CONSTRAINTS OF LANDSCAPE LEVEL PREY AVAILABILITY ON
PHYSIOLOGICAL CONDITION AND PRODUCTIVITY OF GREAT EGRETS AND
WHITE IBISES IN THE FLORIDA EVERGLADES

by

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CONSTRAINTS OF LANDSCAPE LEVEL PREY AVAILABILITY ON
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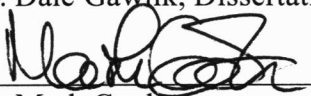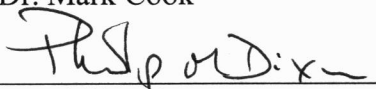WHITE IBISES IN THE FLORIDA EVERGLADES
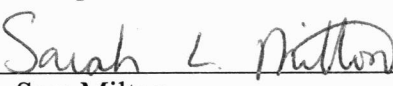
by

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This dissertation was prepared under the direction of the candidate's dissertation advisor,
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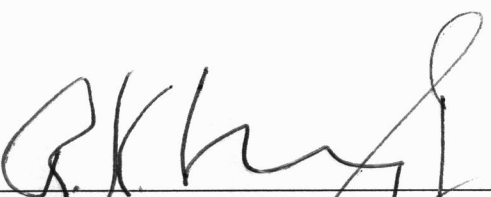for the degree of Doctor of Philosophy.

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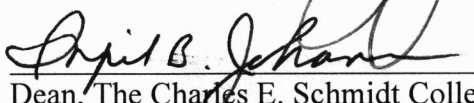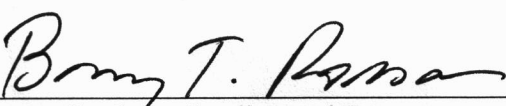Dr. Dale Gawlik, Dissertation Chair

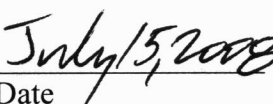Dr. Mark Cook

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ABSTRACT

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Title: Constraints of Landscape Level Prey Availability on Physiological
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Life history strategy suggests long lived bird species will adjust their nesting effort

according to current conditions, balancing the costs of reproduction with their long-term

needs for survival and future reproduction. The habitat conditions that produce these

responses may differ between species, even within the same ecosystem, producing

different nesting and population trends. I traced the pathway by which food availability

influences the physiological condition of pre-breeding great egrets and white ibises

through to reproductive measures, and the physiological condition of chicks. I focused

on these two species with contrasting foraging strategies, in relation to foraging and

habitat conditions to maximize the likelihood of application of these results to other

wading bird species. Experimental food supplementation and physiology research on

white ibis chicks demonstrated that in years with low prey availability white ibis were

food limited, with increased levels of stress protein 60 and fecal corticosterone. This is the first study to demonstrate experimentally the response of stress protein 60 to changing levels of food availability. During a year with low prey availability (2007) white ibis adults and chick physiological condition was lower than that of great egrets. During the same year, fledging success was lower for both species (20% for white ibis versus 27% for great egret) but the magnitude of the decrease was particularly severe for the white ibis (76% decline versus 66% decline for the great egret). Results suggest white ibises modify their clutch size during years with poor habitat in accordance with life history traits of a long-lived species, whereas great egrets maintained their clutch size during years with poor habitat. Increasing recession rates, hydrological reversals, and prey densities influenced white ibis, whereas great egrets were most influenced by prey densities and recession rates, with no effect of hydrological reversals. This study is the first to make the link between landscape hydrology patterns, prey availability, and responses in wading bird nesting. These linkages provide critical insight into how species' nesting patterns could differ given the same time and spatial constraints and how that may be related to long-term nesting trends. This knowledge could ultimately lead to novel predictions about population and community patterns of wetland birds.

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CHAPTER 1: GENERAL INTRODUCTION

INTRODUCTION

Food availability is one of the primary limitations to avian populations,

particularly during the breeding season (Lack 1947, 1954, Skutch 1949, Ricklefs 1968).

Seasonal environmental conditions require most avian species to adjust their physiology,

morphology, and behavior throughout the annual cycle (Hahn 1998). When breeding,

many avian species are able to regulate their body condition when they are faced with

high energy demands (Blem 1990), food scarcity (Stuebe and Ketterson 1982), or food

unpredictability (Cuthill et al. 2000). Food may become a limiting factor during the

breeding cycle due to increased adult physiological demands for egg production and

feeding chicks.

While many species have adapted to varying environmental conditions, their

ability to respond to natural variability coupled with anthropogenic induced changes are

less predictable. Birds can respond to food limitations by abandoning nesting, reducing

clutch size, increasing foraging rates, selecting lower quality but more numerous prey

items, or traveling further to better quality foraging patches. These altered behaviors can

result in adult and chick physiological responses, which can be observed in clutch sizes,

hatching success, growth rates, and survival. Measuring the response to changes in food

availability at both the adult and nest/chick level allows for a quantitative understanding of their relationship and its implication on populations.

Life history theory suggests birds should adjust their level of reproductive effort according to current habitat conditions (e.g., food availability) and life expectancies (Ricklefs 1984, Weimerskirch et al. 2000). This dichotomy suggests that short-lived birds should reproduce during periods of low food availability, with adults bearing the burden of the costs of poor breeding conditions because they have fewer opportunities to reproduce (Daan et al. 1996, Apanius et al. 2008). As birds live longer their opportunities to reproduce increase, and they are less likely to impair their own physiological condition for the sake of reproduction during one particularly lean year (Daan et al. 1996, Apanius et al. 2008). During years with low food abundances, adults could theoretically opt not to reproduce at all, to adjust their level of effort (e.g., clutch size: Lack 1968), incur some physiological penalty themselves, or to pass on the burden of low food availability to their nestlings (e.g., decreased chick physiological condition or survival; Fig. 1).

Critical to understanding how medium to long-lived species respond to changes in their breeding habitats is to understand what limits particular species during the reproductive cycle. Food has long been considered a limiting factor in the clutch size of many species of birds, and ultimately a limiting factor for many bird populations (Skutch 1949, Lack 1954, 1966, Ricklefs 1968). However, tests of food limitation are rare, and present a major obstacle to understanding what regulates avian populations, and from a conservation viewpoint, how anthropogenic impacts might impair avian populations through changes to their habitats and food abundances. Subsequently, understanding

how food availability and habitat factors that influence foraging conditions and food availability (e.g., water depths, recession rates) remains a critical component of conservation and restorations initiatives.

Prey Availability and Nesting Responses

Chick Limiting: As prey availability declines the adults maintain their own body condition but provision less to the chicks, resulting in a decline in chick body condition until the chicks starve.

Adult Limiting: As prey availability declines, adults maintain provisioning rates to chicks but their own body condition declines until they abandon the nest.

Figure 1. Conceptual model to illustrate the hypothetical responses of both adult wading birds and their chicks to changes in prey availability at a landscape level.

Declines in annual breeding success and populations of colonial nesting wading birds (Ciconiiformes) in the Florida Everglades system are believed to be linked to reduced prey availability as result of the historic water management practices (Kahl 1964, Kushlan 1986, Kushlan and Frohring 1986, Frederick and Collopy 1989, Frederick and Spalding 1994, Ogden 1994, Gawlik 2002). Gawlik (2002) tested the prey availability hypothesis, observing that vulnerability and density of prey did not always result in a similar foraging response or strategy across a suite of wading species. Furthermore, not all species of wading birds in the Everglades are declining (Crozier and Gawlik 2003).

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For instance white ibises (*Eudocimus albus*) have declined approximately 87%, while great egrets (*Ardea alba*) increased 270% in the same period across the Everglades (Crozier and Gawlik 2003). These results suggest that differences in life history traits during the breeding season associated with species-specific foraging strategies (searchers versus exploiters; Gawlik 2002) and prey availability across the landscape could be linked to observed nesting trends between these two species.

While wading bird productivity and timing of reproduction may fluctuate within and between years (Kushlan 1975, Frederick and Collopy 1989, Ogden 1994), there appears to be no definitive reason why different species that nest and feed sympatrically would have opposing population trends. Recent research examining reproductive physiology (Heath et al. 2003), reproductive success, chick growth and survival of wading birds (Erwin et al. 1996, Borgia 1999, Sepúlveda et al. 1999) provided insight into critical components of the breeding ecology of these birds. However, these studies fail to provide any connection of variation in these parameters to habitat conditions. The Comprehensive Everglades Restoration Plan (CERP) will be changing ecosystem conditions greatly in the next several decades, therefore understanding the link between habitat conditions and wading bird physiological condition in response to prey availability, chick growth and survival as result of adult responses to the habitat conditions, will significantly increase the certainty of how wading birds will respond to changes in hydrology (Fig. 2).

Physiology allows for a quantitative approach within birds to understand how they respond to changes in their local environments (e.g., food availability). These physiological responses serve as signals to interpret local habitat conditions, and

influence the birds reproductive cycle such that they can overcome short-term deficiencies, moderate their level of nesting effort, or abandon nesting efforts. By measuring physiological factors representing a variety of temporal responses we can improve our understanding of how birds react to immediate day-to-day environmental conditions and long-term landscape habitat conditions that may regulate reproduction and nesting patterns.

Wading Bird Nesting in the Florida Everglades – Prey Availability Hypothesis

MAP = Monitoring and Assessment Plan,
SRF = systematic reconnaissance flights
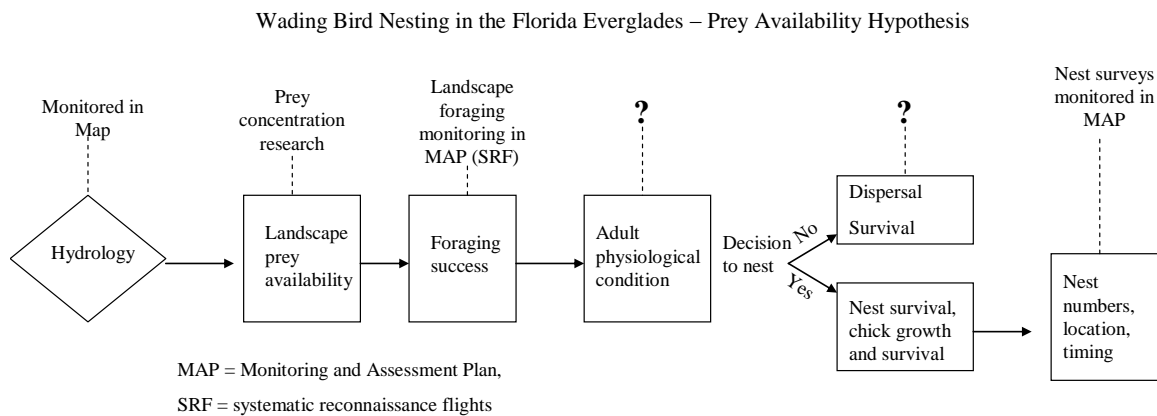
Figure 2. Conceptual model of factors influencing wading bird nest numbers and populations in the Florida Everglades.

Understanding the physiological condition of adult wading birds with different foraging strategies as they approach the nesting cycle could yield important insights into how food abundances (prey availability) and changing habitat conditions might influence their ability to reproduce and how to invest their effort accordingly. While Heath et al. (2003) conducted previous physiological research on white ibises; no such studies exist for great egrets. Paramount to the objectives of a comparative study of adult prebreeding physiology was the capture of large numbers of prebreeding great egrets and white ibises; however few existing methods of capture that were suitable for achieving the objectives

of this study. I developed a new trapping technique specific for wading birds in the Everglades, and evaluate this traps effectiveness relative to existing techniques (Chapter 2).

Traditional avian physiology studies have used a variety of metrics to understand the response of birds to an assortment of environmental conditions. One such approach is the measurement of the steroid corticosterone. There are, however, a number of issues with using corticosterone as a metric of stress in birds and less recognized measures of stress, such as the stress proteins, could provide an alternative, possibly improving our understanding of avian responses to stress. In Chapter 3, I examine the use of corticosterone to measure stress and discuss the potential role that the stress proteins might play in the environmental physiology discipline.

My next objective in this study was to examine the role food plays in wading bird nesting in the Florida Everglades. Collaborating with the South Florida Water Management District, Everglades Division, I used an experimental food supplementation approach to test the physiological responses of supplemented and control chicks (Chapter 4). This approach allowed for a quantitative evaluation of markers of physiological condition being used in Chapter 5 (*Adult Physiology*) and 7 (*Chick Growth and Physiology*). Second, this experimental food supplementation allowed for an evaluation of the magnitude of response of wading birds to changing food abundance, one of the primary hypotheses associated with patterns of change in numbers of nesting Everglades wading birds (Kushlan 1986, Frederick and Collopy 1989, Frederick and Spalding 1994, Ogden 1994, Gawlik 2002).

Accordingly, I then examined the prebreeding physiological condition of adult great egrets and white ibises during the time period leading up to nesting in the Florida Everglades (Chapter 5). If differences in nesting trends are linked to food availability and foraging strategies, physiological differences may mirror those differences, which may lead to an increase or decrease in reproductive potential. During years with differing habitat conditions and prey availability, those differences in adult prebreeding physiology may be translated into changes in nesting effort and nest survival. In Chapter 6, I examine the influence of landscape level prey availability and habitat variables that influenced the accessibility of prey on nest survival of white ibises and great egrets. In Chapter 7, I examine the physiological and growth responses of chicks of both species to years with differing prey availability and habitat conditions, and how those landscape habitat variables influenced metrics of physiological condition and growth patterns. Lastly, in Chapter 8, I integrate the results of the chapters focusing on whether wading birds in the Everglades are food limited, how this might impact the physiological responses of prebreeding adults, how that then translates to changes in chick physiology and growth and nest survival, and discuss what direction future research might head towards to better understanding how food availability and physiology might regulate wading bird nesting.

LITERATURE CITED

Apanius, V., M. A. Westbrock, and D. J. Anderson. 2008. Reproduction and immune homeostasis in a long-lived seabird, the Nazca booby (*Sula granti*). Ornithological Monographs 65:1-46.

Blem, C. R. 1990. Avian energy storage. Current Ornithology 7:59-113.

Borgia, L. 1999. Factors affecting growth and survival of snowy egret nestlings. MS Thesis, Florida International University, Miami, FL.

Crozier, G. E., and D. E. Gawlik. 2003. Wading bird nesting effort as an index of wetland ecosystem integrity. Waterbirds 26:303-324.

Cuthill, I. C., S. A., Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. Behavior Ecology 11:189-195.

Daan, S., C. Deerenberg, and C. Dijkstra. 1996. Increased daily work precipitates natural death in the kestrel. Journal of Animal Ecology 65:539-544.

Erwin, R. M, J. G. Haig, D. B. Stotts, and J. E. Hatfield. 1996. Reproductive success, growth and survival of black-crowned night-heron (*Nyticorax niticorax*) and snowy egret (*Egretta thula*) chicks in coastal Virginia. Auk 113:119-130.

Frederick, P. C., and M. W, Collopy. 1989. Nesting success of Ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625-634.

Frederick, P. C., and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-692 *in* S.

M. Davis and J. C. Ogden (eds.). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Hahn,T. P. 1998. Reproductive seasonality in an opportunistic breeder, the Red Crossbill, *Loxia curvirostra*. Ecology 79:2365-2375.

Heath, J. A., P. C. Frederick, T. M. Edwards, and L. J. Guillette Jr. 2003. Reproductive physiology of free-living White Ibises (*Eudocimus albus*) in the Florida Everglades. General and Comparative Endocrinology 133:118-131.

Kahl, M. P. 1964. Food ecology of the wood stork (*Mycteria Americana*) in Florida. Ecological Monographs 34:97-117.

Kushlan, J. A. 1975. Site selection for nesting colonies of the American White Ibis *Eudocimus albus* in Florida. Ibis 118:590-593.

Kushlan, J. A. 1986. Response of wading birds to seasonally fluctuating water levels: strategiesand their limits. Colonial Waterbirds 9:155-162.

Kushlan, J. A., and P. C. Frohring. 1986. The history of the southern Florida Wood Stork population. Wilson Bulletin 98:368-386.

Lack, D. 1947. The significance of clutch-size. III. Ibis 90:24-45.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, United Kingdom.

Ogden, J. C. 1994. A comparison of wading bird nesting colony dynamics (1931-1946 and 1974-1989) as an indication of ecosystem conditions in the southern

Everglades. Pages 533-570 *in* S. M. Davis and J. C. Ogden (eds.). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Ricklefs, R. E. 1968. On the limitations of brood size in passerine birds by the ability of adults to nourish their young. Proceedings of the National Academy of Science 61:847-851.

Ricklefs, R. E. 1984. The optimization of growth rate in altricial birds. Ecology 65:1602-1616.

Sepúlveda, M. S., G. E. Williams, P. C. Frederick, and M. G. Spalding. 1999. Effects of mercury on health and first-year survival of free-ranging great egrets (*Ardea albus*) from Southern Florida. Archives of Environmental Contamination and Toxicology 37:369-376.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91:69-93.

Stuebe, M. M., and E. D. Ketterson. 1982. A study of fasting in tree sparrows (*Spizella arborea*) and dark-eyed juncos (*Junco hyemalis*). Auk 99:299-308.

Weimerskirch, H., M. P. A. Prince, and L. Zimmermann. 2000. Chick provisioning by the yellow-nosed albatross *Diomedea chlororhynchos*: response of foraging and effort to experimentally increased costs and demands. Ibis 142:103-110.

CHAPTER 2: EVALUATING TWO NEW METHODS FOR CAPTURING

LARGE WETLAND BIRDS

ABSTRACT

Research on waterbirds increasingly involves capturing birds to measure attributes of individuals and for attachment of telemetry devices. There are very few established techniques for capturing wading birds away from their nests and few new techniques have been proposed. I describe the construction and testing of a new trapping technique for wading birds based on a small flip trap used on passerines. This trap design was developed to capture wading birds in the Florida Everglades in water depths less than 30 cm, but has the potential for additional waterbird and upland species capture. The primary advantages of this new trap design are its ability to be easily concealed, ability to selectively capture birds, low injury rate, ease of resetting the trap after captures, ability to be operated by less experienced persons, capacity to be fired remotely, and moderate cost. I also evaluated the effectiveness of using a net gun to capture wading birds in wetlands. Results demonstrated that the net gun was the most effective method for capturing large numbers of wading birds; the modified flip trap, however, provides a safer alternative that may be more appropriate for endangered species.

INTRODUCTION

Existing approaches to capturing wading birds away from nesting colonies or during the non-breeding season include rocket nets (Parris 1977, Heath and Frederick 2003) and mist nets (Bateman 1970, Rojas et al. 1999, Heath and Frederick 2003). Both of these trapping techniques can be effective under certain situations, but they also have limitations. Rocket nets can be difficult to set up in wetlands, and wet charges and wires can result in misfires (Cox and Afton 1994). In addition, the time to reset after firing may be long, resulting in missed capture opportunities (Heath and Frederick 2003). Rocket nets can also ignite fires in combustible wetland vegetation and are costly (Heath and Frederick 2003). Mist nets are non-discriminate, cannot be left unattended when set at wetland trapping sites (Heath and Frederick 2003), and, in wetlands devoid of tall vegetation or under full light conditions, are readily visible to birds (G. Herring, unpubl. data).

Given the low number of options for trapping large wading birds, I developed a new trap that is easily concealed, selective in the birds captured, easily reset after firing, triggered remotely, and relatively inexpensive. This trap design is a highly modified version of a small flip trap, originally intended for capturing upland passerines (Bub 1991). I evaluated the effectiveness of this new trapping technique to capture large wetland birds.

Net guns have also been used to catch a wide variety of birds, including American bitterns (*Botaurus lentiginosus*; Huschle et al. 2002), golden eagles (*Aquila chrysaetos*; O'Gara and Getz 1986), snail kites (*Rostrhamus sociabilis;* Bennetts and Kitchens 1999), and waterfowl (Mechlin and Shaiffer 1980). To my knowledge, the only attempt to use

net guns to capture wading birds was unsuccessful. In that case investigators attempted to capture great egrets (*Ardea alba*) perching or flying into roosting sites (P. Frederick, University of Florida, pers. comm.). I believed that net guns could also be effective on wading birds if we exploited the strong social attraction exhibited by some species (Gawlik and Crozier 2007) and used decoys (Crozier and Gawlik 2003, Heath and Frederick 2003) to lure birds to a gunner. Thus, I chose to also test the effectiveness of the net gun to capture wading birds using decoys and we explored techniques to improve our shooting accuracy once birds were within range.

METHODS

Study Area

I conducted all testing of the modified flip trap and net gun at multiple sites within the Arthur R. Marshall Loxahatchee National Wildlife Refuge and Water Conservation Areas 2A and 3A in the Florida Everglades. Wetlands were dominated by ridge and slough topography, with sawgrass ridges and shallow sloughs interspersed with both submergent and emergent aquatic plants and tree islands. Common aquatic plants included bladderwort (*Utricularia* spp.), fragrant water-lily (*Nymphaea odorata*), and spike rush (*Eleocharis* spp). Water depths at trapping sites averaged 17.8 ± 0.7 (SE) cm (range $13 - 27$ cm).

Trap Design and Construction

The trap consists of two wood frames, an aluminum-throwing arm on each wooden frame, two garage door opener springs on each wooden frame, and a solenoid release mechanism on each arm (Fig. 1, Table 1). Attached to the bottom of each wood frame (5.08 x 10.16 x 304.8 cm) are the two parallel 59 kg garage door opener springs that fasten to the pulling arm with two parallel 0.47 cm diameter braided steel cables. When the throwing arm is pulled over from the extended position to the cocked position, the springs are extended underneath, providing the power to pull the net. The firing rod in the solenoid release mechanism fastened to the end of the wood frame gives way to the aluminum bar as it is cocked (Figs. 1 and 2). The firing rod then slides back into place as the bar passes, and is held in place by a Teflon receiving unit (Fig. 2). Each unit is placed on the end of a furled 10 x 6.1 m nylon net (10.16 cm mesh size). The large mesh size allowed for captured birds to be pulled through the net in most cases. I constructed the

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capture net from gill net material (Memphis Net and Twine, Memphis, TN) and attached

a 0.47 cm diameter nylon rope around the outside of the net for attachment to the throw

arm and to anchor to the ground. The net was anchored at either end to the ground with

steel rods and the top of the net is attached to the two throw arms after cocking. The

throw arms were also secured to the ground by means of cross braces and steel rods (Fig.

3).

Each solenoid firing mechanism consisted of two separate solenoids (F492

external momentary solenoid switch and the internal 12-volt solenoid relay), a Teflon

block that acts as a guide for the release pin, an aluminum flange and rubber gasket to

prevent water from entering the inside of the release mechanism box, and the release pin

(Fig. 2). The F492 solenoids on each unit were fastened temporarily to individual 12-volt

motorcycle batteries (housed in waterproof boxes) during trapping and permanently to

the internal 12-volt solenoid relay. The trap was fired using an electrical switch attached

to the F492 solenoid with 10 m of electrical cable. When the electrical switch was

depressed, it completed an electrical circuit and actuated the solenoids which then

retracted the pin allowing the spring-loaded throw arms to pull the net over. A 12-volt

momentary solenoid switch ensured that that electrical pulse is limited to only a brief

period, pulling the release pin, but not remaining energized, preventing the solenoid from

being damaged.

After completion of trapping, I developed a wireless remote release mechanism,

which provided more flexibility in where the trap was set because the trapper could be far

from tall vegetative cover. A two-channel radio frequency relay board receiver was

wired into the F492 momentary solenoid switch, attached to the outside of the solenoid

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release mechanism box (Fig. 2). The relay board was housed in a waterproof case, mounted on top of the solenoid release box (Fig. 2). The radio frequency relay board on each unit was fastened temporarily to the individual 12-volt motorcycle batteries during trapping. A remote transmitter was then used to send a radio signal to the receiver, completing the electrical circuit and actuating the solenoids which then retracted the pin allowing the spring-loaded throw arms to pull the net over. I test fired the trap using the remote trap release mechanism at 10, 20, 28, 45, and 67 m from each of the cardinal directions, while hidden in dense emergent vegetation.

Net gun. We used a Coda net gun (Coda Enterprises, Mesa, AZ) with a 3.3 m^2 net (model NN11-430WP) and low load .308 rifle cartridges. All nets fired from the net gun had four approximately 500 g weights attached to the corners. Three levels of rifle charge loads were available from the manufacturer. Medium and heavy load charges increased the velocity of the net and distance that the net flew, but would also increased the potential for injuring birds (C. Grey, Coda Enterprises, pers. comm.). We tested the net gun repeatedly (~150 practice shots) prior to trapping birds so we were proficient enough to regularly capture a moving football in the middle portion of the net, thus giving us confidence that there was minimal risk of a bird getting hit by a weight or coming into contact with the heavy lines on the edge of the net. This training also allowed us to determine an effective range for capturing birds. Maximum distances that nets traveled under normal operating conditions was approximately 15 m, but effective capture distance were limited to 10 m, and the ideal distance was from 5 m to 10 m from the gunner.

Trapping site selection and trap setting

We identified potential trapping sites by locating by airboat foraging flocks of mixed wading birds in the Arthur R. Marshall Loxahatchee National Wildlife Refuge and Water Conservation Areas 2A and 3A, Palm Beach County, Florida 1 - 5 d prior to trapping. Trapping sites required shallow water (≤30 cm), sufficient open slough habitat to set the trap (at least 6 x 10 m for the flip trap) or to allow firing of the net gun, and adjacent vegetation (sawgrass or cattail) to conceal the trap operator or net gunner and allow a minimally obstructed view of the capture area. Once these requirements were met, we assembled the modified flip trap for the following day (Fig. 3). For net gunning, we typically set up a 1.25 × 2 m camouflage mesh blind adjacent to the target slough (Fig. 2). We placed a 0.5 × 1.25 m sheet of plywood on the ground behind the blind that provided a stable platform for the shooter. Within the target landing area for the birds we removed excess vegetation that might become caught on the modified flip trap net when released or entangled in the net gun net. When setting the modified flip trap, we set the throw arms flush with the surface of the water, so that only the release mechanisms and roller support brackets (Fig. 1) were above water. We used local vegetation to create a thin bed for the capture net to sit on, typically just above the surface of the water, additional light vegetation was placed on top of the capture net, throw arms, and release mechanisms for concealment. Setup of the modified flip trap took approximately 1 h each time, including camouflaging the wooden braces, the throw arms, and net with local vegetation. Setup for the net gun usually only took 15 min.

On trapping days, we arrived at the trapping site 30 min prior to sunrise to allow for final setting of the trap, placing decoys to attract wading birds (Crozier and Gawlik

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2003), and to position the trap operator or net gunner in adjacent vegetation. During

testing of the modified flip trap and net gun, we used both Snomingos (Union Products,

Leominster, MA) and Carry-Lite egret decoys (EPSCO Industries, Birmingham, AL)

painted to match snowy egrets (*Egretta thula*), great egrets, white ibis (*Eudocimus albus*),

and wood storks (*Mycteria americana*). For wood stork decoys we curved the egret

decoy bill, added additional material to the neck and upper back, and painted the decoys

to match a wood stork. We used a combination of decoy species to increase the realism

of the decoy foraging/trapping site. On average, we used 6.6 ± 0.2 (SE) great egret, $1.0 \pm$

0 snowy egret, 9.3 ± 0.6 white ibis, and 3.2 ± 0.1 wood stork decoys. For net-gun

trapping, we placed decoys in areas closer than 5 m and farther than 10 m from the blind

to encourage birds to land in the optimal range (Fig. 4). We typically placed several ibis

decoys in the capture area of the modified flip trap, with larger heron decoys placed

outside that area and one decoy each placed just at the ends of the aluminum arms when

extended. These end decoys allowed the trapper to more easily delineate the effective

trapping area (Fig. 4). During setup of trapping sites and all trapping efforts, we wore

camouflage and minimized movements to increase the likelihood of wading birds landing

at trapping sites.

I triggered the modified flip trap only when wading birds were at least 2 m within

the outside edge of the trap area to minimize the escape of wading birds. I only fired the

trap when wading birds were 1 m away from the trap throw arms (Fig. 3) to increase the

likelihood of capture, while minimizing the risk of injury by the aluminum throw arms.

During net gunning, we allowed wading birds to land first, and the shooter then stood up

and fired at the bird as it attempted to fly away and was moving relatively slowly. This

technique greatly increased our accuracy and capture rate. We only attempted to capture wading birds within 10 m of the blind and did not fire at birds less than 5 m from the blind to avoid harming them from the impact of the net. We typically carried three nets when net gunning, one in the gun and two in canisters ready for use in the event we missed a bird. After firing all three nets, reloading nets into their canisters took approximately 5 min per net, including time to remove vegetation and shake out excess water from the net. Although we were still successful in capturing birds with wet nets, we did notice that wet nets tended to fly slower and shorter distances.

For evaluating the modified flip trap, I recorded the species and total number of water birds that flew over the trapping area (within approximately 100), the number that approached the decoys and modified flip trap setup (either deviated from their flight path or circled the setup), and the number that landed either in or adjacent to the decoy and trap setup. I assessed the effectiveness of the modified flip trap in six ways: 1) the total number of birds that landed in the slough (a measure of trap concealment), 2) total number of birds captured versus attempts (a measure of trap efficacy), 3) total number of birds that landed in the flip trap net area that were not captured because they were not target species (a measure of the potential to capture additional species), 4) capture rate of the modified flip trap relative to net gunning, 5) number of wading birds injured during trapping, and 6) cost.

To evaluate the net gun, I examined the (1) capture rate of the net gun relative to modified flip trap, (2) number of wading birds injured during trapping, and (3) cost. Values are presented as means ± 1SE.

RESULTS

During 33 days trapping with the modified flip trap, 6673 water birds flew over the trap site, 58.4% ($N = 3896$) of those birds approached the site or circled, 35.1% ($N = 2345$) landed in the trap area, and 9.5% (636) landed in the capture area (Table 2). In addition to white ibises and great egrets, 16 other species responded to decoys and landed adjacent to the flip trap or in the capture area. I did not fire the modified flip trap on nontarget species, although several were captured incidentally when the net was fired on target species. Nontarget species were included in the analysis of the effectiveness of the trap design.

Using the modified flip trap, I captured 42 birds in 56 attempts (75.0%), or an average of 0.75 birds/trap release and 1.27 ± 0.2 birds captured/day during 33 days of testing. In addition to great egrets and white ibises, I also captured roseate spoonbills (*Platalea ajaja*) and snowy egrets (Table 2). Mean time after the firing button was depressed until complete deployment of the net was only 0.6 ± 0.04 sec ($N = 6$). Time to reset the trap averaged 5.8 ± 0.2 min and required only one person, as the arms can be set one at a time. No birds died or experienced major injuries, but two individuals received minor abrasions (feather loss and a mild hematoma). All captured individuals were released adjacent to the trapping site and flew away with no sign of injury. Cost of construction of the modified flip trap was $539 (Table 1).

With the net gun, I captured 175 birds in 366 attempted (47.8%, or 0.47 captures/netgun shot and 1.73 ± 0.1 captures during 101 days of testing. In addition to great egrets and white ibises, I also captured glossy ibis (*Plegadis falcinellus*), roseate spoonbills, and snowy egrets with the net gun. Time to reload another net after taking a

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shot usually took less than 1 min and could be accomplished by the net gunner. I had

four direct mortalities during net gunning, three great egrets and one white ibis,

representing mortality rates of 4.47% for great egrets and 0.96% for white ibises. All

mortalities during net gunning occurred when one of the net weights struck a bird. The

cost of the net gun was $3574, and that included three nets and 100 shells (additional

shells were $0.50 each).

DISCUSSION

The modified flip trap provided an effective and relatively inexpensive method of capturing wading birds at water depths suitable for wading bird foraging (Gawlik 2002). The total cost of the modified flip trap was equivalent to using mist nets, 25% of the cost of a rocket net (Heath and Frederick 2003), and only 15% of the cost of a net gun. The high number of wading birds that landed in the trap net area suggests that increased numbers of wading birds could have been captured had it not been for the need to only capture selected species and process birds after capture. Mean numbers of wading birds captured per day using our modified flip trap were similar to numbers captured using mist nets (1.27 ± 0.1) and rocket nets (1.78 ± 0.7; Heath and Frederick 2003), but lower than the net gun (this study). However, the number of birds captured per day using the net gun was likely biased low because we included data during the period we were refining our capture techniques with this tool. In addition, trapping great egrets in this study reduced the number of birds captured per day because they did not fly into decoys in large numbers like white ibis, the target species for Heath and Frederick (2003). Great egrets also tended to land further away from decoys than White Ibis, making capture more difficult.

No birds were killed using the modified flip trap, suggesting that this technique might be safer than either rocket nets (Cox and Afton 1994, King et al. 1998) or net gunning (this study). Although the number of mortalities associated with the net gun was relatively low (2.28%), that risk increased to nearly 5% with the larger species (great egrets) and may be too high for trapping large endangered wading birds such as wood storks. In contrast, the modified flip trap has the ability to selectively fire only when

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birds are located in a safe portion of the trap area, thus making it more appropriate for capturing endangered species such as wood storks.

The remote release mechanism of the modified flip trap will likely improve the ability to determine if birds are in the trapping zone by allowing a trapper to be further from the trap with an unobstructed view of the trap site. I suggest that the remote release mechanism be used at distances of ≤ 30 m to guarantee successful firing of the trap. Additionally, the two-channel relay board and remote transmitter allowed for two separate traps to be operated using the same remote and it may be possible to amplify the radio signal and increase the rate of successful firing at distances up to 60 m. In the event that concerns for accidental firing of the trap could occur due to local radio frequency interference, the wired electrical switch release mechanism could be used in place of the wireless remote mechanism. Because of the technical aspects involved in the construction of the modified flip trap, I recommend consulting with a professional machinist to ensure proper construction of the trap and execution of the firing mechanism.

The modified flip trap provides a safe, effective alternative to existing wading bird trapping techniques, and has the potential for application to additional species in other habitats, including other waterbird species that can be attracted by either decoys or bait (e.g., shorebirds and some waterfowl) and upland species such as grouse, turkeys, or cranes. Also, the relative low cost and ease of operation of the flip trap allows for multiple trapping setups to be constructed and used for trapping simultaneously. This trap design also allows for relatively untrained persons to operate it; they just need to understand where birds need to be located to increase the likelihood of capture while

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minimizing the chance of harming them. This is in contrast to the net gun, which

requires new users to practice extensively before ever attempting to capture a bird. Also

the heavy weight of the net gun may preclude its use by smaller researchers.

The net gun was more effective for capturing wading birds in our study than mist

nets, the modified flip trap, or rocket nets. Additional benefits of using the net gun

include the short time needed to reload and potentially fire at another wading bird,

flexibility in where shots could be taken, and relative ease of setting up sites for net

gunning. However, the cost of the net gun and greater skill level required for effective

capture of wading birds may detract from its usefulness in some studies where resources

and time may be limited. Additionally, the elevated risk of trapping mortalities

associated with capturing large bodied wading birds may limit its application for

capturing endangered species such as the wood stork. However, in such cases,

researchers can now utilize our modified flip trap and haves a safe and effective

alternative trapping technique.

LITERATURE CITED

Bateman, D. L. 1970. Movement behavior in three species of colonial-nesting wading birds: a radio-telemetry study. Ph.D. dissertation, Auburn University, Auburn, AL.

Bennetts, R. E., and W. L. Kitchens. 1999. Within-year survival patterns of snail kites in Florida. Journal of Field Ornithology 70:268-275.

Bub, H. 1991. Bird trapping and bird banding. Cornell University Press, Ithaca, NY.

Cox, R. R., and A. D. Afton. 1994. Portable platforms for setting rocket nets in open-water habitats. Journal of Field Ornithology 65:551-555.

Crozier, G. E., and D. E. Gawlik. 2003. The use of decoys in attracting wading birds. Journal of Field Ornithology 69:276-287.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Gawlik, D. E. and G. E. Crozier. 2007. A test of cues affecting habitat selection by wading birds. Auk 124:1075-1082.

Heath, J. A., and P. C. Frederick. 2003. Trapping White Ibis with rocket nets and mist nets in the Florida Everglades. Journal of Field Ornithology 69:276-287.

Huschle, G., J. E. Toepfer, W. L. Brininger, Jr., and D. A. Bruce. 2002. Capturing adult American bitterns. Waterbirds 25:505-508.

King, D. T., J. D. Paulson, D. J. Leblanc, and K. Bruce. 1998. Two capture techniques for American white pelicans and great blue herons. Colonial Waterbirds 21:258-260.

Mechlin, L. M., and C. W. Shaiffer. 1980. Net firing gun for capturing breeding waterfowl. Journal of Wildlife Management 44:895-896.

O'Gara, B. W., and D. C. Getz. 1986. Capturing golden eagles using a helicopter and net gun. Wildlife Society Bulletin 14:400-402.

Parris, R. W. 1977. A method for capturing adult great blue herons. Proceedings of Colonial Waterbird Group 1977:163-165.

Rojas, L. M., R. McNeil, T. Cabana, and P. Lachapelle. 1999. Behavioral, morphological and physiological correlates of diurnal and nocturnal vision in selected wading bird species. Brain, Behavior and Evolution 53:227-242.

1. Solenoid release mechanism
2. Radio frequency receiver
3. Release pin
4. 12 volt battery
5. Wood platform
6. Aluminum throw arm
7. Two parallel garage door springs, housed in PVC pipe
8. Roller
9. Support brackets
10. Throw arm pivot
11. Braided steel cables
12. Cross brace
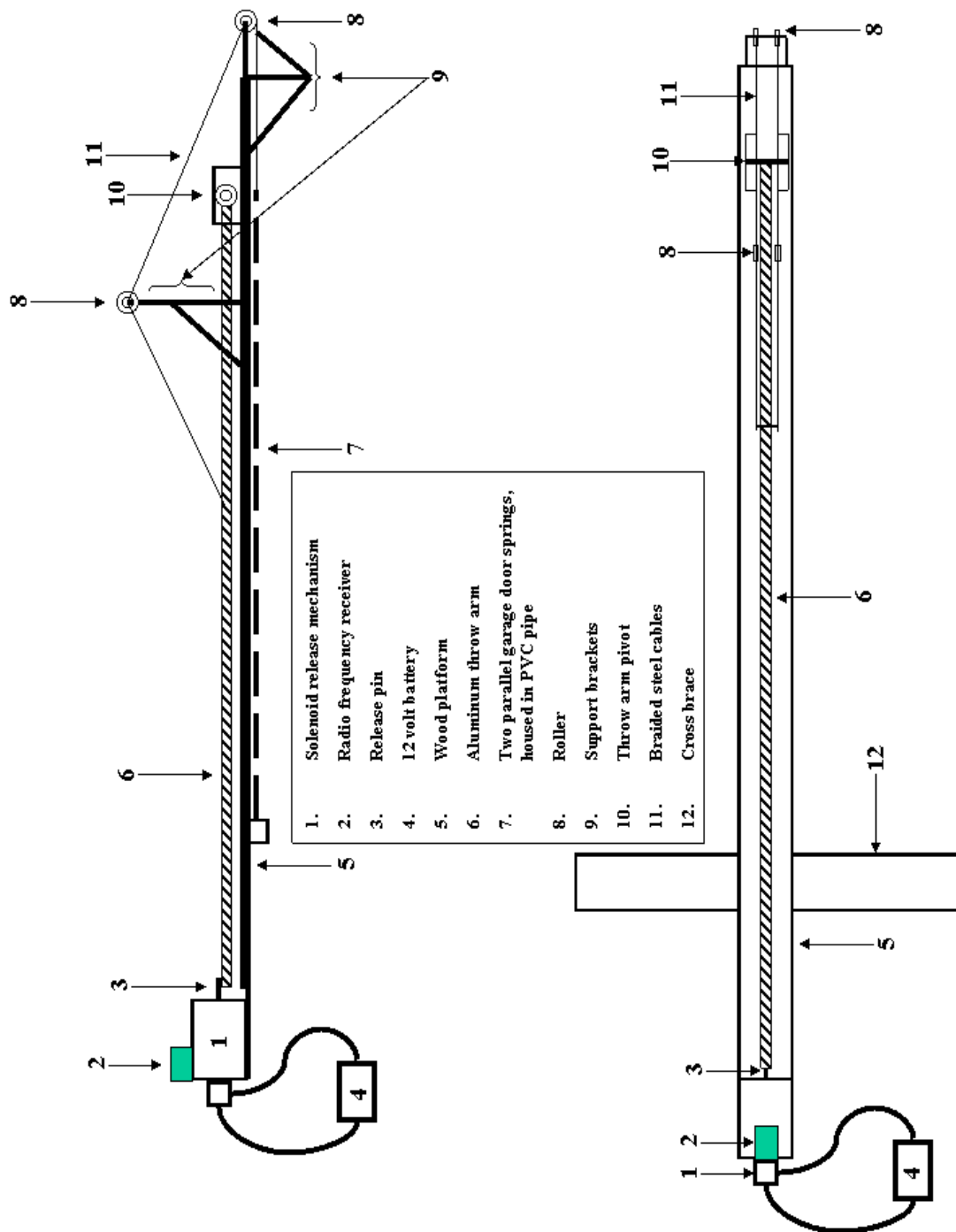
Figure 1. Side and overhead view of the flip trap net-throwing arm and solenoid release mechanism in the set position.
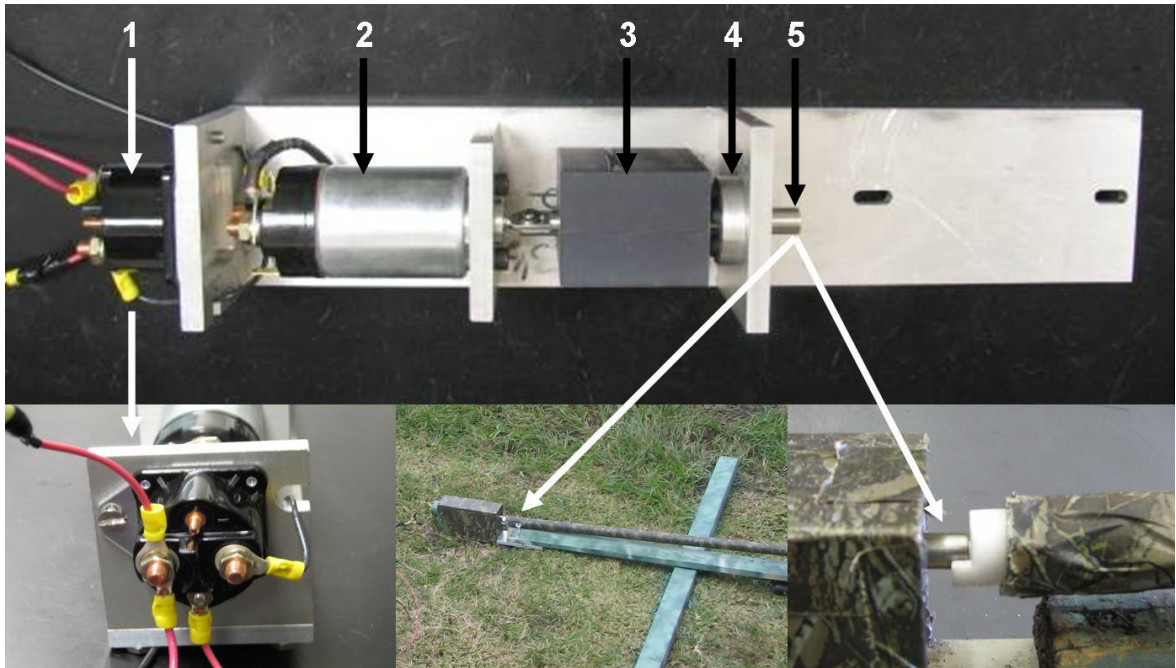
Figure 2. Opposing view of the solenoid release mechanism on the modified flip trap with protective cover taken off, 1 = F492 12-volt solenoid momentary switch, 2 = 12-volt solenoid relay, 3 = Teflon guide, 4 = waterproofing flange, 5 = release pin.
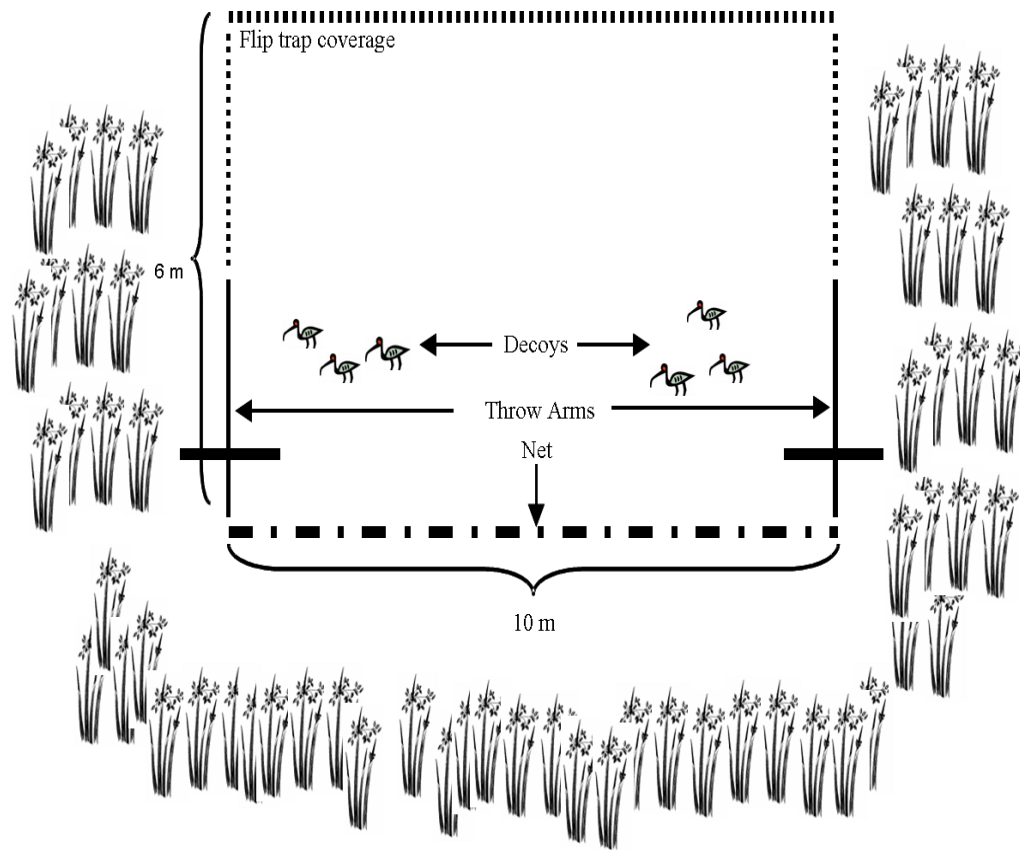
Figure 3. Modified flip trap setup in wetland, including decoys placed within flip net coverage area.
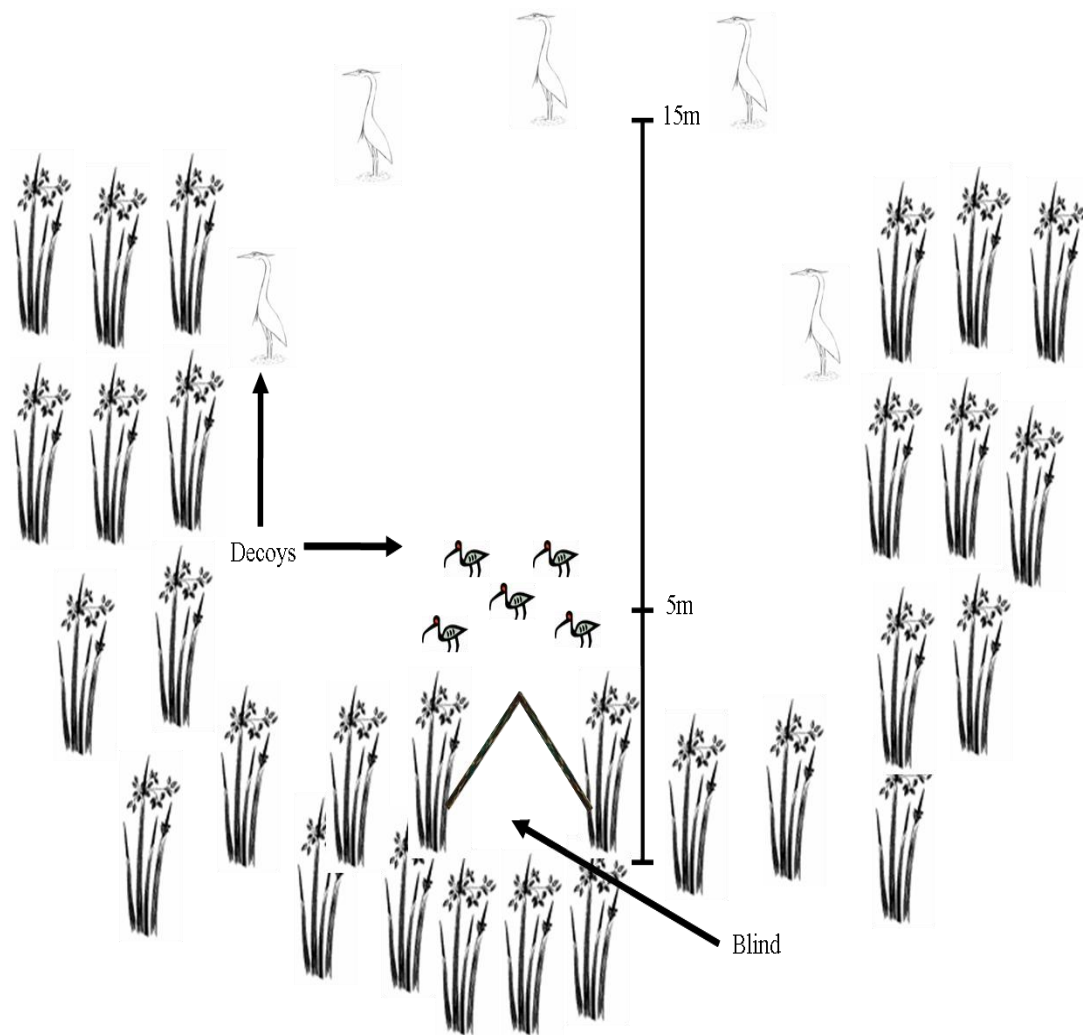
Figure 4. Typical net gun setup, with decoys placed to create an opening to induce birds to land at an optimal distance from the net gunner.

Table 1. List of materials and cost required to construct the modified flip.

Item	Quantity	Purpose	Cost
Wood -5.08 x 10.16 x 304.8 cm (2" x 4" x 10')	2	Throw arm base	10.24
Aluminum tube – 3.17 cm dia	7 m	Throw arm	65.84
Teflon bar – 2.54 cm dia	20 cm	Release pin receiver	10.00
Aluminum round bar – 4.5 cm dia	2 cm	Waterproofing flange	5.00
Stainless steel bar – 1.27 cm dia	20 cm	Release pin	5.00
59.72 kg garage door springs	4	Throw mechanism	58.68
Screen door rollers	8	Cable guides	19.84
Braided steel cable – 0.47 cm dia (3/16") and 8 ferrules	8 m	Pull arm mechanism	22.55
Steel flat bar – 2.54 x 0.47 cm	7 m	Support brackets	23.85
Angle iron – 3.81 x 0.47 cm	61 cm	Throw arm bracket	15.18
Miscellaneous bolts, nuts, washers		Trap construction	50.00
F492 12-volt solenoid switch	2	Release mechanism	28.75
12-volt solenoid relays	2	Release mechanism	28.73
Radio frequency relay board & remote transmitter	2	Remote release mechanism	59.50
Electrical junction box – 10 x 10 x 5 cm	2	Release mechanism receiver	17.28

Release mechanism hardware		Release mechanism	6.10
Spray paint	4	Camouflage	15.96
Nylon gill net material	10 m	Capture net	34.80
6.09 m wide x 10.16 cm mesh size			
Rebar	7 m	Net and trap anchors	4.56
Motorcycle batteries	2	Firing mechanism	56.88
Total cost with wireless remote			$539.14

Table 2. Breakdown of waterbird species responding to trapping efforts with the modified flip trap during 2006 – 2007.

