
3A	N25 55.015	W80 35.917			1												5	1
3A	N26 00.245	W80 35.739			1												3	1
3A	N26 05.676	W80 28.284			1													1
2A	N26 17.326	W80 20.212			1													1

Area	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	YCNH	ROSP	GLIB	CAEG	DCCO	ANHI	TOTAL
3B	N25 45.851	W80 33.716															2	**0**
3B	N25 46.759	W80 33.715															1	**0**
3B	N25 46.234	W80 33.713															1	**0**
3B	N25 46.691	W80 33.712															1	**0**
3B	N25 46.668	W80 33.711															1	**0**
3B	N25 45.842	W80 33.701															6	**0**
3B	N25 47.859	W80 32.995															1	**0**
3B	N25 47.830	W80 32.542															1	**0**
3B	N25 46.485	W80 31.802															1	**0**
3B	N25 46.675	W80 31.781															1	**0**
3B	N25 46.228	W80 31.780															1	**0**
3B	N25 46.004	W80 31.775															1	**0**
3B	N25 46.146	W80 31.767															1	**0**
3B	N25 51.895	W80 30.931																**0**
3B	N25 49.182	W80 30.304																**0**
3B	N25 50.424	W80 30.201															1	**0**
3A	N25 45.959	W80 48.885															1	**0**
3A	N25 47.814	W80 48.431															4	**0**
3A	N25 51.146	W80 48.406															2	**0**
3A	N25 52.142	W80 48.366															1	**0**
3A	N25 48.003	W80 48.219															1	**0**
3A	N25 58.826	W80 48.028															1	**0**
3A	N25 53.306	W80 48.026															1	**0**
3A	N25 52.00	W80 48.00													47			**0**
3A	N25 47.711	W80 47.461															1	**0**
3A	N25 47.987	W80 47.030															1	**0**
3A	N25 50.457	W80 46.959															1	**0**
3A	N25 55.528	W80 46.789															1	**0**
3A	N25 54.914	W80 46.733															1	**0**
3A	N25 56.956	W80 46.656															1	**0**
3A	N25 53.640	W80 46.448															8	**0**
3A	N25 49.002	W80 46.346															5	**0**
3A	N25 56.460	W80 46.247															1	**0**

Unit	**Latitude**	**Longitude**	**Colony**	**GREG**	**GBHE**	**WOST**	**BCNH**	**LBHE**	**SNEG**	**TRHE**	**WHIB**	**GLIB**	**ROSP**	**CAEG**	**ANHI**	**Colony Total***
2A	N26 20.50	W80 20.07		34												34
3A	N25 57.23	W80 28.46		33												33
3A	N26 14.03	W80 36.33		30												30
3A	N25 53.48	W80 48.18							30							30
3A	N26 0.136	W80 43.74						27								27
3A	N26 07.33	W80 30.20		26												26
3A	N25 58.68	W80 44.51						18	2	5					4	25
3B	N25 48.88	W80 36.14		23												23
3A	N25 57.91	W80 44.26						18	2	2					4	22
2B	N26 11.31	W80 18.43		20												20
3A	N26 00.98	W80 47.66						20								20
3A	N25 54.04	W80 31.66		20												20
3A	N26 03.00	W80 46.92						15		3						18
3B	N25 50.76	W80 31.22		15												15
3A	N26 3.219	W80 44.50					4	4		4					6	12
3A	N25 58.27	W80 45.76		12												12
3B	N25 51.98	W80 30.81		12												12
3B	N25 50.81	W80 31.85		12												12
3A	N25 55.09	W80 46.41						7		4						11
3A	N25 46.28	W80 41.61		10	1										30	11
3A	N25 52.06	W80 48.30							10							10
3A	N25 51.04	W80 40.36		6	4										4	10
3B	N25 50.80	W80 31.65		9												9
2A	N26 15.00	W80 19.55		8												8
3B	N25 53.52	W80 30.99		8												8
3A	N25 53.30	W80 46.24					6			2					1	8
3A	N25 57.48	W80 43.35					6			1						7
3B	N25 53.73	W80 30.65		7												7
3A	N25 50.96	W80 46.92						7								7
3A	N26 16.25	W80 31.11		5												5
3A	N26 04.58	W80 37.73		5												5
3A	N26 2.217	W80 47.40								5						5