Species	Flew over area	Approach site	Land at site	Land in net area
American bittern (*Botaurus lentiginosus*)	1	1	1	
Black-crowned night heron (*Nycticorax nycticorax*)	1	1	1	
Black-necked stilt (*Himantopus mexicanus*)	6	6	6	4
Glossy ibis (*Plegadis falcinellus*)	196	113	62	7
Great blue heron (*Ardea herodias*)	13	13	8	
Great egret (*Ardea albus*)	656	470	304	61
Green heron (*Butorides virescens*)	1	1	1	
King rail (*Rallus elegans*)		1	1	1
Limpkin (*Aramus guarauna*)	1	1	1	
Little blue heron (*Egretta. caerulea*)	182	171	121	36
Mottled duck (*Anas fulvigula*)	4	4	4	2
Roseate spoonbill (*Platalea ajaja*)	376	354	240	67
Snowy egret (*Egretta thula*)	813	719	595	261
Sora (*Porzana carolina*)		1	1	1
Tri-colored heron (*Egretta tricolor*)	289	245	205	56
White ibis (*Eudocimus alba*)	3970	1654	734	135
White pelican (*Elecanus erythrorhynchos*)	1	1	1	1

Wood stork (*Mycteria americana*)	100	83	62	4
Total	6608	3839	2348	638

CHAPTER 3: THE ROLE OF STRESS PROTEINS IN THE STUDY OF ALLOSTATIC OVERLOAD IN BIRDS, USE AND APPLICABILITY TO CURRENT STUDIES IN AVIAN ECOLOGY

ABSTRACT

Stress proteins offer a measure of stress in birds at the cellular level that is an alternative to the glucocorticoids. Stress proteins are not biased by handling stress, the increase in stress proteins lasts longer than with other measures (e.g. corticosterone), and therefore may be a more appropriate measure of long term or chronic stress. However, caution should be practiced when using stress proteins, as the level of stress needed to elicit a response may be higher than with corticosterone. Stress proteins have only recently been used to measure the response to competition, food limitation, growth, and parasitism in birds. In other taxa the stress proteins have been used to measure genetic stress, temperature, toxins, UV radiation, and physical activity. Stress proteins increase the options available to avian ecologists for understanding how avian species respond to changes in the environment.

INTRODUCTION

In avian ecology studies, the physiological condition of an individual is often induced by changes in their environment, and can be measured by endocrinological parameters. These non-lethal techniques allow ecologists to assess the physiological condition of species simply through the collection of blood or fecal material. Additional advantages of these techniques are that the same animal can be measured repeatedly throughout time and space (e.g., breeding season) and they can be applied to endangered species. One of the most popular approaches to studying the physiological condition of avian species to an environmental stimulus or stressor is the measurement of corticosterone (CORT), either measured in plasma or fecal samples. There are, however, a number of issues with using CORT as a metric of stress in birds and less recognized measures of stress, such as the stress proteins, could provide an alternative, possibly improving our understanding of avian responses to stress.

In this chapter, I briefly review the conventional use of CORT in avian physiology/ecology studies, detailing the breadth of its use and limitations, including potential problems with using CORT as a measure of stress in birds. I then introduce the stress proteins, providing background on the role they play during stress responses, detail their use across research disciplines, recent use in avian ecology, and lastly examine the limitations of using stress proteins in avian ecology. With this paper I hope to generate further interest in the use of stress proteins in avian ecology, in particular experimental approaches that allow a better understanding the role stress proteins play in birds seasonally, their behavior during normal conditions (non stress periods), and their

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response to stress in the absence of additional factors that often reduce our ability to understand ecological responses beyond correlation.

Defining Stress

Minor fluctuation of CORT in birds as well as other vertebrates is relatively common due to the highly variable environments in which they live. Most species are adapted to these variable environments and can adjust their physiology to cope (Ewen and Wingfield 2002, Buchanan and Goldsmith 2004, Romero 2004). Critical to the overall question being asked of how a species responds to a stressor is the definition of stress. Romero (2004) defined stress as a noxious stimulus that results in a suite of physiological and behavioral coping mechanisms, with long term chronic stress resulting in over stimulation of the coping mechanisms. In the presence of unpredicted, highly variable fluctuations of negative stimuli chronic stress may become a factor that can result in negative impacts on an individual or population (Ewen and Wingfield 2002, Romero 2004). Ewen and Wingfield (2002) proposed that we begin to frame our discussions of stress within the concept of allostasis, the maintenance of physiological homeostasis during times of stress. Allostatic load is how hard an individual must work to maintain that balance, and allostatic overload is when the energy requirements to maintain the balance exceed the capacity of the animal.

Traditional approach to measuring stress: Corticosterone

Corticosterone serves as a physiological signal to the bird to modify its behavior and or metabolism to deal with the potentially adverse environmental conditions. When the cortex of the brain of a bird detects a stressor, a neural signal is sent to the hypothalamus. The hypothalamus then sends a hormone signal to the pituitary gland,

resulting in the pituitary sending a signal to the adrenal or interrenal gland to release CORT. After the stressor has been alleviated a negative feedback loop shuts off the hypothalamus-pituitary-adrenal (HPA) pathway leading to the CORT release. If the stressor persists and CORT remain elevated, the negative feedback loop will cease to function and destructive chronic effects may begin (e.g., reproductive failure) as allostatic overload occurs.

At lower levels, CORT can stimulate foraging activity and lipogenesis (Astheimer et al. 1992, Wingfield 1994). Under conditions of food scarcity, CORT stimulates gluconeogenesis, shifting catabolism away from fats towards proteins (Astheimer et al. 1992, Wingfield 1994). Chronic elevated levels of CORT can reduce the fitness of individuals via immunosuppression and reproductive failure, resulting in harmful effects at various levels (Dunlap and Schall 1985, Verme and Doepker 1985, Wingfield et al. 1992). In birds, fecal CORT levels reflect residue levels of plasma CORT, however, rapid and extensive metabolization before excretion results in lower overall levels than circulating levels (Wasser et al. 2000).

While CORT has played an important role in understanding how wild and captive birds respond to environmental stimuli (e.g., nutritional conditions: Frifinger et al. 2007), it has a major limitation in that CORT production can be stimulated by capture and handling stress. Therefore, unless plasma samples are collected within the first 2-3 minutes they will often be biased high, reflecting the stress induced by the researcher and not the basal level of CORT, which is of interest (Romero and Reed 2005). Measuring fecal CORT is one approach to reduce bias from capture and handling stress, because elevation of fecal CORT does not occur for 2-12 hours after capture in birds (Wasser et

al. 1997, Ludders et al. 2001, Khan et al. 2002, Washburn et al. 2003). However, fecal

CORT measurement also has limitations. This steroid is prone to degradation when fecal

samples are frozen for storage, and as they degrade the concentration of cross-reacting

metabolites can change, potentially giving the impression that hormone levels increased

since sampling (Ludders et al. 2001, Washburn et al. 2003). Often, fecal samples will

include both feces and uric acid; however, CORT may be excreted at different levels in

feces and uric acid resulting in an increase in sample variance (Ludders et al. 2001,

Teskey-Gerstl et al. 2000, Washburn et al. 2003, Millspaugh and Washburn 2004).

Additionally, there are two types of CORT that can be measured, and the

scientific community has not agreed on a standard. Free CORT is available to interact

with receptors and can result in a response to the stressor, whereas total CORT is bound

to a carrier protein and is not available to receptors (Breuner and Orchinik 2001, Romero

et al. 2006). Breuner and Orchinik (2001) suggested that free CORT might be the more

important parameter to measure because it interacts with receptors; however, most studies

to date have measured total CORT. It has been shown that different species may have

opposite relationships between free and total CORT (Breuner and Orchinik 2002,

Romero et al. 2006), and therefore, measuring total CORT in some species may be

sufficient whereas in others it may not. Previous studies found free CORT in house

sparrows (*Passer domesticus*) increased when the individual was stressed, while total

CORT remained relatively constant (Breuner and Orchinik 2001, Romero et al. 2006).

Other studies (see Breuner and Orchinik 2002) have found a different trend, with free

CORT and total CORT having similar trends of circulating levels. Understanding the

response of free CORT and total CORT should be a consideration of future studies using

CORT as a response to a stressor. It is also important for researchers to acknowledge which CORT type they have measured so that comparisons are made properly (e.g., Breuner and Orchinik 2001, Romero et al. 2006).

Alternative approach to measuring stress: Stress Proteins

Stress proteins are a group of highly conserved intracellular polypeptides found in all organisms from bacteria to humans, indicating a crucial role in cellular survival (Sørensen et al. 2003). They function as molecular chaperones for proteins within cells and present a major molecular barrier to alterations in cellular homeostasis (Sørensen et al. 2003, Tomás et al. 2004). The primary role of stress proteins is to limit the interactions of unfolded proteins during the early stages of their synthesis by identifying and binding to exposed proteins. The unfolded protein is stabilized, protecting it from damage from destructive situations, and can then be restored or is tagged for destruction (Tomás et al. 2004, Willmer et al. 1999). Most stress proteins are constitutively expressed, supporting normal protein folding and scouring the cell for damaged proteins. However, some stress proteins are transcriptionally upregulated in a cell upon exposure to a variety of stressors (Sørensen et al. 2003). Heat shock factor (HSF) is a transcription factor that acts as a regulator for HSP (Sørensen et al. 2003).

Under normal cellular conditions, stress proteins are involved in routine cellular protection; however, their molecular chaperone role is amplified during periods of increased stress in order to regulate cell protein damage (Sørensen et al. 2003). There are numerous families of stress proteins, characterized by their molecular weights in kilodaltons, which have been reviewed in detail by Parsell and Linquist (1993) and Feder and Hoffman (1999). The most commonly studied stress proteins in wild animals are

HSP60 and HSP70 (Willmer et al. 1999). Additional families of stress proteins may prove to be beneficial in measuring the response of birds to stress, but little work has been done to assess the validity of using those other families yet.

The HSP70 family consists of 10 homologous members, and is one of the most studied families to date (Tavaria et al. 1996). The two most notable members of the HSP70 family are HSP70B′ and HSP70B, which are only upregulated under conditions of extreme stress (Tavaria et al. 1996, Wegele et al. 2004). Other members of the HSP70 family (e.g., HSP70-1) can be upregulated quickly during stress because they do not contain introns. Similarly, HSP60 is quickly upregulated by a range of cellular damage.

Stress proteins are upregulated in response to a variety of stressors in many different species and taxa, including temperature (Gehring and Wehner 1995, Feder and Hoffman 1999, Zatsepina et al. 2000), heavy metals (Martínez et al. 2001, Werner and Nagel 1997), parasites (Nagasawa et al. 1992, Marinõ et al. 1999), nutritional stress (Merino et al. 2002), hypoxia (Ma and Haddad 1997), anoxia (Prentice et al. 2005), high popultaion density (Sørensen and Loeschcke 2001), pesticides (Yang et al. 2002, Nazir et al. 2003), food limitation, UV radiation, physical activity, and genetic stresses (Feder and Hoffman 1999, Willmer et al. 1999, Nazir et al. 2003). In comparison to CORT, stress proteins may be a more appropriate metric for detecting long term or chronic exposure to stress resulting in allostatic overload (Parsell and Lindquist 1993, Buchanan 2000), because changes may take several hours to show up in blood cells and remain there longer than CORT (Washburn et al. 2001). While stress proteins can serve as metrics of stress from a range of variables, they have only recently begun to be used in avian ecology.

Several recent avian ecology studies have successfully used stress proteins to link environmental stress to physiological factors measured in birds. Merino et al. (2002) examined how stress proteins responded to parasitism in nestling house martins (*Delichon urbica*), observing a negative relationship between chick growth and stress protein levels. These results suggest that house martins may have a limited amount of energy to expand to different nestling functions, the response of elevated stress proteins to increased parasites may reduce energy required for chick growth (Merino et al. 2002). Moreno et al. (2002) also found a negative relationship between stress proteins and chick growth parameters in pied flycatchers (*Ficedula hypoleuca*). These authors observed up to 80% of the variation in some growth parameters of pied flycatchers could be correlated with stress protein levels (Moreno et al. 2002).

Martínez-Padilla et al. (2004) found that stress proteins were an efficient estimator of competitive, nutritional, and parasite-mediated stress in nestling Eurasian kestrels (*Falco tinnunculus*). Smaller Eurasian kestrel nestlings had higher levels of stress proteins, indicative of sibling competition and food shortage (Martínez-Padilla et al. 2004). Garamszegi et al. (2006) examined the response of sexual traits to increased stress proteins in the collared flycatcher (*Ficedula albicollis*), observing that stress proteins may constrain the expression of some specific sexual traits. Male collared flycatchers that produced longer and more versatile songs had higher levels of stress proteins (Garamszegi et al. 2006). While Bourgeon et al. (2006) found that incubating female common eiders (*Somateria mollissima*) decreased their immune function corresponding to an increase in levels of HSP60 and HSP70. Additionally, CORT levels in eiders decreased during the incubation period, while stress proteins increased

(Bourgeon et al. (2006). These authors contend that these results supported the theory that CORT does not regulate immunosuppression, and additionally that stress proteins levels were not triggered by elevated levels of CORT (Bourgeon et al. 2006). Lastly, Tomás et al. (2004) found that blood stress protein levels did not change within 8 hours of sampling in the field when not frozen or centrifuged, a critical issue if collecting samples from wild birds, as in most avian ecology studies.

Common methods to measure the stress proteins include western blotting, slot blotting, radioimmunoassay (RIAs), and enzyme-linked immunosorbent assay (ELISA) (Lewis et al. 1999). Lewis et al. (1999) detailed the use of all methods available for the detection of stress proteins, noting that Western blotting has been the most common method used to measure stress proteins to date. Dot slot blotting was suggested to be a simplified approach to measuring stress proteins, but ELISAs and RIAs provide more quantitative results (Lewis et al. 1999). Stress proteins are measurable in cell lysates, tissue extracts, red blood cells, and serum samples. Levels of stress proteins may differ between these sample types (Lewis et al. 1999), so any comparisons made between studies or sample types should be limited to the response and not specific levels of stress proteins. Blood samples provide a reliable non-lethal approach to measuring stress proteins (Buchanan 2000, Moreno et al. 2002).

Conclusions

When considering the use of stress proteins as a metric of environmental stress, careful consideration should be paid to which family of stress proteins is being measured. Individual families of stress proteins may respond differently to environmental stimuli stressors than other families, where one stress protein family increases in the presence of

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stress another may remain constant. Martínez-Padilla et al. (2004) observed a significant increase in stress protein 60 during the course of a breeding season in Eurasian kestrels, while stress protein 70 remained relatively constant. Moreno et al. (2002) also found stress protein 60 levels to be negatively correlated with tarsus length and high heterophil/lymphocyte ratios, with no relationship to stress protein 70 levels. Stress proteins can also play an important role in normal cellular activities, so understanding which families are involved with specific cellular responses and what basal levels are, is significant in interpreting the response to a stimuli, just as when using CORT.

One aspect of stress protein research that can greatly enhance our understanding of homeostatic and allostatic overload levels of stress proteins in different species of birds, is if there are differences associated with season, reproductive status, sex, etc., how those differences might be expressed with the different families of stress proteins, and in different sample types. Those avian ecology studies that have used the stress proteins as a measure of response to environmental stress to physiological factors measured have largely been correlative to date. Conducting controlled experiments within aviaries could be a valuable approach to understanding the true response of the stress proteins during periods of non-stress, homeostasis, and allostatic overload, in the absence of other variables that in field studies can skew the interpretation of results (e.g., food abundance, temperature).

Recent research on fish (silver sea bream *Sparus sarba*) demonstrated that cortisol (the CORT equivalent found in fishes) could act both as an anti-apoptotic or a pro-apoptotic by either inducing or suppressing stress proteins (Deane et al. 2006). These results suggest understanding the relationship of CORT and stress proteins in birds

should be studied to determine how they might differ in their response to stress and or interact. Understanding the mechanisms behind the expression or transcriptional upregulation of stress protein also remains poorly understood, with regards to avian species. These mechanisms are critical to understanding how apparently stressed individuals (e.g., elevated CORT) might still have lower levels of stress proteins and vice versa.

The use of stress proteins in avian ecology is still in its infancy, but shows promise of being a valuable alternative metric of environmental stress in avian ecology. The stress proteins provide another method to examine the physiological response of species to stressors, and could become routine metrics of physiological condition if avian ecologists become more aware of these options. As with using CORT in avian ecology studies of stress responses to environmental stimuli, the use of stress proteins requires a thorough understanding of the species' physiology, the stressor, and the stress protein measured. Many of these assumptions and issues have already been tested on other vertebrate groups, so our ability to utilize these proteins in avian ecology may not be as limiting as perceived. Stress proteins may not prove to be the best measure of stress in all situations or in all species. They do, however, increase the options available to avian ecologists for understanding how species respond to changes in the environment and may enhance our ability to make more informed decisions regarding the conservation of birds.

LITERATURE CITED

Astheimer, L. B., W. A. Buttemer, and J. C. Wingfield. 1992. Interactions of corticosterone with feeding activity and metabolism in passerine birds. Ornis Scandinavia 23:355-365.

Breuner, C. W., and M. Orchinik. 2001. Seasonal regulation of membrane and intracellular corticosteroid receptors in the house sparrow brain. Journal of Neuroendocrinology 13:412-420.

Breuner, C. W., and M. Orchinik. 2002. Beyond carrier proteins: plasma binding proteins as mediators of corticosteroid action in vertebrates. Journal of Endocrinology 175:99-112.

Bourgeon, S., J. Martínez, F. Criscuolo, Y. L. Maho, and T. Raclot. 2006. Fasting-induced changes of immunological and stress indicators in breeding female eiders. General and Comparative Endocrinology 147:336-342.

Buchanan, K. L. 2000. Stress and evolution of condition-dependent signals. Trends in Ecology and Evolution 14:156-160.

Buchanan, K. L., and A. R. Goldsmith. 2004. Noninvasive endocrine data for behavioral studies: the importance of validation. Animal Behavior 67:183-185.

Deane, E. E., Zhou, L., and Woo, N. Y. S. (2006) Cortisol can be pro- or anti- apototic in Sea Bream cells: potential role of HSP70 induction for cytoprotection. Molecular and Cellular Endocrinology 259:57-64.

Dunlap, K. D., and J. J. Schall. 1985. Hormonal alterations and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. Physiological Zoology 68:608-621.

Ewen, B. S., and J. C. Wingfield. 2002. The concept of allostasis in biology and biomedicine. Hormones and. Behavior 43:2-15.

Feder, M. E., and G. E. Hoffman. 1999. Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. Annul Reviews of Physiology 61:243-282.

Fridinger, R. W., K. M. O'Reilly, S. D. Kildaw, and C. L. Buck. 2007. Removal of a nest-mate elicits an age-dependent increase in plasma corticosterone of nestling black-legged kittiwakes. Journal of Field Ornithology 78:93-99.

Garamszegi, L. Z., S. Merino, J. Török, M. Eens, and J. Martínez. 2006. Indicators of physiological stress and the elaboration of sexual traits in the collared flycatcher. Behavioral Ecology 17:399-404.

Gehring, W. J., and R. Wehner. 1995. Heat shock proteins synthesis and thermotolerance in Cataglyphis, an ant from the Sahara desert. Proceedings of the National Academy of Science USA 92:2994-2998.

Khan, M. Z., I. Altmann, S. S. Isani, and J. Yu. 2002. A matter of time: evaluating the storage of fecal samples for steroid analysis. General and Comparative Endocrinology 128:57-64.

Lewis, S., R. D. Handy, B. Cordi, Z. Billinghurst, and M. H. Depledge. 1999. Stress proteins (HSP): methods of detection and their use as an environmental biomarker. Ecotoxicology 8:351-368.

Ludders, J. W., J. A. Langenberg, N. M. Czekala, and H. N. Erb. 2001. Fecal

corticosterone reflects serum corticosterone in Florida sandhill cranes. Journal of

Wildlife Diseases 37:646-652.

Lynn, S. E., C. W. Breuner, and J. C. Wingfield. 2003. Short-term fasting affects

locomotor activity, corticosterone, and corticosterone binding globulin in a

migratory songbird. Hormones and Behavior 43:150-157.

Ma, E., and G. G. Haddad. 1997. Anoxia regulates gene expression in the central

nervous system of *Drysophila melanogaster*. Molecular Brain Research 46:325-

328.

Marinõ, F., C. Winters, and A. J. Morgan. 1999. Heat shock protein (hsp60, hsp70,

hsp90) expression in earthworms exposed to metal stressors in the field and

laboratory. Pedobiologia 43:615-624.

Martínez, J., J. Pérez-Serrano, W. E. Bernadina, and F. Rodríguez-Caabeiro. 2001. In

vitro stress response to elevated temperature, hydrogen peroxide and mebendazole

in *Trichinella spiralis* muscle larvae. International Journal of Parasitology 29**:**

1457-1464.

Martínez-Padilla, J., J. Martínez, J. A. Dávilla, S. Merino, J. Moreno, and J. Millán.

2004. Within-brood size differences, sex and parasites determine blood stress

protein levels in Eurasian kestrel nestlings. Functional Ecology 18:426-434.

Merino, S., J. Martínez, A. P. Møller, A. Barbosa, F. de Lope, and F. Rodríguez-

Caabeiro. 2002. Blood stress protein levels in relation to sex and parasitism of

barn swallows (*Hirundo rustica*). Ecoscience 9:300-305.

Millspaugh, J. J., and B. E. Washburn. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for applications and interpretation. General and Comparative Endocrinology 138:189-199.

Moreno, J., S. Merino, J. Martínez, J. J. Sanz, and E. Arriero. 2002. Heterophil/lymphocyte ratios and heat shock protein levels are related to growth of nestling birds. Ecoscience 9:434-439.

Nagasawa, H., M. Oka, K. Maeda, C. Jian-Guo, H. Hisaeda, Y. Ito, R. A. Good, and K. Himeno. 1992. Induction of heat-shock protein closely correlates with protection against toxoplasma-gondhii infection. Proceedings of the National Academy of Science USA 89:3155-3158.

Nazir, A., D. K. Saxena, and D. K. Chowdhuri. 2003. Induction of hsp70 in transgenic Drysophila: biomarker of exposure against phthalimide group of chemicals. Biochemical Biophysiology Acta 1621:218-225.

Parsell, D. A., and S. Lindquist. 1993. The function of heat shock proteins in stress tolerance: degradation and reactivation of damaged proteins. Annul Reviews of Genetics 72:19-24.

Prentice, H. M., S. L. Milton, D. Scheurle, and P. L. Lutz. 2005. The upregulation of cognate and inducible heat shock proteins in the anoxic turtle brain. Journal of Cerebral Blood Flow and Metabolism 24:826-828.

Romero, L. M. 2004. Physiological stress in ecology: lessons learned from biomedical research. Trends in Ecology and Evolution 19:249-255.

Romero, L. M., and J. M. Reed. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comparative Biochemical Physiology A 140: 73-79.

Romero, L. M., N. E. Cyr, and R. C. Romero. 2006. Corticosterone responses to change seasonally in free-living house sparrows (*Passer domesticus*). General and Comparative Endocrinology 149:58-65.

Sørenson, J. G., and V. Loeschcke. 2001. Larval crowding in *Drysophila melanogaster* induces Hsp70 expression, and leads to increased adult longevity and adult thermal stress resistance. Journal of Insect Physiology 47:1301-1307.

Sørensen, J. G., T. N. Kristensen, and V. Loeschke. 2003. The evolutionary and ecological role of heat shock proteins. Ecology Letters 6:1025-1037.

Tavaria, M., T. Gabriele, I. Kola, and R. L. Anderson. 1996. A hitchhiker's guide to the human Hsp70 family. Cell Stress Chaperones 1:23-28.

Teskey-Gerstl, A., E. Bamberg, T. Steineck, and R. Palme. 2000. Excretion of cortocosteroids in urine and feces of hares (*Lepus europaeus*). Journal of Comparative Physiology B 170:163-168.

Tomás, G., J. Martínez, and S. Merino. 2004. Collection and analysis of blood samples to detect stress proteins in wild birds. Journal of Field Ornithology 75: 281-278.

Verme, L. J., and R. V. Doepker. 1988. Suppression of reproduction in Upper Michigan white-tailed deer, *Odocoileus virginianus*, by climatic stress during the rut. Canadian Field Naturalist 102:550-552.

Washburn, B. S., J. J. Moreland, A. M. Slaughter, I. Werner, D. E. Hinton, and B. M. Sanders. 2001. Effects of handling on heat shock protein expression in rainbow

trout (*Oncorhynchus mykiss*). Environmental Toxicology and Chemistry 21:557-560.

Washburn, B. E., J. J. Millspaugh, J. H. Schulz, B. S. Jones, and T. Mong. 2003. Using fecal glucocorticoids for stress assessment in mourning doves. Condor 105:696-706.

Wasser, S. K., K. Bevis, G. King, and E. Hanson. 1997. Noninvasive physiologic measures of disturbance in the northern spotted owl. Conservation Biology 11: 1019-1022.

Wasser, S. K., K. E. Hunt, J. L. Brown, K. Cooper, C. M. Crockett, U. Bechert, J. J. Millspaugh, S. Larson, and S. L. Monfort. 2000. A generalized fecal corticosterone assay for use in a diverse array of nondomestic mammalian and avian species. General and Comparative Endocrinology 120:260-275.

Wegele, H., L. muller, and J. Buchner. 2004. Hsp70 and Hsp90—a relay team for protein folding. Reviews of Physiology, Biochemistry and Pharmacology 151:1-44.

Werner, I., and R. Nagel. 1997. Stress proteins HSP60 and HSP70 in three species of amphipods exposed to cadmium, diazinon, dieldrin and flouranthane. Environmental Toxicology and Chemistry 16:2393-2403.

Willmer, P. G., G. N. Stone, and I. A. Johnston. 1999. Environmental physiology of animals. Blackwell Science, Oxford, United Kingdom.

Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds. *In* K.G. Davey, R. E. Peter, and S. S. Tobe (eds). Perspectives in Comparative Endocrinology National Research Council of Canada, Ottawa, Ontario, Canada.

Wingfield, J. C., J. P. Smith, and D. S. Farner, D. S. 1992. Endocrine responses of white-crowned sparrows to environmental stress. Condor 84:399-409.

Yang, D. R., D. U. Lu, W. G. Zhang, and F. S. He. 2002. Biochemical changes in primary culture of skeletal muscle cells following dimethoate exposure. Toxicology 174:79-85.

Zatsepina, O. G., K. A. Ulmasov, S. F. Beresten, V. B. Molodtsov, and M. B. Evgen'ev. 2000. Thermotolerant desert lizards characteristically differ in terms of heat shock system regulation. Journal of Experimental Biology 203:1017-1025.

CHAPTER 4: THE PHYSIOLOGICAL EFFECTS OF VARYING FOOD LEVELS ON WHITE IBIS CHICKS IN A DYNAMIC WETLAND ECOSYSTEM

ABSTRACT

This study experimentally examined the physiological effects of food supplementation on white ibis chicks to determine the consequences of changes in prey intake as reflected by prey availability at a landscape scale. During 2006, a year with above average landscape prey availability, differences between control and provisioned chicks were not detected. In contrast, 2007 was a year with considerably less prey available in the landscape and control chicks had significantly higher levels of stress protein 60 and fecal corticosterone. Physiological responses measured in plasma corticosterone and stress protein 70 were less predictable. Glycerol and triglyceride levels did not differ significantly between years or between supplemented and control chicks. Stress protein 60 and fecal corticosterone both reflected varying levels of prey availability and therefore may be good measures of the physiological response of wild wading birds in the future. The combination of a food supplementation experiment and physiological responses provided new insight into how ecosystem conditions can affect a specialized searcher foraging species. This knowledge could ultimately lead to novel predictions about population and community patterns of wetland birds.

INTRODUCTION

Environmental variability often results in seasonal and interannual differences in the availability of food for the chicks of most avian species. This variability is considered one of the primary influences that have produced specific life-history traits in birds such as small and large clutch sizes (Lack 1968, Ricklefs 1968, Metcalfe and Monaghan 2001). The responses of chicks to changing levels of food have been observed in growth patterns, development, and survival (Gebhart-Henrich and Richner 1998, Brzek and Konarzeewski 2001). Further, the response of chicks to changing food availability can also be observed in physiological markers that reflect a change in the level of food within the landscape.

While many studies have examined the role food limitation plays on the growth and survival of chicks (see Cook and Hamer 1997, Dewey and Kennedy 2001, Gjerdrum 2004), there remains no definitive response of chicks to changing food availability during the breeding season. Understanding this response by wading bird chicks, whose parents often acquire food from large areas over a nesting season can be an important consideration in wetland ecosystem management and restoration. The responses by wading birds are used currently as performance measures or indicators by which to gauge ecosystem restoration and management in the Florida Everglades (Gawlik 2006). An assumption underlying the use of these birds as performance measures is that the ecosystem processes being manipulated, such as water levels, produce a response in the prey community, which subsequently produces a response in birds.

Another factor associated with potential responses of wading bird chicks to changing levels of food availability is the fact that wading bird chicks hatch

asynchronously. Typically, the first born A chick has a size advantage within the nest,

allowing it to obtain more food from the parent (Kushlan and Bildstein 1992, Mock and

Parker 1997). Thus, differences in growth rates and physiological condition between A

hatched chicks and subsequent hatched chicks may not be related to landscape habitat

conditions and food limitations, varying considerably in years with different habitat

conditions (Monaghan et al. 1989, Harding et al. 2007). Given that birds utilize a life

history strategy to time their reproduction with maximum levels of food abundance

(Perrins 1991, Houston 1997, Thomas et al. 2001), during good years differences

between chicks is likely minimal. During years with low prey availability, life history

suggests that long-lived birds should minimize their energy expenditure to chicks and

maintain their own physiological condition (Sæther et al. 1993, Mauck and Grubb 1995).

One approach to understand how wading bird chicks are affected by changes in

landscape level prey availability then is to measure physiological variables that might

respond in a predictable manner to these changes in food availability. If seasonal food

availability fluctuations at the landscape level influence physiological condition of adults

and in turn, the amount of energy they invest in reproduction (see Chapter 6), then certain

physiological parameters should be discernable reflecting those differences at the chick

level as well. Coupling physiological markers with provisioning experiments allows for

measurement of physiological responses related to varying amounts of food. For

example, recent physiology research has shown that food-related stress can account for

lower body mass, depleted lipid reserves, and elevated levels of baseline levels of

corticosterone (CORT) in colonial nesting birds at fledging that were supplementally fed

compared to chicks fed *ad libitum* (Boag 1987, Kitaysky et al. 1999, Romano 2000).

In this experiment I measured changes in the physiological condition of white ibis (*Eudocimus albus*) chicks in response to experimental food supplementation during years (2006 and 2007) with prey densities that differed by up to 73% (Gawlik and Botson 2007). I selected physiological markers that might reflect short-term (e.g., triglycerides [TRIG], glycerol [GLYC]), medium-term (e.g., plasma corticosterone [PCORT]), and long-term (e.g., fecal corticosterone [FCORT], stress protein 60 [SP60], stress protein 70 [SP70]) responses to food limitation.

An important method to examine short-term physiological condition of birds is the use of blood metabolite levels. TRIG in blood are often positively correlated with an increase in body mass, and high levels indicate energy (lipid) storage, while elevated GLYC correlate with decreasing mass (Jenni-Eierman and Jenni 1994, Williams et al. 1999, Masello and Quillfeldt 2004, Quillfedt et al. 2004, Anteau 2006). TRIG and GLYC tend to be short-term measures, and typically represent responses within, at most, the last 2 days (Jenni-Eierman and Jenni 1994, Williams et al. 1999, Anteau 2006).

As stored TRIG are utilized and depleted, birds will begin to catabolize muscle protein (Cherel et al. 1988), which is motivated by the secretion of CORT via the stress response (Quillfeldt et al. 2004). If the stressor persists and CORT remain elevated, destructive chronic effects may begin (e.g., decreased growth rates) as allostatic overload occurs. Under conditions of food scarcity, CORT stimulates gluconeogenesis, shifting catabolism away from fats towards proteins (Astheimer et al. 1992, Wingfield 1994). Chronic elevated levels of CORT can reduce the fitness of individuals via immunosuppression and result in decreased growth and survival rates for chicks (Dunlap and Schall 1985, Wingfield et al. 1992). FCORT levels reflect residue levels of PCORT.

However, rapid and extensive metabolism before excretion results in lower overall levels than circulating levels (Wasser et al. 2000).

Stress proteins are a group of highly conserved intracellular polypeptides (Linquist 1986) that function as molecular chaperones for proteins within cells, and present a major molecular barrier to alterations in cellular homeostasis (Tomás et al. 2004). Their molecular chaperone role is amplified during periods of increased stress in order to regulate cell protein damage (Sørenson 2003). Recent papers have evaluated the effectiveness of using stress proteins to examine physiological condition in avian ecology (Moreno et al. 2002, Martínez-Padilla et al. 2004, Tomás et al. 2004, Herring and Gawlik 2007), suggesting that they can be a valuable metric in avian studies.

My objectives with this experimental food limitation research were threefold: 1) assess whether white ibis chicks were food-limited by comparing chick physiological markers during years with contrasting food availability (*Food Limitation Hypothesis*), 2) examine how chick hatch order affects physiological responses to food limitation (*Hatch Order Hypothesis*), and 3) determine the utility of using physiological markers to measure and test the response of chicks to food limitation (*Physiological Markers*).

I predicted that A chicks would be less stressed than subordinate chicks, shown by lower levels of PCORT, FCORT, SP60 or SP70, and in better physiological condition (e.g., higher levels of TRIG, lower levels GLYC) when food was less available. I also expected that in years with high prey availability, chicks would receive more food on a regular basis so differences between A chicks and subordinate chicks would not be as substantial as in years with low levels of food availability.

METHODS

Study Area

The provisioning experiment was conducted within the Arthur R. Marshall

Loxahatchee National Wildlife Refuge (Lox) during the 2006 and 2007 wading bird

breeding seasons at New Colony 3 (26°31N, 80°17) and New Colony 4 (26°31N,

80°16.5W). Colonies in Lox consisted of up to 50 tree islands, 0.04 – 0.13 ha in size,

dominated by cocoplum (*Chrysobalanus icaco*), willow (Salix spp.), dahoon holly (*Ilex*

cassine), smilax (*Smilax laurifolia*), red bay (*Persea barbonia*), and wax myrtle (*Myrica*

cerifer). Over 90% of the wading bird nests in the colonies in Lox were white ibis, with

the remainder being snowy egret (*Egretta thula*), little blue heron (*E. caerulea*), great

egret (*Ardea alba*), and black-crowned night-heron (*Nycticorax nycticorax*).

Food Supplementation

The food supplementation component of this research was a collaborative effort

with M. Cook at the South Florida Water Management District (SFWMD). Nest

selection and food supplementation were carried out by the SFWMD while I oversaw the

collection and analysis of all physiological samples. White ibis nests in two breeding

colonies were randomly selected and assigned to either the control or experimental group.

Thirty-six nests were studied in 2006 (18 supplemented and 18 control) and 46 nests in

2007 (22 supplemented and 24 control). All chicks were banded to allow individual

identification, and their hatch order was recorded.

Food supplementation began approximately six days after hatching to avoid

abandonment by adults and undue stress to young birds (Bancroft 1990). Supplemented

chicks were fed 10 g of native Everglades fishes per chick 5 consecutive days a week.

The species of Everglades fish were eastern mosquitofish (*Gambusia holbrooki*), flagfish (*Jordanella floridae*), golden topminnow (*Fundulus chrysotus*), and sailfin molly (*Poecilia latipinna*). These species occur in the diet of white ibis chicks (Kushlan 1979, Kushlan and Bildstein 1992, Dorn et al. *In Press*) and are common throughout the Everglades (Trexler et al. 2001). Control nests received no supplement but were visited and handled to standardize the disturbance effect. Growth of chicks was measured every 3-4 d using standard morphometric measurements until approximately 25 d post hatching.

Chick Physiology Sampling

I attempted to collect blood and fecal samples from chicks at two separate stages (~10 d and ~20 d; hereafter early and late chick stages). Mean ages of chicks sampled during early and late stages were 11.6 days ± 0.4 SE and 21.9 days ± 1.0 SE, respectively. On sampling days, chicks were removed from nests and then taken to an adjacent site to minimize disturbance and reduce stress bias in sampled chicks. Because blood samples could not be obtained in less than 3 minutes to achieve a baseline level of CORT (Romero and Reed 2005) I measured time to blood draw to determine if handling time had an effect on PCORT levels (Romero and Reed 2005). I collected up to 1 ml of blood from the brachial or jugular veins using a 27.5-gauge needle. Blood samples were stored in heparinized Vacuutainers and placed on ice until transported to the lab. I then extracted up to 2 ml of fecal material directly from the cloaca of the chick using a micropipette. Fecal samples were stored in micro centrifuge tubes and placed on ice.

In the lab, blood samples were centrifuged (15 min, 10,000 g) and plasma and red blood cells were then separated and frozen at -20° C for later analysis. Fecal samples were also frozen at -20° C for later analysis. TRIG and GLYC were measured using

enzymatic endpoint assays following Williams et al. (1999) using Sigma kits (Sigma, Saint Louis, MO). Assays were then validated using reference values from normal and abnormal human control sera. Inter- and intraassay coefficients of variation for triglycerides internal standards were 6% and 9% and 5% and 8% respectively.

PCORT and FCORT samples were homogenized and then mixed with methanol and vortexed for 30 min. After centrifugation (15 min, 2500 g) I transferred the supernatant to a new vial, which was then evaporated under a stream of nitrogen gas. CORT metabolites were then resuspended in diluted extraction buffer and measured using enzyme-linked immunosorbent assays (ELISA; Neogen, Lexington, KY). Inter- and intraassay coefficients of variation for PCORT and FCORT internal standards were 4% and 7%. I also validated that FCORT levels did not change after freezing, as in the case of mammals (Khan et al. 2003), by freezing and measuring FCORT levels monthly for 6 months (Herring and Gawlik *In Review*). This experiment suggested that cross-reacting metabolites did not change levels of FCORT in my samples and therefore freezing did not bias my results.

Red blood cells were washed three times using phosphate buffered saline, centrifuged and the supernatant was removed after the final wash. Red blood cell supernatant was then mixed with 1✖ extraction reagent and a protease inhibitor cocktail (Sigma), vortexed for 5 min and then sonicated for 1 min. Samples were again centrifuged (15 min, 2500 g) and the supernatant removed. I measured SP60 and SP70 (SP70-1) in the supernatant using ELISA kits (Assay Designs, Inc., Ann Arbor, MI). Inter- and intraassay coefficients of variation for SP60 and SP70 internal standards were 5% and 7% and 6% and 7% respectively. All samples were run in duplicate, and means

of duplicates were used in all analyses. All ELISA kits were validated using serial

dilutions and spike tests to determine percent recovery (Chapter 5).

Chick Physiology Statistical Analysis

I used general linear models (GLM) to test for differences between independent

variables for each physiological metric. Independent variables were year (2006 or 2007),

treatment (control or supplemented), chick hatch order (A or B chick), and sampling date

(early or late). No chicks used in this analysis were sampled more than once. I also

removed C hatched chicks from all analysis due to small samples sizes. The full model

contained terms for all main effects and their interactions. Interaction terms were

dropped from the final model when not significant. Post hoc tests were conducted using

Tukey's HSD to protect for Type I error.

I used correlation analysis to examine the relationship between all physiological

parameters (GLYC, TRIG, PCORT and FCORT metabolites, SP60 and SP70). This

analysis allowed for an assessment of how physiological parameters respond with one

another: positive relationship, negative relationship, or no relationship with changes in

other metrics of physiological condition.

RESULTS

I collected physiological samples from 64 chicks during 2006 (n = 43) and 2007

(n = 21). During 2006, 24 provisioned and 19 control chicks were sampled, and in 2007,

13 provisioned and 8 control chicks were sampled. Samples sizes for hatch order (A, B,

and C chicks) were 31, 11, and 1 respectively in 2006, and 12, 7, and 2 in 2007. I only

used data from the 61 A or B chicks in my analysis.

Chick Physiological Condition

Short-term markers of physiological condition did not show any overall response

to year or treatment differences. GLYC levels did not differ by treatment (P = 0.94),

hatch order (P = 0.98), year (P = 0.72), or collection date (P = 0.98; Table 1). TRIG

levels were similar by year (P = 0.06), treatment (P = 0.22), hatch order (P = 0.44), and

collection date (P = 0.06).

PCORT levels differed by year (P = 0.004, Fig. 1) and had a significant hatch

order × treatment effect (P = 0.02), although the Tukey HSD post hoc test did not reveal

where those differences were. Means suggested A control chicks had higher PCORT

than A provisioned chicks, while B control chicks had lower levels of PCORT than B

provisioned chicks. I observed a significant FCORT year × chick order interaction (P =

0.003), and chick order × collection date interaction (P = 0.003). FCORT levels were

higher in B chicks in 2007 than 2006, while A chicks did not differ between years (Fig.

2). Early B chicks had lower FCORT levels relative to late B chicks, while A chicks did

not differ (Fig. 3). FCORT levels were higher during 2007 than in 2006 (P <0.0001, Fig.

4), lower in A chicks than B chicks (P = 0.005), higher in control than treatment chicks

(P = 0.02), and higher in late than in early sampled chicks (P = <0.001; Table 1).

Overall, SP60 differed significantly between the two years (P < 0.001; Fig. 5) but not by feeding treatment, hatching order or age (Table 1). However, the interactions of year and treatment (P = 0.03) showed that while feeding treatment had little effect on stress levels in a good year (2006), control chicks were more stressed than fed chicks in a poor food year (2007; Fig. 6). Similarly, the interaction of year and hatch order (P = 0.01) showed that stress levels were similar among A and B-hatched chicks in a good food year but B-chicks suffered relatively higher stress than A-chicks in the poor food year (Fig. 7). There was no evidence of difference in SP70 levels between year (P = 0.94), treatment (P = 0.24), or collection date (P = 0.98), but increased with hatch order (P = 0.05; Fig. 8, Table 1).

Correlation analysis

Correlation analysis revealed that SP60 and SP70 (P = 0.0008), SP60 and FCORT (P = 0.02), and SP 60 and GLYC (P = 0.03) all had significant positive relationships (Table 2). However, the amount of variation explained by these models did not exceed 29% (SP60 and SP70), and was only 13% for the remaining two significant models (Table 2). All other combinations of physiological metrics were not correlated significantly (all P's > 0.05; Table 2).

DISCUSSION

Food Limitation Hypothesis

This is the first study to identify a pathway by which food in the Everglades can lead to effects on wading bird reproduction via physiology. Demonstrating food limitation in white ibis chicks is a critical because this species has experienced a long-term decline in nesting numbers in the Everglades (Crozier and Gawlik 2003). While not all wading birds have show long-term declines in nesting trends similar to white ibis, there are several species (e.g., snowy egret, wood stork [*Mycteria americana*]) that have demonstrated similar nesting trends (Crozier and Gawlik 2003). One important similarity between these species that have demonstrated long-term declines in nest effort is that they are all searcher foraging species (Gawlik 2002). Searcher species locate high quality patches, forage there until the patch reaches some level of a give up density (e.g., decreased prey density), and then move on and search for a more profitable patch (Gawlik 2002).

The development of a life history trait such as the searcher foraging strategy is based on a long-term average benefit, such that this particular species has adapted its foraging behavior to take advantage of the environment around it. The searcher foraging strategy likely developed under optimal condition results in a surplus of food captured and returned to the nest with a minimum time or energy investment. This scenario fits the results from this study during 2006, the year with elevated prey densities across much of the Everglades ecosystem. During 2006, white ibis chick physiological condition was elevated relative to their physiological condition during 2007, when prey densities dropped by nearly 80% across much of the Everglades (Gawlik and Botson 2008).

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During years with below average prey densities, the searcher strategy may be mismatched to the current landscape patterns. Historically, white ibis would have had a surplus of potential foraging sites throughout the breeding season in the Everglades, with increased short-hydroperiod wetlands and stable coastal wetlands (Kushlan 1977, Sklar et al. 2002). Coupled with the annual drying cycle during good recession years, high quality foraging patches would likely have been more abundant, and near continuously available at a spatial and temporal pattern matched to reproduction. Large changes in the annual hydrological cycle during the last century, loss of much of the short-hydroperiod wetlands, and the impoundment of much of the Everglades has resulted in fewer, more disperse short-hydroperiod wetlands, with increased sensitivity to hydrological reversal associated with impounding (Sklar et al. 2005). During current below average prey density years, the implications are that white ibis may spend more time and energy searching for high quality patches to provision chicks, resulting in a concomitant reduction in the time and energy available for nestlings.

The physiological response of chicks in this study strongly suggests that white ibis were food limited in 2007, but not 2006. These data were supported by chick growth and survival data (Cook and Herring 2007) that demonstrated associated differences in white ibis chick growth and survival with this same experimental provisioning study, supporting my results that ibis chicks were indeed food limited. Their study found that differences in growth rates between provisioned and control chicks were most apparent during the low habitat quality year, 2007, when prey availability was lower across the Everglades ecosystem. Similarly, my physiological results from those same experimental

ibis chicks differed most during the year with lower prey availability (2007), thus reflecting food limitation at the landscape level scale.

Several prior studies have failed to show a significant effect of food limitation on chick fitness (e.g., mass) using experimental treatments (e.g., Korpimäki 1989, Ward and Kennedy 1996). One of the main arguments for why these studies did not find a significant effect of food limitation on chick fitness is that food is probably not a limiting factor every year for every species, or in every possible region (Dewey and Kennedy 2001, this study), or perhaps only the fittest individuals reproduce in poor years. Tests of food limitation theory often never assess food availability during the period of study (e.g., Ward and Kennedy 1996); interpretation of results can then be complicated because you may in fact not be testing what the experiment was designed to test. This issue often results in the suggestion that predation and disease may be more influential regulators of avian populations than food availability (e.g., Martin 1993, Rostogi et al. 2006). However, research suggests increased food availability can decrease predation rates (Ward and Kennedy 1996, Rostogi et al. 2006, Zanette et al. 2006). Subsequently, it may be more appropriate to ask under what condition populations will be limited, rather than is a population regulated by a process like predation, disease, or food. This key difference is based on recognizing that food limitations probably occur irregularly in most systems and that they likely interact with other potential population regulators.

Hatch Order Hypothesis

While brood reduction is common for white ibises (Kushlan 1977), the mechanistic link between physiological condition and brood reduction or decreased survival remained unclear until this study. Kushlan (1977) demonstrated that hatch order

played an important role in the survival of white ibis chicks, with only A-hatched chicks typically surviving. Differences between clutch sizes and fledging rates in Kushlan's study were hypothesized to be associated with differences in prey availability. In this study, increased stress levels (FCORT and SP60) during 2007 may have played a role in slower growth rates and decreased survival associated with poor prey availability, most notably in B chicks (Cook and Herring 2007).

Given that asynchronous hatching can result in a size advantage during provisioning from adults (Kushland and Bildstein 1992, Mock and Parker 1987), it is not surprising that these stress responses were observed in B chicks, which tend to be smaller than A chicks. Assumingly, increased stress levels in B-hatched chicks mediated a stress response (e.g., increased begging; Kitaysky et al. 2001, Saino et al. 2003) in response to lower prey availability. Collectively, this study demonstrates that changes in landscape level prey availability do influence white ibis chick physiology via food limitation. Those results tend to be only observed in B chicks and between years with large differences in prey availability. Assumingly, these affects would also be observed in C chicks. Given that very few C chicks survived in 2007, it seems likely that the magnitude of the effect might be greater.

Physiological Markers

This study provides support that several of the physiological markers measured did respond to changes in food supplementation, and suggested that food was limited during 2007 but not 2006. Those responses were best observed in SP60, FCORT, and to a limited extent PCORT and SP70. Physiological responses measured in PCORT and SP 70 were less predictable, but still showed differences between years and hatch order of

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chicks. GLYC and TRIG levels provided no indication of the condition of chicks or interannual differences.

While these responses demonstrate differences in physiological condition between provisioned and control chicks and between years, they also reflected the temporal responses of the different physiological markers and their potential value as a metric of response to landscape level prey availability. Not surprisingly, those physiological markers that reflect short-term responses provided no information on the physiological condition of chicks between years or treatments, except for PCORT, which demonstrated that hatch order was important in association with treatment effects. The fact that these short-term markers can respond so rapidly suggests that they likely only reflect the status of the chick on the exact day of sampling, and therefore do not reflect the long-term effects associated with the provisioning experiments (Zajac et al. 2006) or prey availability at the landscape scale. Medium-term responses provided a clearer picture of the difference in physiological responses between provisioned and control chicks, while generally the long-term responses provided the clearest picture if there were physiological differences associated with food limitation between provisioned and control chicks and between years.

To my knowledge, this is the first food supplementation experiment that demonstrates the utility of using stress proteins as a metric of physiological condition associated with prey availability. More importantly, this is the first food supplementation experiment that demonstrates a significant response of a stress protein to a decrease in prey availability at a landscape scale. Interestingly, only SP60 levels increased in response to this apparent landscape stressor. Other recent research in avian ecology using

both SP60 and SP70 provided similar evidence that these two stress proteins may not respond similarly to a common stressor. Martínez-Padilla et al. (2004) observed a significant increase in SP60 during the course of a breeding season in Eurasian kestrels (*Falco tinnunculus*), while SP70 remained relatively constant. Moreno et al. (2002) also found SP60 levels to be negatively correlated with tarsus length and high heterophil/lymphocyte ratios, with no similar relationship for SP70 levels in pied flycatchers (*Ficedula hypoleuca*). Results from this study concur with these results and suggest that SP60 may be a better physiological marker of stress in birds associated with food limitation than SP70.

CORT levels in this study responded similarly to stress proteins in that PCORT and FCORT did not respond in the same manner between provisioned and control chicks. While both PCORT and FCORT were higher in 2007 than 2006, only FCORT showed a treatment response. The fact that PCORT did not show a difference between treatments may be due to the confounding effects of handling time bias. While studies have demonstrated that sampling blood in < 3 min can minimize the potential for bias (Romero and Reed 2005) this was not feasible within these wading bird colonies. PCORT samples in this study likely do not reflect basal levels given that the mean time to plasma collection was > 6 min. Values more likely reflect some level of the additive response of the handling effect on top of basal levels. The time at which chicks begin to respond to disturbance within the colony associated with nest checks and capturing neighboring chicks probably far exceeds the period that I measured handling stress. Accordingly, I suggest that these estimates of PCORT did not accurately describe basal levels of stress

in white ibis chicks, nor did I feel it appropriate to adjust PCORT levels down based on a handling time effect.

Correlation of physiological responses in this study occurred in a predictable manner in most cases: generally as metrics that measure stress increase, so did similar metrics (e.g., SP60 and SP70, albeit a weak correlation). However, not surprising, all response variables that measured stress were not all correlated. This likely stems from differences in the time that these physiological metrics take to respond, how long those responses are present, and potential differences in the stressors to which they respond. Coupling my results with those that reflected interannual and experimental differences, it seems the most parsimonious approach to measuring physiological response of wild wading birds in the future should include at least SP60 and FCORT.

Future experimental provisioning research might use a comparative approach between contrasting species to gain additional insight into how species-specific responses might mitigate the influence of variable prey availability. Results from field studies (Chapter 7) suggested that regardless of landscape habitat condition, great egrets chicks tended to weather conditions better, with better physiological condition that likely played a large role in higher nest success during below average prey availability years (Chapter 6). Understanding the physiological responses of great egrets to prey supplementation may elucidate additional factors that help explain why their populations have remained stable or increased while white ibis populations have declined (Crozier and Gawlik 2003).

LITERATURE CITED

Anteau, M. J. 2006. Ecology of lesser scaup and amphipods in the upper-Midwest: scope and mechanism of the spring-condition hypothesis and implications for migratory habitat conservation. Dissertation, Louisiana State University, Baton Rouge, LA.

Astheimer, L. B., W. A, Buttemer, and J. C. Wingfield. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scandinavia 23:355-365.

Bancroft, G. T., S. D. Jewell, and A. M. Strong. 1990. Foraging and nesting ecology of herons in the lower Everglades relative to water conditions. Final report to South Florida Water Management District West Palm Beach, FL.

Boag, P. T. 1987. Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). Auk 104:155-166.

Brzek, P., and M. Moarzewski. 2001. Effect of food shortage on the physiological and competitive abilities of sand martin (*Riparia riparia*) nestlings. Journal of Experimental Biology 204:3065-3074.

Cherel, Y., J. P. Robin, and Y. Le Mayo. 1988. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66:159-166.

Cook, M. I., and K. C. Hamer. 1997. Effects of supplementary feeding on provisioning rates of nestling puffins *Fratercula artica*; evidence for regulation of growth. Journal of Avian Biology 28:56-62.

Cook, M. I., and H. K. Herring. 2007. Food availability and white ibis reproductive success: an experimental study. *In* Cook and Herring (eds) South Florida wading bird report, Volume 13. South Florida Water Management District, West Palm Beach, FL.

Crozier, G. E., and D. E. Gawlik. 2003. Wading bird nesting effort as an index of wetland ecosystem integrity. Waterbirds 26:303-324.

Dewey, S. R., and P. L. Kennedy. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of northern goshawks. Auk 118:352-365.

Dorn, N. J., G. Herring, and D. E. Gawlik. *In Press*. Estimation of crayfish abundance and size-structure in White Ibis diets. *Waterbirds*.

Dunlap K. D., and J. J. Schall. 1985. Hormonal alterations and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. Physiological Zoology 68:608–621.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Gawlik, D. E., and B. Botson. 2007. Aquatic fauna seasonal concentrations, contract CP040319. Unpublished annual report to the South Florida Water Management District, West Palm Beach, FL.

Gebhardt-Henrich, S., and H. Richner. 1989. Causes of growth variation in and its consequences for firness. *In* Starck and Ricklefs (eds) Avian growth and development. Oxford University Press, New York, NY.