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 53.31	W80 42.03			1			4							5	5
	N25 52.00	W80 30.00		5												5
3B	N25 47.65	W80 31.85	Heron Alley	5												5
2B	N26 08.70	W80 23.01			3										13	3
3A	N25 57.66	W80 28.78		3											2	3
3A	N25 57.62	W80 44.03						1		2						3
3A	N25 52.69	W80 42.55			3											3
3A	N25 47.83	W80 45.58			3										1	3
3A	N25 47.75	W80 41.33			3										1	3
3A	N25 47.02	W80 45.57			3											3
3A	N25 46.89	W80 41.34			3											3
3A	N25 46.29	W80 43.82			3										4	3
3A	N26 02.07	W80 45.60						1		1						2
3A	N25 57.28	W80 41.07			2											2
3A	N25 53.84	W80 42.28			2										1	2
3A	N25 53.62	W80 46.46					1			1					1	2
3A	N25 53.58	W80 40.56			2										6	2
3A	N25 53.18	W80 42.11			2										9	2
3A	N25 52.63	W80 45.32								2					2	2
3A	N25 51.30	W80 40.88			2										6	2
3A	N25 49.65	W80 40.55			2											2
3A	N25 49.59	W80 40.14			2											2
3A	N25 49.35	W80 40.28			2										5	2
3A	N25 48.66	W80 42.51			2										1	2
3A	N25 48.41	W80 47.44			2											2
3A	N25 47.48	W80 46.73			2										1	2
3A	N25 47.45	W80 46.74			2											2
3A	N25 47.20	W80 45.40			2											2
3A	N25 47.16	W80 48.36			2										1	2
3A	N25 47.08	W80 43.65			2											2
3A	N25 46.89	W80 45.66			2											2
															5	2

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 46.77	W80 42.88			2										1	2
3A	N25 46.74	W80 47.93			2										2	2
3A	N25 46.66	W80 42.61			2										4	2
3A	N25 46.65	W80 41.62			2										11	2
3A	N25 46.62	W80 42.69			2											2
3A	N25 46.54	W80 46.24			2											2
3A	N25 46.35	W80 43.68			2											2
3A	N26 3.324	W80 27.86			1											1
3A	N26 3.292	W80 27.97			1											1
3A	N26 00.84	W80 38.01			1										2	1
3A	N25 59.28	W80 40.28			1											1
3A	N25 56.58	W80 40.00			1										1	1
3A	N25 56.41	W80 44.86			1										1	1
3A	N25 56.40	W80 40.86			1										4	1
3A	N25 56.26	W80 44.20			1											1
3A	N25 55.99	W80 42.85			1										5	1
3A	N25 55.96	W80 45.70			1											1
3A	N25 55.82	W80 40.77			1											1
3A	N25 55.82	W80 42.79			1										1	1
3A	N25 55.68	W80 39.21			1											1
3A	N25 55.25	W80 43.40			1										3	1
3A	N25 54.96	W80 45.42			1											1
3A	N25 54.88	W80 46.45			1										7	1
3A	N25 54.84	W80 44.06			1											1
3A	N25 54.77	W80 40.10			1											1
3A	N25 54.76	W80 40.13			1											1
3A	N25 54.48	W80 42.24			1										2	1
3A	N25 54.32	W80 40.74			1											1
3A	N25 53.77	W80 42.81			1											1
3A	N25 53.16	W80 39.99			1										2	1
3A	N25 52.81	W80 42.31			1											1
3A	N25 52.64	W80 42.34			1										2	1

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 52.51	W80 38.72			1											1
3A	N25 52.47	W80 44.11			1											1
3A	N25 51.60	W80 42.46			1											1
3A	N25 50.90	W80 42.86			1											1
3A	N25 50.77	W80 42.18			1										3	1
3A	N25 50.76	W80 40.68			1										3	1
3A	N25 50.45	W80 47.14			1											1
3A	N25 50.12	W80 41.13			1										4	1
3A	N25 49.97	W80 39.41			1											1
3A	N25 49.62	W80 40.09			1										1	1
3A	N25 49.54	W80 40.30			1											1
3A	N25 49.45	W80 42.06			1										2	1
3A	N25 49.42	W80 43.30			1										5	1
3A	N25 49.40	W80 42.80			1											1
3A	N25 49.22	W80 42.44			1											1
3A	N25 49.18	W80 41.40			1											1
3A	N25 49.14	W80 40.32			1										2	1
3A	N25 49.06	W80 40.14			1										2	1
3A	N25 49.02	W80 40.27			1											1
3A	N25 48.99	W80 40.36			1										3	1
3A	N25 48.87	W80 43.66			1											1
3A	N25 48.74	W80 40.59			1										1	1
3A	N25 48.52	W80 48.46			1											1
3A	N25 48.39	W80 47.77			1											1
3A	N25 48.30	W80 40.89			1											1
3A	N25 48.30	W80 46.93			1											1
3A	N25 48.28	W80 42.52			1										2	1
3A	N25 48.23	W80 41.23			1											1
3A	N25 48.23	W80 41.29			1											1
3A	N25 48.11	W80 44.77			1											1
3A	N25 48.10	W80 45.75			1											1
															4	1