Gjerdrum C. 2004. Parental provisioning and nestling departure decisions: a
supplementary feeding experiment in tufted puffins (*Fratercula cirrhata*) on
Triangle Island, British Columbia. Auk 121:463–472

Harding, A. M., J. F. Piatt, J. E. Schmutz, M. T. Shultz, T. I. Van Pelt, A. R. Kettle, and
S. G. Speckman. 2007. Prey density and the behavioral flexibility of a marine
predator: the common murre (*Uria aalge*). Ecology 88:2024-2033.

Herring, G. and D. E. Gawlik. 2007. The role of stress proteins in the study of allostatic
overload in birds, use and applicability to current studies in avian ecology. The
Scientific World Journal 7:1596-1602.

Herring, G. and D. E. Gawlik. *In Review*. Stability of avian fecal corticosterone
metabolite levels in frozen avian feces. General and Comparative Endocrinology.

Houston, D. C. 1997. Nutritional constraints on egg production in birds. Proceedings of
the Nutrition Society 56:1057-1065.

Jenni-Eierman, S., and L. Jenni. 1994. Plasma metabolite levels predict individual body
mass changes in a small long-distance migrant, the Garden Warbler. Auk
111:888-899.

Kitaysky, A. S., J. F. Piatt, J. C. Wingfield, and M. Romano. 1999. The adrenocortical
stress-response of Black-legged Kittiwake chicks in relation to dietary
restrictions. Journal of Comparative Physiology 169:303-310.

Kitaysky A. S., J. C. Wingfield, J. F. Piatt. 2001. Corticosterone facilitates begging and
affects resource allocation in the black-legged kittiwake. Behavioral Ecology
12:619-625.

Korpimaki, E. 1989. Breeding performance on Tengmalm's owl *Aegolius funereus*:
effects of supplementary feeding in a peak vole year. Ibis 131:51-56.

Kushlan, J. A. 1979. Feeding ecology and prey selection in the white ibis. Condor
81:376-389.

Kushlan, J. A., and K. L. Bildstein. 1992. White Ibis. *In* A. Poole and F. Gill (eds.). The
Birds of North America, No. 570. The Birds of North America, Inc., Philadelphia,
PA.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, Oxford, UK.

Linquist, S. 1986. The heat shock response. Annual Review of Biochemistry 55:1151-
1191.

Martin, T. E. 1993. Nest predation and nest sites. New perspectives on old patterns.
Bioscience 43:523-532.

Martínez, J., J. Pérez Serrano, W. E. Bernardina, and F. Rodríguez-Caabeiro. 2001. In
vitro stress response to elevated temperature, hydrogen peroxide and mebendazole
in *Trichinella spiralis* muscle larvae. International Journal of Parasitology
29:1457-1464.

Martínez-Padilla, J., J. Martínez, J. A. Dávilla, S. Merino, J. Moreno, and J. Millán.
2004. Within-brood size differences, sex and parasites determine blood stress
protein levels in Eurasian kestrel nestlings. Functional Ecology 18:426-434.

Masello, J. F., and P. Quillfeldt. 2004. Are haematological parameters related to body
condition, ornamentation and breeding success in wild burrowing parrots
Cyanoliseus patagonus? Journal of Avian Biology 35:445-454.

Mauck, R. A., and T. C. Grubb, Jr. 1995. Petrel parents shunt all experimentally

    increased reproductive costs to their offspring. Animal Behaviour 49:999-1008.

McCrimmon, D. A., Jr., J. C. Ogden, and G. T. Bancroft. 2001. Great egret (*Ardea alba*).

    In A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of

    North America, Inc., Philadelphia, PA.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay

    later?. Trends in Ecology and Evolution 16:254–260.

Mock, D. W., and G. A. Parker. 1997. The evolution of sibling rivalry. Oxford

    University Press, Oxford UK.

Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine, and J. Blackwood. 1989. The

    relationship between food supply, reproductive effort and breeding success in

    Arctic terns *Sterna paradisaea*. *Journal of Animal Ecology* 58:261–274.

Moreno, J., S, Merino, J. Martínez, J. J. Sanz, and E, Arriero. 2002.

    Heterophil/lymphocyte ratios and heat shock protein levels are related to growth

    of nestling birds. Ecoscience 9:434-439.

Perrins, C. M. 1991. Tits and their caterpillar food supply. Ibis 133:49-54.

Quillfeldt, P., J. F. Masello, and E. Möstl. 2004. Blood chemistry in relation to nutrition

    and ectoparasite load in Wilson's storm-petrels *Oceanites oceanicus*. Polar

    Biology 27:168-176.

Ricklefs, R. E. 1968. On the limitations of brood size in passerine birds by the ability of

    adults to nourish their young. Proceedings of the National Academy of Science.

    61:847-851.

Romano, M. D. 2000. Effects of diet on growth and development of nestling seabirds. Thesis, Oregon State University, Corvallis, OR.

Romero, M. L., and J. M. Reed. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comparative Biochemistry and Physiology, Part A 140:73-79.

Rastogi, A. D., L. Zanette, and M. Clinchy. 2006. Food availability affects diurnal nest predation and adult antipredator behavior in song sparrows, *Melospiza melodia*. Animal Behaviour 72:933-940.

Sæther, B. B., R. Andersen, and H. C. Pedersen. 1993. Regulation of parental effort in a long-lived seabird – an experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antartica*. Behavioral Ecology and Sociobiology 33:147-150.

Saino, N., C. Suffritti, R. Martinelli, D. Rubolini, and A. P Møller. 2003. Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). Behavioral Ecology 14:318 -325.

Sklar, F., C. McVoy, R. VanZee. D. E. Gawlik, K. Taroton, D. Rudnick, and S. Miao. 2002. The effects of altered hydrology on the ecology of the Everglades. Pp. 39 – 82, in J. W. Porter and K. G. Porter (eds.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC, Boca Raton.

Sklar, F. H., M. J. Chimney, S. Newman, P. McCormick, D. Gawlik, S. Miao, C.,McVoy, W. Said, J. Newman, C. Coronado, G. Crozier, M. Korvela, and K.

Rutchey. 2005. The ecological-societal underpinnings of Everglades restoration. Frontiers in Ecology and the Environment 3:161-169.

Sørensen, J. G., T. N., Kristensen, and V. Loeschke. 2003. The evolutionary and ecological role of heat shock proteins. Ecological Letters 6:1025-1037.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598-2600.

Tomás, G., J. Martínez, and S. Merino. 2004. Collection and analysis of blood samples to detect stress proteins in wild birds. Journal of Field Ornithology 75:281-278.

Trexler, J. C., W. F. Loftus, C. F. Jordan, J. Chick, K. L. Kandl, T. C. McElroy, and O. L. Bass. 2001. Ecological scale and its implications for freshwater fishes in the Florida Everglades. Pp. 153 – 181, in J. W. Porter and K. G. Porter (eds.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC, Boca Raton.

Ward, J. M., and P. L. Kennedy. 1996. Effects of supplemental food on size and survival of juvenile northern goshawks. Studies in Avian Biology 16:114-118.

Wasser, S. K., K. E. Hunt, J. L. Brown, K. Cooper, C. M. Crockett, U. Bechert, J. J. Millspaugh, S. Larson., and S. L. Monfort. 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. General and Comparative Endocrinology 120:260–275.

Williams, T. D., C. G. Guglielmo, O. Egeler, and C. J. Mortyniuk. 1999. Plasma lipid metabolites provide information on mass change over several days in captive Western Sandpipers. Auk 116:994-1000.

Wingfield, J. C., C. M. Vleck, and M. C. Moore. 1992. Seasonal changes of the

adrenocortical response to stress in birds of Sonoran Desert. Journal of

Experimental Zoology 264:419-428.

Wingfield, J. C., G. Ramos-Fernandez, A. Nunez-de la Mora, and H. Drummond. 1999.

The effects of an *El Nino* southern oscillation event on the reproduction in male

and female Blue-footed Boobies, *Sula nebouxii*. General and Comparative

Endocrinology 114:163-172.

Zajak, R. M., D. J. Cerasale, and C. G. Guglielmo. 2006. The rapid response of plasma

metabolites to changes in feeding rate in a small passerine Wilson's warbler

Wilsonia pusilla. Journal of Avian Biology 37:405-408.

Zanette, L., M. Clinchy, and J. N. M. Smith. 2006. Combined food and predator effects

on songbird nest survival and annula reproductive success: results froma bi-

factorial experimnet. Oecologia 147:632-640.
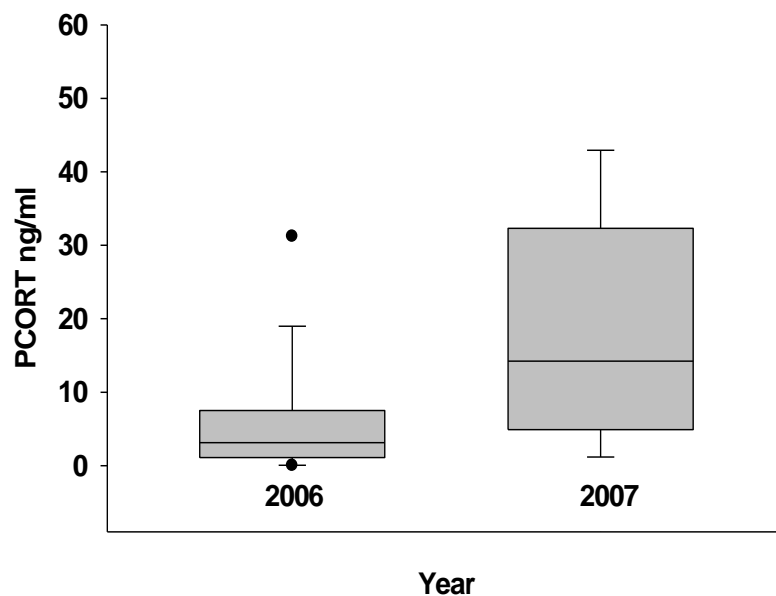
Figure 1. Plasma corticosterone levels in white ibis chicks (all birds pooled) during 2006 – 2007.
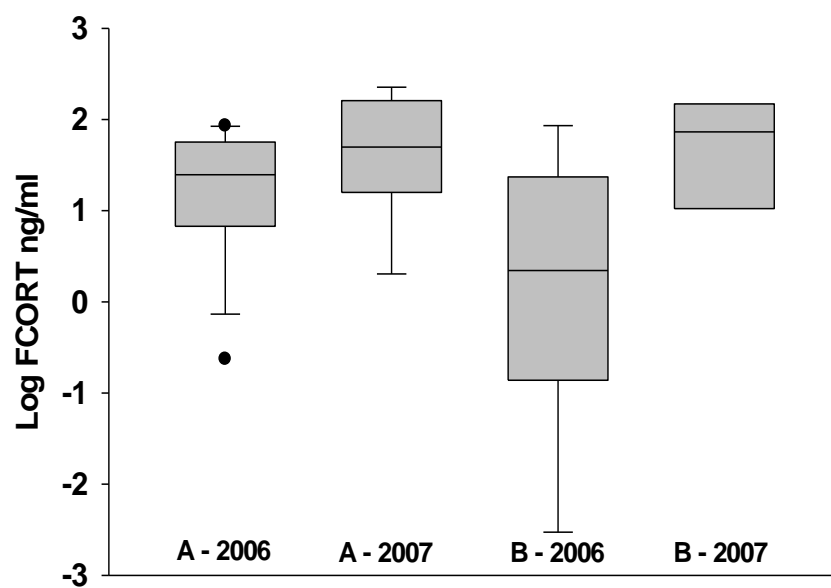
Figure 2. Log fecal corticosterone levels in and A and B-hatched white ibis chicks during 2006 – 2007.

Figure 3. Log fecal corticosterone levels in early versus late sampled white ibis chicks during 2006 – 2007.
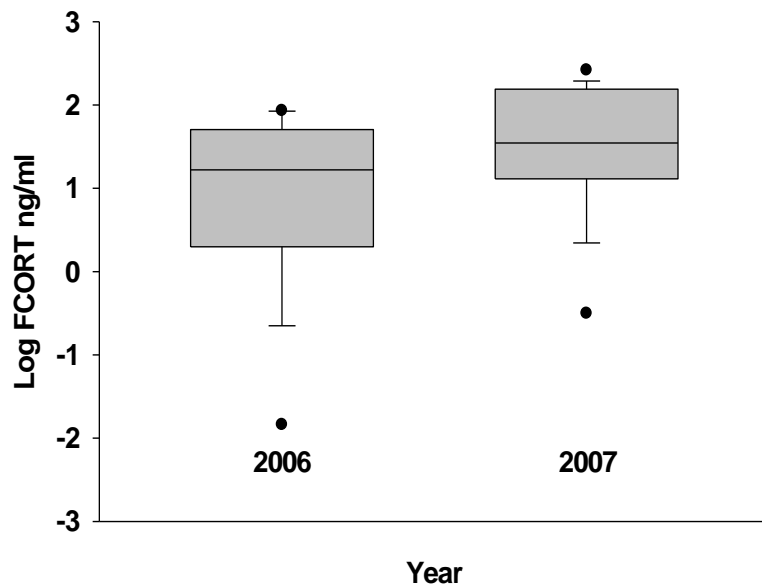
Figure 4. Log fecal corticosterone levels during 2006 – 2007 for white ibis chicks (all birds pooled).
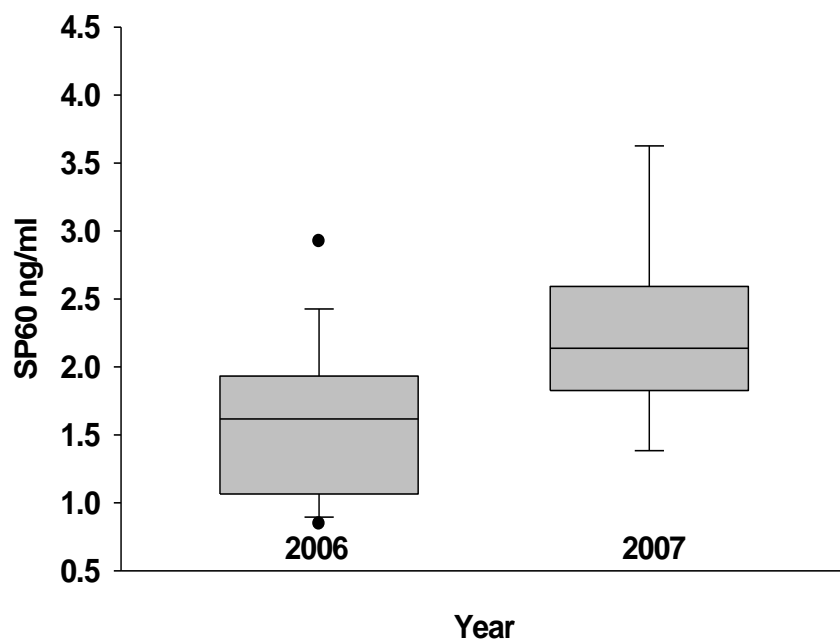
Figure 5. Stress protein 60 levels during 2006 and 2007 in pooled white ibis provisioned and control chicks.
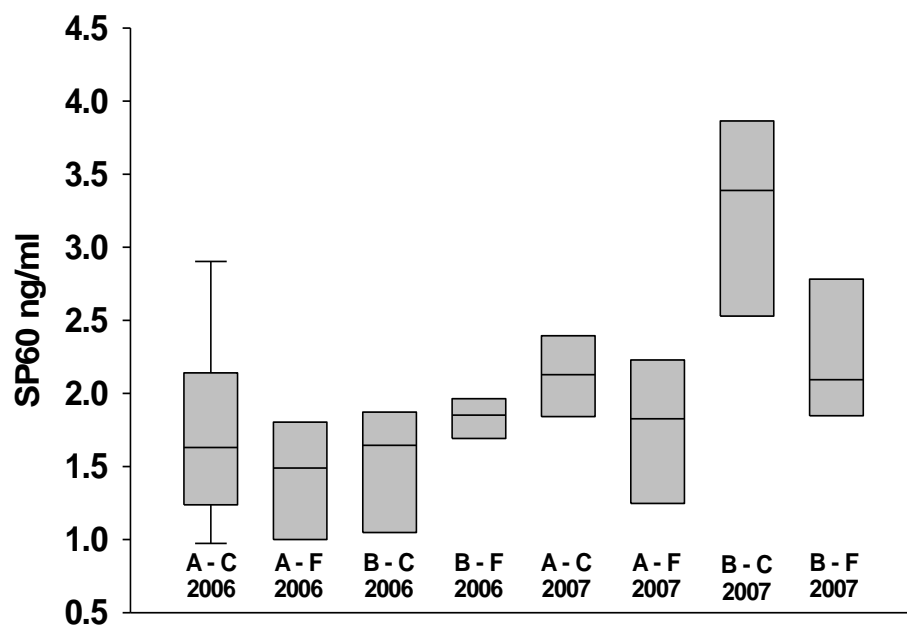
Figure 6. Stress protein 60 levels in A and B-hatched white ibis chicks for control (C) and

fed (F) treatments during 2006 – 2007.
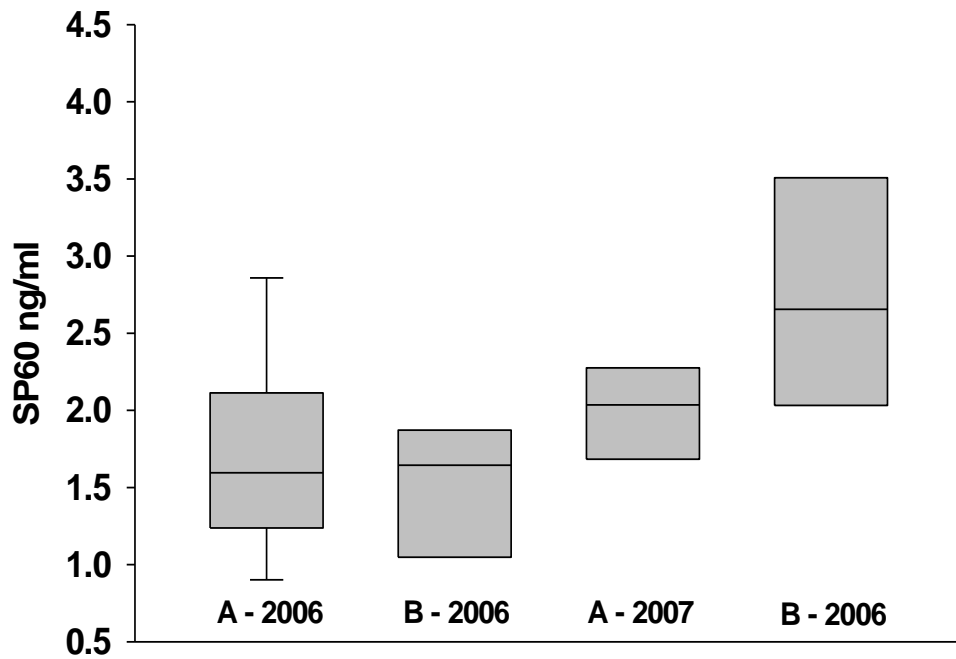
Figure 7. Stress protein 60 levels in pooled A and B-hatched white ibis chicks during
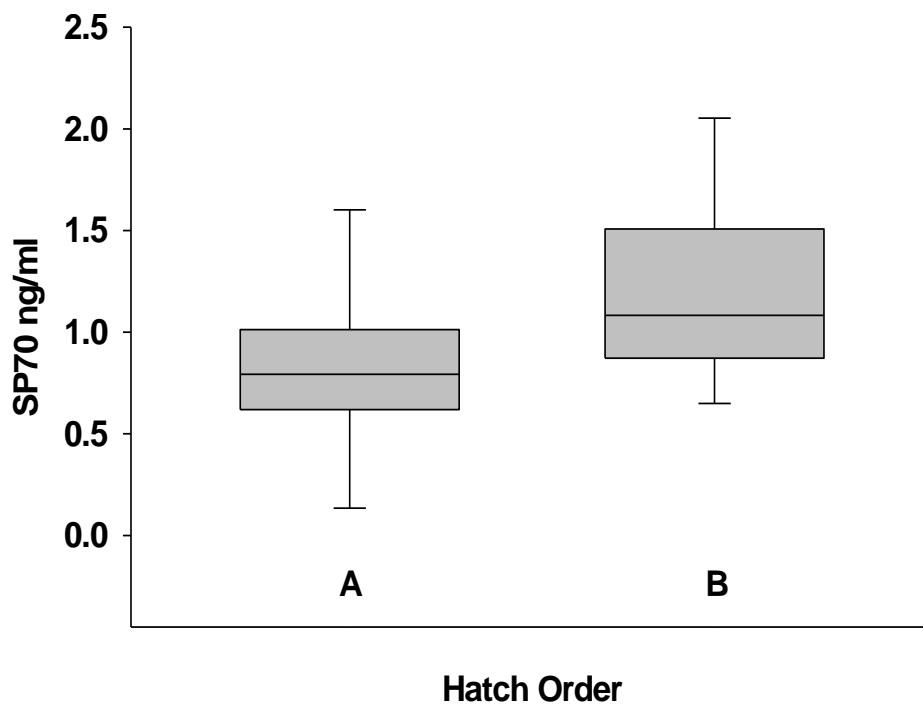
2006 – 2007.

Figure 8. Stress protein 70 levels in pooled A and B-hatched white ibis chicks across

2006 – 2007.

Table 1. General linear model results white ibis chick provisioning experiment physiological condition by year, treatment, hatch order, and collection date during 2006 and 2007 in the Florida Everglades.

	SP 60			SP 70			FCORT			PCORT			GLYC			TRIG		
Effect	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Year	1,32	14.17	<0.0001	1,21	0.003	0.95	1,42	27.01	<0.001	1,46	8.31	0.006	1,32	0.08	0.76	1,36	3.67	0.06
Treatment	1,32	0.19	0.66	1,21	1.10	0.30	1,42	5.05	0.02	1,46	0.51	0.47	1,32	0.002	0.98	1,36	1.51	0.22
Hatch order	1,32	0.75	0.39	1,21	4.23	0.05	1,42	7.09	0.01	1,46	0.12	0.72	2,32	0.22	0.76	1,36	0.59	0.44
Collection date	1,31	0.004	0.94	1,21	0.002	0.98	1,42	7.66	<0.001	1,46	0.27	0.6	1,32	0.04	0.82	1,36	3.73	0.06
Year x treatment	1,32	4.39	0.04															
Hatch order x year	1,32	5.10	0.03				1,42	10.13	0.003									
Hatch order x Treatment										1,46	4.44	0.04						
Hatch order x collection date							1,42	9.48	0.003									

Table 2. Correlation statistics for stress proteins 60 and 70, plasma corticosterone, fecal corticosterone, glycerol, and triglycerides in white ibis chicks during 2006 and 2007 in the Florida Everglades.

	SP 60			SP 70			FCORT			PCORT			GLYC			TRIG		
	r^2	P	n	r^2	P	n	r^2	P	n	r^2	P	n	r^2	P	n	r^2	P	n
SP 60				0.29	<0.01	22	0.13	0.02	38	0.00	0.74	35	0.13	0.03	34	0.10	0.06	35
SP 70	0.29	<0.01	22				0.03	0.36	25	0.03	0.39	23	0.00	0.85	20	0.00	0.83	21
FCORT	0.13	0.02	38	0.03	0.36	25				0.06	0.11	41	0.00	0.77	39	0.01	0.48	40
PCORT	0.00	0.74	35	0.03	0.39	23	0.06	0.11	41				0.00	0.99	38	0.01	0.48	39
GLYC	0.13	0.03	34	0.00	0.77	20	0.00	0.77	39	0.00	0.99	38				0.00	0.62	40
TRIG	0.10	0.06	35	0.00	0.83	21	0.01	0.48	40	0.01	0.48	39	0.00	0.62	40			

CHAPTER 5: PRE-BREEDING PHYSIOLOGICAL RESPONSES OF ADULT GREAT EGRETS AND WHITE IBISES TO LANDSCAPE LEVEL FOOD LIMITATION

ABSTRACT

One of the key conceptual models underlying the Everglades restoration is that hydrologic changes affect prey availability and wading bird nesting. However, the mechanism by which prey availability affects wading birds and produces species-specific nesting patterns has not been identified. I examined the physiological responses of pre-breeding great egrets and white ibises, two species with contrasting foraging strategies, in relation to foraging and habitat conditions in the Everglades. Both species were in good physiological condition (low levels of stress protein 60 and fecal corticosterone) during a year with good habitat conditions (2006). During a year with poor habitat conditions (2007) ibis physiological condition was lower; stress protein 60 and fecal corticosterone metabolite levels were higher in ibis while remaining stable in egrets. Differences in foraging strategies may explain why great egret stress levels remained similar between years, and males of the species were able to increase mass even when habitat conditions were poor. Egrets appear to minimize energy expenditure associated with foraging and are known to forage in a wider range of habitat conditions relative to ibis. During the poor year, female egrets had similar masses; female ibises had lower masses, while male

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egrets and ibises had higher masses than in 2006. During poor years, females likely minimized the cost of reproduction and maintained low masses, possibly increasing the likelihood of future reproductive success while males increase mass, possibly to prepare for unpredictable habitat conditions during the breeding season. During good years both species may maintain lower masses because prey availability is higher and more predictable. Model results confirmed the role of prey biomass and recession rate as the primary habitat variables that were associated with physiological differences. This is the first study that has demonstrated a specific mechanism linked to prey availability that could result in differences in nesting numbers for these two species. The decrease in white ibis physiological condition is expected to result in a concomitant reduction in nest effort, nest success, and chick physiology. If all searcher species respond similarly to poor years, this mechanism could explain the large discrepancy in nesting trends in the Everglades between species that use searcher and exploiter foraging strategies.

INTRODUCTION

Reproduction is a costly undertaking for most species, with those species that reproduce more than once having to balance the cost of in progress reproduction with surviving to future reproduction attempts (Ricklefs 1977, Partridge and Harvey 1988, Golet et al. 1998, Golet and Irons 1999). Factors associated with reproducing annually, no matter what the cost, versus abandoning a reproductive attempt with the hope of reproducing in subsequent years, each have their own distinct selective pressures. Short-term increased energetic investment may enhance an individual's chance of successful reproduction and contribution to the fitness of that species; however, the cost may be an increased risk of mortality for adults (Williams 1966, Stearns 1976, 1992, Roff 1992). One strategy avian species use to increase their ability to reproduce successfully, while minimizing the likelihood of mortality, is to build up energetic/lipid reserves (increased physiological condition or capital breeders; Drent and Daan 1980) prior to reproduction as a buffer to the costs of reproduction (e.g., egg production, incubation, mate attendance, provisioning).

While many studies have documented an increase in the physiological condition of pre-breeding birds (see Ankney and MacInnes 1978, Gauthier et al. 1984), few studies have demonstrated the response of adult birds to spatial and temporal changes in habitat conditions such as prey availability and associated ecological drivers such as hydrology (Bolton et al. 1993, Kitaysky et al. 1999, Williams et al. 2007). Even the numerous studies that have focused on pre-breeding physiological condition offer limited insight into physiological condition of birds because their taxonomic focus has been restricted to seabirds (Alcids) and waterfowl (Anatidae; see citations above). Reproductive studies

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have been conducted on colonial nesting species, but these studies focused on penguins (Cherel et al. 1994, Cockrem and Seddon 1994, McQueen et al. 1998, Lormee et al. 1999; and others) or other sea birds (albatrosses: Hector et al. 1985, Hector 1988; boobies and tropicbirds: Wingfield et al. 1999, Lormee et al. 2000).

To date there has been only one study conducted to examine the breeding physiology of wild wading birds in the Florida Everglades (Heath 2002, Heath et al. 2003). Heath's study documented the chronology of physiological changes in the white ibis but did not examine environmental factors that could have produced those changes (e.g., increasing pectoral muscle mass scores). Physiological metrics present a valuable method for quantifying how wading birds respond to fluctuating environmental conditions in the Florida Everglades. This method can provide insight into how different species cope with a specific set of environmental conditions, and thus provide a greater understanding of species-specific differences in seasonal nest effort and nest success, and thus long-term population trends.

In the Florida Everglades, a variety of environmental conditions are thought to influence wading bird reproductive success, although the exact link between landscape level environmental conditions and the biological and physiological mechanisms for reproductive effort and success have not been identified. Environmental conditions such as water depth, recession rate, and landscape level prey availability are known to influence breeding success and wading bird foraging (Frederick and Collopy 1989, Bancroft et al. 2002, Russell et al. 2002, Gawlik 2002). Frederick and Collopy (1989) demonstrated that wading bird nest success was most influenced by rapid hydrological reversals, while recession rates was most strongly associated with white ibis nest success,

and that the amount of rainfall associated with hydrological reversals was most strongly

associated with great egret nest failure. Bancroft et al (2002) demonstrated the

importance of water depth constraints on foraging wading birds, while and Russell et al.

(2002) demonstrated the influence of steady recession rates for making foraging sites

available for wading birds, and hydrological reversal for making them unavailable.

Gawlik (2002) tested the prey availability hypothesis, observing that vulnerability and

density of prey did not always result in a similar foraging response or strategy across a

suite of wading bird species that utilized searcher and exploiter foraging strategies. The

study proposed that these species-specific differences in foraging strategy could account

for species-specific population trends under the same environmental conditions, although

the mechanistic pathway of effects was unknown.

    For instance, white ibises (*Eudocimus albus*) have declined approximately 87%,

while great egrets (*Ardea alba*) increased 270% in during the last 20 years across the

Everglades (Crozier and Gawlik 2003*a*). Also, wading bird productivity fluctuates

within and between years and timing of reproduction is often variable within and between

years (Kushlan 1975, Frederick and Collopy 1989, Ogden 1994). Apparent

dissimilarities between many wading bird species diets suggest that interspecific species

forage competition does not limit prey availability (Ramo and Busto 1993, Smith 1997).

These results suggest that differences in breeding season physiological condition could be

an important link associated with species-specific foraging strategies (searchers versus

exploiters; Gawlik 2002) and changes in prey availability across the landscape.

    Selecting the correct physiological metric to measure, a species' response to

environmental change is difficult because the magnitude and duration of responses may

differ considerably between metrics. By measuring physiological factors representing a variety of temporal responses we can improve our understanding of how birds react to day-to-day environmental conditions and long-term landscape habitat conditions. It is important to consider that not all short-term responses may affect the long-term physiological condition of the bird and that not all long-term stress markers will be detectable on a day-to-day basis.

An effective method of examining short-term physiological condition of birds is the use of blood metabolite levels. Triglyceride levels (TRIG) in blood are often correlated positively with an increase in body mass and energy (lipid) storage while elevated glycerol levels (GLYC) correlate with decreasing mass (Jenni-Eierman and Jenni 1994, Williams et al. 1999, Masello and Quillfeldt 2004, Quillfedt et al. 2004, Anteau and Afton 2008). TRIG and GLYC tend to be short-term measures, and typically represent responses within approximately 2 days of being affected by an environmental event (Jenni-Eierman and Jenni 1994, Williams et al. 1999, Anteau 2006). Although TRIG and GLYC are considered short-term physiological responses, measuring changes of these blood metabolites in multiple birds across time and space can provide an estimate the population response to longer-term environmental conditions at the landscape level.

Another short-term affect of environmental stress is the production of corticosterone (CORT; Quillfelt et al. 2004). As stored TRIGs are utilized and depleted, birds begin to catabolize muscle protein (Cherel et al. 1988), which is motivated by the secretion of CORT. When the cortex of the brain of a bird detects a stressor (e.g., food shortage, large temperature change), a neural signal is sent to the hypothalamus. The

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hypothalamus then sends a hormone signal to the pituitary gland, resulting in the pituitary sending a signal to the adrenal or interrenal gland to release CORT (short to medium-term length stress response). After the stressor has been alleviated a negative feedback loop shuts off the hypothalamus-pituitary-adrenal (HPA) pathway leading to the CORT release. If the stressor persists and CORT remain elevated, the negative feedback loop will cease to function and destructive chronic effects may begin as allostatic overload occurs.

At lower levels, CORT can stimulate foraging activity and lipogenesis (Astheimer et al. 1992, Wingfield 1994). Under conditions of food scarcity, CORT stimulates gluconeogenesis, shifting catabolism away from fats towards proteins (Astheimer et al. 1992, Wingfield 1994). Chronic elevated levels of CORT can reduce the fitness of individuals via immunosuppression and result in reproductive failure (Verme and Doepker 1985, Wingfield et al. 1992). Fecal CORT metabolites (FCORT; medium-term stress response) levels reflect residue levels of plasma CORT, however, rapid and extensive metabolization before excretion results in lower overall levels than circulating levels (Wasser et al. 2000).

Stress proteins are a group of highly conserved intracellular polypeptides (Linquist 1986), that function as molecular chaperones for proteins within cells, present a major molecular barrier to alterations in cellular homeostasis, and can be used to detect the effects of long-term stress (Tomás et al. 2004). The primary role of stress proteins is to limit the interactions of unfolded proteins during the early stages of their synthesis by identifying and then binding to exposed proteins, thus stabilizing the unfolded protein (Willmer et al. 1999). Differences in stress proteins in central tissues and organs may be

distinguished in peripheral blood as circulating blood cells may be stimulated to amplify stress protein production. Recent papers have evaluated the effectiveness of using stress protein to examine physiological condition in avian ecology (Moreno et al. 2002, Martínez-Padilla et al. 2004, Tomás et al. 2004, Herring and Gawlik 2007), suggesting that they can be a valuable metric for future avian studies for detecting physiological responses to changing environmental conditions. In comparison to CORT, stress proteins may be more appropriate for detecting long-term or chronic exposure to stress, as capture and handling effects are not confounding factors as in CORT (Buchanan 2000, Tomás et al. 2004, Herring and Gawlik 2007).

Here, I investigate potential physiological differences in pre-breeding great egrets and white ibises and related physiological condition to landscape level prey availability and the hydrological variables that influence foraging conditions. Hydrologic patterns differed drastically during the two years of the study, 2006 and 2007, producing a large difference in habitat quality. Prey densities during the January 10 - March 23 adult great egret and white ibis capture period differed greatly between years. Prey biomass during the pre-breeding period decreased by 77% from 42.06 g/m^2 ± 2.48 SE (n = 44) in 2006 to 6.05 g/m^2 ± 0.75 SE during 2007 (n = 43; Gawlik and Botson 2008). This lead to the characterization of 2006 as the year with good habitat conditions and 2007 as the year with poor habitat conditions.

My objectives were threefold; 1) measure the pre-breeding physiological condition of great egrets and white ibises in the Everglades across two years (Physiological Condition), 2) use a modeling framework to determine what habitat parameters (e.g., hydrology, prey biomass, recessions rates) most influenced the response

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of each physiological parameter for each species (Food Limitation Hypothesis), and 3)

relate potential differences in physiological responses across the two species to foraging

strategies (e.g., searchers versus exploiters) and populations trends (Foraging

Strategies).METHODS

Data on the density of wading bird prey that are available to birds were provided

by a project directed by Dale Gawlik as part of the Comprehensive Everglades

Restoration Plan (CERP) Monitoring and Assessment Plan. The prey density estimates

in 2006 and 2007 were calculated from samples collected using a three-stage sampling

design (Cochran 1977); with landscape subunits (LSU), primary sampling units (PSU),

and throw-trap subsamples (SS). LSUs and PSUs remained fixed, whereas the SSs were

randomly selected each year based on the current wetland conditions. Landscape

subunits were selected by a group of Everglades' experts for all Monitoring and

Assessment Plan projects, and were based on differing hydrological and vegetation

characteristics. Within each LSU, 5 PSUs, 500 m^2 in size were randomly selected such

that all points capable of comprising a 500 m^2 plot had an equal probability of being

selected (Philippi 2003). The locations of two 1-m^2 SSs were randomly selected without

replacement at each PSU each year.

Estimates of prey density included all prey (fishes and invertebrates), and all prey

sizes captured during sampling. Because estimates of prey density from the above

methods did not match the exact temporal and spatial scales of the birds captured and

sampled in this study, I pooled prey density data across the period of my adult trapping

and sampling and used the mean estimates in subsequent models. While these estimates

are coarse, they did reflect large differences between years and are the primary ecological

driver thought to influence wading bird populations. Thus a term for prey density was used in place of a term for "year" in subsequent models.

Adult Physiological Condition

I selected the great egret and white ibis because they are representative of contrasting foraging strategies (Gawlik 2002). White ibises (searchers) tend to select high quality patches and abandon them quickly; while great egrets (exploiters) tend to stay at foraging sites where prey densities are low (Gawlik 2002).

Great egrets and white ibises were captured prior to the initiation of the breeding season using either a netgun or modified flip trap (Herring et al. 2008, Chapter 2) and decoys (Crozier and Gawlik 2003*b*, Heath and Frederick 2003). In both years of the study, birds were captured between 10 Jan and 23 Mar in Water Conservation Areas (WCA) 2A, 3A, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox; Fig. 1). Capture dates corresponded with the seasonal pattern of the two species arriving in the Everglades in great numbers prior to the upcoming breeding season, which typically begins in March. During 2006 and 2007, I captured and sampled 209 adult birds [79 great egrets (49 f, 30 m) and 130 white ibis (67 f, 63 m)] and deployed 201 radio-tags on 125 white ibis and 76 great egrets during this pre-breeding period.

Upon capture of birds, I immediately placed a hood on the birds' head to reduce stress and minimize movement during subsequent sampling and measurements. Because blood samples could not be obtained in less than 3 minutes, to achieve a baseline level of corticosterone (Romero and Reed 2005) I standardized the bias by collecting blood samples at 10 min (Michael Romero, Tufts University, pers. comm.). At 10 min after capture I collected up to 2 ml of blood from the brachial vein using a 27.5-gauge needle.

Blood samples were then labeled and stored in heparinized Vacuutainers, and placed on ice until transferred to a freezer in the lab. I then extracted up to 2 ml of fecal material directly from the birds cloaca using a micropipette, fecal samples were labeled and stored in mirco centrifuge tubes and placed on ice. I recorded tarsus length (middle of midtarsal joint to the end of tars-metatarsus), wing chord, wing flattened, exposed culmen length, bill depth, and mass for both species, and additionally curved bill length for white ibis. All measurements were to the nearest 1 mm using calipers or a wing ruler, except mass, which was measured to the nearest 5 g using a spring scale. I then palpated the pectoral muscle to subjectively score pectoral mass (PEC; Heath et al. 2003) on a scale of 1-5 (1: prominent keel, - 5: muscle greater than keel). All measurements were taken by trained individuals and supervised by GH. All birds were captured during the morning (between 0600 and 1000) while most birds were en route to foraging sites, thus I assumed that masses were not biased by ingested food.

Radio transmitters were attached to birds using a figure eight harness around the legs and pelvis. Model A1260 transmitters (Advance Telemetry Systems, Isanti, MN) had a minimum lifespan of 6 months and were in the 152.000-153.999 MHz range. Mean mass of transmitters was16 g, which was 2.6% of the total mass of the lightest bird. Radio tagged adults were used for locating wading bird colonies and nests in Chapters 6 and 7. I banded all captured birds with U.S. Fish and Wildlife Service aluminum bands and color bands to facilitate their relocation within the breeding colonies. Great egrets and white ibises were later sexed using the standard morphometric measurements and discriminate function analysis (Herring et al. 2008). I then validated sexing of all adults captured using DNA testing (Zoogen Services Inc., Davis, CA). DNA sexing was

conducted by Zoogen Services, Inc. (Davis, California), with a reported sex identification accuracy of 99.9 % (Zoogen 2007).

In the lab, blood samples were centrifuged (15 min, 10,000 g); plasma and red blood cells were separated and frozen at -20° C for later analysis. Fecal samples were also frozen at -20° C for later analysis. Plasma TRIG and GLYC were measured using enzymatic endpoint assay following Williams et al. (1999) using Sigma kits (Sigma, Saint Louis, MO). Assays were then validated using reference values from normal and abnormal human control sera. Inter- and intra-assay coefficients of variation for TRIG and GLYC internal standards were 6% and 9% and 6% and 7% respectively.

PCORT and FCORT samples were homogenized and then mixed with methanol and vortexed for 30 min. After centrifugation (15 min, 2500 g) I transferred the supernatant to a new vial, which was then evaporated under a stream of nitrogen gas. CORT metabolites were then resuspended in diluted extraction buffer and measured using enzyme-linked immunosorbent assays (ELISA; Neogen, Lexington, KY). I conducted a standard assay validation for each species, which included an assessment of parallelism, recovery of exogenous CORT, and intra and inter-assay precision to confirm that the ELISAs accurately measured CORT in both great egret and white ibis plasma and fecal samples. I also validated that FCORT levels did not change after freezing as in the case of mammals (Khan et al. 2002) by freezing and measuring FCORT levels monthly for 6 months (Herring and Gawlik *In Review*). This experiment suggested that cross-reacting metabolites do not change levels of FCORT in avian species; subsequently I suggest that levels of FCORT in white ibises and great egrets were not biased.

To measure SP levels, red blood cells were washed three times using phosphate buffered saline, centrifuged and the supernatant removed after the final wash. Red blood cell supernatant was then mixed with a $1\times$ extraction reagent and a protease inhibitor cocktail (Sigma), vortexed for 5 min and then sonicated for 1 min. Samples were again centrifuged (15 min, 2500 g) and the supernatant removed. I measured SP60 and SP70 (SP70-1) using ELISA kits specific to just those stress proteins and not all other SP60 and SP70 family members (Assay Designs, Inc., Ann Arbor, MI). I conducted a standard assay validation, which included an assessment of parallelism, recovery of exogenous SP60 and SP70, and intra and inter-assay precision to confirm that the ELISAs accurately measured SP60 and SP70 in both great egret and white ibis red blood cells. All samples were run in duplicate and means of duplicates were used in all analysis.

Food Limitation Hypothesis

I used the Everglades Depth Estimation Network (EDEN) to estimate all water depths and recession rates at trapping sites during 2006 and 2007. EDEN is a network of real-time water level monitoring, water surface modeling, and ground elevation modeling that is used to model water depth for the entire freshwater portion of the Greater Everglades (USGS 2006). EDEN calculates stage levels at daily time steps to account for daily changes associated with evapo-transpiration drying and rainfall rewetting. The model provides estimates of the average water depth of 400 m by 400 m grid cells across the entire landscape.

To estimate stage and recession rates at trapping sites I first used ArcGIS 9.1 to establish a 3-km radius buffer around all sites where birds were captured. I used a 3-km radius buffer, because during, trapping radio-tagged birds often returned to sites within a

3-km radius of their capture site on subsequent days. I assumed that birds had been

foraging in the same general area on days prior to their capture. The 3-km radius buffer

was then used to identify all of the associated 400 m by 400 m grid cells associated with

EDEN and I used the Joint Ecosystem Modeling EDEN module to extract stage levels for

each cell for 1 week prior to capture for each site, averaging across these to get an overall

estimate of water depth and recession rates for all capture sites.

Statistical Analysis

Food Limitation Hypothesis

To validate ELISA test kits for PCORT, FCORT, SP60, and SP70, I tested for

equality of two slopes (parallelism) using a t-test (Zar 1996) to determine if curves of

serially diluted PCORT and FCORT metabolites, and SP60 and SP70 from both great

egrets and white ibises, were parallel to standard curves for corticosterone and SP60 and

SP70. Similar slopes between serially diluted samples and standard curves would

demonstrate the ELISA kits were in fact measuring the parameter as purported by the

manufacturer.

I used Proc Mixed in SAS, specifying the maximum likelihood variance estimator

(Littell et al. 1996) to determine which habitat parameters most influenced the response

of each physiological parameter for each species using an information theoretic approach

(Akaike 1973, Burnham and Anderson 2002).   I built and ranked competing models

(Burnham and Anderson 2002). Competing models were developed based on a

biologically meaningful understanding of wading foraging ecology based on evidence

from previous studies. Bancroft et al (2002) demonstrated the importance of water depth

constraints on foraging wading birds, while Russell et al. (2002) demonstrated the

influence of steady recession rates for making foraging sites available for wading birds, and hydrological reversal for making them unavailable. Gawlik (2002) tested the prey availability hypothesis, observing that vulnerability and density of prey did not always result in a similar foraging response or strategy across a suite of wading bird species that utilized searcher and exploiter foraging strategies.

I ran separate models for each species to understand their individual physiological responses to differing habitat conditions (e.g., hydrology, prey densities). Each physiological response variable (TRIG, GLYC, PCORT, FCORT, SP60, SP70, PEC, and body size scaled mass (MASS) was examined using the variables prey biomass (Biomass), sex, Julian date (Julian), mean depth at capture site (Depth), the quadratic form of depth during the week prior to capture (Depth + $Depth^2$), recession rate during the week prior to capture (Recess), and the quadratic form of recession during the week prior to capture (Recess + $Recess^2$). Global models included all environmental terms as well as interactions of main effects.

I used the AIC_C values adjusted for small samples sizes in all models (Burnham and Anderson 2002). I calculated delta AIC (Δ_i, Akaike's Information Criterion) and AIC weights (ω_i) from AIC_c values. Models with the lowest AIC_c value was considered to be the best explanatory model; although, additional competing models with $\Delta AIC_c < 2$ were considered to be equally plausible given the data (Burnham and Anderson 2002). Models with $\Delta AIC_c > 4$ were considered to have little to no support (Burnham and Anderson 2002). I calculated the unconditional estimates for coefficients and unconditional standard error terms for each parameter across all models (Burnham and Anderson 2002) based on all models with AIC_C weights ≥ 0.001. Model-averaged

coefficients were calculated by only using the exponentiated AIC_C values from models that contained the parameter, the exponentiated values were then summed, the original exponentiated AIC_C value was then divided by the new sum to get new Akaike weights. I then multiplied the raw (individual model) parameters by the new weights and summed the products. To assess magnitude of individual parameters, I calculated weights or parameter likelihoods by summing the model weights for each variable in the most parsimonious model for every model that it occurred in, this allowed for a quantitative assessment of the contribution of each variable to the response variable. In the results, I limit discussion of the sign and magnitude of effects to parameters that were in the most parsimonious models and that did not have estimates of SE that overlapped the estimated coefficient greatly

RESULTS

Adult Physiological Condition

GLYC

The model with the most support for great egret GLYC levels contained only the variable Recess. The weight of the evidence for this model was 70%, and this model received 3.3× the support of the second best model (Table 1). The most parsimonious model explain GLYC levels in pre-breeding white ibises contained only the variable for Recess, with 54% of the model evidence, and 3.0× the support of the second top model. Recess rate was identified as the most important variable for describing both great egret and white ibis GLYC levels based on its high parameter likelihood value (Table 2). However, unexpectantly great egret GLYC levels increased and white ibis GLYC levels decreased with increasing recession rate (Table 2). Great egret and white ibis GLYC levels were similar between years (Figs. 2-3).

TRIG

Two models were identified that explained great egret TRIG levels, containing the variables for Recess rate (46% weight of evidence) and the Recess + Recess^2 rate (20% weight of evidence). The Recess model received 2.3× the support of the CV model, which received 2.0× the support of next model (Table 1). The model selection process identified three separate models to explain TRIG levels in pre-breeding white ibises. The first model contained the variables Sex + Biomass + Recess with 30% of the model evidence, and 1.5× the support of the second candidate model, which contained only Sex + Biomass with 19% of the model evidence. The third most parsimonious model included the additional variable Depth with 17% of the model evidence. Parameter

likelihood values suggested the great egret TRIG levels were most influenced by Recess rate, albeit it weak support (0.55 likelihood; Table 2), while white ibis adult TRIG levels were equally influenced by Sex, Biomass, and to a lesser extent Recess (Table 2). Great egret TRIG levels increased with increasing recession rates. White ibis TRIG levels were higher in males, decreased with increasing biomass, recession rate, and Julian date, and increased with decreasing water depth (Table 2). Great egret TRIG levels were similar between years (Fig. 4), while female white ibis TRIG levels decreased during 2007 (Fig. 5).

PCORT

Serial dilutions of great egret and white ibis plasma extracts yielded displacement parallel to the standard corticosterone curves ($t_9 = 0.99$, $P = 0.34$, $t_{10} = -0.52$, $P = 0.61$ respectively; Figs. 6-7). Mean recovery of the added exogenous corticosterone spike was 86.3% ± 7.7SE. Assay sensitivity was 0.05 ng/ml. Inter- and intra-assay coefficients of variation for corticosterone internal standards for great egrets and white ibises were 5% and 7% and 6% and 9% respectively.

The model selection process identified three separate models to explain PCORT levels in pre-breeding great egrets. The first model contained the variables for Sex + Biomass + Recess + Depth + Julian + Sex×Biomass with 42% of the weight of the evidence and 2.4× the support of the next model (Table 1). The second and third models included all the variables from the first model with the exception of Sex×Biomass and Julian + Sex×Biomass, with 17% and 11% of the weight of the evidence, and 1.0× and 2.2× respectively the support of the next models (Table 1). The model selection process identified two separate models with near equal support to explain PCORT levels in pre-

breeding white ibises. The first model contained the variables Sex + Biomass + Recess, with 34% of the model evidence. The second model included the variables Sex + Biomass, with 32% of the model evidence. Both models had at least 3.5× the support of the next model. Parameter likelihood values suggested great egret PCORT levels were most influenced by Sex and Biomass, followed by weaker support for Recession and Depth (Table 2), while white ibis adult PCORT levels were near equally influenced by Sex and Biomass (Table 2). Great egret PCORT levels increased with increasing recession rate and prey biomass, decreased with increasing CV, and was higher in males (Table 2). White ibis PCORT levels were higher in females, decreased with increase in prey densities, and decreased with increasing recession rate (Table 2). Great egret PCORT levels were similar between years (Fig. 8), while female white ibis PCORT levels increased during 2007 (Fig. 9).

FCORT

Serial dilutions of great egret and white ibis fecal corticosterone metabolite extracts yielded displacement parallel to the standard corticosterone curves ($t_9 = 1.02$, P = 0.33, $t_9 = 1.10$, P = 0.30 respectively; Figs. 10-11). Mean recovery of the added exogenous corticosterone spike was 86.3% ± 7.7SE. Assay sensitivity was 0.05 ng/ml. Inter- and intra-assay coefficients of variation for corticosterone internal standards for great egrets and white ibises were 7% and 11% and 8% and 9% respectively.

The model selection process identified two separate models to explain FCORT metabolite levels in pre-breeding great egrets. The first model contained the variables Sex + Biomass + Recess, while the second model contained the same variables but with the quadratic form of recession (Table 1). The weight of the evidence for these models

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were 42% and 31% respectively, and these models received 1.3× and 2.8× the support of the next models respectively (Table 1). The second top model included the same variables but with the Recess + Recess^2 form of Recess, and had 24% of the support of being the top model. The third model with only 14% of the weight of the evidence included only the variable Recess, with 1.5× the support of the next model. The model selection process identified two separate models to explain FCORT metabolites levels in pre-breeding white ibises. The first model contained the variables Sex + Biomass + Recess, with 48% of the model evidence, and 1.5× the support of the second candidate model (Table 1). The second most parsimonious model included the variables Sex + Biomass, with 31% of the model evidence, and 2.0× the support of the next model. Parameter likelihood values suggested great egret FCORT metabolite levels were equally influenced by Sex, Biomass, and Recession (Table 2), while white ibis adult FCORT metabolite levels were equally influenced by Sex and Biomass (Table 2). Great egret FCORT metabolite levels were higher in females, decreased with increasing prey biomass, and increased with increasing recession rates (Table 2). White ibis FCORT levels were higher in males, decreased with increasing prey biomass, and increased with increasing recession rates (Table 2). Great egret FCORT metabolite levels were similar between years (Fig. 12), while white ibis FCORT metabolite levels increase during 2007 (Fig. 13).

SP60

Serial dilutions of great egret and white ibis red blood cells extracts yielded displacement parallel to the standard SP60 curves ($t_8 = 0.78$, $P = 0.45$, $t_7 = 1.44$, $P = 0.19$ respectively; Figs. 14-15). Mean recovery of the added exogenous SP60 spike was 87%

± 8 SE. Assay sensitivity was 3.0 ng/ml. Inter- and intra-assay coefficients of variation for SP60 internal standards for great egrets and white ibises were 7% and 9% and 6% and 8% respectively.

The model selection process did not identify a parsimonious model to explain SP60 levels in pre-breeding great egrets. Three models were identified with similar support. The best model was the Global model with 30% of the weight of the evidence, and this model received 1.1× the support of the second model (Table 1). The second top model included the variables Sex + Biomass + Recess, with 26% of the weight of the evidence and 1.1× the support of the next model. The third model included the additional variables Depth + Julian + Sex×Biomass, with 24% of the weight of the evidence and 3.0× the support of the next model (Table 1). The model selection process identified two models with equal support to explain SP60 levels in pre-breeding white ibises. The first model contained the variables Sex + Biomass + Recess, with 38% of the model evidence, and 1.58× the support of the next model. The second model included the additional variables Julian + Sex×Julian, with 18% of the model evidence, and 1.38× the support of the next model. Parameter likelihood values suggested great egret SP60 levels were equally influenced by Sex and Biomass, and near equally by Recess, and to a lesser extent Depth and Julian date (Table 2). White ibis adult SP60 levels were equally influenced by Sex and Biomass, and to a lesser extent Recess (Table 2). Great egret SP60 levels were higher in females, decreased with increasing biomass, recession rates, depths, and Julian date. White ibis SP60 levels were higher in females, decreased with increasing prey biomass and recession rates, and increased with increasing depth and

Julian date (Table 2). Female great egret SP60 levels increased during 2007 (Fig. 16), while both male and female white ibis increased during 2007 (Fig. 17).

SP70

Serial dilutions of great egret and white ibis red blood cells extracts yielded displacement parallel to the standard SP70 curves (t_8 = -0.80, P = 0.44, t_9 = 1.46, P = 0.17 respectively; Figs. 18-19). Mean recovery of the added exogenous SP70 spike was 81% ± 9 SE. Assay sensitivity was 0.09 ng/ml. Inter- and intra-assay coefficients of variation for SP70 internal standards for great egrets and white ibises were 8% and 11% and 7% and 12% respectively.

The model with the most support for great egret SP70 levels contained only the variable for Recess. The weight of the evidence for this model was 49%, and this model received 3.2× the support of the second best model. The model selection process identified three models with similar support for white ibis SP70 levels, the first contained only the variable Recess + Recess^2, with 43% of the model evidence weight, and 1.4× the support of the second top model (Table 1). The second contained only the variable for Recess, with 30% of the model evidence weight, and 1.8× the support of the next model. The third model contained only the variable for Depth, with 16% of the model evidence weight, and 5.3× the support of the next model. Parameter likelihood values suggested both great egrets and white ibises SP70 levels were most influenced by Recess, albeit it weak support (0.49 and 0.43 likelihood respectively; Table 2). Great egret SP70 levels increased with increasing recession rates, while white ibis SP70 levels increased with increasing recession rates (Table 2). Both great egret and white ibis SP70 levels were similar between years (Figs. 20-21).

MASS

The model selection process identified two models to explain MASS in pre-breeding great egrets. The first model contained the variables Sex + Biomass + Recession. The weight of the evidence for this model was 60%, and this model received 2.1× the support of the second model (Table 1). The second top model included the variables Sex + Biomass + Recess +Recess^2, and had 28% of the weight of the evidence and 4.6× the support of the next model (Table 1). The model selection process identified two models with the most support for white ibis MASS, the first contained the variables Sex + Biomass + Recess, with 42% of the model evidence weight, and 2.2× the support of the second top model. The second model contained the additional variables for Depth, Julian, and Sex×Biomass interaction, with 19% of the model evidence weight and 1.3× the support of the next model. Parameter likelihood values suggested great egret MASS was equally influenced by Sex, Biomass, and Recess, while white ibis MASS was equally supported by Sex and Biomass, and to a lesser extent Recession, Depth, and Julian date, albeit it weaker support (0.79 – 0.36 likelihood; Table 2). Great egret mass was higher in males, increased with increasing biomass, and decreased with increasing recession rates (Table 2). White ibis mass was higher in males, increased with increasing biomass and decreasing water depths, and each Julian day of the pre-breeding period, and decreased with increasing recession rates (Table 2). Great egret and white ibis male MASS increased during 2007, was similar for great egret females between years, and decreased in female white ibis during 2007 (Figs. 22-23).

PEC

The model selection process identified two models with equal support to explain

PEC levels in pre-breeding great egrets. The first model contained the variables Sex,

Biomass, and Recess, while the second model had the variables for Sex, Biomass, and

Recess + Recess^2. The weight of the evidence for each model was 42%, and they

received 7.0× the support of the next model (Table 1). The model selection process

identified three separate models to explain PEC levels in pre-breeding white ibises. The

first model contained the variables Sex + Biomass + CV, with 34% of the model

evidence, and1.2 the support of the second model. The second model included only the

variable Recess, with 27% of the model evidence, and 2.0× the support of the third

model. The third top candidate model contained the variable Sex + Biomass + Recess,

with 13% of model evidence weight, and 1.3× the support of the next model. Parameter

likelihood values suggested great egret PEC levels were most influenced by Recess,

followed closely by Sex and Biomass (Table 2), while white ibis adult PEC levels were

near equally by Sex, and Biomass, albeit weak support for all two variables (≤0.59

likelihood; Table 2). Great egret PEC levels were higher in males, increased with

increasing biomass, and decreased with increasing recession rates (Table 2). White ibis

PEC increased with increasing biomass (Table 2). Male great egrets and white ibises had

similar PEC scores between years, while female great egret and white ibis PEC scores

decreased in 2007 (Fig. 24-25).

To further identify variables, post hoc, common among all of top models (e.g., <2

Δi AIC$_C$ units) for all physiological variables that were identified as being influential to

adult physiological metrics based on parameter likelihood values I summed the parameter

likelihood values across all models. For great egrets, the variable that influenced all physiological metrics the most was Recess (sum parameter likelihood = 6.6), while Sex (sum parameter likelihood = 4.63), Biomass (sum parameter likelihood = 4.63) had similar but considerably less influence. White ibis physiological condition was largely influenced by three variables, Recess (sum parameter likelihood = 5.38), Sex (sum parameter likelihood = 5.34), and Biomass (sum parameter likelihood = 5.34).

Food Limitation Hypothesis

Model selection results overwhelmingly demonstrated strong support for the *Food Limitation Hypothesis*, with >60% of all physiological parameters responding negatively to decreasing prey availability (Table 3). Hydrological factors that influence prey availability (recession rates, water depths) also had strong support given for increasing physiological metrics during the pre-breeding period for both species when prey densities were lower (Table 3).

DISCUSSION

Physiological Condition

Metrics of pre-breeding physiological condition suggested white ibises and great egrets differed both in their response to differing habitat quality years, and in the variables that influenced those physiological metrics. While the two species responded similarly by both exhibiting good physiological condition during 2006, a year with good habitat conditions, that was not the case during the 2007, the year with poor habitat conditions. Great egret physiological condition appeared to remain comparatively stable leading up to the reproductive stage during 2007, even though habitat conditions were poor. White ibises responded negatively to the poor habitat conditions during 2007, and their physiological condition decreased considerably from the previous year, with males having increased SP60 levels and FCORT metabolites, and females having lower mass, higher SP60 levels, and higher FCORT metabolite levels.

Many studies have examined the physiological condition of pre-breeding and breeding birds, however the focus has almost exclusively been on female condition (see Ankney and MacInnes 1978, Gauthier et al. 1984, Hanssen et al. 2003, Kellett et al. 2005). The rationale for this has been that in most cases, males play a lesser role in nesting, and thus because of the anisogamous nature of reproduction, female physiological condition is considered paramount. Male great egrets and white ibises play a critical role in nest construction, guarding females, incubation, and provisioning chicks (Kushlan and Bildstein 1992, McCrimmon et al. 2002). I suggest that pre-breeding physiological condition of males is equally as important as female condition, because if

males cannot maintain or improve their physiological condition leading up to nesting, nesting may not occur at all.

Results from this study cannot definitively explain the mass differences observed in male and female great egrets and white ibises, in particular why they would differ during good and poor years. However, the costs and benefits of the approaches used can provide some insight into each strategy. During good years, both male and female great egrets and white ibises may not need to maximize their physiological condition leading up to breeding, to successfully fledge multiple chicks and increase their long-term fitness because prey availability is high and predictable. Models of foraging strategies (McNamara and Houston 1987, Anholt and Werner 1998) predict that animals in rich environment will spend less time feeding than those in poor environments. These models assume that mass/lipid reserve levels and the benefits of harvesting energy is a decelerating function of the cumulative harvest (Houston et al, 1997). Most research in this field has focused on the response of birds to condition of low food availability (see Gosler et al. 1995, Rogers and Reed 2003) or unpredictable food (see Pravosudov and Grubb 1997, Cuthill et al. 2000) demonstrating a positive increase in mass or lipid reserves storage. A key point that all of these studies have also demonstrated inadvertently is that during good years, birds do not need to have high mass levels.

This strategy would be suited to the Everglades ecosystem in its natural state, when short hydroperiod wetlands were abundant, thus increasing predictability of locating food. These wetlands would have been well matched to a strategy of acquiring food on a regular basis and not increasing reserve levels in preparation for breeding: this response assumes those high quality patches were more common and predictable in the

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Everglades than they are now (Gawlik 2002). During the last 100 years, the compartmentalization of the Everglades has resulted in large differences in hydrology between regions that can result in one compartment having a surplus of water, while an adjacent region may have considerably lower water levels. These factors combined with management of water resources for flood protection, consumptive use, and wildlife needs often produces conditions very different across the Everglades. Current conditions do not mimic the natural landscape in any sense of the original hydrological cycle; subsequently habitat conditions across the Everglades can vary greatly, and change rapidly.

This study found that in poor or below average years, male egrets and ibises had higher pre-breeding mass than in the year with good habitat conditions, possibly to prepare for unpredictable prey availability experienced during the period of increased demands for nest construction, mate defense, and incubation duties. Using an experimental approach Pravosudov and Grubb (1997) demonstrated that when tufted titmice (*Parus bicolor*) experienced unpredictable food availability they increased their mass and lipid reserves. Similarly, Rogers and Reed (2003) experimentally demonstrated that dark-eyed juncos (*Junco hyemalis*) responded to proximate environmental cues related to resource deterioration and increased fat stores. While this apparent strategy of males preparing for unpredictable food availability fits results from this study, it does not explain the response of females during the year with poor food availability.

Females had similar or slightly lower masses to 2006 and likely fueled their energy demands on a daily basis. The advantage might be that females may not have to expend as much energy acquiring large amounts of prey when food may be less predictable, instead reserving nutrient reserves for egg production and nesting.

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Ultimately, this strategy might benefit females because if the nesting season fails, the long-term female costs are reduced, increasing the likelihood of potential future reproductive success for this long-lived species (Drent and Daan 1980). Alternatively, Velando et al. (2003) suggested females may be at some physiological maximum during this period and cannot increase levels beyond those observed.

Food Limitation Hypothesis

Great egret adult physiological condition was most influenced by recession rate during this study, and in the case of those metrics that reflected medium to long-term stress (e.g., FCORT, SP60) increasing recession rates resulted in an increase in stress. Correspondingly, an increase in recession rate resulted in a decrease in mass for pre-breeding great egrets. Biomass, a surrogate for interannual differences in habitat conditions in this study was less influential in the physiological condition of pre-breeding great egrets based on model weights and parameter likelihood values. Although the response of adult egrets to higher levels of prey biomass was predictable, higher biomass resulted in a positive increase in MASS, with decreasing levels of medium to long-term stress markers (e.g., FCORT, SP60) based on parameter estimates.

Pre-breeding white ibises presented a more complex scenario, where their physiological condition was most influenced by the Biomass, Recess, and Sex. Higher levels of prey biomass resulted in an increase in white ibis MASS, with a concurrent decrease in both SP60 and FCORT levels. However, increased recession rates increased levels of FCORT, SP70, while decreasing mass. Unexpectedly, increased Recess resulted in a decrease in SP60 levels counter to both FCORT and SP70 results. While no prior studies have examined the pre-breeding physiological condition of great egrets,

Heath et al. (2003) did examine the physiology of reproductive white ibises in the Florida Everglades. Heath et al. observed similar levels of PCORT during the pre-breeding and display period during the four years of their study in both male and female ibises. Results from this study found an interannual increase in female PCORT during 2007, an increase in male and female FCORT metabolites during 2007, and an increase in SP60 levels in ibises during 2007, the poor year during the same period of the pre-breeding season as in Heath et al.'s study. While direct comparisons between this study and Heath et al.'s ought to be considered cautiously due to differences in research objectives and techniques (e.g., ELISA vs. radioimmunoassay sample testing), they do demonstrate that white ibis pre-breeding physiological condition can differ considerably between years.

Comparatively, great egret PCORT and FCORT metabolite levels in both sexes were similar between years, as were SP60 levels. These results suggest egrets may not respond as acutely to variability in habitat conditions between breeding years, as in the case of white ibises. Indeed, egret physiological condition was most influenced by Recess, while Biomass and Recess near equally influenced white ibis physiological condition. These differential responses to changes in landscape habitat conditions between species resulted in associated responses throughout the remainder of the breeding season. During the poor year, white ibises laid smaller clutches and fledged fewer chicks (Chapter 6), and the physiological condition of those chicks was lower (Chapter 7). Great egrets maintained their clutch sizes, but did fledge fewer chicks (Chapter 6), although those chicks generally were in similar physiological condition compared to the good year (Chapter 7).

Studies have suggested that long-lived (e.g., seabirds) and short-lived species (e.g., passerines) will have different stress responses with increased stress suppression in short-lived species and an increased likelihood of trade-offs in long-lived species (Kitaysky et al. 1999). The rational for this is that short-lived species have fewer reproductive opportunities, so they have to make every one count, so suppressing stress responses can be beneficial to building up pre-breeding reserves, egg production, or nest/chick attendance. Long-lived species may have many opportunities to reproduce, so responding to stress and abandoning nesting is not as critical if a stress response occurs (Stearns 1992). Both white ibis and great egrets are intermediate in their life span (15-20 years; Clapp et al. 1982) and reproductive potential relative to short-lived passerines and long-lived seabirds. White ibis in this study followed the life-history strategy of a long-lived species. When food availability was poor, resulting in a pre-breeding decrease in physiological condition, ibis responded by decreasing their clutch size (Chapter 6), and did not invest as much energy in their chicks (Chapter 7). Great egrets may have used an intermediate strategy, approaching the breeding season in similar physiological condition to good years, they maintained their clutch sizes, and adjusted nest effort later resulting in fewer chicks fledged, but maintained the physiological condition of those chicks, similar to good years (Chapters 6 and 7). Alternatively, egrets may be less constrained by prey availability because of their ability to forage in a wider range of habitats (exploiter foraging strategy; Gawlik 2002, Beerens 2008) and the fact that they forage closer to colonies (Beerens 2008). The cues that drive this process for both species are likely a combination of hydrology and prey availability parameters that make prey more or less available (Gawlik 2002, Gawlik and Crozier 2007).

Foraging Strategies

Results from this study suggest that searcher species (e.g., white ibis) may not be well suited to environment changes that can produce an internal stress response and ultimately a decrease in the pre-breeding physiological condition. Alternatively, exploiters (great egrets) appear to use a stress response suppression approach, which could explain the fact that their physiological conditions remained relatively constant during the year with lower habitat conditions. This could be mitigated by their ability to forage in a wider range of habitats (exploiter foraging strategy; Gawlik 2002, Beerens 2008) and the fact that they forage closer to colonies (Beerens 2008). Other avian species with specialized foraging needs similar to white ibises, such as expensive food-searching behaviors (e.g., common terns *Sterna hirundo,* snail kites *Rostrhamus sociabilis*) have also been show to be more vulnerable to food shortages during the nesting period than those species that do not use expensive food-searching behaviors (Pearson 1968, Beissinger 1983, Sykes 1987, Monaghan et al. 1989).

The inclusion of the parameter for Recess during one week prior to capture of birds suggests that short-term habitat conditions play an important role in the pre-breeding physiological condition of both egrets and ibis. This variable also suggests that the physiological condition of pre-breeding egrets and ibises is not strictly a function of how much prey biomass is present in the landscape, but includes hydrological factors that make prey more or less accessible and the predictability of those sites. While Gawlik and Crozier (2007) observed that foraging wading birds were strongly attracted to social and water depth cues and not recession rate, the importance of recession rate in this study suggests there is a response but that it may occur at a larger scale than their experiment

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captured. Kushlan (1976), Frederick and Collopy (1989), and Frederick and Spalding (1994) also demonstrated a linkage between breeding success in wading birds and water level fluctuations, suggesting that a similar connection is also important during the period of time leading up to breeding in the Everglades. The importance of recession rate in almost every egret and ibis physiological model also demonstrates the essentialness of maintaining good foraging habitat throughout the period of time leading up to reproduction for these species. While shallow water conditions may be important for attracting wading birds to the Everglades during the early dry season, steady recession rates associated with suitable foraging depths may act together as a switch to initiate the pre-breeding stage where both species begin to prepare for reproduction. Given most years will not have excellent habitat conditions similar to 2006, maintaining stable recession rates during average years is probably the most critical factor to consider in managing Everglades wetlands for breeding wading birds. The response to these conditions is probably not static year to year, but variable and dependent on the influence of the previous season's dry and rainy seasons that preset hydrological and prey community conditions for the following year.

This study provides the first documentation of different patterns in adult pre-breeding physiological condition and the landscape habitat variables that influenced them for great egrets and white ibises during years with differing habitat conditions. The significance of these differences may not be limited to these two species alone, but may also be linked to other species of wading birds in the Florida Everglades that either remained stable or had decreasing populations during the alteration of this ecosystem. Understanding how landscape habitat variability can influence the physiological

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condition of pre-breeding searcher and exploiter species may be an important facet of

future research, and could identify a tipping point for whether waders decide to breed,

and if so how much energy to invest given current habitat conditions. Examining other

searcher and exploiter species' pre-breeding responses to variability in landscape level

habitat conditions will improve our understanding of the generalized patterns within these

two groups and also potentially yield new insights into how near identical species may

respond completely different to their local environment, with implications for subsequent

nesting and populations patterns.

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19:716-723.

Anteau, M. J., and A. D. Afton. 2008. Using plasma lipid metabolites to index changes in lipid reserves of free-living lesser scaup (*Aythya affinis*). Auk 125:354-357.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459-471.

Anholt, B. R., and E. E. Werner. 1998. Predictable changes in predation mortality as a consequence of changes if food availability and predation risk. Evolutionary Ecology 12:729-738.

Astheimer, L. B., W. A, Buttemer, and J. C. Wingfield. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scandinavia 23:355-365.

Bancroft G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. Waterbirds 25:265–277.

Beerens, J. E. 2008. Hierarchial habitat selection in Great Egrets and White Ibises in the Florida Everglades. Thesis, Florida Atlantic University, Boca Raton , FL.

Beissinger, S. R. 1983. Hunting behavior, prey selection, and energetics of snail kites in Guyana: consumer choice by a specialist. Auk 100:84-92.

Bolton, M., P. Monaghan, and D. C. Houston. 1993. Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition. Canadian Journal of Zoology 71:273-279.

Buchanan, K. L. 2000. Stress and evolution of condition-dependent signals. Trends in Ecology an Evolution 14:156-160.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cherel, Y., J. P. Robin, and Y. Le Mayo. 1988. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66:159-166.

Cherel, Y., R. Mauget, A. Lacroix, and J. Gilles. 1994. Seasonal and fasting-related changes in circulating gonadal steroids and prolactin in King Penguins, *Aptenodytes patagonicus*. Physiological Zoology 67:1154-1173.

Clapp, R. B., M. K. Klimkiewicz, and J. H. Kennard. 1982. Longevity records of North American birds: Gaviidae through Alcidae. Journal of Field Ornithology 53:81-124.

Cochran, W. G. 1977. Sampling techniques. John Wiley and Sons Inc., New York.

Cockrem, J. F., and P. J. Seddon. 1994. Annual cycle of sex steroids in the Yellow-eye Penguin (*Megadyptes antipodes*) on South Island, New Zealand. General and Comparative Endocrinology 94:113-121.

Crozier, G. E., and D. E. Gawlik. 2003*a*. Wading bird nesting effort as an index of wetland ecosystem integrity. Waterbirds 26:303-324.

Crozier, G. E., and D. E. Gawlik. 2003*b*. The use of decoys in attracting wading birds. Journal of Field Ornithology 69:276-287.

Cuthill, I. C., S. A. Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. Behavioral Ecology 11:189-195.

Drent, R. H., and S, Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Frederick, P. C., and M. W, Collopy. 1989. Nesting success of Ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625-634.

Frederick, P. C., and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-692 *in* S. M. Davis and J. C. Ogden (eds.). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Gauthier, G., J. Bédard, J. Huot, amd Y. Bédard. 1984. Spring accumulation of fat by greater snow geese in two staging habitats. Condor 86:192-199.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Gawlik, D. E., and G. E. Crozier. 2007. A test of cues affecting habitat selection by wading birds. Auk 124:1075-1082.

Golet, G. H., and D. B. Irons. 1999. Raising young reduces body condition and fat scores in black-legged kittiwakes. Oecologia 120:530-538.

Golet, G. H., D. B. Irons, and J. A. Estes. 1998. Survival costs of chick rearing in black-legged kittiwakes. Journal of Animal Ecology 67:827-841.

Golet, G. H., J. A. Schmutz, D. B. Irons, and J. A. Estes. 2004. Determinants of
reproductive costs in the long-lived black-legged kittiwake: a multiyear
experiment. Ecological Monographs 74:353–372.

Gosler, A. G., J. J. Greenwood, and C. Perrins. 1995. Predation risk and the cost of being
fat. Nature 337:621-623.

Hanssen, S. A., K. E. Erikstad, V. Johnsen, and J. O. Bustness. 2003. Differential
investment and costs during avian incubation determined by individual quality: an
experimnetal study of the common eider (*Somateria mollissima*). Proceeding of
the Royal Society London B 270:531-537.

Heath, J. A. 2002. White ibis (*Eudocimus albus*) reproductive physiology. Dissertation,
University of Florida, Gainesville, FL.

Heath, J. A., P. C. Frederick, T. M. Edwards, and L. J. Guillette Jr. 2003. Reproductive
physiology of free-living white ibises (*Eudocimus albus*) in the Florida
Everglades. General and Comparative Endocrinology 133:118-131.

Heath, J. A., and P. C. Frederick. 2003. Trapping white ibis with rocket nets and mist
nets in the Florida Everglades. Journal of Field Ornithology 69:276-287.

Hector, J. A. L. 1988. Reproductive endocrinology of albatrosses. In: H. Oullet, editor.
Acta XIX Congressus International Ornithology 2:1702-1709.

Hector, J. A. L., J. P. Croxall, and B. K. Follet. 1985. Reproductive endocrinology of the
wandering albatross *Diomedea exulans* in relation to biennial breeding and
deferred sexual maturity. Ibis 128:9-22.

Herring, G. and D. E. Gawlik. 2007. The role of stress proteins in the study of
allostatic overload in birds, use and applicability to current studies in avian

ecology. The Scientific World Journal 7:1596-1602.

Herring, G. and D. E. Gawlik. *In Review*. Stability of avian fecal corticosterone

metabolite levels in frozen avian feces. General and Comparative Endocrinology.

Herring, G., D. E. Gawlik, and J. M. Beerens. 2008. Evaluating two new methods

for capturing large wetland birds. Journal of Field Ornithology 79:102-110.

Herring, G., D. E. Gawlik, and J. M. Beerens. 2008. Predicting the sex of great

egrets and white ibises. Waterbirds 31:306-311.

Houston, A. I., J. M. McNamara, and J. M. Hutchinson. 1997. General results

concerning the trade-off between gaining energy and avoiding predation.

Philosophical Transaction of the Royal Society of London B 341:375-397.

Jenni-Eierman, S., and L. Jenni. 1994. Plasma metabolite levels predict individual body

mass changes in a small long-distance migrant, the garden warbler. Auk 111:888-899.

Kellett, D. K., R. T. Alisauskas, K. R. Mehl, K. L. Drake, J. J. Traylor, and S. L. Lawson.

2005. Body mass of long-tailed ducks (*Clangula hyemalis*) during incubation.

Auk 122:313-318.

Khan, M. Z., I. Altmann, S. S. Isani, and J. Yu. 2002. A matter of time: evaluating the

storage of fecal samples for steroid analysis. General and Comparative

Endocrinology 128:57-64.

Kitaysky, A. S., J. C. Wingfield, and J. F. Piatt. 1999. Dynamics of food   availability,

body condition and physiological stress response in breeding black-legged

kittiwakes. Functional Ecology 13:577:584.

Kushlan, J. A. 1975. Site selection for nesting colonies of the American white ibis *Eudocimus albus* in Florida. Ibis 118:590-593.

Kushlan J. A. 1976. Site selection for nesting colonies by the American White Ibis *Eudocimus albus* in Florida. Ibis. 118:590–593.

Kushlan, J. A., and K. L. Bildstein. 1992. White ibis. *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of North America, Inc., Philadelphia, PA.

Linquist, S. 1986. The heat shock response. Annual Review of Biochemistry 55:1151-1191.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina.

Lormee, H., P. Jouventin, P. Chastel, and O, Mauget. 1999. Endocrine correlates of parental care in the Antarctic winter breeding seabird, the emperor penguin, *Antenodytes forsteri*. Hormonal Behavior 35:9-17.

Lormee, H., P. Jouventin, P. Lacroix, A. Lallemand, and O. Chastel. 2000. Reproductive endocrinology of tropical seabirds: sex-specific patterns in LH, steroids, and prolactin secretion in relation to patterns of parental care. General and Comparative Endocrinology 117:413-426.

Martínez-Padilla, J., J. Martínez, J. A. Dávilla, S. Merino, J. Moreno, and J. Millán. 2004. Within-brood size differences, sex and parasites determine blood stress protein levels in Eurasian kestrel nestlings. Functional Ecology 18:426-434.

Masello, J. F., and P. Quillfeldt. 2004. Are haematological parameters related to body
condition, ornamentation and breeding success in wild burrowing parrots
Cyanoliseus patagonus? Journal of Avian Biology 35:445-454.

McCrimmon, D. A., Jr., J. C. Ogden, and G. T. Bancroft. 2001. Great egret (*Ardea alba*).
In A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of
North America, Inc., Philadelphia, PA.

McNamara, J. M., and A. I. Houston. 1987. Starvation and predation as factors limiting
population size. Ecology 68:1515-1519.

McQueen, S. M., L. S. Davis, and G. Young. 1998. The reproductive endocrinology of
fiorland crested penguins *Eudyptes pachyrhynchus*. Emu 98:127-131.

Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine, and J. Blackwood. 1989. The
relationship between food supply, reproductive effort and breeding success in
Arctic terns *Sterna paradisaea*. Journal of Animal Ecology 58:261–274.

Moreno, J., S, Merino, J. Martínez, J. J. Sanz, and E, Arriero. 2002.
Heterophil/lymphocyte ratios and heat shock protein levels are related to growth
of nestling birds. Ecoscience 9:434-439.

Ogden, J. C. 1994. A comparison of wading bird nesting colony dynamics (1931-1946
and 1974-1989) as an indication of ecosystem conditions in the southern
Everglades. Pages 533-570 *in* S. M. Davis and J. C. Ogden (eds.). Everglades: the
ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Partridge, L., and P. H. Harvey. 1988. The ecological context of life history evolution.
Science 241:1449-1455.

Pearson, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology 37: 521–552.

Philippi, T. 2003. CERP monitoring and assessment plan: stratified random sampling plan. Final Report to South Florida Water Management District, West Palm Beach, Florida.

Pravosudov, V. V., and T. C. Grubb, Jr. 1997. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. Behavioral Ecology 8:332-339.

Quillfeldt, P., J. F. Masello, and E. Möstl. 2004. Blood chemistry in relation to nutrition and ectoparasite load in Wilson's storm-petrels *Oceanites oceanicus*. Polar Biology 27:168-176.

Ramo, C., and B. Busto. 1993. Resource use by herons in a Yucatan wetland during the breeding season. Wilson Bulletin 105:573-586.

Ricklefs, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. American Naturalist 111:453-478.

Rogers, C. M., and A. K. Reed. 2003. Does avian winter fat storage integrate temperature and resource conditions? A long-term study. Journal of Avian Biology 34:112-118.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York, New York.

Romero, M. L., and J. M. Reed. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comparative Biochemistry and Physiology, Part A 140:73-79.

Russell, G. J., O. L. Bass, Jr., and S. L. Pimm. 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. Animal Conservation 5:185-199.

Smith, J. P. 1997. Nesting season food habits of 4 species of herons and egrets at Lake Okeechobee, Florida. Colonial Waterbirds 20:198-220.

Stearns, S. C. 1976. Life history tactics: a review of ideas. Quarterly Review of Biology 51:3-47.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.

Sykes, P. W. 1987. The feeding habits of the snail kite in Florida, USA. Waterbirds 10: 84-92.

Tomás, G., J. Martínez, and S. Merino. 2004. Collection and analysis of blood samples to detect stress proteins in wild birds. Journal of Field Ornithology 75:281-278.

U. S. Geological Survey. 2006. The Everglades Depth Estimation Network (EDEN) for Support of Ecological and Biological Assessments. U. S. Department of the Interior. Fact Sheet 2006-3087.

Velando, A., and C. Alonso-Alvarez. 2003. Differential body condition regulation by males and female in response to experimental manipulations of brood size and parental effort in the blue-footed booby. Journal of Animal Ecology 72:846-856.

Verme, L. J., and R. V. Doepker. 1988. Suppression of reproduction in Upper Michigan white-tailed deer, *Odocoileus virginianus*, by climatic stress during the rut. Canadian Field Naturalist 102:550-552.

Wasser, S. K., K. E. Hunt, J. L. Brown, K. Cooper, C. M. Crockett, U. Bechert, J. J.
    Millspaugh, S. Larson, and S. L. Monfort. 2000. A generalized fecal
    corticosterone assay for use in a diverse array of nondomestic mammalian and
    avian species. General and Comparative Endocrinology 120:260-275.

Williams, T. D. 1966. Natural selection, the costs of reproduction and refinement of
    Lack's principle. American Naturalist 100:687-690.

Williams, T. D., C. G. Guglielmo, O. Egeler, and C. J. Mortyniuk. 1999. Plasma lipid
    metabolites provide information on mass change over several days in captive
    Western sandpipers. Auk 116:994-1000.

Williams, C. T., S. D. Kildaw, and C. L. Buck. 2007. Sex specific differences in body
    condition indices and seasonal mass loss in tufted puffins. Journal of Field
    Ornithology 78:369-378.

Willmer, P. G., G. N. Stone, and I. A. Johnston. 1999. Environmental physiology of
    animals. Blackwell Science, Oxford, United Kingdom.

Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds. *In*
    K.G. Davey, R. E. Peter, and S. S. Tobe (eds). Perspectives in Comparative
    Endocrinology National Research Council of Canada, Ottawa, Ontario, Canada.

Wingfield, J. C., C. M. Vleck, and M. C. Moore. 1992. Seasonal changes of the
    adrenocorticalesponse to stress in birds of Sonoran Desert. Journal of
    Experimental Zoology 264:419-428.

Wingfield, J. C., G. Ramos-Fernandez, A. Nunez-de la Mora, and H. Drummond. 1999.
    The effects of an *El Nino* southern oscillation event on the reproduction in male

and female blue-footed boobies, *Sula nebouxii*. General and Comparative

Endocrinology 114:163-172.

Zar, J. H. 1996. Biostatistical Analysis. Prentice Hall, Upper Saddle River, NJ.

Zoogen. 2007. Sex Made Easy™ avian gender determination test.

http://www.zoogen.biz/sme.html, accessed 18 June 2007.

Table 1. Akaike's Information Criterion (adjusted for small sample sizes; AICc) model selection for adult great egret and white ibis plasma triglycerides, plasma glycerol, plasma corticosterone, fecal corticosterone, stress proteins 60 and 70, pectoral muscle mass scores, and size structure controlled mass. Samples were collected in Water Conservation Areas 2A, 3A, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge between 10 Jan – 23 Mar in both 2006 and 2007. Models presented only include those that were within 5 AIC_c values of the top model ($\Delta i = 0$).

Great egret model	K	AIC_c	Δi	ω_i
GLYC				
Recess	3	114.7	0	0.70
Recess + Recess^2	3	117.1	2.4	0.21
Sex + Biomass + Recess	5	119.6	4.9	0.06
Intercept	1	130.0	15.3	0.00
Global	23	147.8	33.1	0.00
TRIG				
Recess	3	116.2	0	0.46
Recess + Recess^2	3	117.8	1.6	0.20
Depth	3	119.1	2.9	0.10
Sex + Biomass + Recess	5	119.9	3.7	0.07
Intercept	1	131.0	14.8	0.00
Global	22	138.0	21.8	0.00
PCORT				
Recess	3	214.6	0	0.42

Sex + Biomass + Recess	5	216.4	1.8	0.17
Recess + Recess^2	3	216.5	1.9	0.16
Sex + Biomass	4	217.9	3.3	0.08
Sex + Biomass + Recess + Recess^2	5	218.2	3.6	0.06
Global	23	233.7	19.1	0.00
Intercept	1	234.0	19.4	0.00

FCORT

Sex + Biomass + Recess	5	181.4	0	0.32
Sex + Biomass + Recess + Recess^2	5	182.0	0.6	0.24
Recess	3	183.0	1.6	0.14
Recess + Recess^2	3	183.8	2.4	0.09
Sex + Biomass + Recess + Depth + Julian + Sex×Biomass	8	183.9	2.5	0.09
Sex + Biomass + Recess + Depth	6	185.5	4.1	0.04
Global	23	189.7	8.3	0.00
Intercept	1	189.7	8.3	0.00

SP60

Global	23	347.4	0	0.45
Sex + Biomass + + Recess + Recess^2 + Depth + Depth^2	6	348.8	1.4	0.22
Sex + Biomass + Recess + Depth + Julian + Sex*Biomass	8	349.5	2.1	0.16
Sex + Biomass + Recess	5	351.5	4.1	0.05
Sex + Biomass + Recess + Recess^2 + Depth + Depth^2	6	351.6	4.2	0.05
Intercept	1	399.4	52.0	0.00

SP70

Recess	3	88.6	0	0.49

Recess + Recess^2	3	90.9	2.3	0.15
Intercept	1	91.1	2.5	0.14
Biomass	3	92.9	4.3	0.05
Sex	3	93.6	5.0	0.04
Global	23	126.9	38.3	0.00

Mass

Sex + Biomass	4	172.8	0	0.39
Sex + Biomass + Recess	5	173.0	0.2	0.35
Sex + Biomass + Recess + Recess^2	5	174.6	1.8	0.16
Sex×Biomass	3	176.9	4.1	0.05
Global	23	190.3	17.5	0.00
Intercept	1	215.7	42.9	0.00

PEC

Recess	3	112.7	0	0.32
Recess + Recess^2	3	113.4	0.7	0.22
Sex + Biomass + Recess	5	114.0	1.3	0.16
Sex + Biomass + Recess + Recess^2	5	114.0	1.3	0.16
Sex×Biomass	3	116.7	4.0	0.04
Intercept	1	119.8	7.1	0.00
Global	23	135.5	22.8	0.00

White ibis model	K	AIC$_c$	Δi	ω$_i$
GLYC				
Recess	3	213.0	0	0.49
COV	3	214.8	1.8	0.20
Recess + Recess^2	3	215.8	2.8	0.12
Sex + Biomass	4	216.9	3.9	0.07
Sex + Biomass + Recess	5	217.6	4.6	0.04
Depth	3	217.9	4.9	0.04
Intercept	1	238.9	25.9	0.00
Global	23	247.9	34.9	0.00
TRIG				
Sex + Biomass + Recess	5	245.4	0	0.30
Sex + Biomass + Recess + Depth + Julian + Sex×Biomass	8	246.3	0.9	0.19
Sex + Biomass + Recess + Depth	6	246.6	1.1	0.17
Sex + Biomass + Recess + Depth + Julian	7	247.9	2.5	0.08
Sex + Biomass + Recess + Recess^2	5	248.1	2.7	0.08
Sex + Biomass + Recess	5	248.2	2.8	0.07
Recess	3	249.4	4.0	0.04
Global	23	258.8	13.4	0.00
Intercept	1	291.6	46.2	0.00
PCORT				
Sex + Biomass + Recess	5	328.5	0	0.34
Sex + Biomass	4	328.6	0.1	0.32
Sex + Biomass + Recess + Recess^2	5	331.0	2.5	0.09

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Sex + Biomass + Recess + Julian + Sex×Biomass	7	331.0	2.5	0.09
Recess	3	331.0	2.5	0.09
Sex + Biomass + Recess + Depth	6	332.6	4.1	0.04
Global	23	352.2	23.7	0.00
Intercept	1	363.8	35.3	0.00

FCORT

Sex + Biomass + Recess	5	225.9	0	0.48
Sex + Biomass	4	226.8	0.9	0.31
Sex + Biomass + Recess + Recess^2	5	226.8	2.3	0.15
Sex + Biomass + Recess + Depth	6	226.8	4.8	0.04
Global	23	247.7	21.8	0.00
Intercept	1	270.6	44.7	0.00

SP60

Sex + Biomass + Recess	5	701.0	0	0.30
Sex + Biomass + Recess + Depth + Julian + Sex×Biomass	8	701.1	0.1	0.29
Sex + Biomass + Recess + Depth	6	703.2	2.2	0.10
Sex + Biomass + Recess + Recess^2	5	703.2	2.2	0.10
Global	23	703.3	2.3	0.09
Sex + Biomass	4	704.4	3.4	0.05
Sex + Biomass + Recess + Depth + Julian	7	705.2	4.2	0.03
Intercept	1	811.1	110.1	0.00

SP70

Recess	3	116.7	0	0.43
Recess + Recess^2	3	118.7	2.0	0.16
Depth	3	121.5	4.8	0.03
Intercept	1	122.6	5.9	0.02

Global	23	157.2	40.5	0.00

Mass

Sex + Biomass + Recess	5	702.4	0	0.42
Sex + Biomass + Recess + Depth + Julian + Sex×Biomass	8	704.0	1.6	0.19
Sex + Biomass + Recess	5	704.6	2.2	0.14
Sex + Biomass + Recess + Recess^2	5	705.0	2.6	0.11
Sex + Biomass	4	706.2	3.8	0.06
Global	23	708.8	6.4	0.01
Intercept	1	784.9	82.5	0.00

PEC

Sex + Biomass	4	203.2	0	0.34
Recess	3	203.6	0.4	0.27
Sex + Biomass + Recess	5	205.1	1.9	0.13
Recess + Recess^2	3	205.6	2.4	0.10
Sex + Biomass + Recess + Recess^2	5	207.1	3.9	0.04
Global	23	236.5	33.3	0.00
Intercept	1	257.3	54.1	0.00

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Table 2. Parameter likelihoods and weighted parameter estimates ± unconditional

standard error (SE) from general linear mixed models evaluating the response of white

ibis and great egret plasma triglycerides, plasma glycerol, plasma corticosterone, fecal

corticosterone, stress proteins 60 and 70, pectoral muscle mass scores, and size structure

controlled mass. Explanatory variables were included if they exceeded 0.10, with the

greatest relative support have parameter likelihoods close to 1.0.

MODEL	Explanatory variable	Parameter likelihood	Parameter estimate	± SE
Great egret				
GLYC	Recess	1.00	0.38	0.22
TRIG	Recess	0.55	0.34	0.33
	Recess + Recess^2	0.23	0.13	0.13
	Depth	0.12	-0.03	0.01
PCORT	Recess	0.84	0.14	0.80
	Sex	0.96	-0.09	0.21
	Biomass	0.96	0.22	0.51
	Depth	0.75	-0.007	0.04
	Julian	0.59	0.005	0.01
FCORT	Sex	0.90	0.24	0.29
	Biomass	0.90	-0.72	0.66
	Recess	0.91	2.14	1.09
SP60	Sex	0.99	1.00	0.67
	Biomass	0.99	-0.40	1.90
	Recess	0.97	-4.22	2.98

	Depth	0.65	-0.10	0.16
	Julian	0.57	-0.08	0.07
SP70	Recess	0.49	0.20	0.19
	Recess + Recess^2	0.15	0.06	0.08
Mass	Sex	0.92	-36.41	9.81
	Biomass	0.92	-40.76	18.28
	Recess	0.91	29.94	31.53
PEC	Recess	0.92	-0.60	0.23
	Sex	0.86	-0.01	0.05
	Biomass	0.86	0.38	0.13

White ibis

GLYC	Recess	0.72	-0.14	0.14
	Sex	0.22	0.02	0.05
	Biomass	0.22	0.23	0.12
TRIG	Sex	0.86	0.16	0.12
	Biomass	0.86	-0.70	0.52
	Recess	0.81	0.65	0.40
	Depth	0.44	0.03	0.04
	Julian	0.27	0.04	0.02
PCORT	Sex	0.79	0.007	0.11
	Biomass	0.79	-0.64	0.23
	Recess	0.47	-0.22	0.31
FCORT	Sex	0.98	-0.19	0.14
	Biomass	0.98	-1.44	0.31
	Recess	0.54	0.36	0.39
	Recess + Recess^2	0.15	-0.12	0.15

SP60	Sex	0.99	1.35	0.78
	Biomass	0.99	-6.03	1.90
	Recess	0.86	-0.54	2.38
	Depth	0.48	0.10	0.15
	Julian	0.36	0.06	0.06
SP70	Recess	0.43	0.007	0.10
	Recess + Recess^2	0.16	-0.007	0.03
Mass	Sex	0.99	-61.78	10.01
	Biomass	0.99	15.35	20.74
	Recess	0.79	-28.79	27.94
	Depth	0.36	2.82	1.81
	Julian	0.36	2.16	0.83
PEC	Sex	0.51	-0.06	0.05
	Biomass	0.51	0.24	0.10

Table 3. Summary of responses of physiological metrics to changing prey availability (Food Limitation Hypothesis) and landscape factors that influence prey availability. Symbols indicate associated physiological responses, positive (+) or negative (-) of adult great egrets and white ibises for plasma triglycerides, plasma glycerol, plasma corticosterone, fecal corticosterone, stress proteins 60 and 70, pectoral muscle mass scores, and size structure controlled mass to decreasing prey densities.

Food Limitation Hypothesis

Response	GLYC	TRIG	PCORT	FCORT	SP60	SP70	MASS	PEC
GREG								
Prey biomass			+	+	+		+/-	-
WHIB								
Prey biomass	+	-	+	+	+		+/-	-

Landscape Factors Influencing Food Limitation Hypothesis

	GLYC	TRIG	PCORT	FCORT	SP60	SP70	MASS	PEC
GREG								
Recess	-	+	+	-	+	-	+	-
Recess + Recess2		+	+			-		
Water Depth		+	+		-			
WHIB								
Recess	+	+	+	-	+	-		-
Recess + Recess2				+		+		
Water Depth		+				-		+
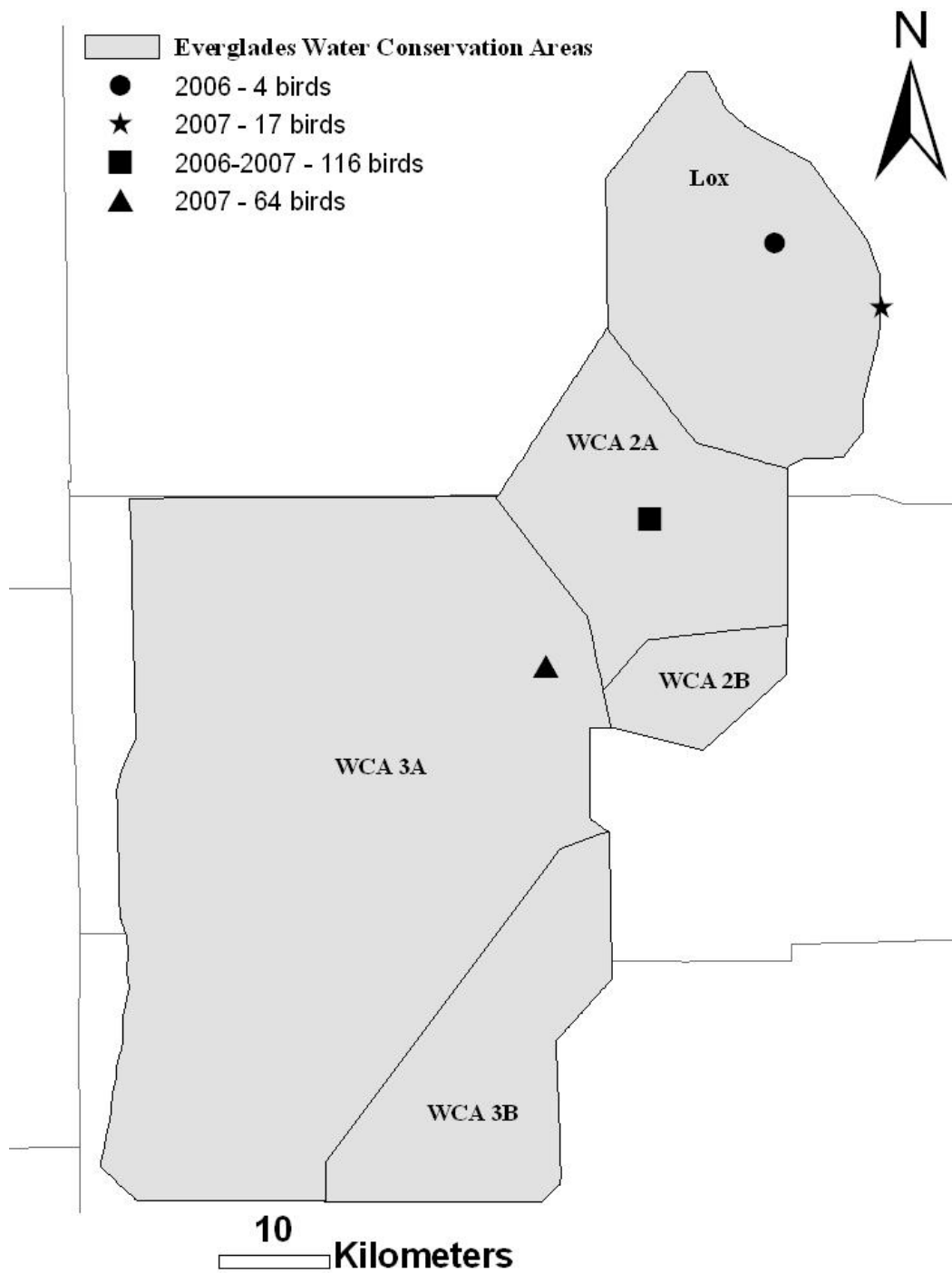
Figure 1. Trapping sites of adult great egrets and white ibises during 2006 – 2007 in the

Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox), Water Conservation

Areas 2A (WCA 2A), and 3A (WCA 3A).
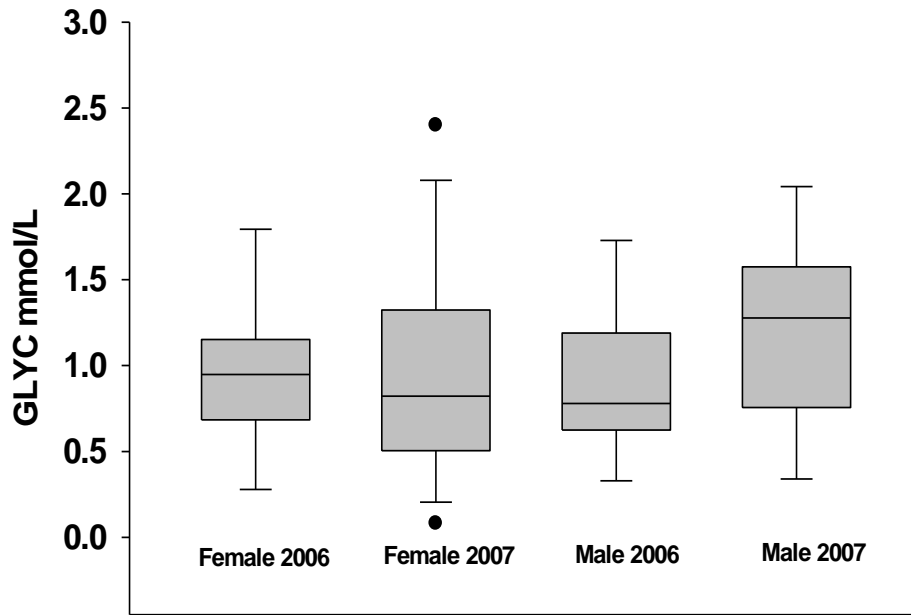
Great Egrets
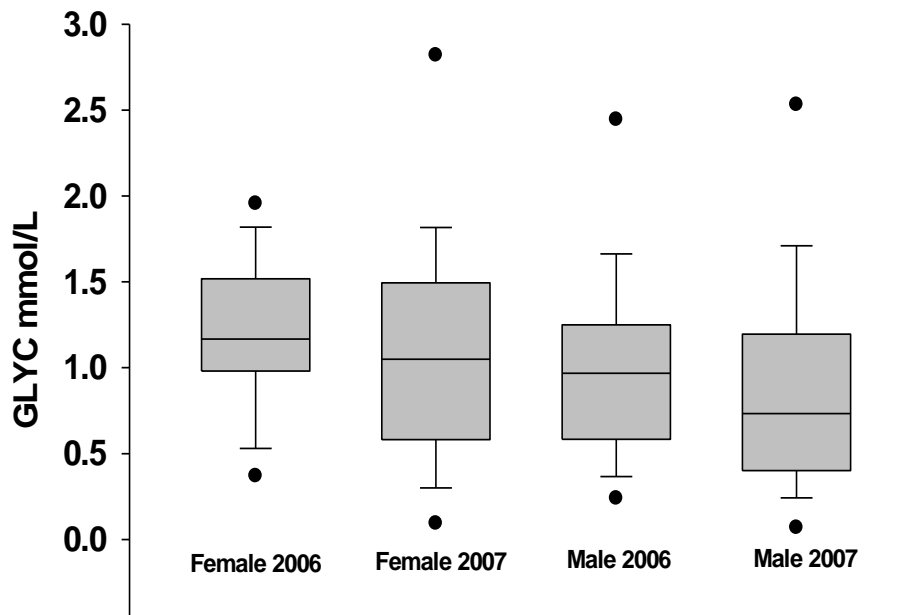
White Ibises

Figure 2-3. Great egret and white ibis GLYC levels during the 2006-2007 pre-breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.

Great Egrets

White Ibises

Figure 4-5. Great egret and white ibis TRIG levels during the 2006-2007 pre-breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

Conservation Area 2A, and 3A of the Florida Everglades.
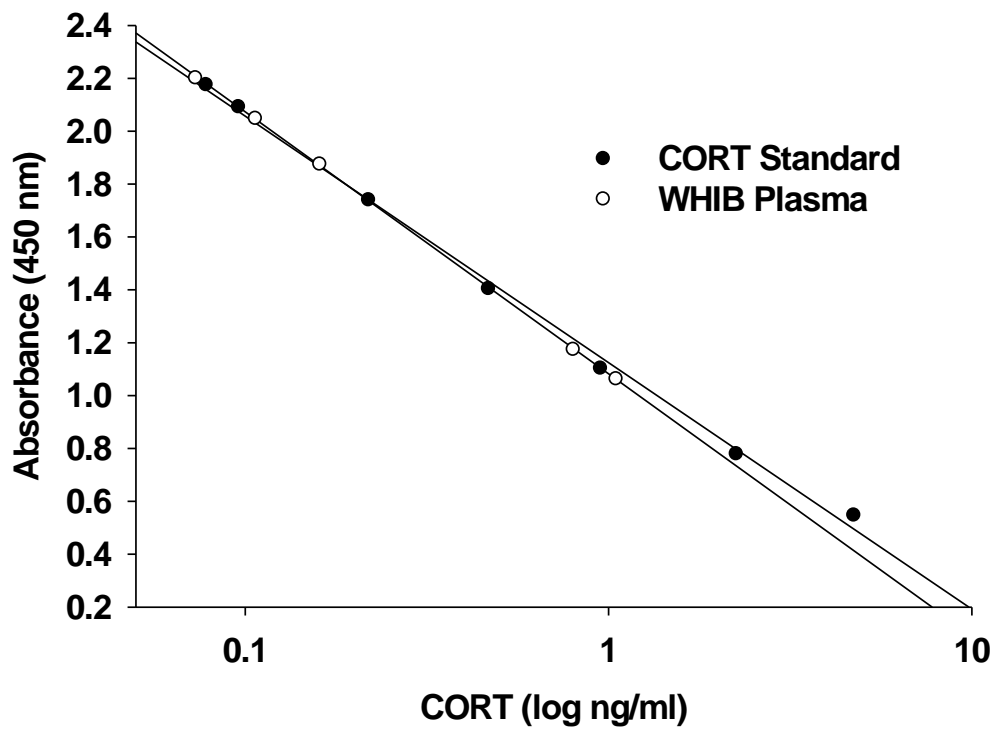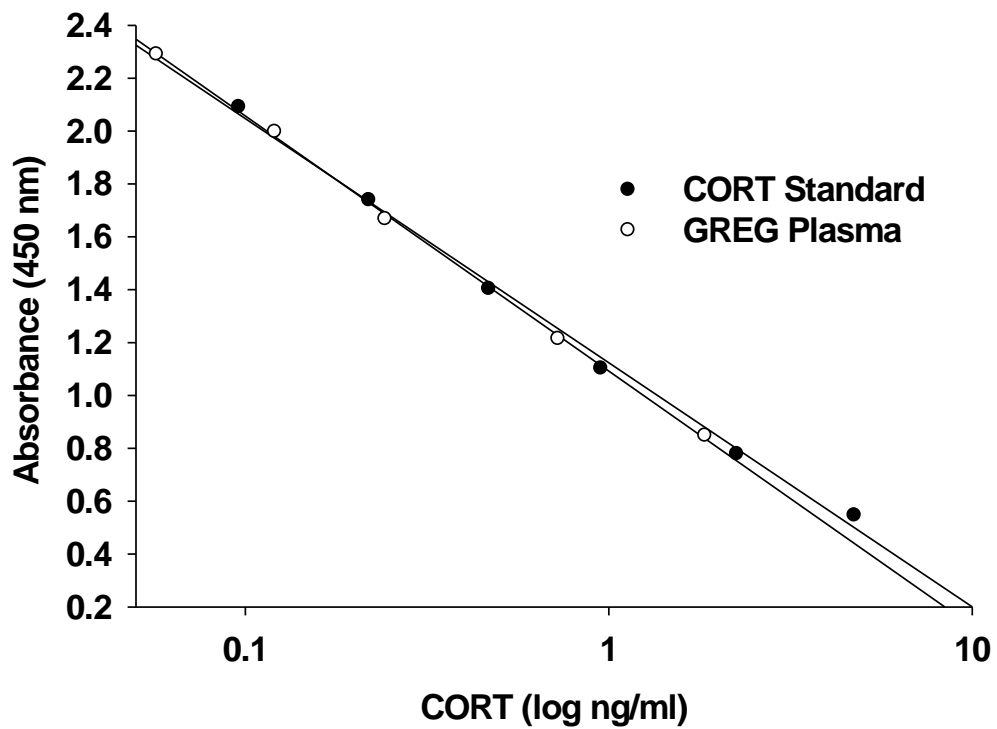
Figure 6-7. Serial dilution results from great egret and white ibis plasma corticosterone extracts.