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 48.01	W80 40.83			1										5	1
3A	N25 47.90	W80 46.94			1										4	1
3A	N25 47.77	W80 46.22			1											1
3A	N25 47.72	W80 41.10			1										2	1
3A	N25 47.60	W80 43.760			1											1
3A	N25 47.59	W80 45.81			1											1
3A	N25 47.58	W80 43.89			1											1
3A	N25 47.54	W80 43.89			1											1
3A	N25 47.53	W80 43.43			1											1
3A	N25 47.52	W80 46.11			1											1
3A	N25 47.36	W80 45.71			1										1	1
3A	N25 47.28	W80 46.33			1											1
3A	N25 47.20	W80 45.64			1											1
3A	N25 47.00	W80 41.52			1											1
3A	N25 46.95	W80 48.45			1											1
3A	N25 46.93	W80 46.51			1											1
3A	N25 46.91	W80 47.64			1										2	1
3A	N25 46.90	W80 45.62			1											1
3A	N25 46.85	W80 48.07			1											1
3A	N25 46.83	W80 47.64			1											1
3A	N25 46.81	W80 45.82			1											1
3A	N25 46.80	W80 47.92			1											1
3A	N25 46.75	W80 44.46			1											1
3A	N25 46.70	W80 45.24			1										3	1
3A	N25 46.67	W80 43.01			1											1
3A	N25 46.66	W80 43.97			1											1
3A	N25 46.64	W80 47.05			1											1
3A	N25 46.64	W80 44.02			1											1
3A	N25 46.62	W80 44.72			1											1
3A	N25 46.62	W80 41.97			1										3	1
3A	N25 46.61	W80 47.59			1											1
3A	N25 46.61	W80 46.92			1											1

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 46.56	W80 47.78			1										3	1
3A	N25 46.52	W80 42.00			1											1
3A	N25 46.42	W80 47.14			1											1
3A	N25 46.36	W80 41.77			1											1
3A	N25 46.34	W80 47.81			1										2	1
3A	N25 46.31	W80 47.47			1											1
3A	N25 46.30	W80 42.50			1											1
3A	N25 46.30	W80 42.50			1											1
3A	N25 46.10	W80 47.34			1											1
3A	N25 46.05	W80 47.86			1											1
3A	N25 46.01	W80 46.64			1											1
3A	N25 45.98	W80 47.78			1											1
3A	N25 45.95	W80 48.86			1											1
3A	N26 00.67	W80 44.12													1	0
3A	N25 57.05	W80 41.63													3	0
3A	N25 56.72	W80 40.44													4	0
3A	N25 56.64	W80 44.00													7	0
3A	N25 56.47	W80 39.87													1	0
3A	N25 56.45	W80 41.06													2	0
3A	N25 56.42	W80 39.85													1	0
3A	N25 56.37	W80 44.74													1	0
3A	N25 55.90	W80 44.36													1	0
3A	N25 55.83	W80 41.26													1	0
3A	N25 55.75	W80 45.10													4	0
3A	N25 55.71	W80 41.24													2	0
3A	N25 55.56	W80 41.16													4	0
3A	N25 55.07	W80 40.05													3	0
3A	N25 55.04	W80 42.96													1	0
3A	N25 54.95	W80 39.66													1	0
3A	N25 54.86	W80 43.24													2	0
															2	0

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 54.60	W80 43.26													2	0
3A	N25 54.58	W80 44.85													1	0
3A	N25 54.41	W80 43.84													1	0
3A	N25 54.35	W80 43.26													1	0
3A	N25 54.24	W80 42.48													1	0
3A	N25 54.12	W80 39.49													1	0
3A	N25 54.08	W80 44.30													5	0
3A	N25 54.06	W80 44.47													1	0
3A	N25 54.03	W80 39.22													1	0
3A	N25 53.92	W80 39.84													1	0
3A	N25 53.79	W80 40.89													1	0
3A	N25 53.79	W80 45.30													3	0
3A	N25 53.73	W80 39.72													2	0
3A	N25 53.62	W80 44.62													4	0
3A	N25 53.00	W80 38.23													2	0
3A	N25 52.82	W80 42.59													2	0
3A	N25 52.71	W80 42.67													1	0
3A	N25 52.47	W80 47.48													1	0
3A	N25 52.21	W80 40.89													1	0
3A	N25 52.12	W80 39.62													3	0
3A	N25 52.05	W80 44.89													1	0
3A	N25 51.93	W80 42.10													1	0
3A	N25 51.90	W80 42.57													1	0
3A	N25 51.86	W80 46.62													2	0
3A	N25 51.84	W80 45.02													3	0
3A	N25 51.65	W80 39.95													1	0
3A	N25 51.58	W80 44.71													1	0
3A	N25 51.19	W80 45.46													1	0
3A	N25 51.10	W80 42.44													1	0
3A	N25 51.05	W80 41.59													2	0
3A	N25 51.03	W80 42.28													1	0
3A	N25 50.84	W80 41.12													1	0