Figure 8-9. Great egret and white ibis PCORT levels during the 2006-2007 pre-breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

Conservation Area 2A, and 3A of the Florida Everglades.
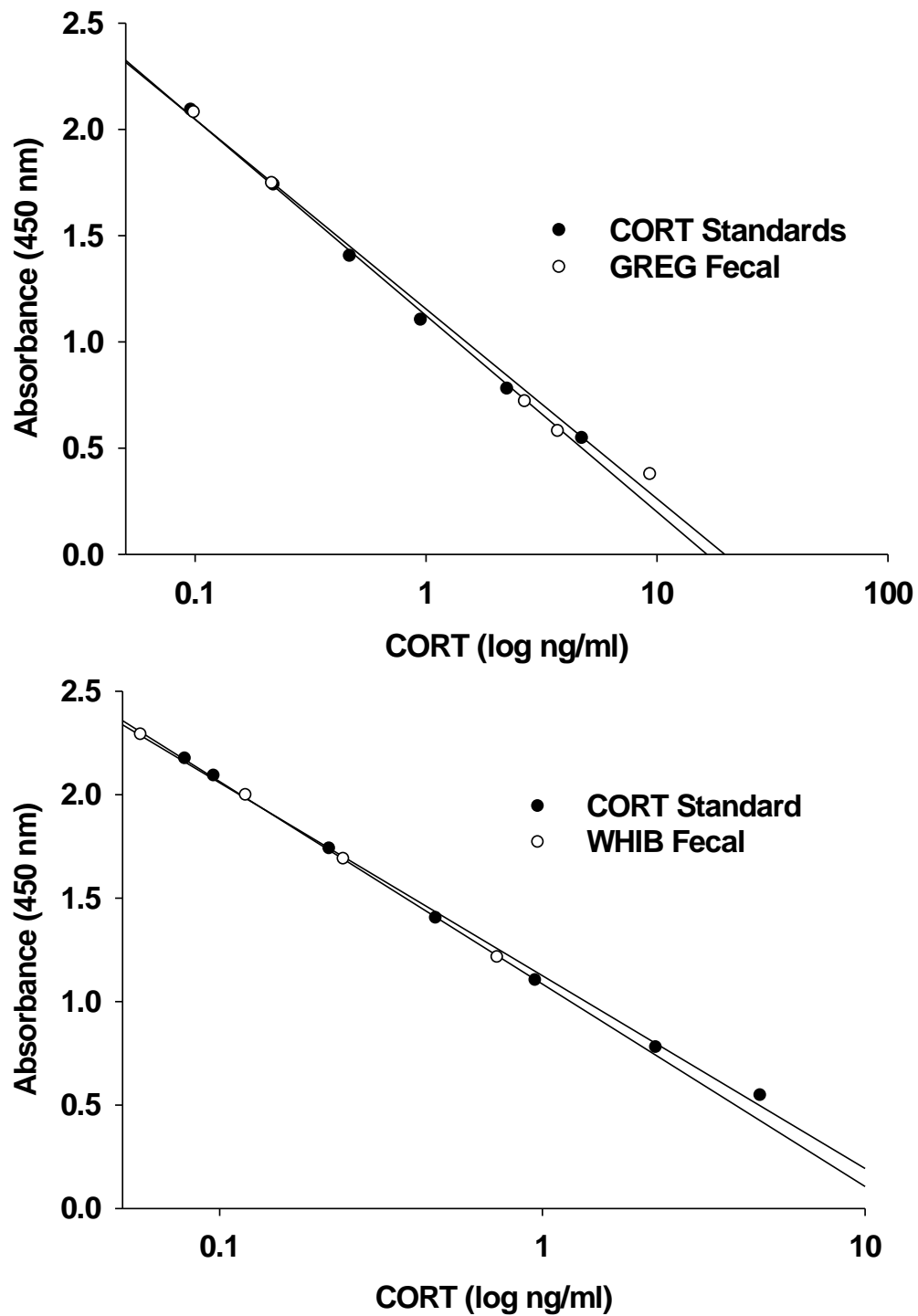
Figure 10-11. Serial dilution results from great egret and white ibis fecal corticosterone extracts.

Great Egrets
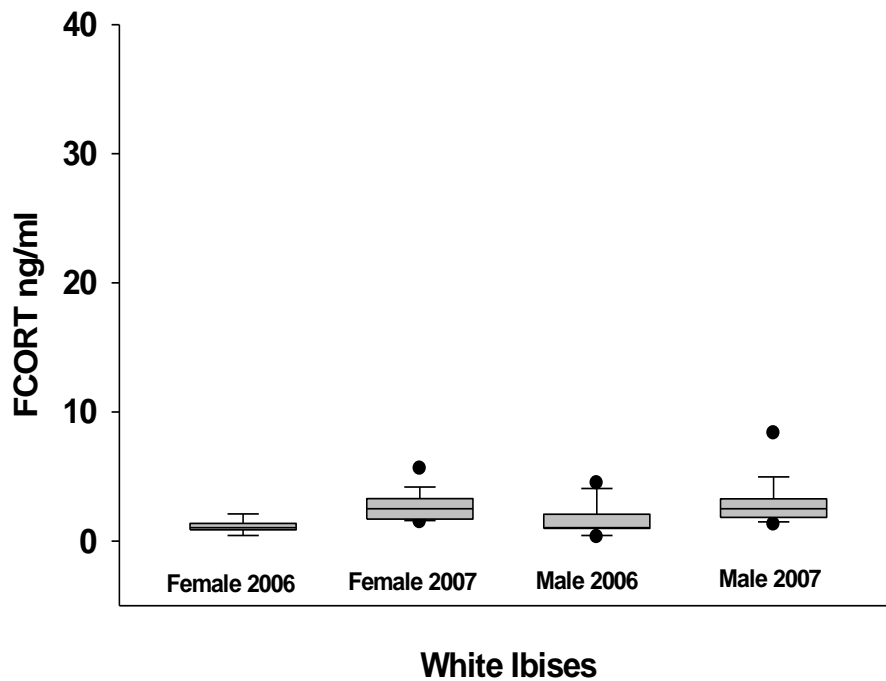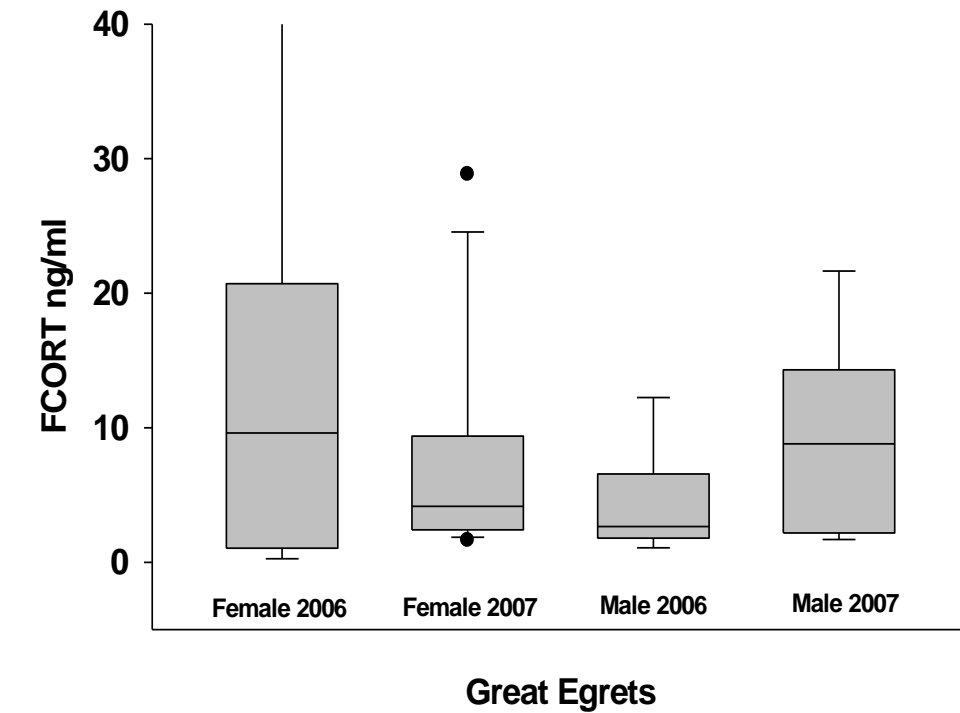
White Ibises

Figure 12-13. Great egret and white ibis FCORT levels during the 2006-2007 pre-breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.
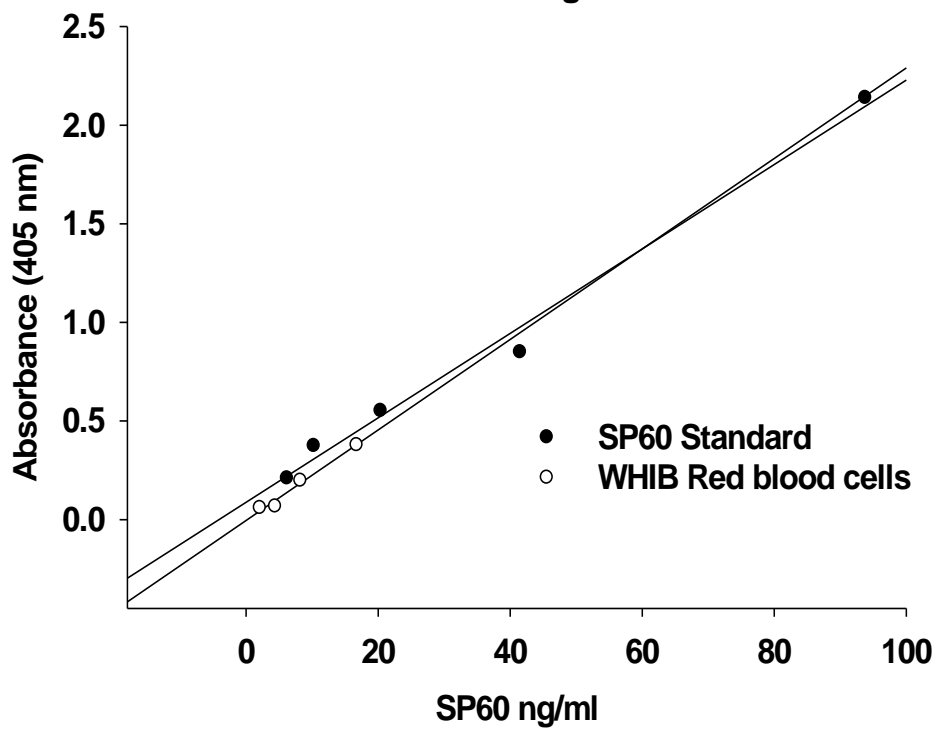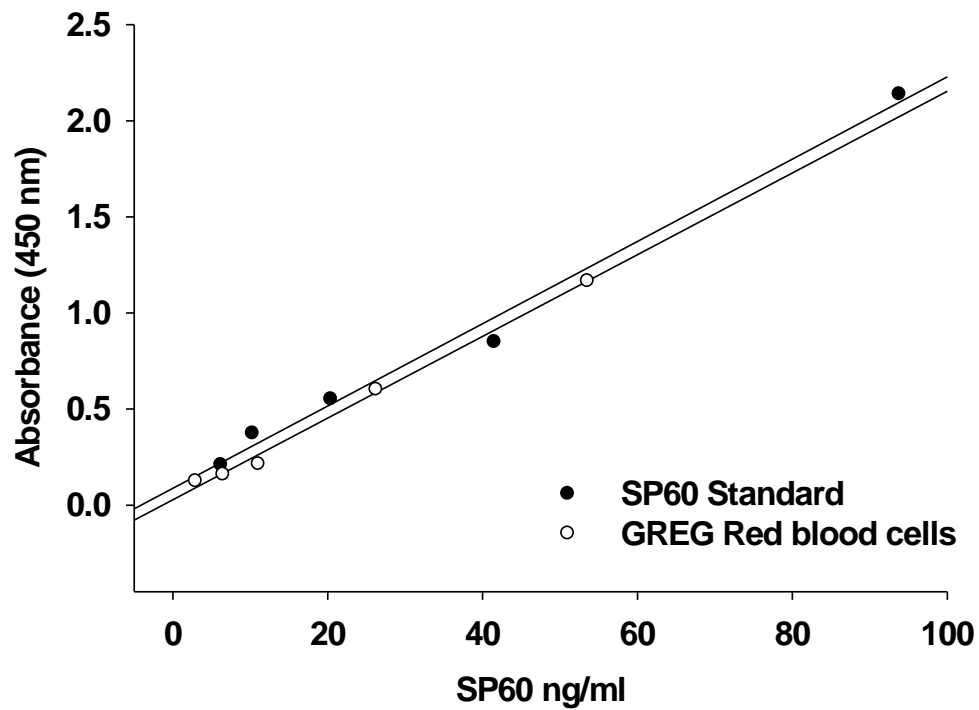
Figure 14-15. Serial dilution results from great egret and white ibis red blood cell SP60
extracts.
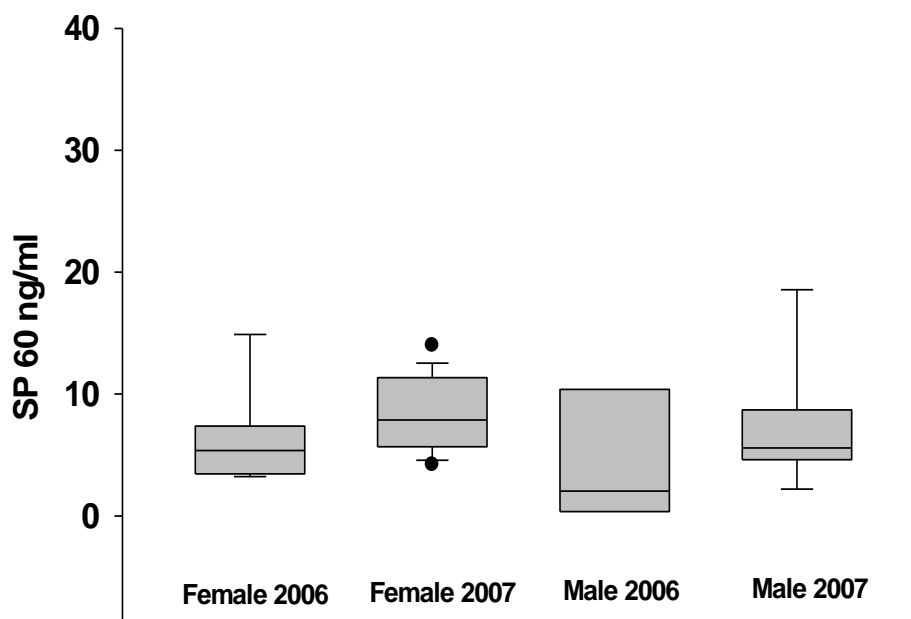
Great Egrets
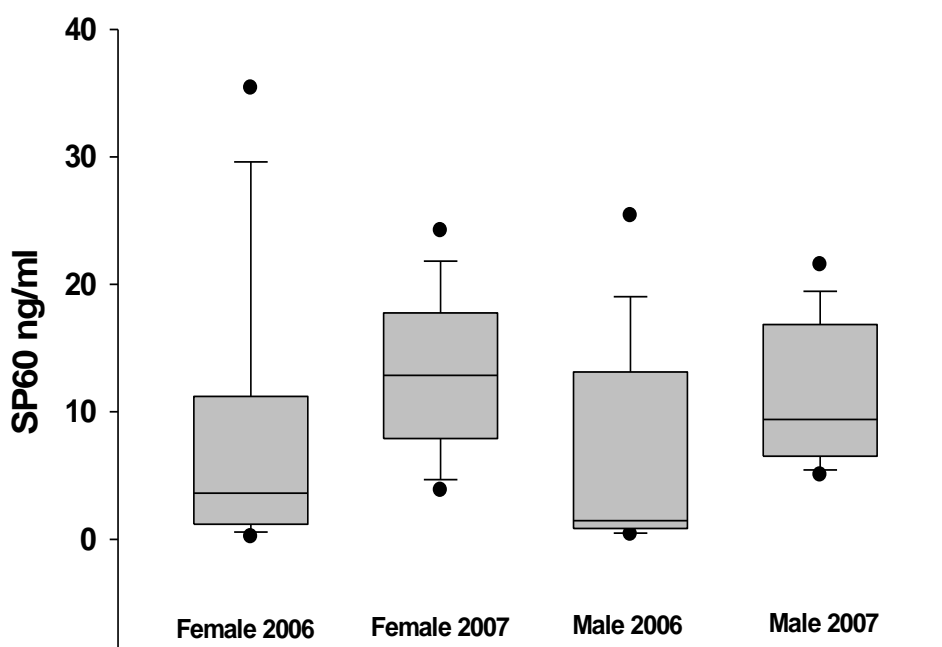
White Ibises

Figure 16-17. Great egret and white ibis SP60 levels during the 2006-2007 pre-breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

Conservation Area 2A, and 3A of the Florida Everglades.
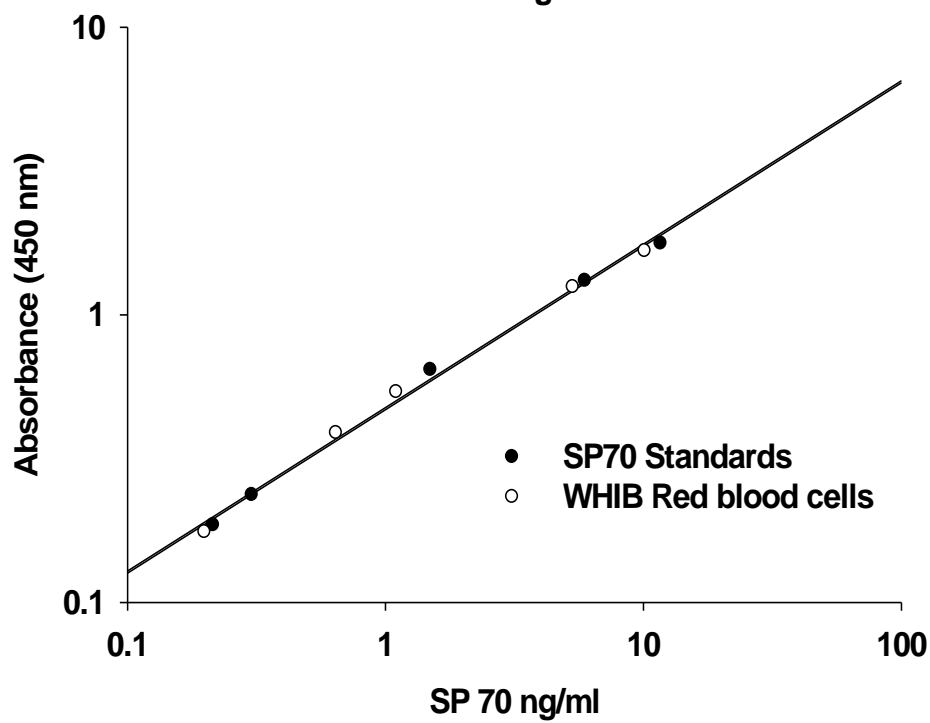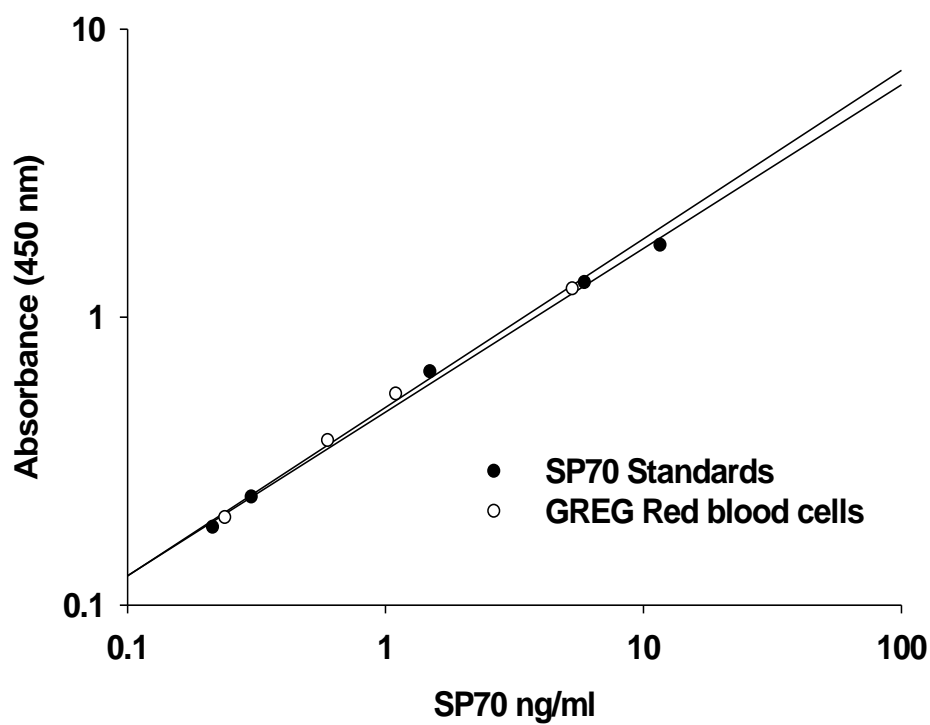
Figure 18-19. Serial dilution results from great egret and white ibis red blood cell SP70 extracts.
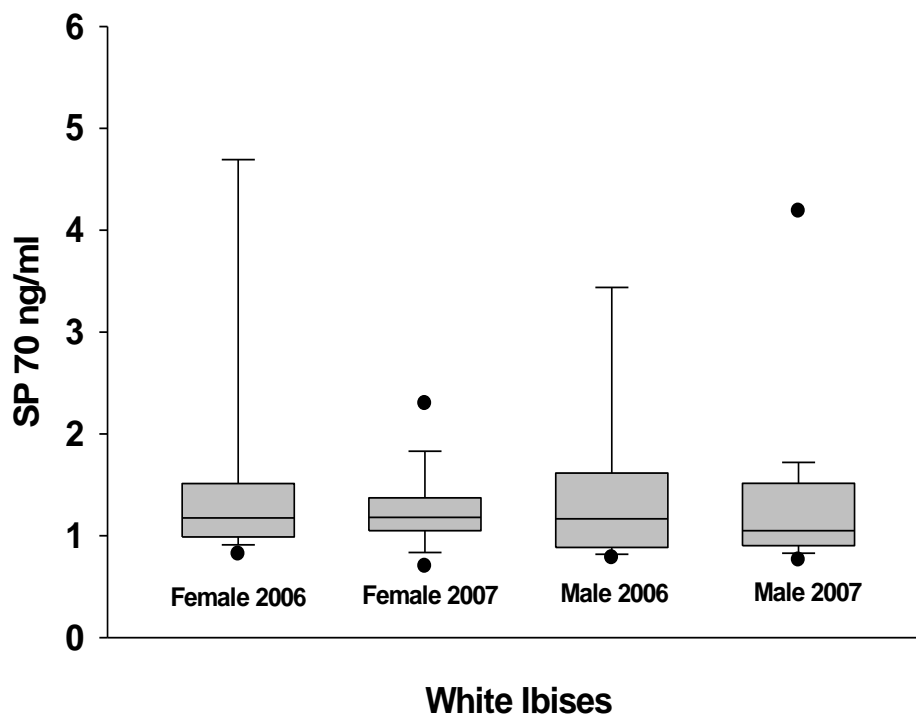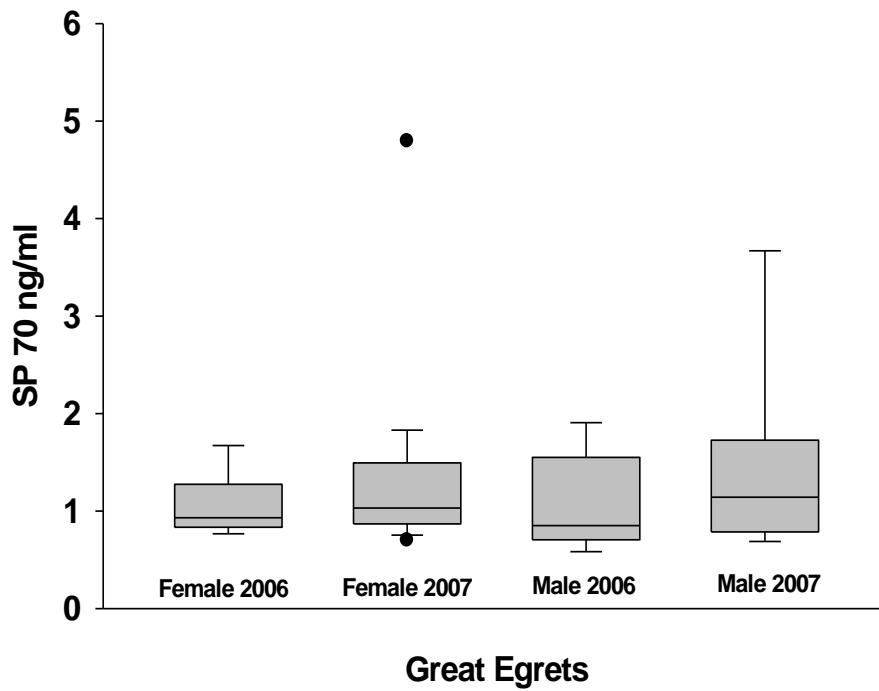
Figure 20-21. Great egret and white ibis SP70 levels during the 2006-2007 pre-breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.
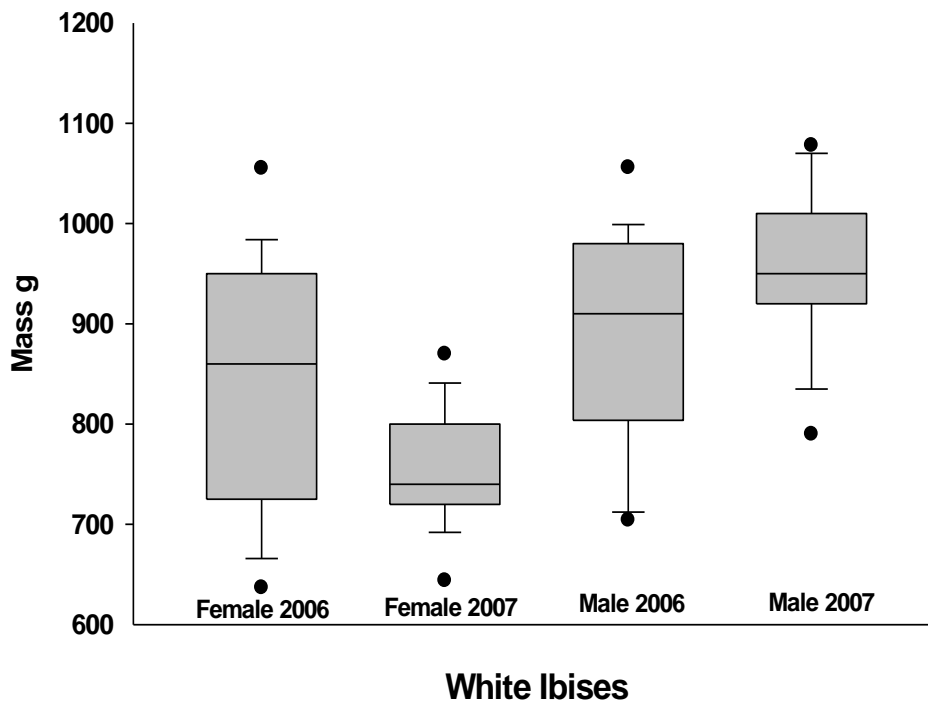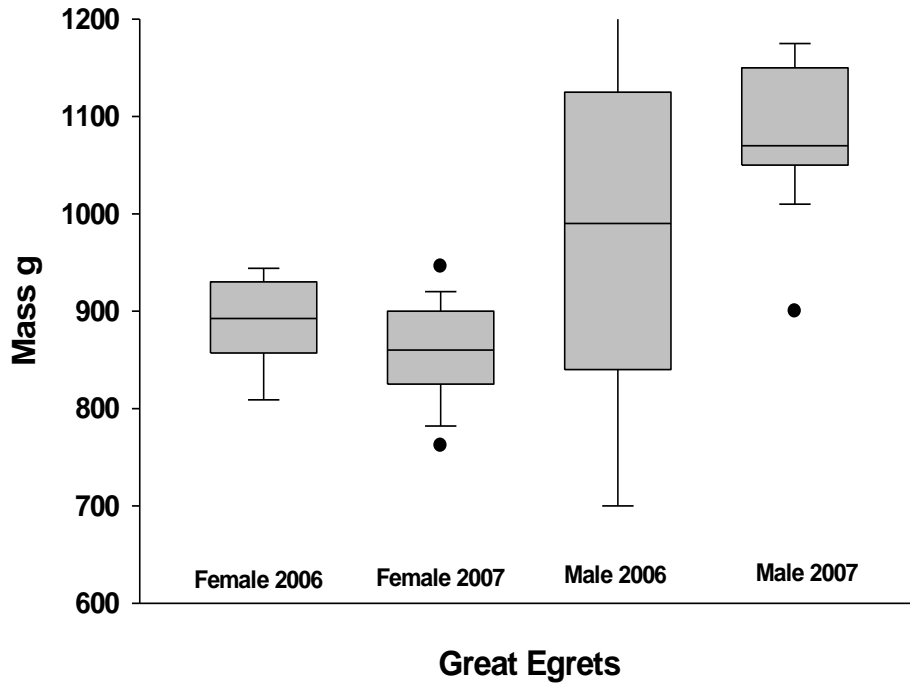
Figure 22-23. Great egret and white ibis mass during the 2006-2007 pre-breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.
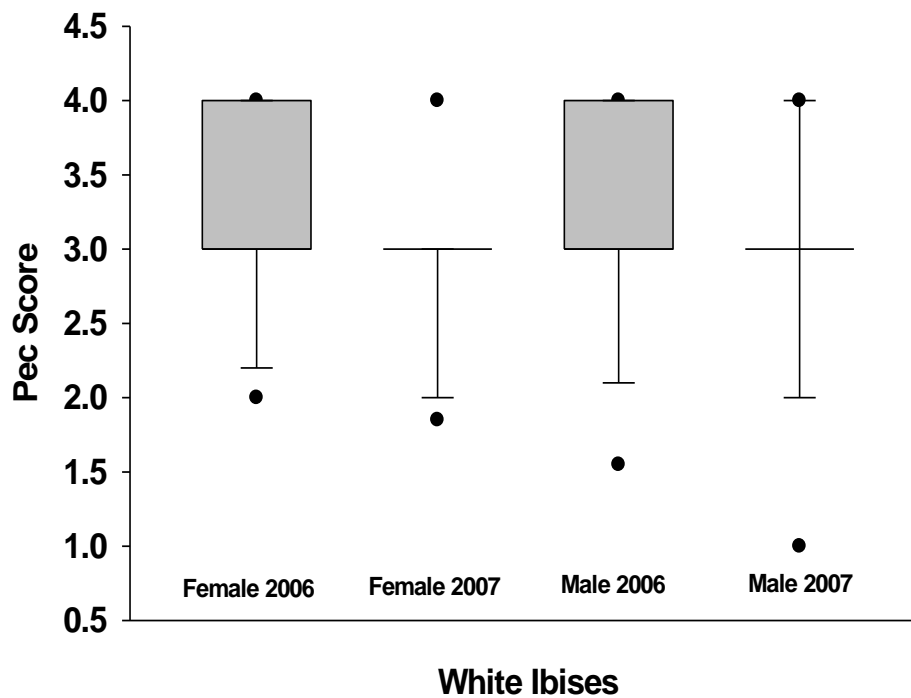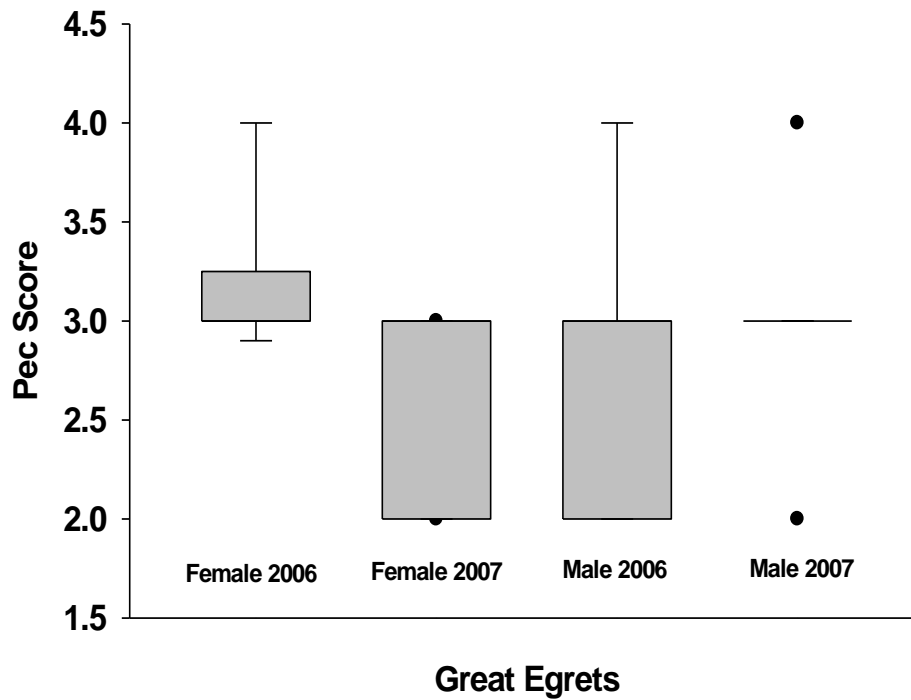
Figure 24-25. Great egret and white ibis PEC levels during the 2006-2007 pre-breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

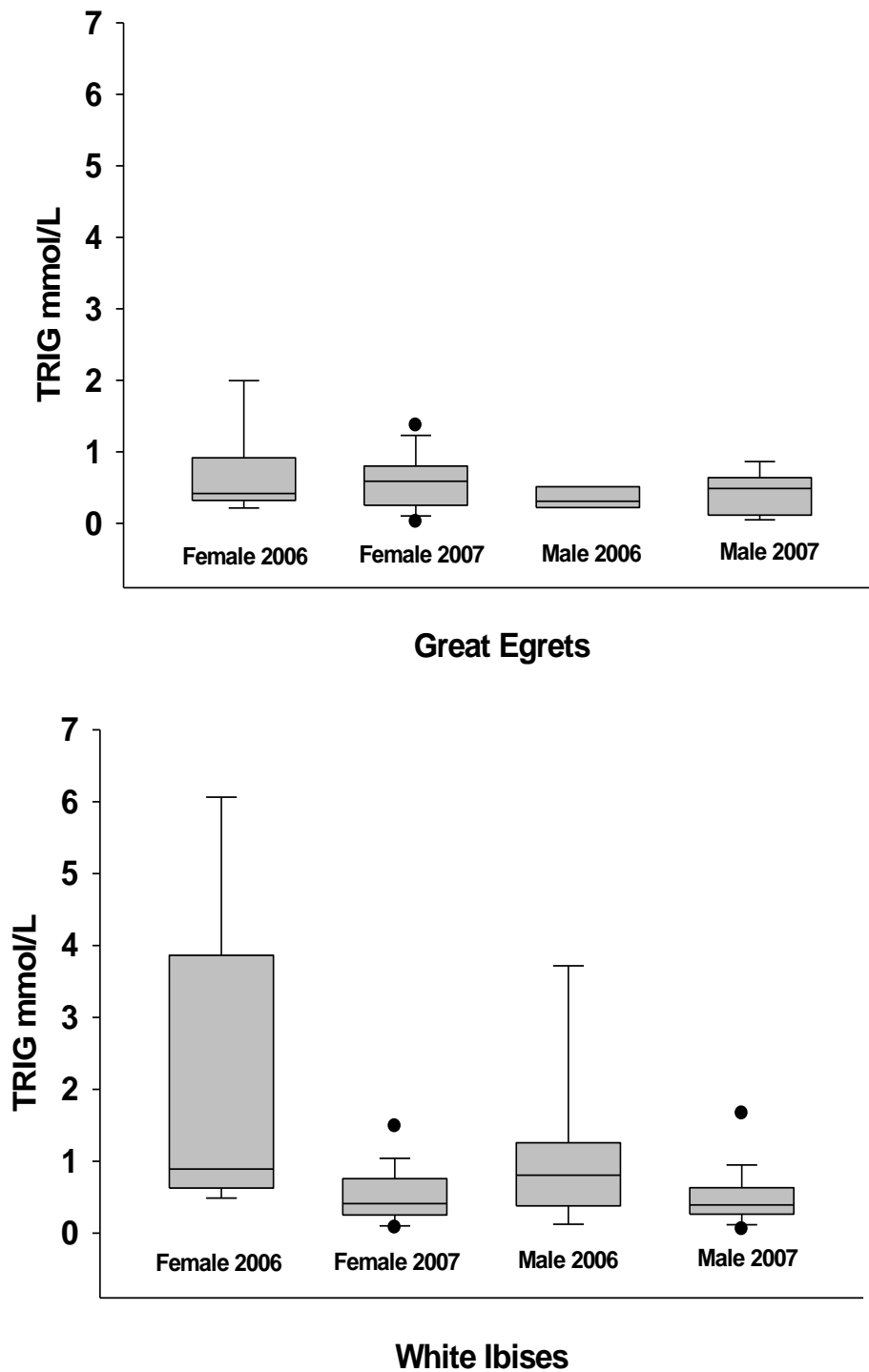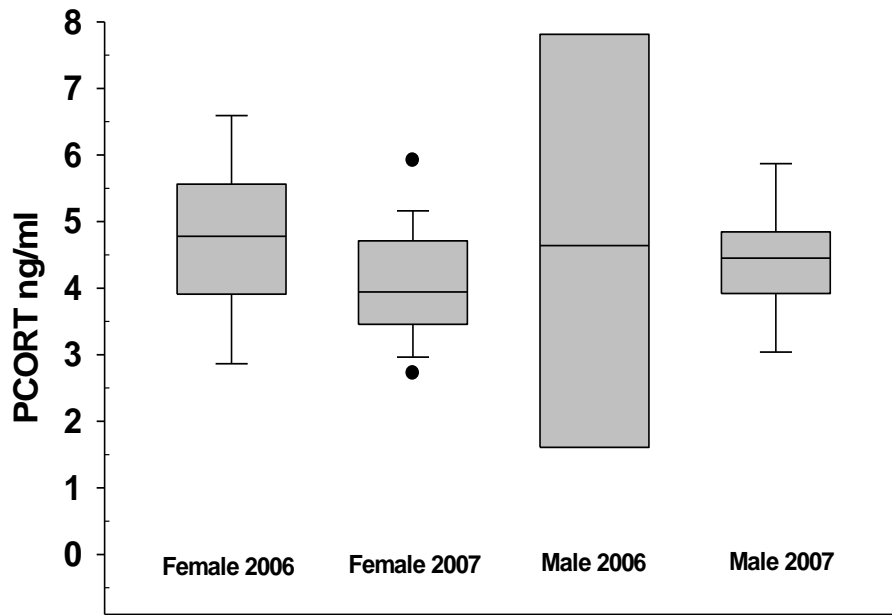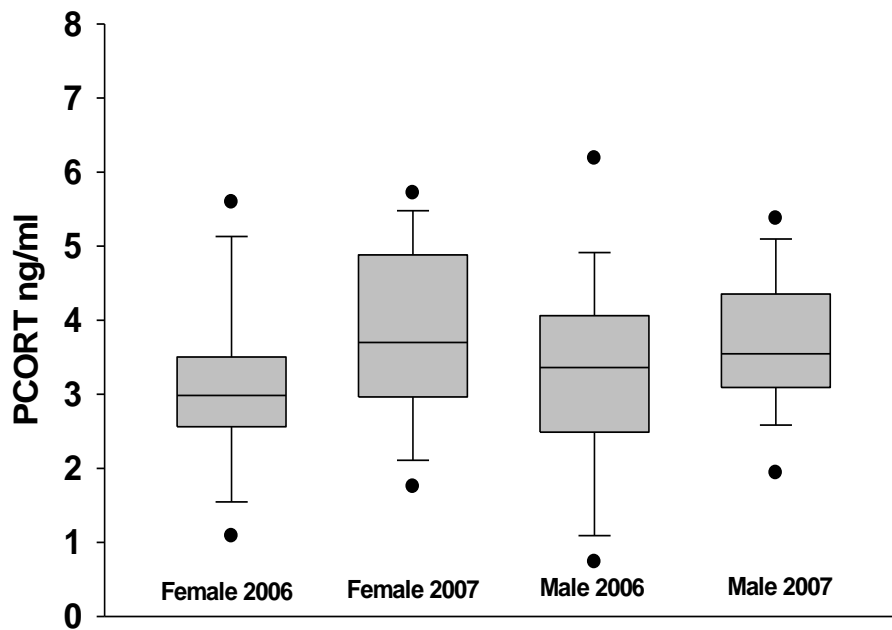Conservation Area 2A, and 3A of the Florida Everglades.

CHAPTER 6: SENSITIVITY OF GREAT EGRET AND WHITE IBIS NESTING TO FOOD LIMITATION

ABSTRACT

Life history strategy suggests long lived bird species will adjust their nesting effort according to current conditions, balancing the costs and benefits of current reproduction with their long-term needs for survival and future reproduction (Williams 1966). However, the habitat conditions that produce these responses may differ between species, even within the same ecosystem, producing different nesting and population trends. I compared the nesting responses of two sympatric wading bird species with different foraging strategies in two years that differed greatly in habitat conditions (e.g., food abundance). The reproductive parameters examined were nest effort, nest success, and fledging success of white ibises and great egrets in the Florida Everglades. Increasing recession rates, hydrological reversals, and prey densities influenced white ibis nest survival, whereas great egret nest survival was most influenced by prey densities and recession rates, with no effect from hydrological reversals. Fledging success was high and similar between the two species during the year with good habitat conditions (2006). However, in the year with poorer habitat conditions, fledging success was lower for both species (20% for white ibis versus 27% for great egret) but the magnitude of the decrease was particularly severe for the white ibis (76% decline versus 66% decline for the great

egret). Results suggest white ibises modify their clutch size during years with poor

habitat in accordance with life history traits of a long-lived species, whereas great egrets

maintained their clutch size during years with poor habitat. The strategy of the great

egret is advantageous in years with poor habitat if birds are more likely to experience

brood reduction rather than total nest failure, or if habitat conditions improve rapidly

during the nesting period, allowing for the third egg to hatch and or chick to fledge. This

bet hedging approach appears to allow great egrets to produce successful nests in poor

years, and may maximize their reproductive efforts during average to above average

years. The strategy of white ibises favors a searcher foraging strategy for wading birds

with short legs. These species have less ability to withstand change in hydrological

conditions (e.g., depth) and require more numerous high quality foraging patches. Poor

prey availability may be a cue for this species to lower its clutch size in preparation for

increased costs of locating suitable high quality foraging patches to provision chicks.

INTRODUCTION

Food availability is one of the primary limitations to avian populations,

particularly during the breeding season (Skutch 1949, Lack 1947, 1954, Ricklefs 1968).

Seasonal environmental conditions require most avian species to adjust their physiology,

morphology, and behavior throughout the annual cycle (Hahn 1998). When breeding,

many avian species are able to regulate their body condition when they are faced with

high-energy demands (Blem 1990), food scarcity (Stuebe and Ketterson 1982), or food

unpredictability (Cuthill et al. 2000). Food may become a limiting factor during the

breeding cycle due to increased adult physiological demands for egg production and

increased food required to maintain and fledge chicks (Drent and Daan 1980, Bolton et

al. 1993, Erikstad et al. 1998). Thus, most species time their breeding cycle to coincide

with maximum food production (Perrins 1991, Houston 1997, Thomas et al. 2001).

Subsequently, it during years with poor habitat conditions (e.g., low prey availability) the

demands of self-maintenance and future reproduction may outweigh the benefits of

reproducing that year more than during years with good habitat conditions.

Nesting birds can respond to food limitations by increasing foraging rates,

selecting lower quality but more abundant prey items, or traveling further to better quality

foraging patches (Hahn 1998, Beerens 2008). The response to a food limitation can

result in adult physiological responses and life history tradeoffs, which can be observed

in lower clutch sizes, lower hatching success, slower growth rates, and decreased nest

survival when breeding habitat conditions are below average. Measuring the response to

changes in food availability in terms of adult physiology and productivity allows for a

quantitative understanding of their relationship and its implication on populations. While

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many species have adapted to varying environmental conditions, their ability to respond to natural variability when amplified by anthropogenic induced changes is less certain. Life history traits have evolved over countless breeding periods to maximize reproduction, while minimizing costs to the adult. Most human impacts of avian species have occurred in such short time frames with very abrupt changes to habitat conditions, resulting in a mismatch of life history strategies and current ecosystem conditions.

Declines in annual breeding success and populations of colonial nesting wading birds (Ciconiiformes) in the Florida Everglades system are believed to be linked to reduced prey availability as result of historic water management practices (Kahl 1964, Kushlan 1986, Kushlan and Frohring 1986, Frederick and Collopy 1989, Powell et al. 1989, Frederick and Spalding 1994, Ogden 1994, Gawlik 2002). Gawlik (2002) tested the prey availability hypothesis, observing that vulnerability and density of prey did not always result in a similar foraging response or strategy across a suite of wading species. Furthermore, not all species of wading birds in the Everglades are declining (Crozier and Gawlik 2003). For instance white ibises (*Eudocimus albus*) have declined approximately 87%, while great egrets (*Ardea alba*) increased 270% during the last 20 years across the Everglades (Crozier and Gawlik 2003).

While wading bird productivity may fluctuate within and between years and timing of reproduction is often variable within and between years (Kushlan 1975, Frederick and Collopy 1989, Ogden 1994), there appears to be no definitive reason why different species nesting and feeding sympatrically have opposite population trends. The Comprehensive Everglades Restoration Plan (CERP) will be changing ecosystem conditions, therefore understanding the link between these habitat conditions and wading

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bird reproduction in response to landscape habitat parameters as result of adult responses to those conditions will significantly increase the certainty of how wading birds will respond to changes in hydrology.

My objectives with this study were threefold; 1) measure the nesting responses (e.g., clutch size, nest survival, fledging success) of two sympatric species with differing foraging strategies across years with differing habitat conditions (e.g., hydrology and prey availability), 2) use a modeling framework to test *A priori* hypotheses regarding the effects of habitat variables (e.g., hydrology, prey biomass, recessions rates) on the nest survival responses of great egrets and white ibises, and 3) discuss any differences in nest responses between the two species can be related to foraging strategies (e.g., searchers versus exploiters) and populations trends.

METHODS

During 2006 and 2007 great egret and white ibis nests were monitored in colonies in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (n = 7 colonies; Lox), and Water Conservation Areas 2A (n = 2 colonies) and 3A (n = 5 colonies; Fig. 1). Nesting colonies for white ibises and great egrets were located throughout the Everglades using a combination of ground and aerial surveys, the locations of the radio tagged adults (Chapter 5) from Beerens' (2008) research, and from known colony sites from previous research (e.g., South Florida Wading Bird Reports, South Florida Water Management District). I attempted to monitor nests in colonies with both great egrets and white ibises, although some colonies contained only one or the other species. Most colonies contained nest of additional species including snowy egret (*Egretta thula*), little blue heron (*E. caerulea*), tricolored heron (*E. tricolor*), great blue heron (*Ardea herodias*), and black-crowned night-heron (*Nycticorax nycticorax*).

I located nests of radio tagged adults by first flying fixed wing aerial telemetry surveys at night, where I used a left-right control box and two side view directional yagi antennas to locate radio tagged birds. This approach allowed for a rapid assessment of where radio tagged adults were located throughout the Everglades, and with which colony, if any they were associated. I then visited occupied colonies during the daytime to verify nesting or the development of nesting at that site. If I detected radio tagged great egrets or white ibises when visiting colonies on the ground, I would locate those birds using a hand held yagi antenna. Located nests were marked with flagging tape, and GPS coordinates were recorded. Random nests were also marked in these colonies as well and were included in all analysis with radio tagged nests. I also randomly marked

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and collected data from nests in colonies that did not have radio tagged nesting birds. I recorded total clutch size as a measure of nesting effort and revisited all nests approximately every 5 - 7 days until chicks fledged or the nests failed. Successful nests were those that fledged at least one chick.

I used the Everglades Depth Estimation Network (EDEN) to estimate all water depths and recession rates at nesting colonies during 2006 and 2007. EDEN is a network of real-time water level monitoring, water surface modeling, and ground elevation modeling that is used to model water depth for the entire freshwater portion of the Greater Everglades (USGS 2006). EDEN calculates stage levels at daily time steps to account for daily changes associated with evapo-transpiration drying and rainfall rewetting. The model provides estimated depth information on a 400 m by 400 m grid across the entire landscape.

To estimate stage and recession rates at nesting colonies I first used ArcGIS 9.1 to establish buffers around colonies based on mean distances flown ± 1 SE by radio-tagged great egrets and white ibises from those colonies based on estimates provided by Beerens (2008). Mean distances flown were 13.71 km ± 0.37 SE and 7.0 ± 0.47 SE for white ibises and 7.98 km ± 0.76 SE and 4.83 km ± 0.3 SE for great egrets during 2006 and 2007 respectively. These buffers were used to identify all of the associated 400 m by 400 m grids associated with EDEN around specific colonies by year and species. I then used SAS (9.1) to extract stage levels for each 400 m by 400 m grid for each day an estimate of daily nest survival was calculated, and 1 and 2 weeks prior to that day to calculate recession rate. I averaged these estimates across cells to get an overall estimate of stage and recession rates for each colony. I also calculated the coefficient of variation (CV) for

recession rate for 1 and 2 weeks prior to capture. The CV measures the variation of daily

recession rates over the 1-week period to capture variations in recession rates associated

with hydrological reversals. This method is preferable to only using mean recession rate

because calculating the mean recession rates for 1-week prior may mask any small

hydrological reversal events that occurred.

To estimate prey densities associated with colonies, I used data provided from

Beerens' (2008) associated research on ibises and egrets. Beerens (2008) located radio-

tagged egrets and ibises across the Everglades using telemetry techniques then sampled

those sites to estimate prey densities using throw traps (Kushlan 1981) within 1 day of

aerial surveys. Foraging site locations were mapped in ArcGIS 9.1 and prey density

estimates from sites within the flight distance buffers of each species around nesting

colonies (the mean distance flown plus one standard error) were used to represent and

index prey availability for each colony. Prey availability estimates were only used if they

were collected within a colony's buffer within 7 days of an estimate of nest survival. I

averaged all estimates of prey availability during that 7-day period to provide a mean

estimate of landscape level prey availability for each weekly time step.

Statistical Analyses

I used a three-way analysis of variance (ANOVA) to test for differences in white

ibis and great egret clutch sizes by species, year, region, and their interactions. I

observed a significant species×region interaction ($P = 0.01$) and ran separate ANOVA

models to interpret results for each species.

I used a logistic exposure approach in a mixed model setting to model nest

survival rather than the Mayfield Method (Mayfield 1961, 1975) or logistic regression

(Shaffer 2004). The model is based on a binomial distribution (nest fate = 0 when failed

and 1 if successful) and uses a logit link function to estimate daily nest success and

evaluates potential factors that influence nest success (Shaffer 2004). I used the modified

logit link function $(g(\theta) = \log_e (\theta^{1/t}/[(1 - \theta^{1/t}])$; where θ = nest interval survival rate and t

is the interval length) to account for differences in duration of time between nest visits

(Shaffer 2004). A major advantage of using the logistic exposure approach for simple

models is that the appropriateness of those models can be judged by comparing them to

more complex models via information-theoretic techniques (Shaffer 2004, Rotella 2007).

Logistic exposure models also do not require assumptions about when nest losses occur

and they allow for continuous categorical variables and random and fixed effects as in

Mayfield and logistic regression approaches (Shaffer 2004, Rotella 2007).

I then used an information theoretic approach using PROC GENMOD to build

and rank competing models (Burnham and Anderson 2002). Competing models were

developed based on a biologically meaningful understanding of the nesting responses of

wading birds from previous studies (see Frederick and Collopy 1989, Butler 1994). I

included terms for prey biomass 1 (Biomass 1) and 2 (Biomass 2) weeks prior to the nest

survival estimate because food abundance is considered to be one of the most important

determinants of nesting effort (Lack 1968, Ricklefs 1968). I included variables for Year

and Julian date, because interannual conditions and nest initiation date have been

demonstrated to be important in determining the likelihood of successful nesting

(Frederick and Collopy 1989). Recession rates 1 (Recess 1) and 2 (Recess 2) weeks prior

to capture and the quadratic form of recession rate 1 and 2 weeks prior to an estimate of

nest success (Recess 1 + Recess 1^2, Recess 2 + Recess 2^2) were included in the model

because they have been previously linked to nesting in colonial nesting wading birds in the Everglades (Frederick and Collopy 1989) and the distribution of foraging wading birds (Bancroft 2002, Russell et al. 2002). I included the CV of recession rate 1 (CV 1) and 2 (CV 2) weeks prior to chick sampling for any potential hydrological reversals that would be missed in the recession rate variables due to the averaging effect smoothing out small amounts of variability that might be important to nesting otherwise. I evaluated the goodness-of-fit of the global models and verified that the models fit the data before proceeding with additional model analyses. Prior to model selection I visually examined the residuals of model variables to identify outliers or other patterns that required transformation.

I ran separate models for each species because prior research suggested differences in nesting success (e.g., Frederick and Collopy 1989), and differences in foraging strategies (Gawlik 2002) might result in different variables explaining nest success for each species. I used the AIC_C values adjusted for small samples sizes in all models (Burnham and Anderson 2002). Global models included terms for Biomass 1 and Biomass 2, region, Julian date, Recess 1 and Recess 2, Recess1 + Recess 1^2 and Recess 2 + Recess 2^2, CV 1and CV 2, and all biologically meaningful interactions. I calculated delta AIC (Δ_i, Akaike's Information Criterion) and AIC weights (ω_i) from AIC_C values. Models with the lowest AIC_C value was considered the best explanatory model; although, additional competing models with $\Delta AIC_C < 2$ were considered equally plausible given the data (Burnham and Anderson 2002). Models with $\Delta AIC_C > 4$ were considered to have little to no support (Burnham and Anderson 2002). I calculated the unconditional estimates for coefficients and unconditional standard error terms for each parameter

across all models (Burnham and Anderson 2002) based on all models with AIC_C weights ≥ 0.001.

I then calculated daily survival rates (DSR) of nests based on model-averaged coefficients from my best fitting model using the equation $S(x) = e^{\beta 0 + \beta 1x}/1 + e^{\beta 0 + \beta 1x}$. Model-averaged coefficients were calculated by only using the exponentiated AIC_C values from models that contained the parameter, the exponentiated values were then summed, the original exponetiated AIC_C value was then divided by the new sum to get a new Akaike weights. Lastly, I multiplied the raw (individual model) parameters by the new weights and summed the products. DSRs were raised to a constant power for both species to allow comparisons of nest success or fledging rate. Given the large differences in the time great egret and white ibis chicks spend at nests before fledging, I used a conservative fledging chick age of 15 days. The 15 days of age for fledging was added to the 21 and 25 day incubation periods for white ibis and great egret respectively (Kushlan and Bildstein 1992, McCrimmon et al. 2001), giving a combined period of nest survival estimation of 36 and 40 days respectively. While these chick ages do not reflect the true age at which either species chicks fledge, they do represent a period during which chicks can be reliably associated with their specific nests and the period at which most mortality occurs.

Lastly, I tested for differences in the number of chicks fledged per year by each species using nonparametric Wilcoxon tests after determining data did not meet assumptions of equal variance (Levene's test; JMP 2001). For white ibis chicks, I used a 15-day chick age as an assessment of chick fledging, after this age chicks have increased mobility and become increasingly difficult to locate as per Frederick and Collopy (1989).

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I considered great egret chicks to be fledged when they were 15 days old to allow for direct comparisons with white ibis results, although in many cases, I observed great egret chicks when they were over 60 days old still at their nests.

RESULTS

I marked and monitored a total of 318 nests, 117 during 2006 and 201 during 2007. I monitored 178 white ibis nests for a total of 450 nest intervals; 119 nests were successful. I monitored 140 great egret nests for a total of 536 nest intervals; 79 nests were successful.

Great egret clutch size was similar by location ($F_{2, 151} = 1.33$, $P = 0.26$, n = 155) and year ($F_{1, 151} = 2.60$, $P = 0.11$; Fig. 2). White ibis clutch size was 18% lower in WCA 3A than Lox ($F_{1, 173} = 12.65$, $P = 0.0005$, n = 176), and 21% higher during 2006 than 2007 ($F_{1, 173} = 4.26$, $P = 0.0002$; Fig. 2).

Great Egret Daily Nest Survival and Fledging Rate

The model selection process did not identify one singular model that best explained daily survival of great egret nests; rather there were two models with similar AIC_C values. Those top two models were 1) Region, Julian date, Biomass 1, Biomass 2, Recession 1 + Recession 1^2, Recession 2 + Recession 2^2, and 2) Region, Julian date, Biomass 1, B, Biomass 2, Recession 1 + Recession 1^2, Recession 2 + Recession 2^2, CV 1, with 35% and 21% of the weight of the evidence respectively (Table 1). Combined these models weight of evidence was 56%, and they received 2.7× and 1.6× the support of the next best model respectively (Table 1). Daily survival of great egret nests in 2006 and 2007 was 0.996 and 0.968 respectively (Fig 3). When daily survival rates were scaled to fledging estimates, nest success was 0.837 and 0.277 during 2006 and 2007 respectively. Numbers of chicks fledged decreased by 30% in great egret nests between 2006 and 2007 ($Z_{1, 65}$, $P < 0.0001$; Fig. 4).

Daily survival probability of great egret nests was 12% higher in Lox than WCA2A, 10% higher in Lox than WCA3A, and 13% higher in WCA3A than WCA2A (Table 2). The probability of daily nest survival increased by 2% with every additional gram of prey biomass at sites within the mean foraging range of colonies during two weeks before a daily nest survival estimate. It increased by 41% with every 1-cm increase in recession rate two weeks before a daily nest survival estimate (Table 2). Daily survival of great egret nests decreased by 3% with 1-g/m^2 decrease in prey density and by 4% with every 1-cm increase in recession rate during one week before an estimate of daily nest survival. No change in great egret daily survival was observed across the nesting period (e.g., Julian date odds ratio = 1.0). The variable importance weight was highest in this order: Year, Region, Biomass 1, Biomass 2, and Recess1 + Recess 1^2, and Recess2 + Recess 2^2 (Table 2). The odds ratio confidence interval for WCA3a vs. WCA2A, Biomass 1, and Recess 1 + Recess 1^2 all included 1.0, suggesting a weak effect, with stronger effects observed in Year, Biomass 2, and Recess 2 + Recess 2^2 (Table 2).

White Ibis Daily Nest Survival and Fledging Rate

The model selection process did not identify one singular model that best explained white ibis daily nest survival; rather there were two models with similar AIC_C values. Those top two models were 1) Region, Julian date, Biomass 1, Biomass 2, Recession 1, Recession 2, CV 1, CV 2 and 2) Region, Julian date, Biomass 1, Biomass 2, Recession 1 + Recession 1^2, Recession 2 + Recession 2^2, CV 1, CV 2, with 47% and 44% of the weight of the evidence respectively (Table 1). The combined weight of evidence for these models was 91%, and they received 11.7× and 11.0× the support of the next best model respectively (Table 1). Daily white ibis nest survival in 2006 and 2007 was

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0.996 and 0.957, respectively (Fig. 3). When daily survival rates were scaled to fledging estimates, nest success was 0.868 and 0.208 during 2006 and 2007 respectively. Numbers of white ibis chicks fledged decreased by 26% between 2006 and 2007 ($Z_{1, 60}$, P = 0.001; Fig. 4).

Daily survival probability of white ibis nests was 3% higher in Lox than WCA3A. It increased by 11% and 7% with 1 cm increases in recession rates one and two weeks, respectively, before a daily nest survival estimate. Daily nest survival increased by 19% with a one-unit increase in CV one week before an estimate of a daily nest survival (Table 2). Probability of white ibis daily nest survival decreased by 3% with every day of exposure across the breeding season, by 6% with a 1-g/m^2 decrease in prey density two weeks prior to an estimate of nest success, and by 19% with every unit increase in CV two weeks before a daily nest survival estimate (Table 2). The variable importance weight was the same for Year, Region, Julian, Biomass 1, and Biomass 2, followed then by CV 1, CV 2, Recess 1, and Recess 2 (Table 2). The odds ratio confidence interval for Julian, Biomass 1, Recess 1, and Recess 2 all included 1.0, suggesting a weak effect, with stronger effects for Year, Region, Biomass 2, CV 1, and CV 2 (Table 2).

DISCUSSION

Great egrets and white ibises used different strategies during years with low prey availability; assumingly each strategy has its own costs and benefits that affect their populations. Clutch size during this study suggested that white ibises responded more dramatically than great egrets to the significant change in prey densities across years with a decrease in clutch size by ~21%, with no concomitant decrease in egret clutch size. Clutch size is largely considered to be determined by the availability of food (Lack 1954, Ricklefs 1968, Monaghan et al. 1995).

During below average years, life history theories suggests long-lived birds should not increase their level of effort when undue changes to habitat conditions occur, but rather they should either reduce clutch size or produce offspring whose physiological condition reflects current habitat conditions (Apanius et al. 2008). For these species, the physiological condition of the chicks, not their parents, should reflect any shortfall between the chicks' needs and what is obtainable (Sæther et al. 1993, Mauck and Grubb 1995). Results from this study suggest that both great egrets and white ibises neither wholly utilize a short-lived or long-lived approach to the costs of reproduction. Both species demonstrated some level of pre-breeding physiological response to changes in year-to-year habitat conditions (although the response was greater in white ibises), and both demonstrated a response at the nest level, with lower nest success. Given the decrease in white ibis clutch size and their lower fledging success during the below average year relative to great egrets it seems that they exhibited stronger response to the interannual differences in prey availability.

The strategy of white ibises favors a searcher foraging strategy for wading birds that are constrained in their choice of foraging habitat. Short-legged birds or tactile foragers have less ability to withstand change in hydrological conditions (e.g., depth) and require more numerous high quality foraging patches. Poor prey availability may be a cue for this species to lower its clutch size in preparation for increased costs of locating suitable high quality foraging patches to provision chicks. While the strategy of the great egret is advantageous in years with poor habitat if birds are more likely to experience brood reduction rather than total nest failure, or if habitat conditions improve rapidly during the nesting period, allowing for the third egg to hatch and or chick to fledge. This bet-hedging approach appears to allow great egrets to produce successful nests in poor years, but may not maximize their reproductive efforts during average to above average years.

The model selection process demonstrated that overall there were differences in habitat variables that influenced great egret and white ibis nest survival. White ibis nest survival was most influenced by Year, Region, Biomass 2, CV 1, and CV 2, while great egret nest survival was most influenced by Year, Biomass 2, and Recess 2 + Recess 2^2. Also associated with these differences between ibis and egrets in the habitat variables that influenced daily nest survival were considerable differences between species in fledging success. While both species had elevated and comparable estimates of fledging success during the above average habitat conditions year (2006), in the poor year egret fledging success decreased by ~66%, while ibis fledging success declined by ~76%.

Given the evidence provided by the model selection process (model weights, variable importance weights, odds ratios) for variables influencing great egret daily nest

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survival it appeared that most influential parameters were Year, Region, and the one-

week Recession + Recession^2 rate. Taken as a whole, this indicates that egret daily nest

survival depends on when and where they nest, and how much food is available (either

density or vulnerability) via steady recession rates within their average foraging range of

colonies. The great egret's ability to withstand hydrological variability and forage

successfully (e.g., rainfall reversals or deep water; Gawlik 2002) was supported by the

exclusion of the variables for CV 1 and CV 2, and additionally while the Recession +

Recession 2^2 rate was in the final model it had little influence on egret nest success based

on its variable importance weight.

Conversely, model results suggested white ibis daily nest survival was influenced

by Year, Region, Julian date, Biomass 1 and 2, Recess 1, Recess 2, and CV 1 and 2.

These results suggest that ibis daily nest survival was more influenced by variability in

habitat conditions in the landscape (e.g., rainfall reversals). The inclusion of both CV 1

and 2 demonstrates that hydrological reversals played a larger role in influencing fledging

success for white ibis relative to great egrets. Some of this may be explained by their

shorter leg length, which could limit their ability to forage successfully after a

hydrological reversal (Powell 1987, Gawlik 2002).

The responses of each species to these landscape habitat variables should be noted

as considerably different. For instance, great egret daily nest success increased an

additional 2% more than white ibis nest success with relatively small (+1 g/m^2) changes

in landscape prey densities during the week before a nest survival estimate. Further, a

decrease in prey densities by 1g/m^2 during the period two weeks before a daily nest

survival estimate only decrease the egret estimate by 3%, while ibis daily nest survival

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decreased by 6%. Egrets might either be using resources more efficiently, or minimizing their energy expenditure when obtaining prey. This result fits the paradigm for a species that chooses to remain at foraging patches when prey densities decrease beyond a giving up density which results in searcher species (e.g., white ibis) abandoning the site and searching for a more profitable site (Gawlik 2002). For exploiter species, the cost of remaining at a patches must outweigh expending energy and searching for a patch with better foraging conditions to make this foraging strategy energetically profitable. For great egrets, this may be alleviated by their ability to forage in a wider variety of habitat conditions (e.g., depth; Gawlik 2002) and the fact they expend less energy by foraging closer to colonies (Beerens 2008). During years with lower prey availability (e.g., 2007) the cost of obtaining prey for self maintenance and provisioning to chicks may be increased for searcher species if the likelihood of detecting a higher quality foraging site is lower, because either the quality or number of quality sites has decreased across the landscape. While selection pressure may have refined the ability of searchers to locate high quality patches, that process may now be mismatched to a landscape like the Everglades where large changes in wetland hydrology have occurred during the last 100 years and in years when prey availability is lower than in average to above average years.

The response of white ibis nest success to CV 1 and CV 2, demonstrated that they were more sensitive to an increase in water depth associated with hydrological reversals than was the great egret. White ibis daily nest success declined by up to 19% when a one-unit increase in CV occurred during the week before a daily nest survival estimate. Although Frederick and Collopy (1989) demonstrated a similar response to hydrological reversals by great egrets, it was not apparent in this study. The difference may be due to

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fewer or less severe hydrologic reversals in this study. If that were the case, data from this study would suggest that ibis should have had even higher nest abandonment rates than great egrets. Frederick and Collopy (1989) did not report rates of abandonment associated with hydrological reversal, but they did acknowledge that white ibises abandoned their nests synchronously during or immediately following periods of heavy rainfall.

Similarly, white ibis daily nest success increased by 11% with every 1 cm increase in recession rate during the nesting season, while egret daily nest success actually decreased by up to 4% with the same level of increase in recession rate. Past studies have demonstrated the importance of recession rate to nesting and foraging of wading birds, suggesting that a minimal recession rate of >5mm/d is required for successful nesting or optimal foraging (Kushlan 1979, Frederick and Collopy 1989, Frederick and Spalding 1994, Russell et al. 2002). The quadratic terms for recession rate in this study suggest that rather than a minimal recession rate, there is an optimal recession rate that results in prey being concentrated in shallow depressions at a temporal and spatial scale to meet the reproductive requirements of wading birds (Kushlan 1989, Gawlik 2002, Russell et al. 2002, Gawlik and Crozier 2007). This appears to be more important for species like great egrets that regularly forage on larger prey species (Dimalexis et al. 1997, Smith 1997, McCrimmon et al. 2001), a rapid recession rate could result in the loss of large prey species to mortality via starvation and desiccation before they can be captured (Gaff et al. 2004) while smaller prey species can locate refugia more easily (Chick et al. 2004). Further, white ibises can continue to forage at sites without

surface water conditions by utilizing invertebrate prey species such as crayfish that do not die under these conditions (Dorn and Trexler 2007).

Hydrological reversals, changes in recession rates, and lower prey availability all likely play a large role in influencing nest success during poor and average years, similar to 2007. Birds can respond to lower levels of prey availability by either extending their search distance or spending more times searching for prey within a smaller distance (Suryan et al. 2000). The response chosen can be influenced by the current conditions and the species knowledge of habitat conditions (e.g., available prey; Anderson and Ricklefs 1987, Golet et al. 1998, Iron 1998). It appears that both species responded to lower quality habitat conditions (e.g., lower prey availability) by reducing their energy expenditures by flying shorter distances to foraging sites (Beerens 2008). However, white ibises continued to fly up to 45% further to foraging sites during the below average year than great egrets (Beerens 2008). Given the results of this study, it appears that the shortening of flying distances benefited great egrets more than white ibises. Flying shorter distances may not benefit searcher species like white ibis if they continue to search for higher quality patches when those patches might not exist (Gawlik 2002).

Estimates of nest success for both species were within the range of previous studies of nest success in the Everglades (see Frederick and Collopy 1989, McCrimmon et al. 2001, Semones 2003). Direct comparisons were not possible due to large differences in techniques to monitor nests, and most importantly, differences in the way daily survival rates and nest success (fledging rate) were calculated (Shaffer 2004). Nonetheless, some trends detected in prior research were also apparent during this study. Similar to Frederick and Collopy (1989), I observed lower estimates of fledging success

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during years with poor habitat conditions. Results also suggested that white ibis fledging success was associated with prey densities and increased recession rates corresponding to Frederick and Collopy's (1989) findings. However, those authors suggested that this was not associated with densities of fish but possibly crayfish (*Procambarus* spp). Recent studies (Dorn et al. *In Press*) have shown that Everglades' fishes can play a larger role in the diets of white ibis during the breeding season than was previously suspected, although there were spatial differences in the use of fish as a prey species across the Everglades. The proportion of fishes in the diet of white ibises was higher during 2006 than 2007 (Nate Dorn, Florida Atlantic University, pers. comm.), and given the increased caloric value of fishes over crayfish in the Everglades (Kushlan et al. 1986), it suggests that differences in diet as well as overall prey densities may play a role in fledging success between years with different habitat conditions.

Frederick and Collopy (1989) suggested that rainfall which results in hydrological reversals was the most important landscape habitat variable associated with great egret fledging success. Interestingly, great egret nests in Frederick and Collopy's (1989) study took over a week to fail after major rainfall events, while white ibis nests typically were abandoned very soon after a major rainfall event. While I did not include rainfall in my nest survival models, minor hydrological reversals did occur during my study, which correlate with rainfall events, but not to the extent to result in egret nest abandonment.

Model results for white ibis did suggest that hydrological reversals (CV 1 and 2) influenced daily nest survival. These differences may be an artifact of year differences in habitat conditions and when nests were initiated (seasonal effects) between Frederick and Collopy's study and this study. White ibis nesting during this study were largely initiated

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during March – April, while in Frederick and Collopy's study ibis nesting occurred

during May – June and in years with differing hydrological conditions. Regardless,

results from this study suggest ibises responded acutely to minor hydrological reversals in

the Everglades.

Differences in daily nest survival were highest in Lox for both species, although

egret daily nest survival estimates were 7% higher than white ibis within Lox. Water

depths within Lox remained deeper throughout much of the breeding seasons compared

to those adjacent to breeding colonies in WCA 2A and WCA 3A (Gawlik and Botson

2008). Increased depths, coupled with incomplete drying during the 2005, and 2006

breeding seasons would likely have allowed for larger fishes to survive and be available

for foraging egrets in Lox. Recent data on fauna concentrations across the Everglades

during the wading bird breeding season suggests prey biomass in Lox was higher during

the period of this study (Gawlik and Botson 2008). Potentially, larger fishes may be

available to great egrets earlier in the season when they initiate nesting, when depths

preclude white ibis foraging in Lox. Larger prey fishes may minimize energy

expenditure for foraging great egrets in Lox during this study. Fauna concentration data

(Gawlik and Botson 2008) may be mismatched with the timing of egret nest initiation,

potentially explaining why the biomass of large fish does not appear to be different from

other areas within the Everglades, but could allow for improved nest survival in Lox.

Bolus data from white ibis chicks in Lox suggests that they were fed mostly invertebrates

during the breeding season (Dorn et al. *In Press*). Differences in energy content between

invertebrates and fishes may have played a role in the differences in daily survival rates

between species in Lox.

Results from this study benefited from a refined understanding of prey selection by white ibises, prey densities across the breeding season, and perhaps more importantly a major refinement of our understanding of and accuracy of hydrology measurements across the Everglades associated with the development of the Everglades Depth Estimation Network (EDEN). The EDEN allowed for modeling of the effects of recession rates and the coefficient of variation for recession rates in daily time steps at a 400-m^2 resolution. Past modeling efforts to understand the influence of hydrology on wading bird nesting in the Everglades have often relied on only several water gauges across large regions of the Everglades (e.g., Frederick and Collopy 1989, Strong et al. 1997). The use of daily recession rates calculated on a smaller scale, coupled with estimates of prey densities specific to colonies studied during this research provided a much better picture of habitat conditions available to birds.

The results of this study and those of Chapter 5 (*Adult Physiology*) support a growing body of evidence that links reproductive investment with foraging conditions and physiological condition of adults. This study also suggests that multiple variables (e.g., physiological condition, nesting investment, foraging strategies, hydrologic conditions) may be important mechanisms for shaping divergence between wading bird nesting trends in response to changing habitat conditions (e.g., hydrology, prey densities) in the Everglades. A better understanding of the true long-term costs and benefits of reproduction between species that utilize searcher and exploiter foraging strategies may yield factors critical to those differences and provide insight on to better manage and restore the Everglades to meet the needs of all wading bird species.

LITERATURE CITED

Anderson, D. J., and R. E. Ricklefs. 1987. Radio-tracking masked and blue-footed

boobies (*Sula* spp.) in the Galapagos Islands. National Geographic Research

3:152-163.

Apanius, V., M. A. Westbrock, and D. J. Anderson. 2008. Reproduction and immune

homeostasis in a long-lived seabird, the Nazca booby (*Sula granti*).

Ornithological Monographs 65:1-46.

Bancroft G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative

to vegetation and water depths in the northern Everglades of Florida, USA.

Waterbirds 25:265–277.

Beerens, J. E. 2008. Hierarchial habitat selection in Great Egrets and White Ibises in the

Florida Everglades. Thesis, Florida Atlantic University, Boca Raton , FL.

Beissinger, S. R. 1983. Hunting behavior, prey selection, and energetics of snail kites in

Guyana: consumer choice by a specialist. Auk 100:84-92.

Blem, C. R. 1990. Avian energy storage. Current Ornithology 7:59-113.

Bolton, M., P. Monaghan, and D. C. Houston. 1993. Proximate determination of clutch

size in lesser black-backed gulls: the roles of food supply and body condition.

Canadian Journal of Zoology 71:273-279.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical

information-theoretic approach. Springer-Verlag, New York, New York, USA.

177

Butler, R. W. 1994. Population regulation of wading Ciconiiform birds. Colonial Waterbirds 17:189-199.

Chick, J. H., C. R. Ruetz III, and J. C. Trexler. 2004. Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. Wetlands 24:652-664.

Crozier, G. E., and D. E. Gawlik. 2003. Wading bird nesting effort as an index of wetland ecosystem integrity. Waterbirds 26:303-324.

Cuthill, I. C., S. A., Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. Behavioral Ecology 11:189–195.

Dimalexis, A., M. Pyroveysi, and S. Sgardelis. 1997. Foraging ecology of the grey heron (*Ardea cinerea*), great egret (*Ardea alba*) and little egret (*Egretta garzetta*) in response to habitat, at 2 Greek wetlands. Colonial Waterbirds 20:261-272.

Dorn, N. J., and Trexler. 2007. Crayfish assemblage shifts in a large drought-prone wetland: the roles of hydrology and competition. Freshwater Biology 52:2399-2411.

Dorn, N. J., G. Herring, and D. E. Gawlik. *In Press*. Estimation of crayfish abundance and size-structure in White Ibis diets. *Waterbirds*.

Drent, R. H., and S, Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.

Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788.

Frederick, P. C., and M. W, Collopy. 1989. Nesting success of Ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625-634.

Frederick, P. C., and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-692 *in* S. M. Davis and J. C. Ogden (eds.). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Gaff, H., J. Chick, J. Trexler, D. DeAngelis, L. Gross, and R. Salinas. 2004. Evaluation of and insights from ALFISH: a spatially explicit, landscape-level simulation of fish populations in the Everglades. Hydrobiologia 520:73-87.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Gawlik, D. E., and B. Botson. 2008. Aquatic fauna seasonal concentrations, contract CP040319. Unpublished annual report to the South Florida Water Management District, West Palm Beach, FL.

Gawlik, D. E., and G. E. Crozier. 2007. A test of cues affecting habitat selection by wading birds. Auk 124:1075-1082.

Golet, G. H., D. B. Irons, and J. A. Estes. 1998. Survival costs of chick rearing in black-legged kittiwakes. Journal of Animal Ecology 67:827-841.

Hafner, H. 1997. Ecology of wading birds. Colonial Waterbirds 20:115-120.

Hahn, T. P. 1998. Reproductive seasonality in an opportunistic breeder, the red crossbill, *Loxia curvirostra*. Ecology 79:2365–2375.

Houston, D. C. 1997. Nutritional constraints on egg production in birds. Proceedings of the Nutrition Society 56:1057-1065.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79:647-655.

Jenni-Eierman, S., and L. Jenni. 1994. Plasma metabolite levels predict individual body mass changes in a small long-distance migrant, the garden warbler. Auk 111:888-899.

JMP. 2001. A guide to statistics and data analysis using JMP and JMP IN software. Second Edition. SAS Institute, Cary, North Carolina, USA.

Kahl, M. P. 1964. Food ecology of the wood stork (*Mycteria Americana*) in Florida. Ecological Monographs 34:97-117.

Kushlan, J. A. 1975. Site selection for nesting colonies of the American White Ibis *Eudocimus albus* in Florida. Ibis 118:590-593.

Kushlan, J. A. 1979. Feeding ecology and prey selection in the white ibis. Condor 81:376-389.

Kushaln, J. A. 1981. Sampling characteristics of enclosure fish traps. Transactions American Fisheries Society 110:557-562

Kushlan, J. A. 1986. Response of wading birds to seasonally fluctuating water levels: strategies and their limits. Colonial Waterbirds 9:155-162.

Kushlan, J. A., and K. L. Bildstein. 1992. White Ibis. *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of North America, Inc., Philadelphia, PA.

Kushlan, J. A., and P. C. Frohring. 1986. The history of the southern Florida Wood Stork population. Wilson Bulletin 98:368-386.

Kushlan J. A, S. A. Voorhees, W. F. Loftus, and P. C. Frohring. 1986. Length, mass, and calorific relationships of Everglades animals. Florida Scientist 49:65–79.

Lack, D. 1947. The significance of clutch-size. Ibis 90:24-45.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, United Kingdom.

Masello, J. F., and P. Quillfeldt. 2004. Are haematological parameters related to body condition, ornamentation and breeding success in wild burrowing parrots *Cyanoliseus patagonus*? Journal of Avian Biology 35:445-454.

Mauck, R. A., and T. C. Grubb, Jr. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. Animal Behaviour 49:999-1008.

Mayfield , H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

Mayfield , H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

McCrimmon, D. A., Jr., J. C. Ogden, and G. T. Bancroft. 2001. Great Egret (*Ardea alba*). *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of North America, Inc., Philadelphia, PA.

Monaghan, P., M. Bolton, and D. C. Houston. 1995. Egg production constraints and the evolution of avian clutch size. Proceedings of the Royal Society of London B 259:189-191.

Ogden, J. C. 1994. A comparison of wading bird nesting colony dynamics (1931-1946 and 1974-1989) as an indication of ecosystem conditions in the southern

Everglades. Pages 533-570 *in* S. M. Davis and J. C. Ogden (eds.). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Perrins, C. M. 1991. Tits and their caterpillar food supply. Ibis 133:49-54.

Powell, G. V. N. 1987. Habitat use by wading birds in a subtropical estuary: implications for hydrology. Auk 104:740-749.

Powell, G. V. N., R. D. Bjork, J. C. Ogden, R. T. Paul, A. H. Powell, and R. B. Robertson, Jr. 1989. Population trends in some Florida Bay wading birds. Wilson Bulletin 101:436-457.

Quillfeldt, P., J. F. Masello, and E. Möstl. 2004. Blood chemistry in relation to nutrition and ectoparasite load in Wilson's storm-petrels *Oceanites oceanicus*. Polar Biology 27:168-176.

Ricklefs, R. E. 1968. On the limitations of brood size in passerine birds by the ability of adults to nourish their young. Proceedings of the National Academy of Science. 61:847-851.

Rotella, J. J. 2007. Modeling nest-survival data: recent improvements and future directions. Studies in Avian Biology 34:145-148.

Russell, G. J., O. L. Bass, Jr., and S. L. Pimm. 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. Animal Conservation 5:185-199.

Sæther, B. B., R. Andersen, and H. C. Pedersen. 1993. Regulation of parental effort in a long-lived seabird – an experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antartica*. Behavioral Ecology and Sociobiology 33:147-150.

Semones, J. D. 2003. Consequences of nesting date on nesting success and juvenile survival in White Ibis. Thesis, University of Florida, Gainesville, FL.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91: 69-93.

Smith, J. P. 1997. Nesting season food habits of 4 species of herons and egrets at Lake Okeechobee, Florida. Colonial Waterbirds 20:198-220.

Strong A. M., G. T. Bancroft, and S. D. Jewell. 1997. Hydrological constraints on Tricolored Heron and Snowy Egret resource use. Condor. 99:894–905.

Stuebe, M. M., and E. D. Ketterson. 1982. A study of fasting in tree sparrows (*Spizella arborea*) and dark-eyed juncos (*Junco hyemalis*): ecological implications. Auk 99:299–308.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598-2600.

U. S. Geological Survey. 2006. The Everglades Depth Estimation Network (EDEN) for Support of Ecological and Biological Assessments. U. S. Department of the Interior. Fact Sheet 2006-3087.

Wasser, S. K., K. E. Hunt, J. L. Brown, K. Cooper, C. M. Crockett, U. Bechert, J. J. Millspaugh, S. Larson, and S. L. Monfort. 2000. A generalized fecal corticosterone assay for use in a diverse array of nondomestic mammalian and avian species. General and Comparative Endocrinology 120:260-275.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of

    Lack's principle. American Naturalist 100:687–690.

Willmer, P. G., G. N. Stone, and I. A. Johnston. 1999. Environmental physiology of

    animals. Blackwell Science, Oxford, United Kingdom.

Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds. *In*

    K.G. Davey, R. E. Peter, and S. S. Tobe (eds). Perspectives in Comparative

    Endocrinology National Research Council of Canada, Ottawa, Ontario, Canada.

Table 1. Logistic exposure models for nest success of Great Egrets and White Ibises in the Florida Everglades during 2006 and 2007, with corresponding number of parameters (*K*), Akaike's Information Criterion (adjusted for small sample sizes; AIC_c) scores and weights (ω_i). Nests were monitored in Water Conservation Areas 2A, 3A, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge between 10 Jan – 23 Mar in both 2006 and 2007. Model parameters included year, mean biomass 1 and 2 weeks prior to survival estimate (Biomass 1, Biomass 2), mean water level recessions rate 1 and 2 weeks prior to survival estimate (Recess 1, Recess 2), the quadratic function of water recessions rates 1 and 2 weeks prior to a survival estimate, and the coefficient of variation for mean recession rates 1 and 2 weeks prior to survival estimate (CV 1, CV 2). Models presented only include those that were within 5 AIC_c values of the top model ($\Delta i = 0$), the global model and the intercept model, and are ranked by Δi values.

Model	*K*	AIC_c	Δi	ω_i
Great Egret Nest Survival				
Year + Region + Julian + Biomass 1 + Biomass 2 + Recess 1^2 + Recess 2^2	9	360.448	0.00	0.35
Year + Region + Julian + Biomass 1 + Biomass 2 + Recess 1^2 + Recess 2^2 + CV1	11	361.506	1.05	0.21
Year + Region + Julian + Biomass 1 + Biomass 2 + Recess 1^2 + Recess 2^2 + CV1 + CV2	11	362.464	2.01	0.13
Region + Julian + Biomass 1 + Biomass 2 + Recess 1 + Recess 2	8	363.214	2.76	0.08
Region + Julian + Biomass 1 + Biomass 2 + Recess 1 + Recess 2 + CV1	9	364.072	3.62	0.05
Year + Region + Julian + Biomass 1 + Recess 1 + Recess 2 + CV1 + CV2	6	364.777	4.32	0.04

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Model	K	AIC$_c$	Δi	ω$_i$
Julian*Region	3	365.258	4.81	0.03
Global Model	16	387.761	27.31	0.00
Intercept	1	400.002	39.55	0.00

Model	K	AIC$_c$	Δi	ω$_i$
White Ibis Nest Survival				
Year + Region + Julian + Biomass 1 + Biomass 2 + Recess 1 +Recess 2 + CV 1 + CV 2	11	440.185	0.00	0.47
Year + Region + Julian + Biomass 1 + Biomass 2 + Recess 1^2 + Recess 2^2 + CV 1 + CV 2	12	440.333	0.14	0.44
Global Model	16	445.005	4.82	0.04
Intercept	1	493.685	53.49	0.00

Table 2. Summary of variable importance weights and odds ratios for parameters occurring in competitive models explaining variation in nest success for great egrets and white ibises nesting in Water Conservation Areas 2A, 3A, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge between 10 Jan – 23 Mar in both 2006 and 2007. Values calculated as the summed weights of all models that include the variable.

Parameter	Variable importance weight	Odds ratio[1]	95% CI
Great Egret			
Year (2006 vs. 2007)	0.967	0.18	0.04 – 0.75
Region (Lox vs. WCA2A)	0.967	1.88	1.07 – 3.22
Region (Lox vs. WCA3A)		1.90	1.09 – 3.29
Region (WCA3A vs. WCA2A)		1.87	0.63 – 5.51
Julian	0.980	1.00	0.99 – 1.02
Biomass 1	0.932	1.02	0.98 – 1.07
Biomass 2	0.916	0.97	0.93 – 1.00
Recess 1 + Recess1^2	0.710	0.96	0.87 – 1.07
Recess 1 + Recess 2^2	0.696	1.41	1.02 – 1.71
White Ibis			
Year (2006 vs. 2007)	0.999	7.82	3.07 – 19.91
Region (Lox vs. WCA3A)	0.999	1.19	1.13 – 2.01
Julian	0.999	0.97	0.96 – 1.03
Biomass 1	0.999	1.00	0.96 – 1.03
Biomass 2	0.999	0.94	0.92 – 0.97
Recess 1	0.496	1.11	0.87 – 1.41

Recess 2	0.496	1.07	0.81 – 1.43
CV 1	0.991	1.19	1.01 – 1.47
CV 2	0.924	0.81	0.02 – 0.95

[1]Odds ratios >1 indicate a positive relationship; <1 indicate a negative relationship.

[2]Confidence intervals that do not include 1 indicate evidence of effects.
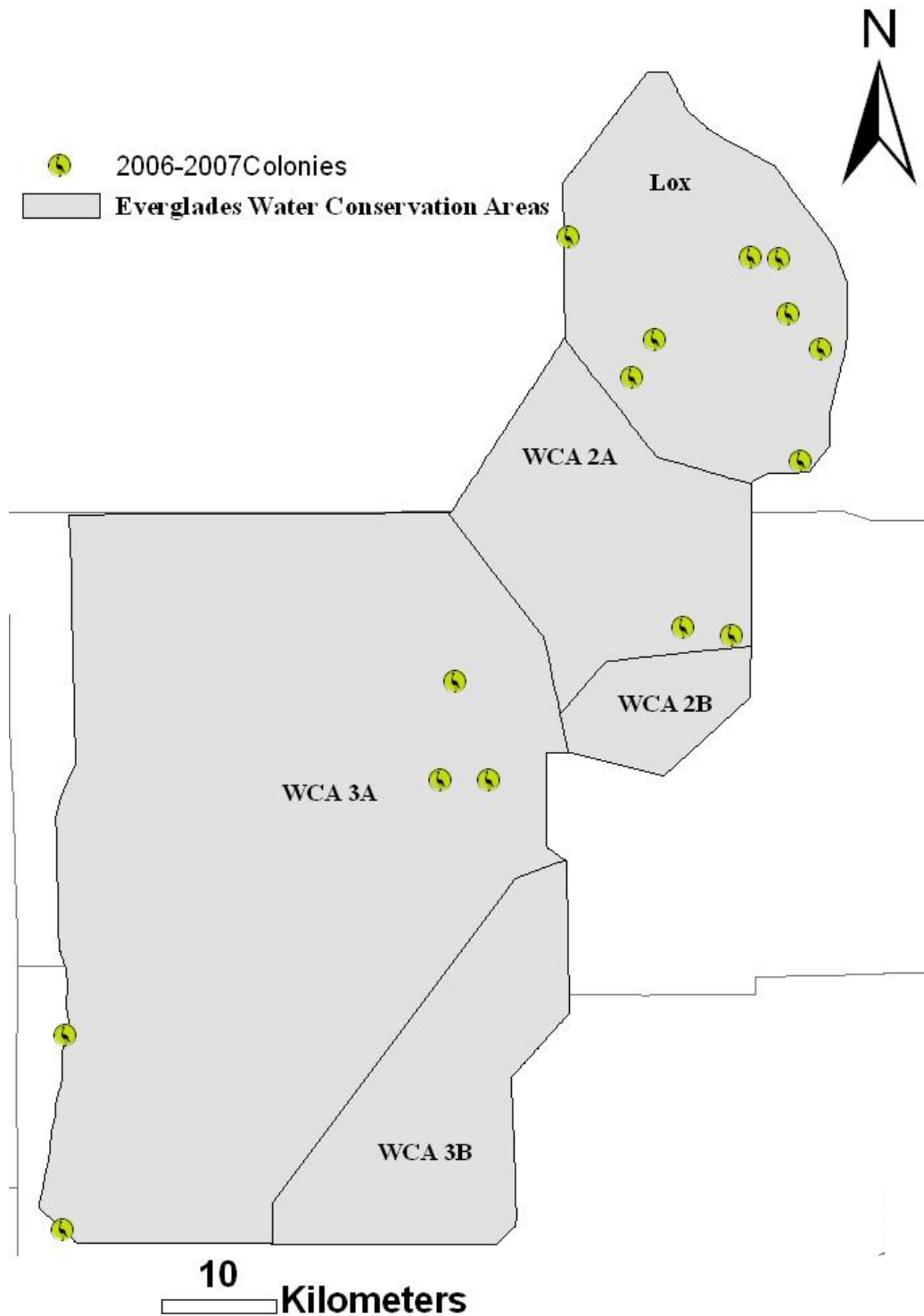
Figure 1. Wading bird colonies in Arthur R. Marshall Loxahatchee National Wildlife

Refuge (Lox), Water Conservation Area 2A (WCA 2A), 2B (WCA 2B), 3A (WCA 3A),

and 3 B (WCA 3B) that were included in this study during 2006 – 2007.

Figure 2. Mean clutch size (± SE) of white ibises (WHIB) and great egrets (GREG) during the 2006 – 2007 breeding seasons in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox), Water Conservation Area 2A (WCA2A), and 3A (WCA 3A) of the Florida Everglades. Differences were determined using 2-way analysis of variance (ANOVA) and sample sizes indicated in bars.
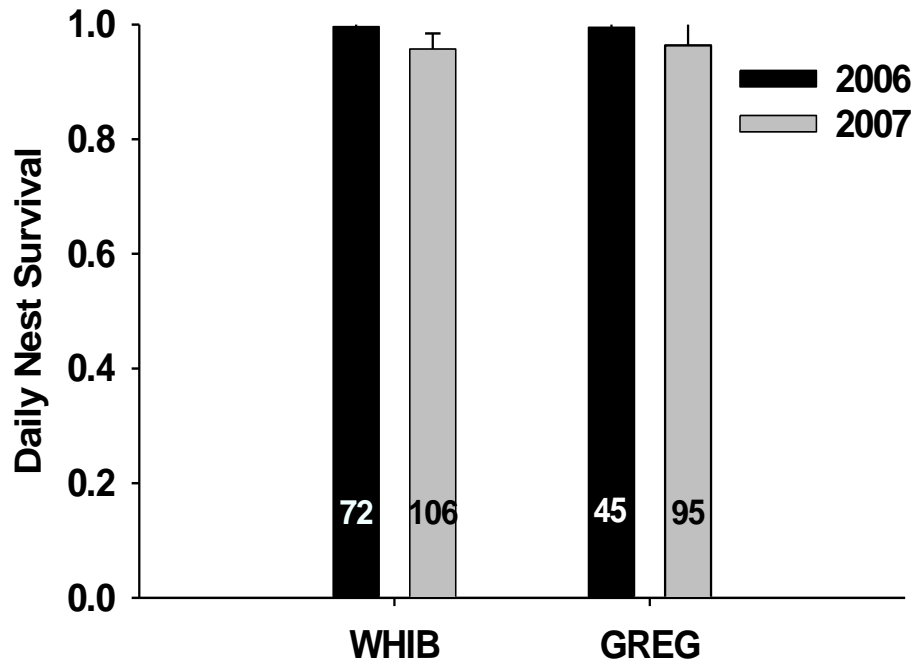
Figure 3. Mean daily nest survival (± SE) of white ibises (WHIB) and great egrets

(GREG) during the 2006 – 2007 breeding seasons in the Arthur R. Marshall Loxahatchee

National Wildlife Refuge (Lox), Water Conservation Area 2A (WCA2A), and 3A (WCA

3A) of the Florida Everglades. Sample sizes indicated in bars.

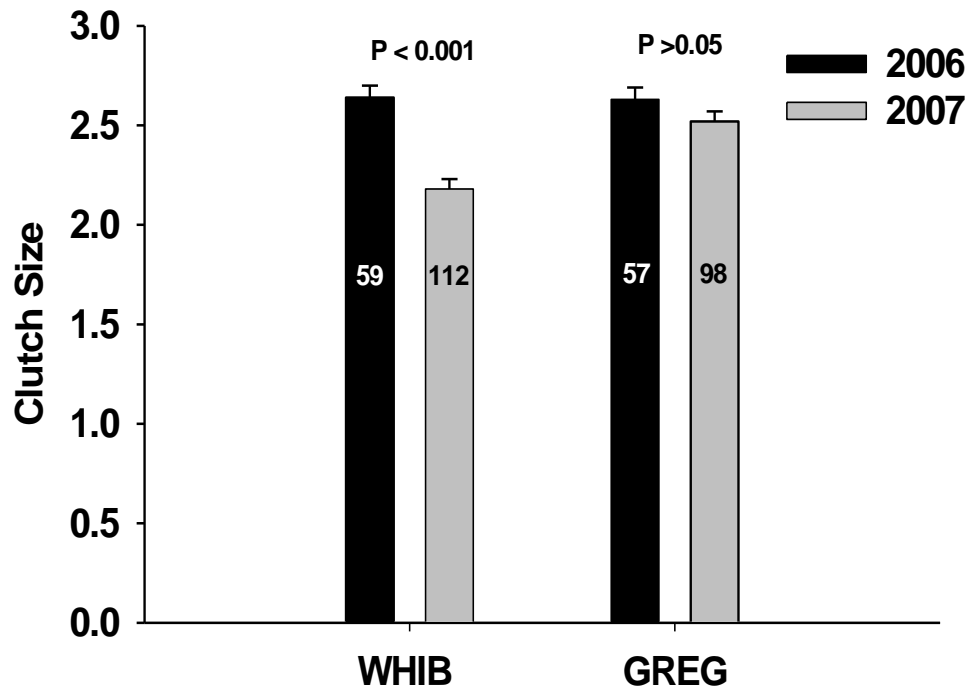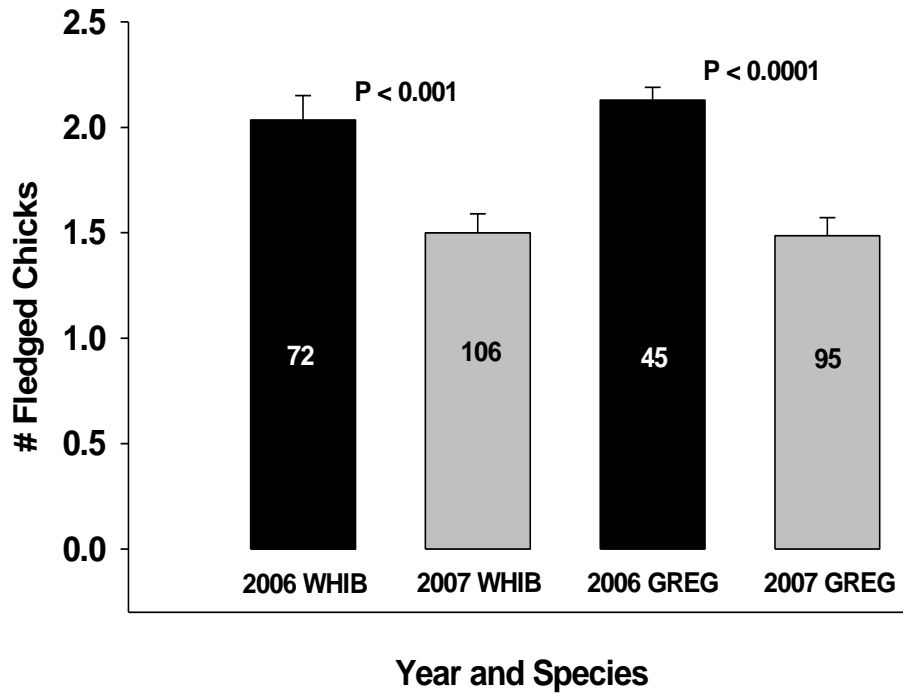Figure 4. Numbers of chicks fledged by white ibises (WHIB) and great egrets (GREG) during the 2006 – 2007 breeding season in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades. Differences determined by Wilcoxon nonparametric tests and nest samples sizes are indicated in bars.

CHAPTER 7: COMPARATIVE GROWTH AND PHYSIOLOGICAL RESPONSES OF GREAT EGRET AND WHITE IBIS CHICKS TO FOOD LIMITATION

ABSTRACT

Life history strategies can influence the physiological condition of chicks if adults decrease their level of provisioning in response to variability in landscape habitat conditions to maintain their own physiological condition or minimize their risk of mortality. Understanding those physiological responses of chicks can broaden our understanding of how life history strategies influence populations, particularly when similar, sympatric species have differing long-term nesting trends and experience years with large variation in habitat quality. I examined the physiological responses of great egret and white ibis chicks, two species whose adults have contrasting foraging strategies, in relation to foraging and habitat conditions in the Everglades. White ibis chicks were in poorer physiological condition based on measures of long-term stress (fecal corticosterone, stress protein 60) and growth rates (mass) during a year with poor prey availability relative to a good year, 2007. During the same poor prey availability year, great egret chicks had increased levels of fecal corticosterone, but no response in the growth rates (mass) of A and B-hatched chicks. Great egrets were also more likely to have hatched a third chick and provisioned that C-hatched chick for at least 8-10 days

before it failed during the poor year. While both great egret chicks and white ibis chicks were influenced by year and the age of chicks, only white ibis chick physiological condition decreased with increasing recession rates. This study is the first to demonstrate a landscape scale response to food limitation in the physiological condition and growth of great egret and white ibis chicks. The consistent pattern of white ibis chicks being in poorer physiological condition, coupled with slower growth rates during poor habitat years, demonstrates an important mechanism for limiting their population in the Florida Everglades.

INTRODUCTION

Food availability is one of the primary limitations to avian populations, particularly during the breeding season (Skutch 1949, Lack 1954, 1966, Ricklefs 1968). Seasonal environmental conditions require most avian species to adjust their physiology, morphology, and behavior throughout the annual cycle (Hahn 1998). When breeding, many avian species are able to regulate their body condition when they are faced with high-energy demands (Blem 1990), food scarcity (Stuebe and Ketterson 1982), or food unpredictability (Cuthill et al. 2000). Food may become a limiting factor during the breeding cycle due to increased adult physiological demands for egg production, increased food required for maintaining and fledging chicks, and environmental variability that can make food less available (Lack 1968).

While many species have adapted to varying environmental conditions, their ability to respond to natural variability coupled with anthropogenicly induced changes are less predictable. Birds can respond to food limitations by increasing foraging rates, selecting lower quality prey items, or traveling further to better quality foraging patches. These altered behaviors can result in adult and chick physiological responses, which can be observed in clutch sizes, hatching success, growth rates, and nest survival. Measuring the response to changes in habitat conditions can occur at a coarser scale (e.g., nest success) or at a finer scale (chick growth and physiological condition). While nest success is often used as a coarse measure of the response of individual species to their surrounding landscape, it lacks focus on what physiological mechanisms within the nest ultimately produce the successful or unsuccessful outcome.

Basic measures of nest success indicate the probability of a nest being successful within some level of certainty (e.g., standard error). While two years might have similar levels of nest success, they could differ largely by the number of chicks that are fledged, the factors within nest that influenced those differences, and the physiological condition of fledged chicks. Species with altricial chicks present an additional level of complexity because altricial nests typically are asynchronous. Typically, the first born (A) chick has a size advantage within the nest, allowing it to obtain more food from the parent (Mock and Parker 1997). Thus, differences in growth rates and physiological condition between A hatched chicks and subsequent hatched chicks may be related to, hatch order, landscape habitat conditions and food limitations, varying considerably in years with different habitat conditions (Monaghan et al. 1989, Harding et al. 2007). Most birds utilize a life history strategy to time their reproduction with maximum levels of food abundance (Perrins 1991, Houston 1997, Thomas et al. 2001), consequently during good years responses between chicks is likely minimal. During years with poor prey availability, life history suggests that long-lived birds should minimize their energy expenditure to chicks and maintain their own physiological condition (Sæther et al. 1993, Mauck and Grubb 1995) resulting in decreased chick physiological condition, with the smallest changes observed in A-hatched chicks.

In the Florida Everglades, a variety of environmental conditions are thought to influence wading bird reproductive success, although the exact link between landscape level environmental conditions and the biological and physiological mechanisms for reproductive effort and success have not been identified. Environmental conditions such as water depth, recession rate, and landscape level prey availability are known to

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influence breeding success and wading bird foraging (Frederick and Collopy 1989, Bancroft et al. 2002, Russell et al. 2002, Gawlik 2002). Frederick and Collopy (1989) demonstrated that wading bird nest success was most influenced by rapid hydrological reversals, while recession rates was most strongly associated with white ibis nest success, and that the amount of rainfall associated with hydrological reversals was most strongly associated with great egret nest failure. Bancroft et al (2002) demonstrated the importance of water depth constraints on foraging wading birds, while and Russell et al. (2002) demonstrated the influence of steady recession rates for making foraging sites available for wading birds, and hydrological reversal for making them unavailable. Gawlik (2002) tested the prey availability hypothesis, observing that vulnerability and density of prey did not always result in a similar foraging response or strategy across a suite of wading bird species that utilized searcher and exploiter foraging strategies. The study proposed that these species-specific differences in foraging strategy could account for species-specific population trends under the same environmental conditions, although the mechanistic pathway of effects was unknown.

For instance, white ibises (*Eudocimus albus*) have declined approximately 87%, while great egrets (*Ardea alba*) increased 270% in the same period across the Everglades (Crozier and Gawlik 2003*a*). Also, wading bird productivity fluctuates within and between years and timing of reproduction is often variable within and between years (Kushlan 1975, Frederick and Collopy 1989, Ogden 1994). Apparent dissimilarities between many wading bird species' diets suggest that interspecific forage competition does not limit prey availability (Ramo and Busto 1993, Smith 1997). White ibises (searchers) tend to select high quality patches and abandon them quickly; while great

egrets (exploiters) tend to stay at foraging sites where prey densities are low (Gawlik 2002). Species-specific foraging strategies (searchers versus exploiters; Gawlik 2002) and prey availability across the landscape could result in differences between searchers and exploiters at the nest level, and those differences could be identified in physiological metrics.