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 50.58	W80 38.73													2	0
3A	N25 50.46	W80 39.74													2	0
3A	N25 50.27	W80 42.02													1	0
3A	N25 50.14	W80 39.95													1	0
3A	N25 50.06	W80 41.23													1	0
3A	N25 49.86	W80 45.20													4	0
3A	N25 49.84	W80 45.41													2	0
3A	N25 49.75	W80 39.80													2	0
3A	N25 49.46	W80 39.40													2	0
3A	N25 49.36	W80 43.14													1	0
3A	N25 49.30	W80 42.57													1	0
3A	N25 49.29	W80 46.11													5	0
3A	N25 49.14	W80 46.21													1	0
3A	N25 49.01	W80 46.36													1	0
3A	N25 48.67	W80 41.23													3	0
3A	N25 48.42	W80 42.27													2	0
3A	N25 48.40	W80 42.62													3	0
3A	N25 48.40	W80 41.27													1	0
3A	N25 48.28	W80 42.76													1	0
3A	N25 48.25	W80 42.54													1	0
3A	N25 48.16	W80 42.45													2	0
3A	N25 48.10	W80 45.13													2	0
3A	N25 48.07	W80 41.58													1	0
3A	N25 47.62	W80 46.22													1	0
3A	N25 47.60	W80 43.09													1	0
3A	N25 47.58	W80 42.09													1	0
3A	N25 47.48	W80 43.10													1	0
3A	N25 47.33	W80 41.82													7	0
3A	N25 46.86	W80 42.13													2	0
3A	N25 46.85	W80 42.22													2	0
3A	N25 46.74	W80 42.14													9	0
[illegible]	[illegible]	[illegible]													1	0

Unit	Latitude	Longitude	Colony	GREG	GBHE	WOST	BCNH	LBHE	SNEG	TRHE	WHIB	GLIB	ROSP	CAEG	ANHI	Colony Total*
3A	N25 46.36	W80 43.87													3	0
		Totals:		**4,168**	**206**	**450**	**142**	**584**	**1,884**	**1,050**	**4,540**	**106**	**14**	**224**	**682**	**13,144**

COLONY	Latitude decimal	Longitude degrees	WOST	WHIB	GREG	SNEG	TRIC	LBHE	GRBH	GLIB	CAEG	BCNH	DCCO	GBHE	ANHI	RoSP	Total
North 3A	26.1358	80.7821					10	3									**13**
west3A	25.8035	80.8034					10								3		**13**
west3A	25.9334	80.7584											10		3		**13**
3B-NAGCA	25.8470	80.5274					7	2						1	2		**12**
west3A	25.8168	80.7726													12		**12**
west3A	25.9607	80.7302												1	11		**12**
3A	25.9517	80.7270												1	10		**11**
west3A	25.9640	80.7526												2	9		**11**
west3A	25.8477	80.7496												1	10		**11**
Unknown	25.8168	80.7665			10												**10**
west3A	25.9128	80.7324												3	7		**10**
3A	25.8194	80.6714													9		**9**
Unknown	26.1105	80.7522			6									3			**9**
Unknown	25.9154	80.6308												2	7		**9**
3A	25.7558	80.6722												1	7		**8**
Unknown	25.9296	80.6797												1	7		**8**
Unknown	26.1163	80.6589					2	2						1	3		**8**
Unknown	25.9792	80.6579													8		**8**
Unknown	26.1633	80.4347			8												**8**
west3A	25.9139	80.7329												1	7		**8**
west3A	25.8935	80.3667												3	5		**8**
3BNAg Ca	25.8947	80.5039			1		4		1					1			**7**
3B-NAGCA	25.8475	80.5762			2		4							1			**7**
3B-NAGCA	25.8475	80.5315			7												**7**
Unknown	26.1348	80.7369					2	5									**7**
west3A	26.0021	80.7619												2	5		**7**
3A	25.8273	80.7056												1	5		**6**