Understanding respective differences between great egret and white ibis chick growth and physiological condition may provide important insight into how the populations of these two species have shown such divergent trends while experiencing the same changes in habitat conditions across the Everglades. The Comprehensive Everglades Restoration Plan (CERP) will be changing ecosystem conditions greatly over the next several decades. Therefore, understanding the link between these habitat conditions and wading bird chick growth and physiological condition, will significantly increase the certainty of how wading birds will respond to the restoration efforts. Further, the linkage between foraging strategies and reproductive success remains poorly understood and understanding mechanism within nests that influence nest success could be valuable to restoration and management efforts.

Selecting the correct physiological metric to measure, a species' response to environmental change is difficult because the magnitude and duration of responses may differ considerably between metrics. By measuring physiological factors representing a variety of temporal responses we can improve our understanding of how birds react to day-to-day environmental conditions and long-term landscape habitat conditions. It is important to consider that not all short-term responses may affect the long-term

physiological condition of the bird and that not all long-term stress markers will be detectable on a day-to-day basis.

An effective method of examining short-term physiological condition of birds is the use of blood metabolite levels. Triglyceride levels (TRIG) in blood are often correlated positively with an increase in body mass and energy (lipid) storage while elevated glycerol levels (GLYC) correlate with decreasing mass (Jenni-Eierman and Jenni 1994, Williams et al. 1999, Masello and Quillfeldt 2004, Quillfedt et al. 2004, Anteau and Afton 2008). TRIG and GLYC tend to be short-term measures, and typically represent responses within approximately 2 days of being affected by an environmental event (Jenni-Eierman and Jenni 1994, Williams et al. 1999, Anteau 2006). Although TRIG and GLYC are considered short-term physiological responses, measuring changes of these blood metabolites in multiple birds across time and space can provide an estimate of the population response to longer-term environmental conditions at the landscape level.

Another short-term affect of environmental stress is the production of corticosterone (CORT; Quillfelt et al. 2004). As stored TRIGs are utilized and depleted, birds begin to catabolize muscle protein (Cherel et al. 1988), which is motivated by the secretion of CORT. When the cortex of the brain of a bird detects a stressor (e.g., food shortage, large temperature change), a neural signal is sent to the hypothalamus. The hypothalamus then sends a hormone signal to the pituitary gland, resulting in the pituitary sending a signal to the adrenal or interrenal gland to release CORT (short to medium-term length stress response). After the stressor has been alleviated a negative feedback loop shuts off the hypothalamus-pituitary-adrenal (HPA) pathway leading to the CORT

release. If the stressor persists and CORT remain elevated, the negative feedback loop will cease to function and destructive chronic effects may begin as allostatic overload occurs.

At lower levels, CORT can stimulate foraging activity and lipogenesis (Astheimer et al. 1992, Wingfield 1994). Under conditions of food scarcity, CORT stimulates gluconeogenesis, shifting catabolism away from fats towards proteins (Astheimer et al. 1992, Wingfield 1994). Chronic elevated levels of CORT can reduce the fitness of individuals via immunosuppression and reproductive failure, resulting in harmful effects at various levels (Verme and Doepker 1985, Wingfield et al. 1992). Fecal CORT metabolites (FCORT; medium-term stress response) levels reflect residue levels of plasma CORT, however, rapid and extensive metabolization before excretion results in lower overall levels than circulating levels (Wasser et al. 2000).

Stress proteins are a group of highly conserved intracellular polypeptides (Linquist 1986), that function as molecular chaperones for proteins within cells, present a major molecular barrier to alterations in cellular homeostasis, and can be used to detect the effects of long-term stress (Tomás et al. 2004). The primary role of stress proteins is to limit the interactions of unfolded proteins during the early stages of their synthesis by identifying and then binding to exposed proteins, thus stabilizing the unfolded protein (Willmer et al. 1999). Differences in stress proteins in central tissues and organs may be distinguished in peripheral blood as circulating blood cells may be stimulated to amplify stress protein production. Recent papers have evaluated the effectiveness of using stress protein to examine physiological condition in avian ecology (Moreno et al. 2002, Martínez-Padilla et al. 2004, Tomás et al. 2004, Herring and Gawlik 2007), suggesting

that they can be a valuable metric for future avian studies for detecting physiological

responses to changing environmental conditions. In comparison to CORT, stress proteins

may be more appropriate for detecting long-term or chronic exposure to stress, as capture

and handling effects are not confounding factors as in CORT (Buchanan 2000, Tomás et

al. 2004, Herring and Gawlik 2007).

Here, I investigate potential physiological differences in great egret and white ibis

chicks and related physiological condition to landscape level prey availability and the

hydrological variables that influence foraging conditions for adults. Hydrologic patterns

differed drastically during the two years of the study, 2006 and 2007, producing a large

difference in habitat quality. Prey densities during the January 10 - March 23 adult great

egret and white ibis capture period differed greatly between years. Prey biomass during

the prey-breeding period decreased by 77% from 42.06 g/m^2 ± 2.48 SE (n = 44) in 2006

to 6.05 g/m^2 ± 0.75 SE during 2007 (n = 43; Gawlik and Botson 2008). This lead to the

characterization of 2006 as the year with good habitat conditions and 2007 as the year

with poor habitat conditions.

My objectives with this study were threefold; 1) measure the physiological

responses of great egret and white ibis chicks across two years (*Chick Physiological*

Condition) using metrics of physiological condition, 2) use a mixed model framework to

determine which landscape variables (e.g., hydrology, prey biomass, recessions rates)

identified *a priori* most influenced the growth rates and physiological condition of great

egret and white ibis chicks (*Food Limitation Hypothesis*), and, 3) explore whether

differences in responses between the two species were related to differences in adult

foraging strategies (e.g., searchers versus exploiters) and populations trends (*Foraging*

Strategies).

METHODS

Chick Physiological Condition

Nesting colonies for white ibises and great egrets were located throughout the Everglades using a combination of ground and aerial surveys, the locations of the radio tagged adults (Chapter 5) and from Beerens' (2008) research, and from known colony sites from previous research (e.g., South Florida Wading Bird Reports, South Florida Water Management District). I attempted to monitor nests in colonies where both great egrets and white ibis were observed nesting, although some colonies contained only one or the other species, although most colonies contained additional species including snowy egret (*Egretta thula*), little blue heron (*E. caerulea*), tricolored heron (*E. tricolor*), great blue heron (*Ardea herodias*), and black-crowned night-heron (*Nycticorax nycticorax*). During 2006 and 2007 great egret and white ibis nests were monitored in colonies that occurred in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (colonies n = 7; Lox), and Water Conservation Areas 2A (colonies n = 2) and 3A (colonies n = 5; Fig. 1).

I located nests of radio tagged adults by first flying fixed wing aerial telemetry surveys at night, where I used a left-right control box and two side view directional yagi antennas to located radio tagged birds. This approach allowed for a rapid assessment of where radio tagged adults were throughout the Everglades, and what colonies they were associated with if they were at a colony at all. I then visited those colonies during the daytime to verify nesting or the development of nesting at that site. If I detected radio tagged great egrets or white ibises when visiting colonies on the ground I would locate those birds using a hand held yagi antenna. Located nests were marked with flagging

tape, and GPS coordinates were recorded. Random nests were also marked in these

colonies and included in analysis with radio tagged nests. If colonies were located that

did not have radio tagged nesting birds I would still randomly mark nests for data

collection. Hatched nests were revisited approximately every 7 days. Upon arrival at

each monitored nest I immediately removed the chicks from the nest and held them in a

either a cloth bag or large plastic container to keep them calm, and to minimize potential

stress and movement during subsequent sampling and measurements. When possible, I

sampled all chicks in each nest; first hatched (A), second hatched (B), and third hatched

(C). During 2006, I sampled 69 A, 39 B, 8 C, and 60 A, 24 B, and 4 C-hatched great

egret and white ibis chicks respectively. During 2007, I sampled 109 A, 109 B, 16 C, and

74 A, 36 B, and 4 C-hatched great egret and white ibis chicks respectively.

Because blood samples could not be obtained in less than 3 minutes to achieve a

baseline level of CORT (Romero and Reed 2005), I attempted to standardized the time (5

min) from capture until blood samples were collected. Mean time to blood collection for

egret chicks was 5.16 min ± 0.29 SE, and 6.80 min ± 0.44 SE for ibis chicks. I collected

up to 1 ml of blood from the brachial or jugular vein using a 27.5-gauge needle. Blood

samples were then labeled and stored in heparinized Vacuutainers, and placed on ice until

transported to the lab. I then extracted up to 2 ml of fecal material directly from the birds

cloaca using a micropipette, fecal samples were labeled and stored in mirco centrifuge

tubes and placed on ice. I then recorded tarsus length (middle of midtarsal joint to the

end of tars-metatarsus), wing chord, wing flattened, exposed culmen length, bill depth,

and mass for both species. All measurements were to the nearest 1 mm using calipers or

a wing ruler, except mass, which was measured to the nearest 5 g using a spring scale.

All measurements were taken by trained individuals and supervised by GH. I attempted to capture and sample all chicks during the morning to minimize heat stress and time of day effects on physiological metrics.

In the lab, blood samples were centrifuged (15 min, 10,000 g); plasma and red blood cells were separated and frozen at -20° C for later analysis. Fecal samples were also frozen at -20° C for later analysis. Plasma TRIG and GLYC were measured using enzymatic endpoint assay following Williams et al. (1999) using Sigma kits (Sigma, Saint Louis, MO). Assays were then validated using reference values from normal and abnormal human control sera. Inter- and intra-assay coefficients of variation for TRIG and GLYC internal standards were 6% and 9%, and 6% and 7%.

PCORT and FCORT samples were homogenized and then mixed with methanol and vortexed for 30 min. After centrifugation (15 min, 2500 g) I transferred the supernatant to a new vile, which was then evaporated under a stream of nitrogen gas. CORT metabolites were then resuspended in diluted extraction buffer and measured using enzyme-linked immunosorbent assays (ELISA; Neogen, Lexington, KY). Inter- and intra-assay coefficients of variation for PCORT internal standards were 5% and 7%, and 6% and 9% respectively for great egrets and white ibises. Inter- and intra-assay coefficients of variation for FCORT internal standards were 7% and 11%, and 8% and 9% respectively for great egrets and white ibises. ELISAs were validated for the measurement of both PCORT and FCORT metabolites (Chapter 5). I also validated that FCORT levels did not change after freezing as in the case of mammals (Khan et al. 2003) by freezing and measuring FCORT levels monthly for 6 months (Herring and Gawlik *In Review*). This experiment showed that cross-reacting metabolites do not change levels of

FCORT in avian species, and lead me to conclude that levels of FCORT in white ibis and great egret chicks were not biased.

Red blood cells were washed three times using phosphate buffered saline, centrifuged and the supernatant removed after the final wash. Red blood cell supernatant was then mixed with a $1\times$ extraction reagent and a protease inhibitor cocktail (Sigma), vortexed for 5 min and then sonicated for 1 min. Samples were again centrifuged (15 min, 2500 g) and the supernatant removed. I measured SP60 and SP70 (SP70-1) using ELISA kits specific to just those stress proteins and not all other SP60 and SP70 family members (Assay Designs, Inc., Ann Arbor, MI). ELISAs were validated for the measurement of SP60 and SP70 (Chapter 5). Inter- and intra-assay coefficients of variation for SP60 internal standards were 7% and 9% and 6% and 8%, respectively for great egrets and white ibises. Inter- and intra-assay coefficients of variation for SP70 internal standards were 8% and 11% and 7% and 12%, respectively for great egrets and white ibises. All samples were run in duplicate and means of duplicates were used in all analysis.

Food Limitation Hypothesis

I used the Everglades Depth Estimation Network (EDEN) to estimate all water depths and recession rates at nesting colonies during 2006 and 2007. EDEN is a network of real-time water level monitoring, water surface modeling, and ground elevation modeling that is used to model water depth for the entire freshwater portion of the Greater Everglades (USGS 2006). EDEN calculates stage levels at daily time steps to account for daily changes associated with evapo-transpiration drying and rainfall

rewetting. The model provides estimated depth information on a 400 m by 400 m grid across the entire landscape.

To estimate stage and recession rates at nesting colonies I first used ArcGIS 9.1 to establish buffers around colonies based on mean distances plus 1 standard error flown by radio-tagged great egrets and white ibises from those colonies based on estimates provided by Beerens (2008). Mean distances flown were 13.71 km ± 0.37 SE and 7.0 km ± 0.47 SE for white ibises and 7.98 km ± 0.76 SE and 4.83 km ± 0.3 SE for great egrets during 2006 and 2007 respectively. These buffers were used to identify all of the associated 400 m by 400 m EDEN cells that were likely to be used by each species each year around specific colonies. I then used SAS (9.1) to extract stage levels for each of the grid cells for each day chicks were sampled, and 1 and 2 weeks prior to that day. I calculated recession rate by first calculating the mean stage of the cells surrounding each colony for each species each day and then subtracted. I also calculated the coefficient of variation (CV) for recession rate for 1 and 2 weeks prior to chick sampling. The CV measures the variation of daily recession rates over the 1-week period to capture variations in recession rates associated with hydrological reversals. This method is preferable to only using mean recession rate because calculating the mean recession rates for 1-week prior may mask any small hydrological reversal events that occurred.

To estimate prey densities associated with colonies, I used data provided from Beerens' (2008) associated research on ibises and egrets. Beerens (2008) located radio-tagged egrets and ibises across the Everglades using telemetry techniques outlined in Chapter 5. Beerens (2008) then sampled those sites to estimate prey densities using throw traps (Kushlan 1981) within 1 day of aerial surveys. I then plotted those locations

in ArcGIS 9.1, created buffers around nesting colonies based on the mean plus 1 standard

error of foraging distances of egrets and ibises as above, and identified those prey density

estimates that were associated with my breeding colonies both spatially and temporally. I

only included an estimate of prey density within a colonies buffer if it was collected

within 7 days of an estimate of nest survival. All estimates of prey densities during that

7-day period were averaged to provide a mean estimate of prey densities within the mean

+ 1 standard error foraging flight distance of a colony for each weekly time step.

Statistical Analyses

I used an information theoretic approach to build and rank competing models in a

mixed model framework (Burnham and Anderson 2002) using a repeated measures

model to account for measuring the same nestlings multiple times (Proc Mixed; Littell et

al. 1996, Littell et al. 1998). I selected the autoregressive(1) covariance matrix after

examining the covariance structure of each response variable. Competing models were

developed based on a biologically meaningful understanding of the nesting responses of

wading bird chicks from previous studies as follows. Frederick and Collopy (1989)

demonstrated that wading bird nest success was most influenced by rapid hydrological

reversals, while recession rates was most strongly associated with white ibis nest success,

and that the amount of rainfall associated with hydrological reversals was most strongly

associated with great egret nest failure. Bancroft et al (2002) demonstrated the

importance of water depth constraints on foraging wading birds, while and Russell et al.

(2002) demonstrated the influence of steady recession rates for making foraging sites

available for wading birds, and hydrological reversal for making them unavailable.

Gawlik (2002) tested the prey availability hypothesis, observing that vulnerability and

density of prey did not always result in a similar foraging response or strategy across a suite of wading bird species that utilized searcher and exploiter foraging strategies.

Because I chose species that differed markedly in their foraging strategy, it was inappropriate to include both species in the same model. Thus, I ran separate models for each species to understand their individual physiological responses to differing habitat conditions (e.g., hydrology, prey densities). I evaluated the goodness-of-fit of the global models and verified model fit before proceeding with additional model analyses. Prior to model selection I visually examined the residuals of model variables to identify outliers or other patterns that required transformation.

Each physiological response variable [TRIG, GLYC, PCORT, FCORT, SP60, SP70, PEC, and mass growth rate (MASS)] were examined using the variables for Year, Region, chick hatch order (Hatch), chick age (Age), prey biomass one and two weeks before chick sampling (Biomass 1, Biomass 2), Julian date (Julian), recession rate one and two weeks prior to capture (Recess 1, Recess 2), and the quadratic form of recession during one and two weeks prior to capture (Recess 1 + Recess 1^2, Recess 2 + Recess 2^2). Global models included all environmental terms as well as interactions of main effects.

I used the AIC_C values adjusted for small samples sizes in all models (Burnham and Anderson 2002). I calculated delta AIC (Δ_i, Akaike's Information Criterion) and AIC weights (ω_i) from AIC_c values. Models with the lowest AIC_c value was considered the best explanatory model; although, additional competing models with $\Delta AIC_c < 2$ were considered equally plausible given the data (Burnham and Anderson 2002). Models with $\Delta AIC_c > 4$ were considered to have little to no support (Burnham and Anderson 2002).

I calculated the unconditional estimates for coefficients and unconditional standard error terms for each parameter across all models (Burnham and Anderson 2002) based on all models with AIC_C weights ≥ 0.001. Model-averaged coefficients were calculated by only using the exponentiated AIC_C values from models that contained the parameter, the exponentiated values were then summed, the original exponentiated AIC_C value was then divided by the new sum to get new Akaike weights. I then multiplied the raw (individual model) parameters by the new weights and summed the products. To assess magnitude of individual parameters, I calculated weights or parameter likelihoods by summing the model weights for each variable in the most parsimonious model for every model that it occurred in, this allowed for a quantitative assessment of the contribution of each variable to the response variable. In the results, I limit discussion of the sign and magnitude of effects to parameters that were in the most parsimonious models and that did not have estimates of SE that did not overlap the estimated coefficient greatly.

RESULTS

Chick Physiological Condition

GLYC

The most parsimonious model for great egret chick GLYC levels only contained the variable Age. The weight of the evidence for this model was 75%, and the model received 3.7× the support of the second best model (Table 1). White ibis chick glycerol levels were best explained by two candidate models; the top model was Year + Age + Hatch with 42% of the weight of the evidence and 1.8× the support of the second best model (Table 1). The second top model included the variables Year + Age + Hatch + Region; with 23% of the weight of the evidence and 1.9× the support of the next model (Table 1). Model variable importance results suggested great egret chick GLYC levels were most influenced by Age, and to a lesser extent Year (Table 2). Model variable importance results suggested white ibis chick GLYC levels most influenced by Year, Age, Hatch, with Region having a smaller influence (Table 2). Great egret and white ibis chick GLYC levels decreased as chicks got older and decreased with hatch order. Ibis chick GLYC levels were also lower in Lox than WCA 3A. Great egret and white ibis chick GLYC levels were similar between years (Figs. 2-3).

TRIG

Great egret chick TRIG levels were best described by three models, 1) Age, 2) Year + Age, and 3) Year + Age + Hatch. The weight of the evidence was 39%, 23%, and 14% respectively, with 1.7 ×, 1.6 ×, and 14 × the support of the next candidate models respectively (Table 1). There were two models with similar support for white ibis chick TRIG levels: 1) Year + Age, + Hatch + Region, and 2) Year + Age + Hatch + Region +

Biomass 1 (Table 1). The first model had 55% of the support and was 1.4× as likely to be the most parsimonious model. The second model had 37% of the support and was 13.4× the support of the next model. Model variable importance results suggested great egret chick TRIG levels were most influenced by Year, Age, and to a lesser extent Hatch (Table 2). Model variable importance results suggested white ibis chick TRIG levels were most influenced by Year, Age, Hatch, and Region, with Biomass 1 having a smaller influence (Table 2). Great egret and white ibis chick TRIG decreased with hatch order. Ibis TRIG increased with chick age and increasing biomass, and was higher in Lox than WCA 3A. Great egret and white ibis chick TRIG levels were similar between years (Figs. 4-5).

PCORT

The model selection process did not identify a top candidate model for great egret PCORT levels; rather there were four models with similar levels of support. Those models included: 1) Year + Age + Hatch + Region, 2) Year + Age + Hatch + Region + Biomass 1, 3) Year + Age + Hatch, and 4) Year + Age (Table 1). The weight of the evidence of these models were 29%, 21%, 19%, and 15% respectively, and 1.3×, 1.1×, 1.2×, and 3.7× the support of the next successive candidate model (Table 1). However, there were 8 models that had $\Delta AIC_C \leq 4$, indicating a high degree of uncertainty and a general lack of explanatory power for all great egret PCORT models. The most parsimonious model for white ibis chick PCORT was the Global model, with 60% of the weight of the evidence and 1.5× the support of the second model. The second model with the variables Year + Age + Hatch + Region + Biomass 1, had similar support with 42% of the weight of the evidence and 3.2× the support of the next model (Table 1). Model

variable importance results suggested great egret chick PCORT levels were most influenced by Year, Age, Hatch, and to a lesser extent Region (Table 2). Model variable importance results suggested white ibis chick PCORT levels were influenced similarly by Year, Age, Hatch, and Region, and Biomass 1 (Table 2). Great egret PCORT increased with chick age, hatch order, and was lower in Lox. Great egret and white ibis chick PCORT levels were similar between years (Figs. 6-7).

FCORT

The top candidate models for great egret chick FCORT level included the variables Year + Age + Hatch with 43% of the weight of the evidence and 1.4× the support of the next model, and Year + Age + Hatch + Region with 30% of the weight of the evidence and 2.5× the support of the next model (Table 1). The most parsimonious model for white ibis chick FCORT included the variables Year + Age + Hatch + Region + Biomass 1, with 70% of the weight of the evidence and 7.0× the support of the next top model (Table 1). Model variable importance results suggested great egret chick FCORT levels were most influenced by Year, Age, Hatch, and to a lesser extent Region (Table 2). Model variable importance results suggested white ibis chick FCORT levels were influenced similarly by Year, Age, Hatch, and Region, and to a lesser extent Biomass 1 (Table 2). Great egret and white ibis chick FCORT metabolites levels increased with hatch order, decreased with age, and were lower in Lox (Table 2). Levels of FCORT increased in all chicks during 2007 for both great egrets and white ibises (Figs. 8-9).

SP60

The model selection process did not identify any of the candidate models for great egret SP60 levels as being parsimonious; the global model had 91% of model weight and

the 15.1× support of the next model (Table 1). The high degree of support for the saturated global model suggests there was a lack of explanatory power for simpler less parameterized candidate models. The model selection process identified two models with similar support for white ibis chick SP60 levels. The first model included the variables Year + Age + Hatch + Region + Biomass 1 + Biomass 2, with 54% of the weight of the evidence and 1.7× the support of the next model (Table 1). The second model included the same variables but with the quadratic form of the 1 and 2 week recession rates, with 31% of the weight of the evidence and 4.4× the support of the next model (Table 1). Model variable importance results suggested white ibis chick SP60 levels were influenced equally by Year, Age, Hatch, and Region, Biomass 1, and Biomass 2, and Recess 1 (Table 2). Great egret chick SP60 levels were similar between years (Fig. 10), while white ibis chick SP60 levels increased during 2007 (Fig. 11) and decreased with chick age (Table 2). White ibis chick SP60 decreased with chick age, hatch order, increasing biomass, and increasing recession rate, while being lower in Lox (Table 2)

SP70

Two top models were identified for great egret chick SP70 levels; Age with 61% of the weight o the evidence and 2.3× the support of the second, Year + Age, with 26% of the weight of the evidence and 2.8× the support of the next model (Table 1). Two top models were identified for white ibis chick SP70 levels, Year + Age + Hatch + Region with 49% of the weight of the evidence and 1.3× the support of the second top model, and Year + Age + Hatch, with 36% of the weight of the evidence and 7.2× the support of the next model (Table 1). Model variable importance results suggested great egret chick SP70 levels were most influenced by Age and to a lesser extent by Year (Table 2).

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Model variable importance results suggested white ibis chick SP70 levels were influenced similarly by Year, Age, and Hatch, and to a lesser extent Region (Table 1). Great egret and white ibis SP70 increased with increasing chick age. Great egret and white ibis chick PCORT levels were similar between years (Figs. 12-13) but increased with chick age (Table 2).

MASS

Two models with similar support were identified for great egret chick mass, Year + Age + Hatch + Region with 55% of the weight of the evidence and 1.2× the support of the second model, and Year + Age + Hatch; with 43% of the weight and 107.5× the support of the next model (Table 1). White ibis chick mass was best described by the model Year + Age + Hatch, with 85% of the weight and 7.0× the support of the next model (Table 1). Model variable importance results suggested great egret chick mass levels were most influenced equally by Year, Age, Hatch, and to a lesser extent Region (Table 2). Model variable importance results suggested white ibis chick mass levels were influenced equally by Year, Age, and Hatch (Table 2). Only C-hatched great egret chicks had lower growth rates and between years and compared to A and B-hatched chicks (Fig 14-18). A and B-hatched egret chick growth rates were similar inter and intra specifically (Figs. 14-17). White ibis A and B-hatched growth rates were similar during 2006 (Fig. 19), but B-hatched chicks had slower growth rates during 2007 (Fig. 20). Both A and B-hatched chicks had similar growth rates within their respective hatch orders (Figs. 21-22).

PEC

Great egret chick PEC was best explained by the model Year + Age + Hatch + Region + Biomass 1 + Biomass 2, with 80% of the weight of the evidence and 8.8× the support of the next model (Table 1). White ibis chick PEC was best explained by the model Year + Age + Hatch + Region + Biomass 1 + Biomass 2 + Recess 1, with 82% of the weight of the evidence and 5.1× the support of the next model (Table 1). Model variable importance results suggested great egret and white ibis chick PEC levels were most influenced by Year, Chick Age, Hatch Order, Region, Biomass 1, Biomass 2, and Recess 1 (Table 2). Great egret PEC scores decreased in both A and B-hatched chicks during 2007, while C-hatched chicks were similar between years; and PEC increased with chick age (Table 2). White ibis chicks had higher PEC scores during 2006 than 2007 (Figs. 23-24), and PEC scores decreased with ibis chick age (Table 2). Both egret and ibis PEC increased with increasing biomass (Table 2).

To further identify, post hoc, variables common among all of top models (e.g., <2 Δi AICC units) for all physiological variables that were identified as being influential to chick physiological metrics based on parameter likelihood values, I summed the parameter likelihood values across all models. For great egret chicks, the variable that influenced all physiological metrics the most was Age (sum parameter likelihood = 6.90), while Year (sum parameter likelihood = 5.56), and Hatch (sum parameter likelihood = 4.12), were also important, but with slightly less influence. White ibis chick physiological condition was equally influenced by three variables, Year (sum parameter likelihood = 7.65), Age (sum parameter likelihood = 7.66), and Hatch (sum parameter

likelihood = 7.40), with Region (sum parameter likelihood = 5.57), and Biomass 1 (sum

parameter likelihood = 4.03) were also important but with slightly less influence.

Food Limitation Hypothesis

Model selection results demonstrated strong support for the *Food Limitation*

Hypothesis in white ibis chicks, with 50% of all long-term physiological parameters

responding positively to increasing prey availability (Table 3). No support was found for

the *Food Limitation Hypothesis* in great egret chicks (Table 13). Hydrological factors

that influence prey availability (recession rates) also show support for positively

increasing physiological metrics during the pre-breeding period for both species (Table

3).

DISCUSSION

Food Availability Theory

The role of food availability may be critical to the physiological condition of both great egret and white ibis chicks, the pathway however may not be the same for these two species, resulting in differences in their physiological condition. White ibis and great egret chicks' physiological condition tended to be influenced by several habitat variables in common, year, and the age of chicks. Given the large differences in prey availability between years (Beerens 2008, Gawlik and Botson 2008) this result seems intuitive, but would suggest that the two estimates for prey biomass should have been more important for the both species physiological condition. Prey biomass was observed to be an important landscape variable in explaining white ibis chick physiological condition, as suggested by the fact that 50% of the ibis physiological models included either the 1or 2-week estimates of biomass with moderate to high parameter likelihood estimates. However, great egret chick physiological condition was less influenced by landscape level prey availability, with only great egret PEC including biomass in the top two candidate models.

Can it be inferred from this result then that prey densities did not influence great egret chick physiological condition, and if so what were the factors that did influence egret chick physiological condition? The large reduction in prey densities did not influence the condition of great egrets' physiology correspondingly to white ibis chicks (increase in SP60 levels), but this does not indicate that there was no overall response in egrets. There was a substantial reduction in nest success in egrets between 2006 and 2007, as well in ibis (Chapter 6). Further, the number of chicks fledged for egret nests

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was lower in 2007, the poor habitat year (Chapter 6). So, while great egret nesting success and chick physiological condition (e.g., increased long-term stress: FCORT) demonstrates a potential life-history strategy, passing the costs of lower habitat quality to chicks (Ricklefs 1984, Zera and Harshman 2001), it also raises the question, why do great egrets chicks not experience a similar response (elevated long-term stress marker SP60) to that of white ibis chicks in the same spatial and temporal frame, and why don't they decrease their clutch size if pre-breeding prey availability suggest it is a poor year?

The reduction in energy expenditure by adult great egrets (e.g., shorter foraging flight distances; Beerens 2008) in the poor year suggests that adults may play a larger role in the physiological condition of their chicks than in traditional long-lived birds such as white ibis. Reducing the costs of provisioning could allow for provisioning rates to be maintained for egret chicks even during poor years. This strategy would seem to fit the model for an exploiter foraging strategy best, given their ability to forage in a wider range of depths (Gawlik 2002), and on a wider size range of prey species (Smith 1997). Additionally, on numerous nocturnal radio telemetry colony surveys, I failed to detect nesting radio tagged adult great egrets in colonies (Herring, unpublished data). Nesting radio tagged adults were located in sloughs on several occasions during nocturnal aerial surveys. These adults were likely foraging during the nocturnal period, as evidenced by the return of many egret adults associated with my nesting study during the period just before adults normally leave the nest in the morning (Herring, unpublished data).

While this foraging behavior has not been documented previously for great egrets (McCrimmon et al. 2001), it does occur on a regular basis for other long-legged exploiter species such as great blue herons (Butler 1992). Great blue herons possess a high degree

of rod photoreceptors in their eyes, presumably an adaptation to for night vision (Lish 1982). Measuring the proportion of cones to rods in the eyes of great egrets could help determine if they are also adapted to night vision and night foraging.

Landscape Effects

Model selection results demonstrated that there were differences in the landscape habitat variables that influenced the physiological condition of great egret and white ibis chicks during the 2006 – 2007 breeding seasons in the Florida Everglades. Similar to nest success results for these two species (Chapter 6), white ibis chick physiological condition was influenced by both variables for 1 and 2 week recession rate estimates prior to estimates of chick physiological condition.

The inclusion of the recession rate variable for ibis SP60 levels suggests that consistent recession rates were important for the physiological condition of ibis chicks, but less important for egret chicks. Stress proteins are considered to be a measure on long-term stress, suggesting that measures of SP60 in this study for white ibis chicks were reflecting changes occurring at the landscape scale in at least recession rates. While in great egret chicks, recession rate was not found to be important in explaining variability in any measure of chick physiological condition.

Interestingly, only SP60 levels increased in response to this apparent landscape stressor. This is consistent with other recent research using both SP60 and SP70, which found only SP60 responded to environmental stressors in birds. Martínez-Padilla et al. (2004) observed a significant increase in SP60 during the course of a breeding season in Eurasian kestrels (*Falco tinnunculus*), while SP70 remained relatively constant. Moreno et al. (2002) also found SP60 levels to be negatively correlated with tarsus length and

high heterophil/lymphocyte ratios, with no similar relationship for SP70 levels in pied flycatchers (*Ficedula hypoleuca*). These studies combined with my results demonstrate that SP60 is a better physiological marker of stress in birds than SP70.

Foraging Strategies

If the exploiter foraging strategy does benefit nesting egrets yet they still fledge similar numbers of chicks relative to white ibis in poor prey availability years, then perhaps benefits were gained in the chicks' physiological condition, not the total number of chicks fledged. Indeed, growth rates of A and B-hatched egret chicks were similar between years and hatch order, suggesting that the increased stress levels (FCORT) were not deleterious to them. Perhaps the increase in corticosterone in great egret chicks is not above a threshold that results in deleterious effects. Alternatively, the increase in great egret chick corticosterone levels may facilitate increased begging and provisioning (Kitaysky et al. 2001, Saino et al. 2003). If this were the case, adult egrets would have to make a trade-off of their own physiological condition. This may also explain why great egret chicks did not show an increase in the other long-term stress marker, SP60. White ibis chick growth rates in this study did however decreased in the poor year, but only for B chicks. During a food supplementation experiment, Cook and Herring (2007) also observed lower growth rates and survival rates for B-hatched chicks but not A chicks during the poor year, 2007.

One additional possibility to describe how these species' responses to landscape habitat conditions could be related to population trends is the response of C-hatched chicks. Results from the nesting study suggest white ibises switch to a strategy of

minimizing the costs of reproduction early one in the breeding cycle by decreasing their clutch size, while great egrets maintained their clutch size from good to poor years.

This strategy would benefit searcher species, which require high quality patches, which may be less available during below average prey availability years or years with poor hydrological conditions. During the poor prey availability year in this study, the white ibis already committed to lowering its energetic costs, which may allow for less successful foraging because only two chicks need to be fed, not potentially three as in good years. Great egrets maintained their clutch size through poor years, which may require more successful foraging, more trips, or better quality food to maintain three chicks. While results from this study suggest in below average years the number of chicks being fed drops rapidly from three to two in most colonies across the Everglades, there remain two possible scenarios where this strategy could be beneficial and result in more chicks fledged. If either the A or B-hatched chick dies early on in the nestling stage, the C chick can replace it, or if landscape level prey availability or hydrological conditions changed rapidly then perhaps the C chick can be fledged (Mock and Parker 1997). This hypothesis has been called the Insurance Egg Hypothesis, and suggests that individuals that use this strategy are not constrained and is an adaptation to uncertain offspring viability (Dorward 1962, Cash and Evans 1986). Alternatively, Lack's Resource Tracking Hypothesis (1947) proposes that surplus offspring act as a bet-hedging function; during good years, the third chick in this case might be fledged as well.

One scenario where either the Insurance Egg or Resource Tracking Hypotheses might occur is when hydrological conditions are poor early in the breeding season (e.g., hydrological reversals, or low recession rates). If nesting was initiated and then recession

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rates improved, more prey could become available to provision and fledge the third

chick. Additionally, this response may be beneficial during poor years because the

likelihood of either the A or B-hatched chicks failing is probably higher than in good

years. Although, during average years, it may not require much of an improvement in

habitat conditions (either prey or hydrological) to fledge C-hatched chicks. However, for

white ibis, if they have handicapped their nest effort early by decreasing their clutch size

from three to two, the maximum number of chicks fledged will always be 2, assuming a 3

egg clutch. Correspondingly, during poor years if one egg or chick fails, then the

reduction in potential number of chicks fledged relative to egrets could be as much as

66% lower per nest. Results from this study do not refute or positively support either

hypothesis for egrets, suggesting egrets may in fact lay third eggs in poor years as an

insurance policy and to fledge third chicks during good years. Future experimental food

supplementation of both species adults may help elucidate these facts for great egret and

white ibis reproductive strategies.

This study is the first to demonstrate a landscape scale response to food limitation

in the physiological condition and growth of great egret and white ibis chicks. The

consistent pattern of white ibis chicks being in poorer physiological condition, coupled

with slower growth rates during poor habitat years demonstrates an important mechanism

for limiting their population in the Florida Everglades. Given that in a year with low prey

availability, white ibis chicks fledged in poor physiological condition relative to great

egret chicks, there could be further differences between the two species not elucidated by

this study. Poor physiological condition in white ibis chicks could lead to lower survival

rates during their first year. Future research might address survival rates of fledging

egrets and ibises to understand if they differ between species, and how they relate to

differences in prey availability and those hydrological factors that influence prey

availability.

LITERATURE CITED

Anteau, M. J., and A. D. Afton. 2008. Using plasma lipid metabolites to index changes in lipid reserves of free-living lesser scaup (*Aythya affinis*). Auk 125:354-357.

Astheimer, L. B., W. A, Buttemer, and J. C. Wingfield. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scandinavia 23:355-365.

Bancroft G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. Waterbirds. 25:265–277.

Beerens, J. E. 2008. Hierarchial habitat selection in great egrets and white ibises in the Florida Everglades. Thesis, Florida Atlantic University, Boca Raton , FL.

Blem, C. R. 1990. Avian energy storage. Current Ornithology 7:59-113.

Buchanan, K. L. 2000. Stress and evolution of condition-dependent signals. Trends in Ecology an Evolution 14:156-160.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Butler, R. W. 1992. Great blue heron (*Ardea herodias*). *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 25. The Birds of North America, Inc., Philadelphia, PA.

Cash, K. J., and R. M. Evans. 1986. Brood reduction in the American white pelican (*Pelecanus erythrorhyncus*). Behavior Ecology and Sociobiology 18:413-418.

225

Cherel, Y., J. P. Robin, and Y. Le Mayo. 1988. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66:159-166.

Cook, M. I., and H. K. Herring 2007. South Florida wading bird report, Volume 13. South Florida Water Management District, West Palm Beach, FL.

Crozier, G. E., and D. E. Gawlik. 2003. Wading bird nesting effort as an index of wetland ecosystem integrity. Waterbirds 26:303-324.

Cuthill, I. C., S. A. Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. Behavioral Ecology 11:189-195.

Dorward, D. R. 1962. Comparative biology of the white booby and the brown booby *Sula* spp. at Ascension. Ibis 103:174-200.

Frederick, P. C., and M. W, Collopy. 1989. Nesting success of Ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625-634.

Gawlik, D. E. 2002. The effects off prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Gawlik, D. E., and B. Botson. 2008. Aquatic fauna seasonal concentrations, contract CP040319. Unpublished annual report to the South Florida Water Management District, West Palm Beach, FL.

Hahn,T. P. 1998. Reproductive seasonality in an opportunistic breeder, the Red Crossbill, *Loxia curvirostra*. Ecology 79:2365-2375.

Harding, A. M., J. F. Piatt, J. E. Schmutz, M. T. Shultz, T. I. Van Pelt, A. R. Kettle, and S. G. Speckman. 2007. Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). Ecology 88:2024-2033.

Herring, G. and D. E. Gawlik. 2007. The role of stress proteins in the study of allostatic overload in birds, use and applicability to current studies in avian ecology. The Scientific World Journal 7:1596-1602.

Herring, G. and D. E. Gawlik. *In Review*. Stability of avian fecal corticosterone metabolite levels in frozen avian feces. General and Comparative Endocrinology.

Houston, A. I., J. M. McNamara, and J. M. Hutchinson. 1997. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transaction of the Royal Society of London B 341:375-397.

Kitaysky A. S., J. C. Wingfield, J. F. Piatt. 2001. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. Behavioral Ecology 12:619-625.

Kushlan, J. A. 1975. Site selection for nesting colonies of the American white ibis *Eudocimus albus* in Florida. Ibis 118:590-593.

Kushlan, J. A. 1981. Sampling characteristics of enclosure fish traps. Transactions American Fisheries Society 110:557-562

Kushlan, J. A., and K. L. Bildstein. 1992. White Ibis. *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of North America, Inc., Philadelphia, PA.

Lack, D. 1947. The significance of clutch-size. Ibis 90:24-45.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, United Kingdom.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, Oxford, UK.

Lish, J. W. 1982. Comparative eye morphology of ciconiiform birds. Dissertation, University of Oklahoma, Norman, OK.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS System for Mixed Models*. SAS Institute, Cary, North Carolina.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. Journal of Animal Science 76:1216-1231.

Martínez-Padilla, J., J. Martínez, J. A. Dávilla, S. Merino, J. Moreno, and J. Millán. 2004. Within-brood size differences, sex and parasites determine blood stress protein levels in Eurasian kestrel nestlings. Functional Ecology 18:426-434.

McCrimmon, D. A., Jr., J. C. Ogden, and G. T. Bancroft. 2001. Great egret (*Ardea alba*). *In* A. Poole and F. Gill (eds.). The Birds of North America, No. 570. The Birds of North America, Inc., Philadelphia, PA.

Mauck, R. A., and T. C. Grubb, Jr. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. Animal Behaviour 49:999-1008.

Mock, D. W. and G. A. Parker. 1997. The evolution of sibling rivalry. Oxford Series in Ecology and Evolution. Oxford University Press, New York.

Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine, and J. Blackwood. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea*. *Journal of Animal Ecology* 58:261–274.

Moreno, J., S, Merino, J. Martínez, J. J. Sanz, and E, Arriero. 2002. Heterophil/lymphocyte ratios and heat shock protein levels are related to growth of nestling birds. Ecoscience 9:434-439.

Ogden, J. C. 1994. A comparison of wading bird nesting colony dynamics (1931-1946 and 1974-1989) as an indication of ecosystem conditions in the southern Everglades. Pages 533-570 *in* S. M. Davis and J. C. Ogden (eds.). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.

Perrins, C. M. 1991. Tits and their caterpillar food supply. Ibis 133:49-54.

Ramo, C., and B. Busto. 1993. Resource use by herons in a Yucatan wetland during the breeding season. Wilson Bulletin 105:573-586.

Ricklefs, R. E. 1968. On the limitations of brood size in passerine birds by the ability of adults to nourish their young. Proceedings of the National Academy of Science. 61:847-851.

Ricklefs, R. E. 1984. The optimization of growth rate in altricial birds. Ecology 65:1602-1616.

Romero, M. L., and J. M. Reed. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comparative Biochemistry and Physiology, Part A 140:73-79.

Russell, G. J., O. L. Bass, Jr., and S. L. Pimm. 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. Animal Conservation 5:185-199.

Sæther, B. B., R. Andersen, and H. C. Pedersen. 1993. Regulation of parental effort in a long-lived seabird – an experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antartica*. Behavioral Ecology and Sociobiology 33:147-150.

Saino, N., C. Suffritti, R. Martinelli, D. Rubolini, and A. P Møller. 2003. Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). Behavioral Ecology 14:318 -325.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91: 69-93

Smith, J. P. 1997. Nesting season food habits of 4 species of herons and egrets at Lake Okeechobee, Florida. Colonial Waterbirds 20:198-220.

Stuebe, M. M., and E. D. Ketterson. 1982. A study of fasting in tree sparrows (*Spizella arborea*) and dark-eyed juncos (*Junco hyemalis*). Auk 99:299-308.

Tomás, G., J. Martínez, and S. Merino. 2004. Collection and analysis of blood samples to detect stress proteins in wild birds. Journal of Field Ornithology 75:281-278.

U. S. Geological Survey. 2006. The Everglades Depth Estimation Network (EDEN) for Support of Ecological and Biological Assessments. U. S. Department of the Interior. Fact Sheet 2006-3087.

Williams, T. D., C. G. Guglielmo, O. Egeler, and C. J. Mortyniuk. 1999. Plasma lipid metabolites provide information on mass change over several days in captive Western sandpipers. Auk 116:994-1000.

Zera, A. J., and L. G. Lawrence. 2001. The physiology of life-history trade-offs in animals. Annual Review of Ecology and Systematics 32:95-126.

Table 1. Akaike's Information Criterion (adjusted for small sample sizes; AIC_c) model selection for adult great egret and white ibis chick plasma triglycerides, plasma glycerol, plasma corticosterone, fecal corticosterone, stress proteins 60 and 70, pectoral muscle mass scores, and size structure controlled mass. Samples were collected in Water Conservation Areas 2A, 3A, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge between 10 Jan – 23 Mar in both 2006 and 2007. Models presented only include those that were within 5 AIC_c values of the top model ($\Delta i = 0$) except in the case of the Global and Intercept models.

Great Egret Chick Model	K	AIC_c	Δi	ω_i
GLYC				
Age class	3	288.5	0	0.75
Year + age class	4	291.1	2.6	0.20
Intercept	1	305.3	16.8	0.00
Global	11	321.5	33.0	0.00
TRIG				
Age class	2	463.5	0	0.39
Year + age class	4	464.5	1.0	0.23
Year + age class + Order	5	465.5	2.0	0.14
Intercept	1	469.5	6.0	0.01
Global	11	481.5	18.0	0.00
PCORT				
Year + Age class + Order + Region	6	793.4	0.0	0.29
Year + Age class + Order + Region + Biomass 1	7	794.0	0.6	0.21

Year + Age class + Order	5	794.2	0.8	0.19
Year + Age class	4	794.7	1.3	0.15
Year + Age class + Order + Region + Biomass 1 + Biomass 2	8	796.8	3.4	0.04
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1	9	797.2	3.8	0.01
Global	11	802.1	8.7	0.00
Intercept	1	834.2	40.8	0.00
FCORT				
Year + Age class + Order	5	908.1	0.00	0.43
Year + Age class + Order + Region	6	908.7	0.7	0.30
Year + Age class + Order + Region + Biomass1	7	910.6	2.5	0.12
Year + Age class	4	912.1	4.0	0.05
Year + Age class + Order + Region + Biomass1 + Biomass2	8	912.9	4.8	0.03
Intercept	1	305.3	16.8	0.00
Global	11	315.5	27.0	0.00
SP60				
Global	11	1280.0	0.0	0.91
Intercept	1	1402.0	127.9	0.00
SP70				
Age class	3	413.7	0.00	0.61
Year + Age class	4	415.4	1.7	0.26
Year + Age class + Order	5	417.4	3.7	0.09
Intercept	1	428.3	14.6	0.00
Global	11	434.9	25.3	0.00
Mass				
Year + Age class + Order + Region	6	253.1	0.00	0.55

Year + Age class + Order	5	253.6	0.50	0.43
Global	11	310.9	57.8	0.00
Intercept	1	965.6	712.5	0.00

PEC

Year + Age class + Order + Region + Biomass 1 + Biomass 2	8	586.9	0.00	0.80
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1	9	591.1	4.2	0.09
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1^2	9	591.4	4.5	0.08
Global	11	616.6	29.7	0.00
Intercept	1	788.7	201.8	0.00

White Ibis Chick Model	K	AIC$_c$	Δi	ω_i
GLYC				
Year + Age class + Order	5	105.1	0	0.42
Year + Age class + Order + Region	6	106.3	1.2	0.23
Year + Age class	4	107.5	2.4	0.12
Age class	3	108.3	3.2	0.08
Year	3	108.7	3.6	0.07
Intercept	1	111.8	6.7	0.01
Global	11	129.4	24.3	0.00
TRIG				
Year + Age class + Order + Region	6	194.5	0.00	0.55
Year + Age class + Order + Region + Biomass 1	7	195.3	0.8	0.37
Global	11	204.7	10.2	0.00
Intercept	1	235.7	41.2	0.00
PCORT				
Global	11	398.7	0.0	0.60
Year + Age class + Order + Region + Biomass 1	7	399.4	0.7	0.42
Year + Age class + Order + Region + Biomass 1 + Biomass 2 +Recess1^2	8	401.7	3.0	0.13
Year + Age class + Order + Region + Biomass 1 + Biomass 2	8	401.8	3.1	0.12
Year + Age class + Order + Region	6	403.1	4.4	0.06
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1^2 + Recess 2^2	10	403.2	4.5	0.06
Year + Age class + Order + Region + Biomass 1 + Recess 1	8	403.4	4.7	0.05
Year + Age class + Order + Region + Biomass 1	9	403.7	4.7	0.05

Recess 1 + Recess 2

Year + Age class + Order	5	404.4	5.0	0.03
Intercept	1	436.5	37.1	0.00

FCORT

Year + Age class + Order + Region + Biomass 1	7	535.8	0.00	0.70
Year + Age class + Order + Region	6	539.6	3.8	0.10
Year + Age class + Order	5	540.6	4.8	0.06
Global	11	555.2	19.4	0.00
Intercept	1	605.9	70.1	0.00

SP60

Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1^2 + Recess 2^2	10	437.1	0.0	0.54
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1 + Recess 2	10	438.2	1.1	0.31
Global	11	441.1	4.0	0.07
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1	9	442.1	5.0	0.04
Intercept	1	560.4	132.3	0.00

SP70

Year + Age class + Order + Region	6	166.6	0.00	0.49
Year + Age class + Order	5	167.2	0.6	0.36
Year + Age class + Order + Region + Biomass 1	7	171.1	4.5	0.05
Global	11	176.9	9.9	0.00
Intercept	1	188.0	21.4	0.00

Mass

Year + Age class + Order	5	161.2	0.00	0.85
Year + Age class + Order + Region	6	165.0	3.8	0.12
Global	11	187.6	26.4	0.00

Intercept	1	406.6	245.4	0.00

PEC

Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1	9	314.6	0	0.82
Year + Age class + Order + Region + Biomass 1 + Biomass 2 + Recess 1 + Recess 2	10	317.8	3.2	0.16
Global	11	328.9	14.3	0.00
Intercept	1	385.0	70.4	0.00

Table 2. Parameter likelihoods and weighted parameters estimates ± unconditional standard error (SE) from general linear mixed models evaluating the response of white ibis and great egret chick plasma triglycerides, plasma glycerol, plasma corticosterone, fecal corticosterone, stress proteins 60 and 70, pectoral muscle mass scores, and size structure controlled mass. Explanatory variables with the greatest relative support have parameter likelihoods close to 1.0.

MODEL	Explanatory variable	Parameter likelihood	Parameter estimate	± SE
Great Egret				
GLYC	Chick age	0.99	-0.048	0.565
	Year	0.24	-0.001	0.109
TRIG	Year	0.96	0.049	0.118
	Chick age	0.96	-0.029	0.485
	Hatch order	0.32	-0.103	0.188
PCORT	Year	0.95	-0.366	0.146
	Chick age	0.96	0.010	0.017
	Hatch order	0.86	0.229	0.289
	Region	0.51	-0.221	0.448
FCORT	Year	1.0	-1.764	0.160
	Chick age	0.98	-0.518	0.423
	Hatch order	0.92	0.439	0.228
	Region	0.51	-0.131	0.167
SP60	No candidate models were parsimonious			
SP70	Chick age	0.99	1.990	0.862
	Year	0.38	0.004	0.160

Mass	Year	0.99	0.019	0.045
	Chick age	0.99	-1.109	0.205
	Hatch order	0.99	0.279	0.053
	Region	0.56	0.005	0.193
PEC	Year	1.0	-0.061	0.058
	Chick age	1.0	0.037	0.003
	Hatch order	1.0	-0.162	0.059
	Region	0.99	0.011	0.109
	Biomass 1	0.99	0.014	0.004
	Biomass 2	0.99	0.021	0.004
White Ibis				
GLYC	Year	0.89	-0.049	0.565
	Chick age	0.88	-0.029	0.485
	Hatch order	0.66	-0.103	0.188
	Region	0.27	-0.121	0.088
TRIG	Year	0.99	-0.014	0.209
	Chick age	0.99	0.227	0.822
	Hatch order	0.99	-0.179	0.262
	Region	0.99	-0.122	0.199
	Biomass 1	0.44	0.005	0.009
PCORT	Year	0.84	-0.408	0.213
	Chick age	0.84	-0.006	0.031
	Hatch order	0.84	-0.106	0.529
	Region	0.84	0.298	0.423
FCORT	Year	1.0	-1.695	1.217
	Chick age	1.0	-0.524	1.653
	Hatch order	0.97	0.458	0.228

	Region	0.90	-0.116	0.176
	Biomass 1	0.80	-0.004	0.011
SP60	Year	0.97	3.724	5.534
	Chick age	0.97	-0.627	0.371
	Hatch order	0.97	-5.283	11.343
	Region	0.97	-4.705	5.724
	Biomass 1	0.97	-0.160	0.535
	Biomass 2	0.97	-0.592	0.627
	Recess 1	0.97	0.812	2.494
	Recess 2	0.85	-2.894	2.972
SP70	Year	0.97	0.006	0.180
	Chick age	0.99	2.034	0.858
	Hatch order	0.97	-0.065	0.294
	Region	0.60	0.005	0.193
Mass	Year	1.0	0.023	0.046
	Chick age	1.0	-1.232	0.314
	Hatch order	1.0	0.262	0.053
PEC	Year	0.98	-0.156	0.121
	Chick age	0.98	0.019	0.007
	Hatch order	0.98	-0.329	0.105
	Region	0.98	-0.264	0.114
	Biomass 1	0.98	0.046	0.013
	Biomass 2	0.98	0.048	0.014

Table 3. Response of great egret and white ibis chick physiological metrics to changing prey availability (Food Limitation Hypothesis) and landscape factors that influence prey availability. Symbols indicate associated physiological responses to a decrease in prey densities, positive (+) or negative (-) of great egret and white ibis chicks for plasma triglycerides, plasma glycerol, plasma corticosterone, fecal corticosterone, stress proteins 60 and 70, pectoral muscle mass scores, and size structure controlled mass.

Food Limitation Hypothesis

	GLYC	TRIG	PCORT	FCORT	SP60	SP70	MASS	PEC
GREG								
Prey biomass								
WHIB								
Prey biomass		-		+	+			-

Landscape Factors Influencing Food Limitation Hypothesis

	GLYC	TRIG	PCORT	FCORT	SP60	SP70	MASS	PEC
GREG								
Recess								
WHIB								
Recess				+				
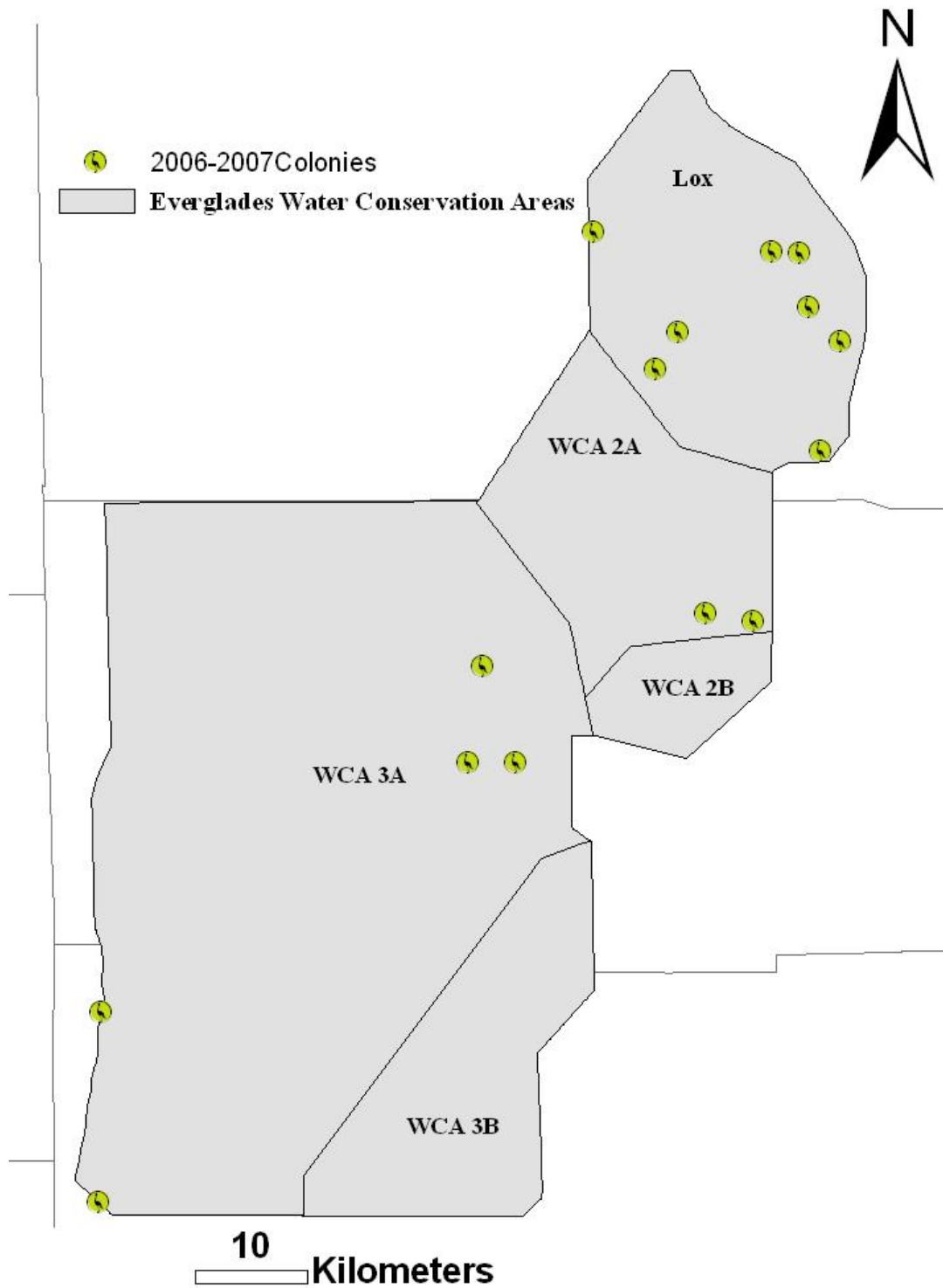
Figure 1. Wading bird colonies in Arthur R. Marshall Loxahatchee National Wildlife

Refuge (Lox), Water Conservation Area 2A (WCA 2A), 2B (WCA 2B), 3A (WCA 3A),

and 3 B (WCA 3B) that were included in this study during 2006 – 2007.
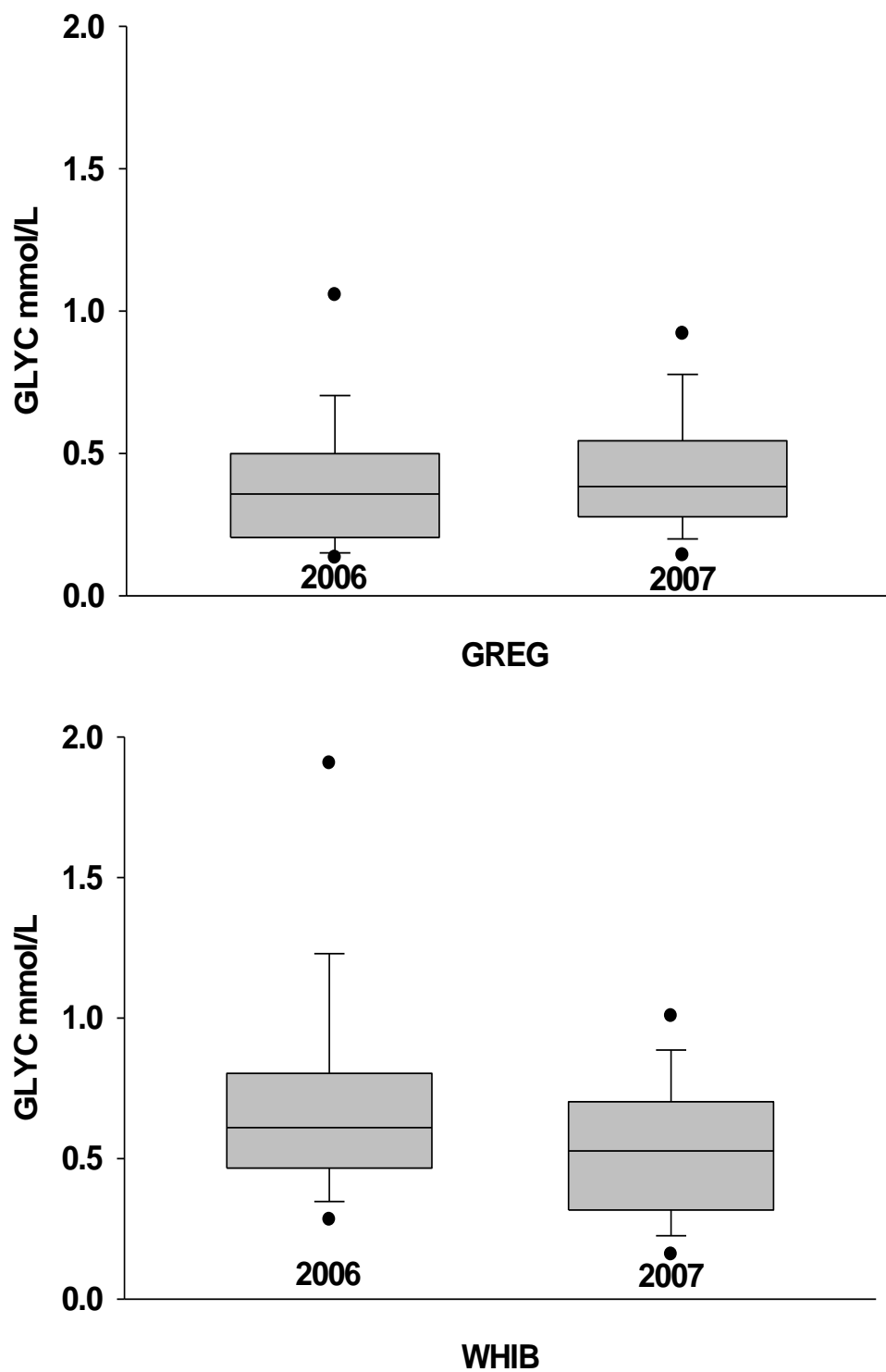
Figure 2-3. Great egret and white ibis chick GLYC levels during the 2006-2007 breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water
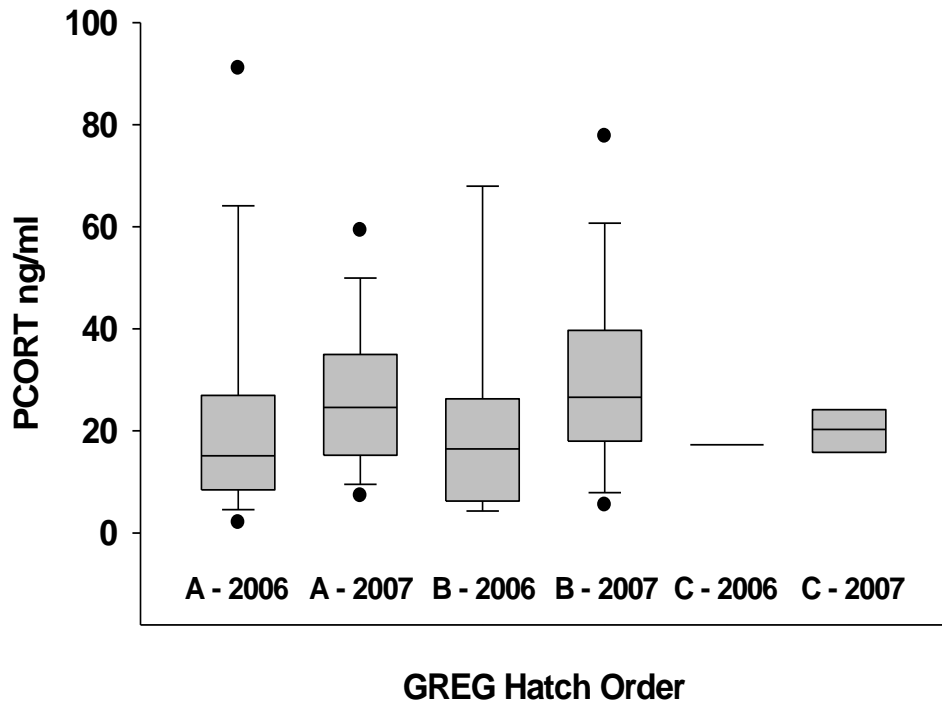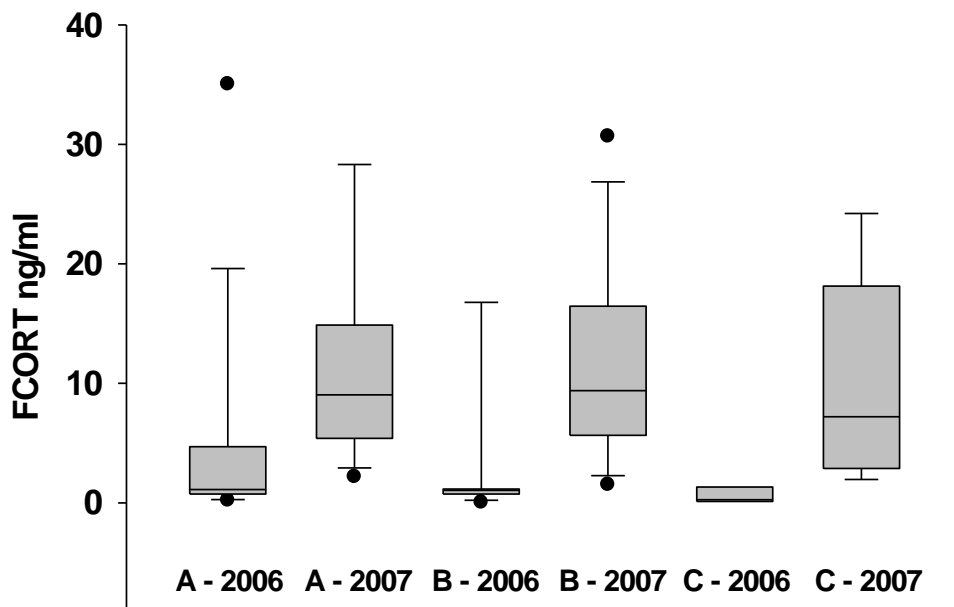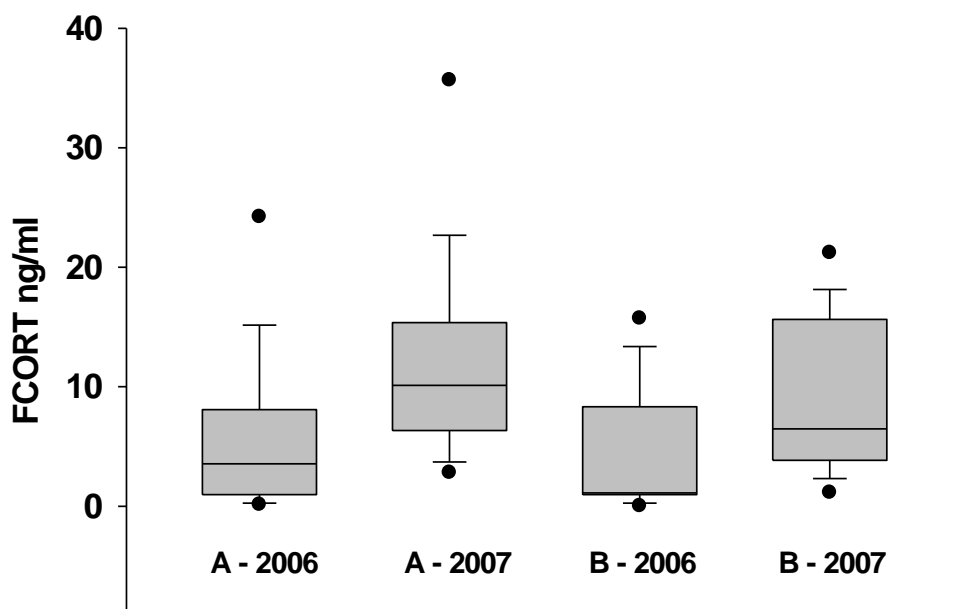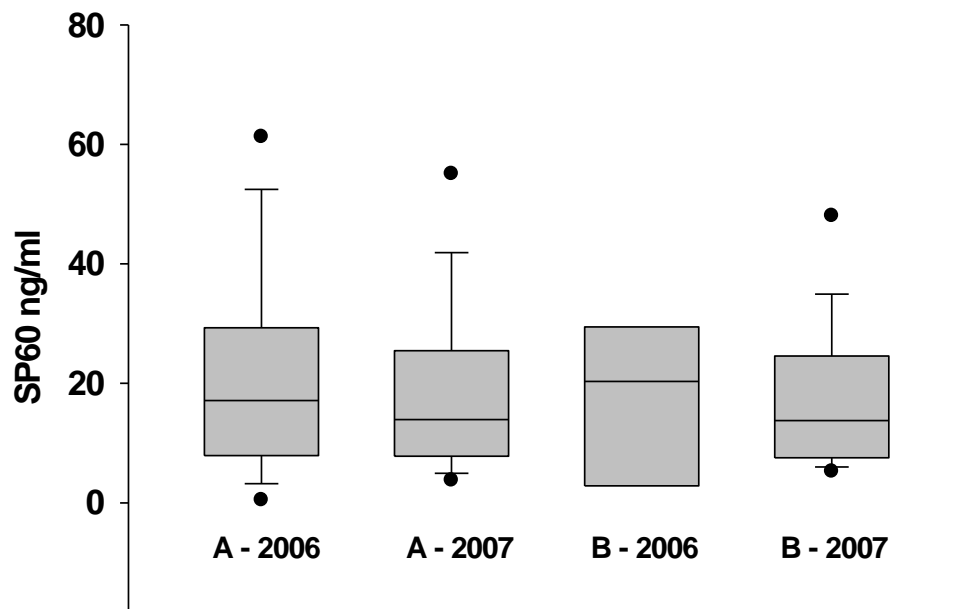
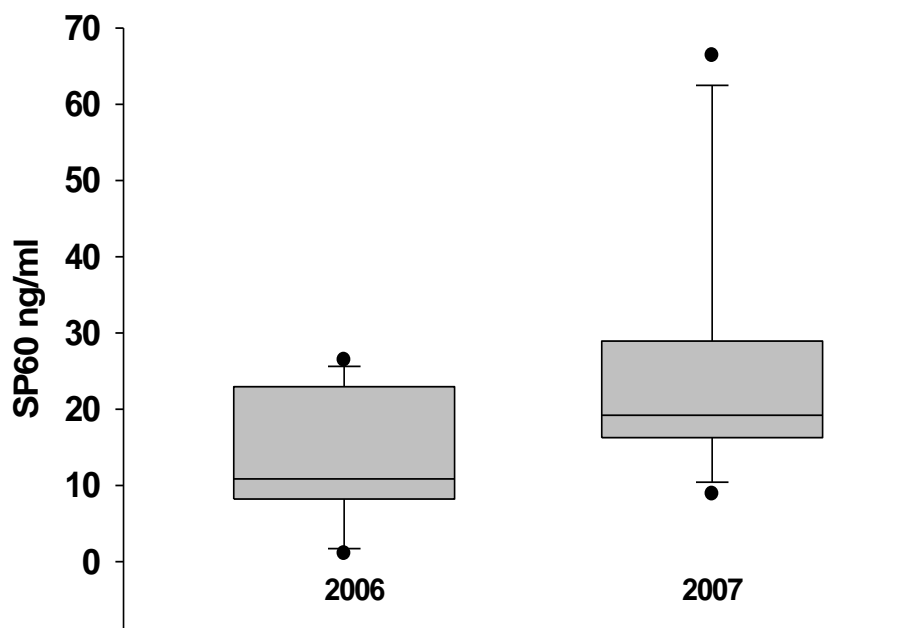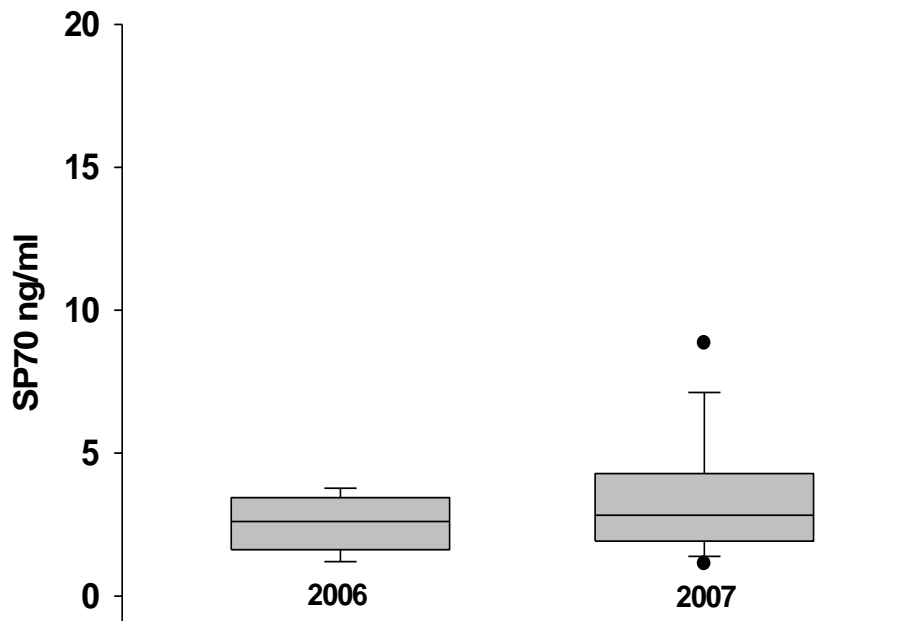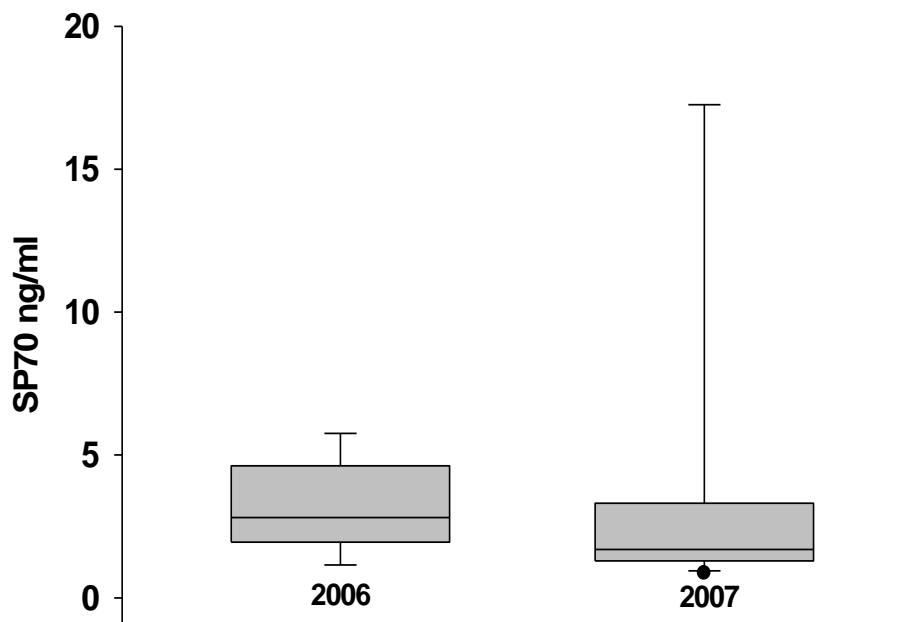Conservation Area 2A, and 3A of the Florida Everglades.
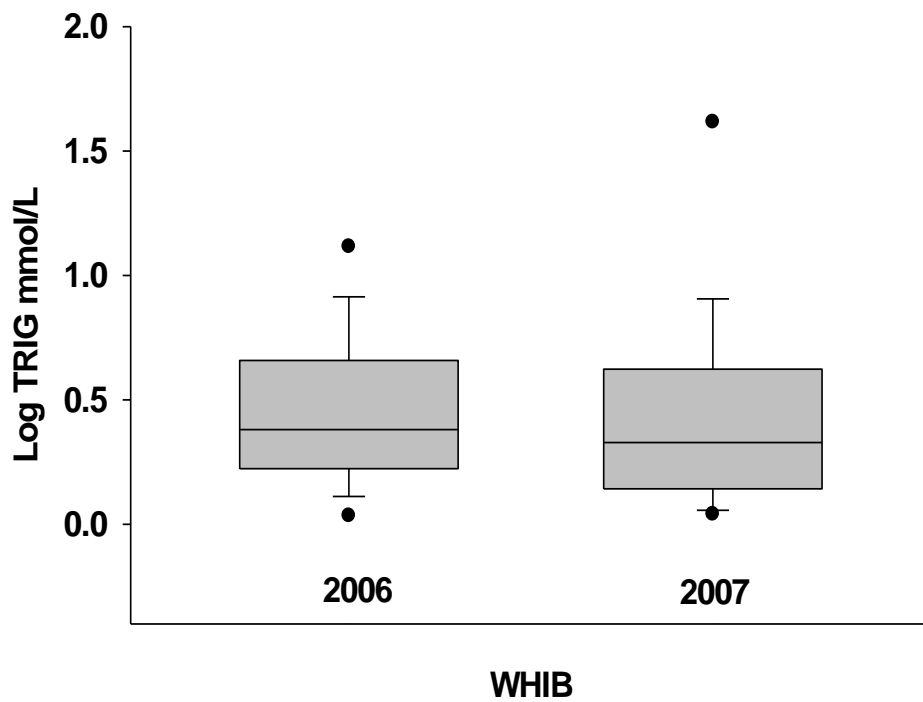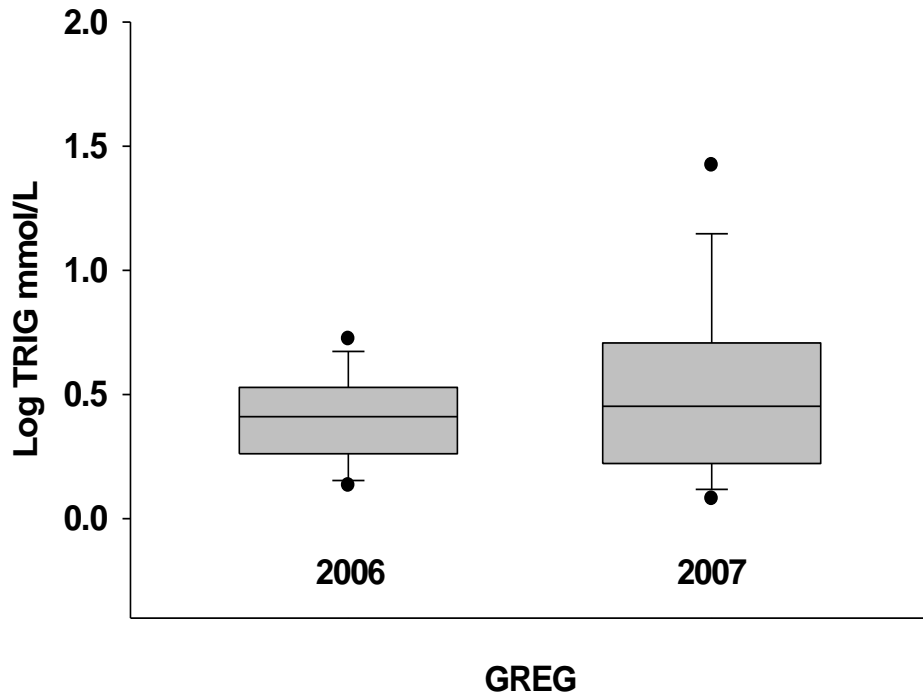
Figure 4-5. Great egret and white ibis chick TRIG levels during the 2006-2007 breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

Conservation Area 2A, and 3A of the Florida Everglades.
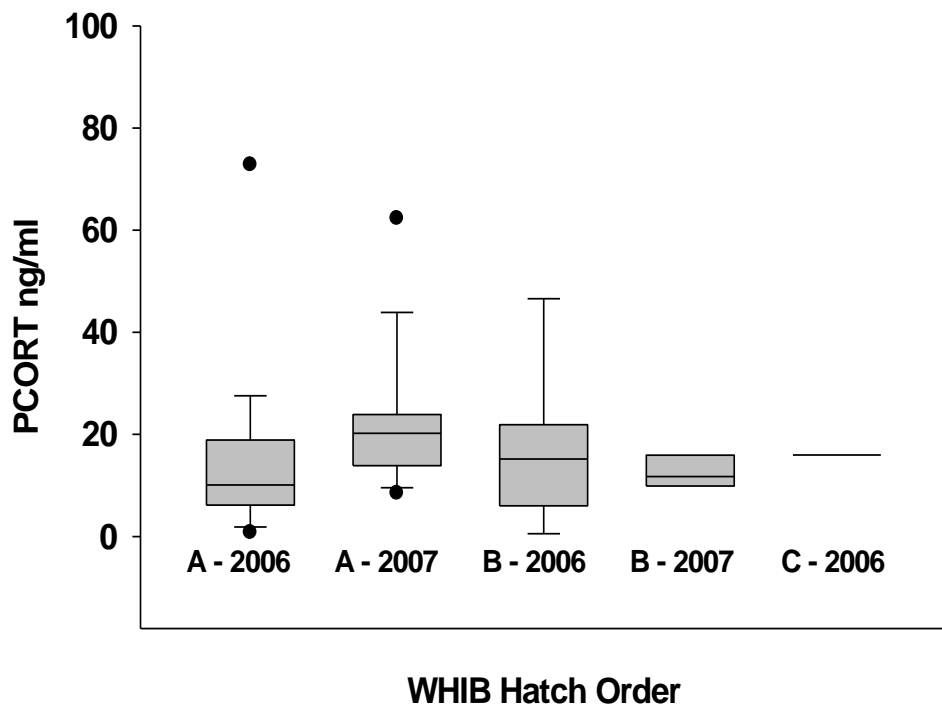
Figure 6-7. Great egret and white ibis chick PCORT levels during the 2006-2007

breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

Conservation Area 2A, and 3A of the Florida Everglades.

Figure 8-9. Great egret and white ibis chick FCORT metabolite levels during the 2006-2007 breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.
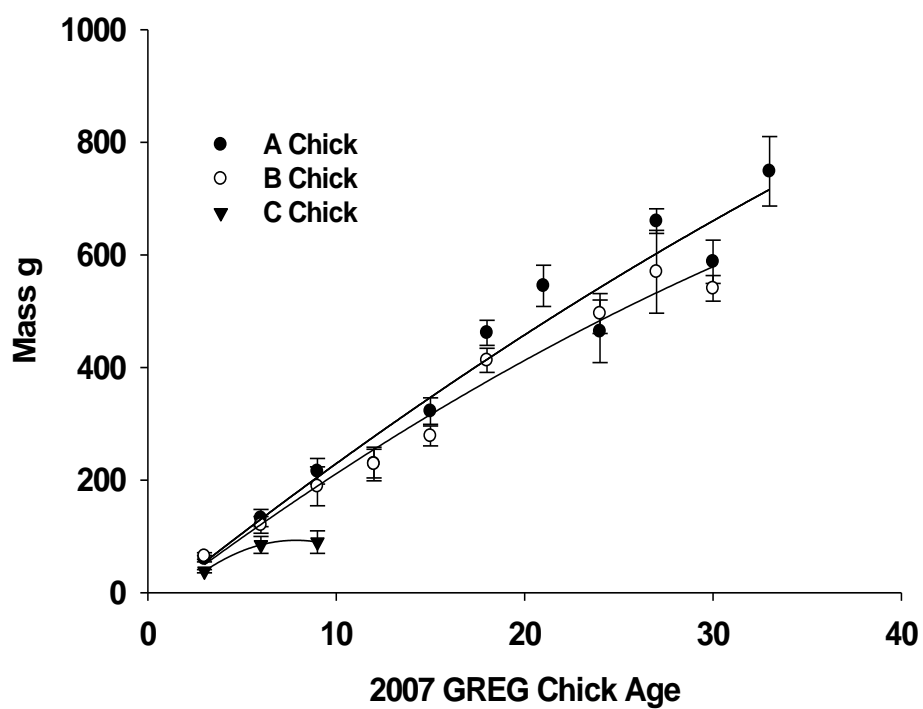
Figure 10-11. Great egret and white ibis chick SP60 levels during the 2006-2007 breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.

Figure 12-13. Great egret and white ibis chick SP70 levels during the 2006-2007 breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.
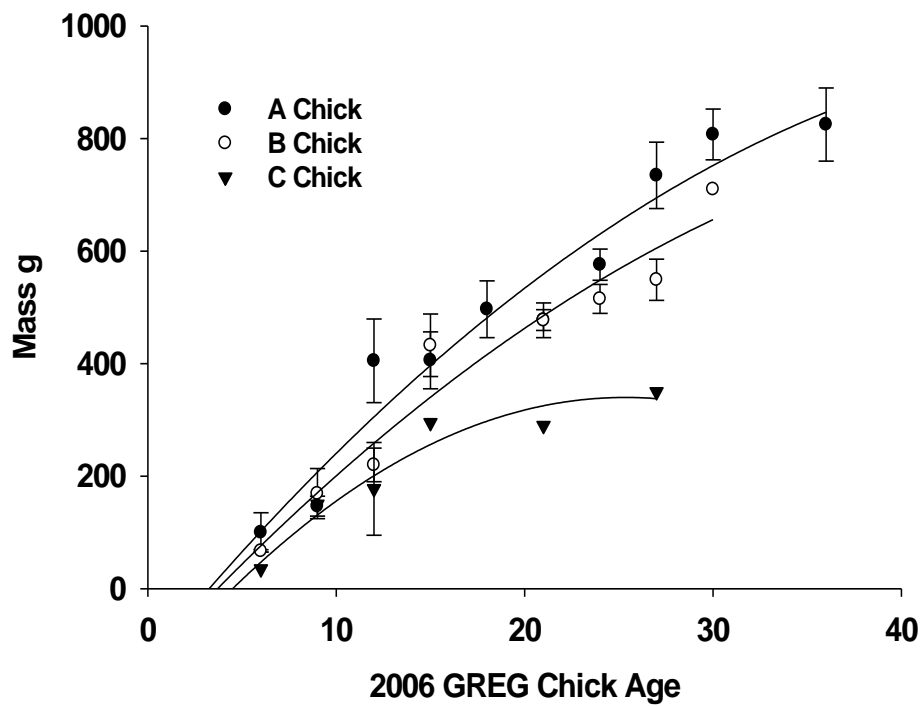
Figure 14-15. Mass growth rates for great egret chicks during the 2006-2007 breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

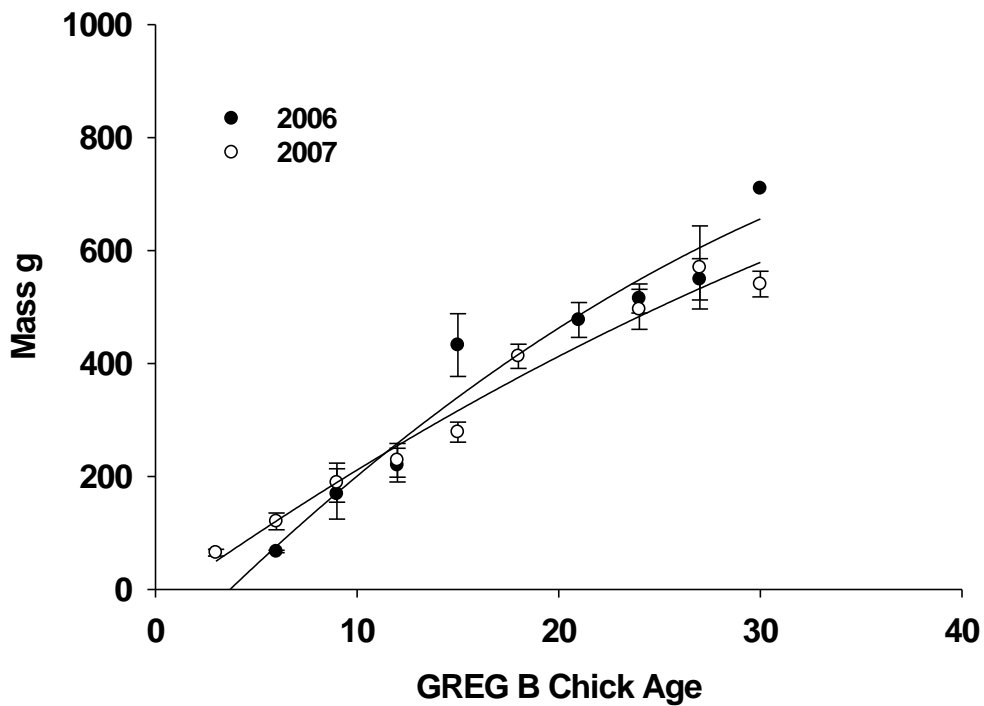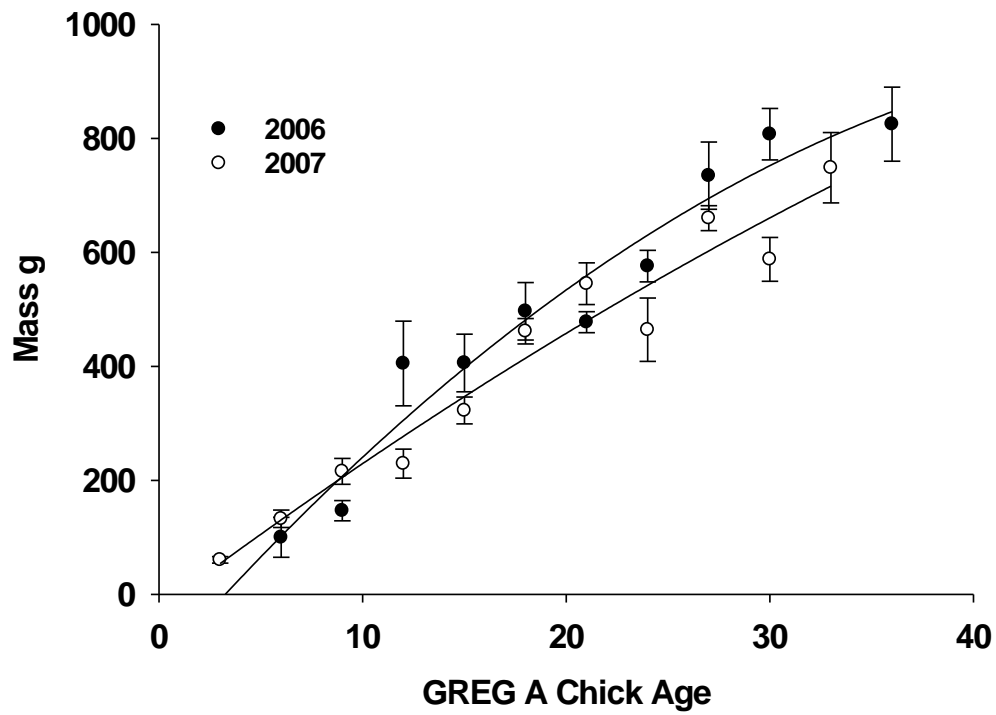Conservation Area 2A, and 3A of the Florida Everglades.

Figure 16-17. Mass growth rates for A and B-hatched great egret chicks by year during

the 2006-2007 breeding period in the Arthur R. Marshall Loxahatchee National Wildlife

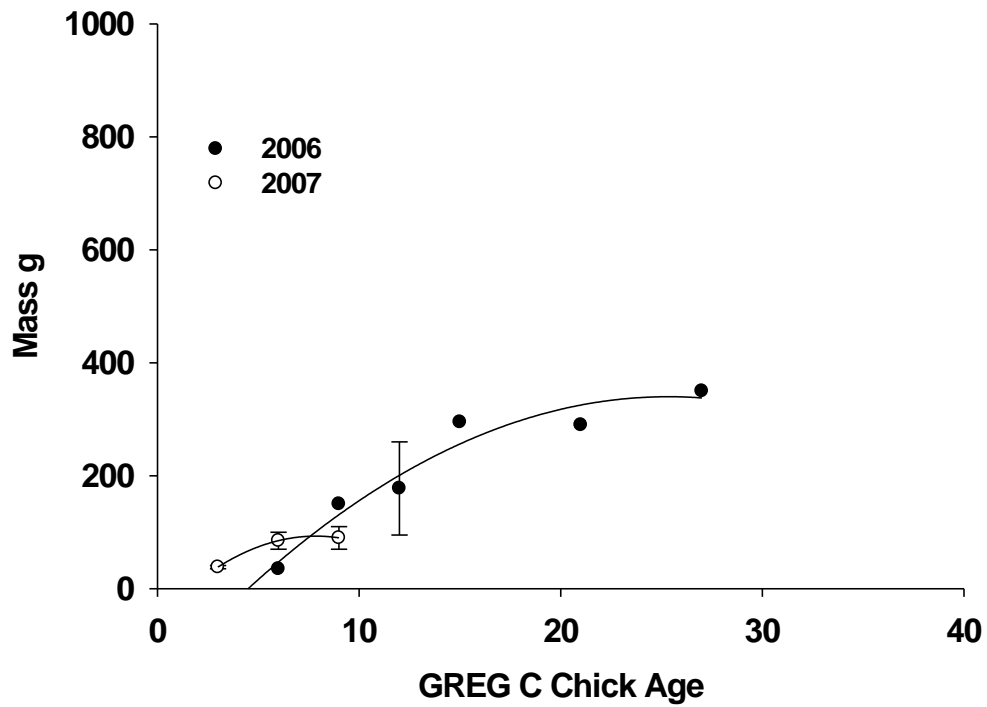Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.

Figure 18. Mass growth rates for C-hatched great egret chicks by year during the 2006-2007 breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.
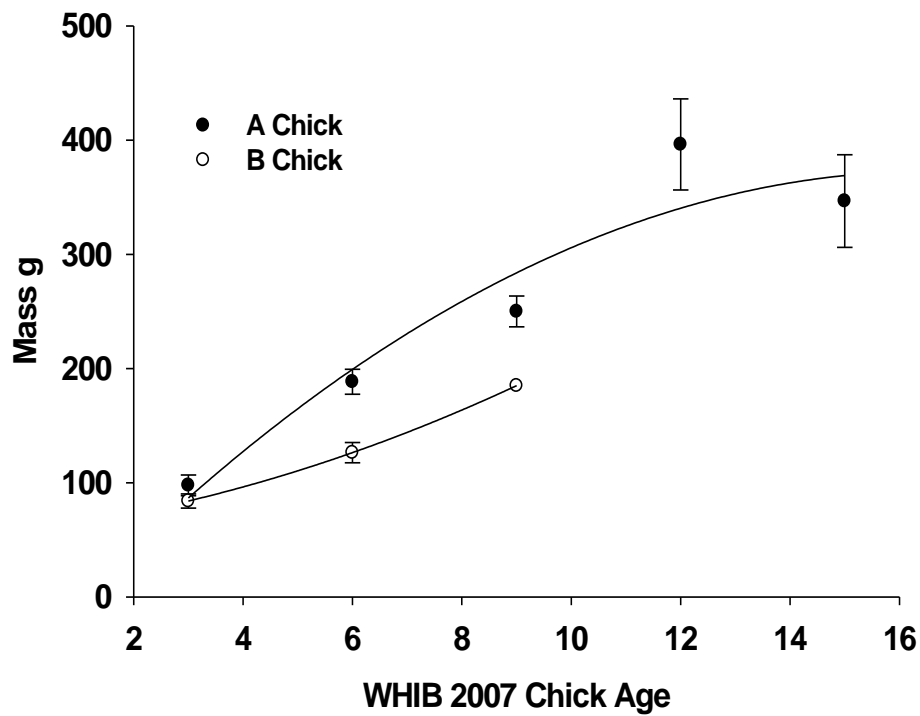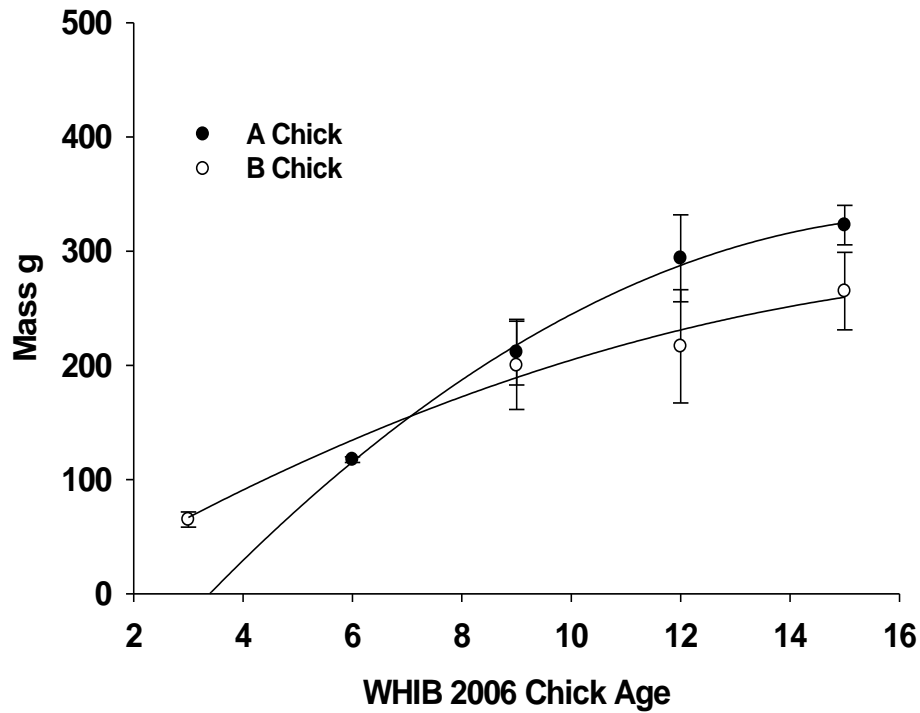
Figure 19-20. Mass growth rates for white ibis chicks during the 2006-2007 breeding

period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water

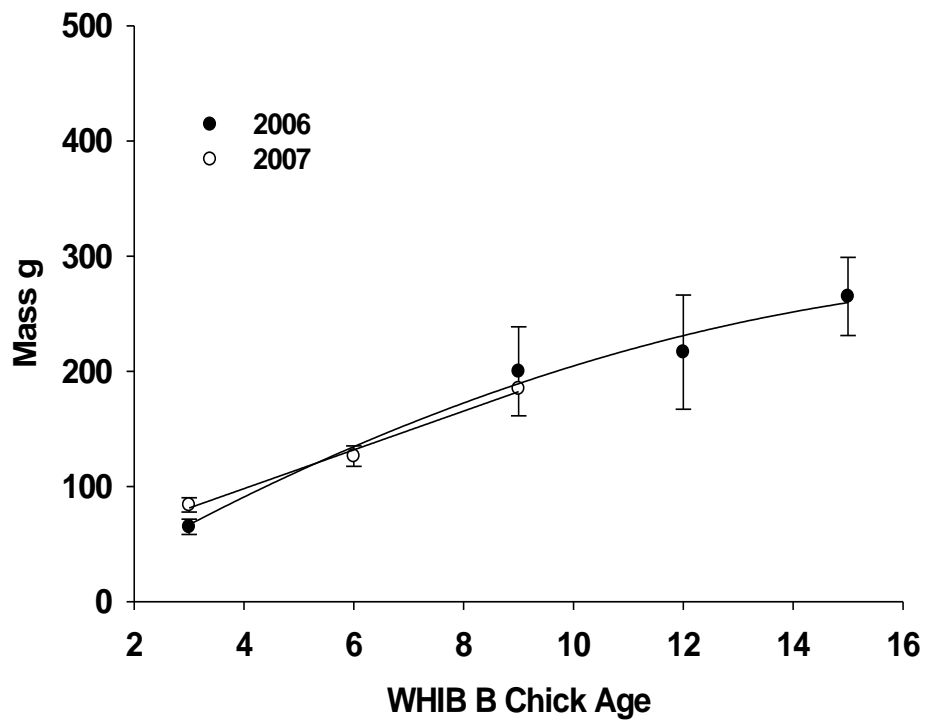Conservation Area 2A, and 3A of the Florida Everglades.

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Figure 21-22. Mass growth rates for A and B-hatched white ibis chicks by year during the

2006-2007 breeding period in the Arthur R. Marshall Loxahatchee National Wildlife

Refuge, Water Conservation Area 2A, and 3A of the Florida Everglades.

Figure 23-24. PEC scores for great egret and white ibis chicks during the 2006-2007
breeding period in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Water
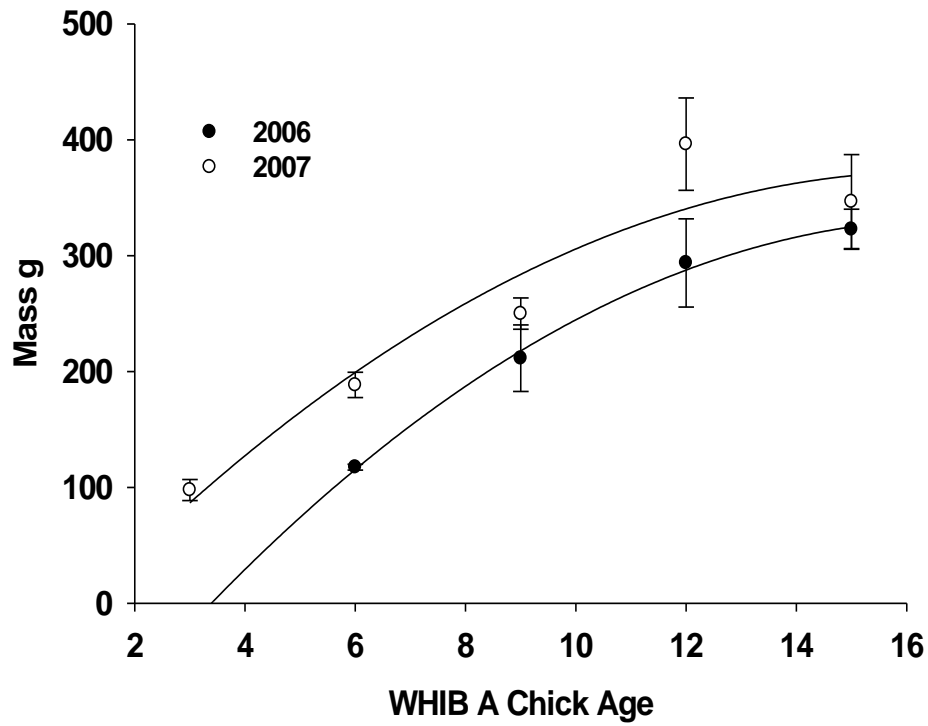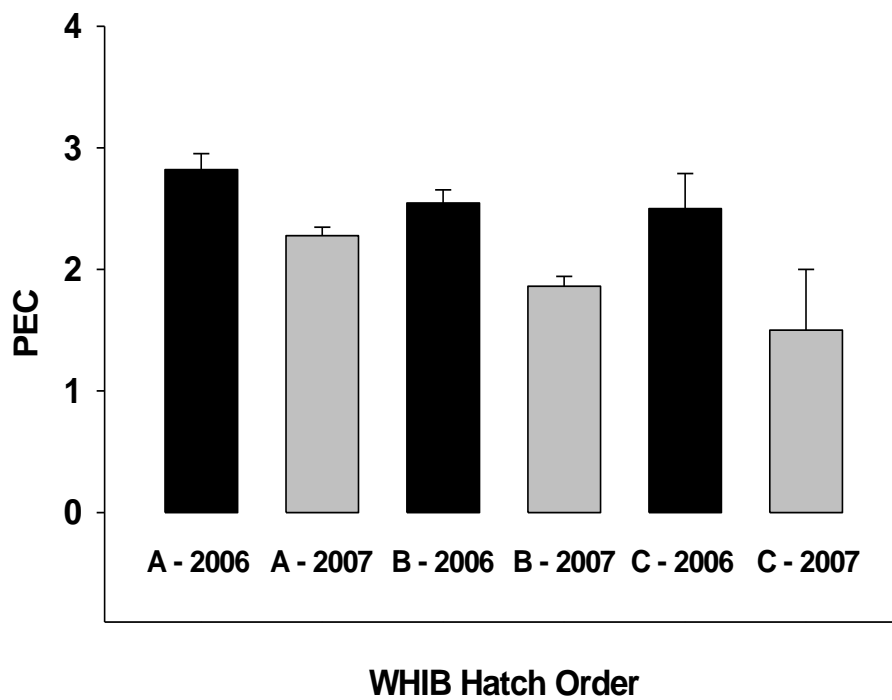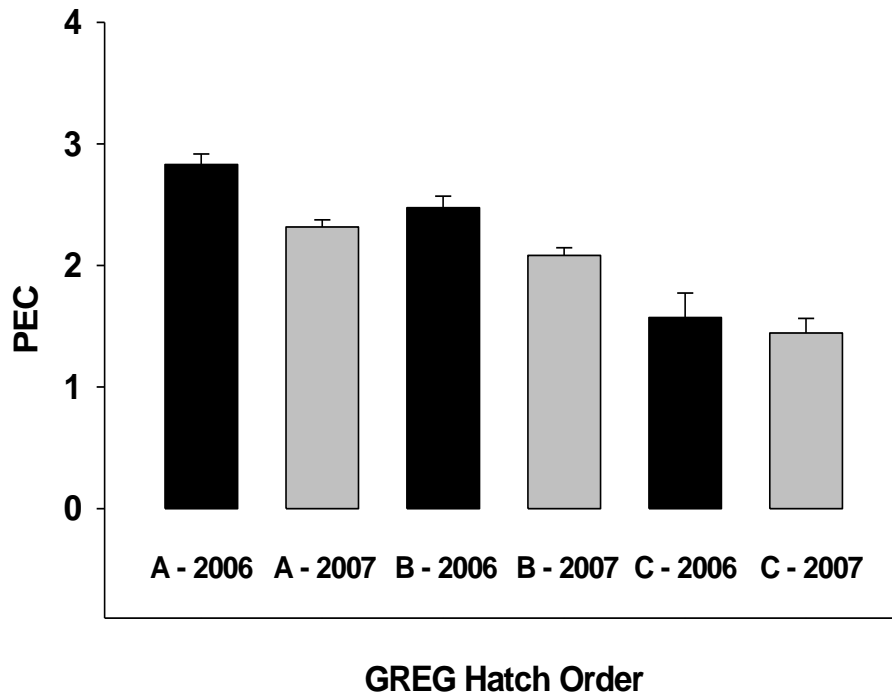Conservation Area 2A, and 3A of the Florida Everglades.

CHAPTER 8. SYNTHESIS

Food Limitation Hypothesis and Corresponding Physiological Responses

One of the key conceptual models underlying Everglades restoration is that hydrologic changes affect prey availability and wading bird nesting. However, the mechanism by which prey availability affects wading birds and produces species-specific nesting patterns has not been identified. This study is the first to make the link between landscape hydrology patterns, prey availability, and wading bird nesting effort and success. These linkages provide critical insight into how species' nesting patterns might differ given the same environmental conditions and how this relates to long-term nesting trends.

Experimental food supplementation research demonstrated that in years with high prey densities physiological condition of white ibis chicks were similar between control and provisioned treatments (Chapter 4). In contrast, 2007 was a year with considerably less prey available in the landscape and control chicks had significantly higher levels of stress protein 60 and fecal corticosterone, confirming that white ibis are a food-limited species. Stress protein 60 and fecal corticosterone both reflected varying levels of prey availability and therefore may be good measures of the physiological response of wild wading birds in the future.

This was the first study to identify a pathway by which food in the Everglades can lead to effects on wading bird reproduction via physiology (Chapter 4). Demonstrating food limitation in white ibis chicks is critical because this species has experienced a long-term decline in nesting numbers in the Everglades (Crozier and Gawlik 2003). While not all wading birds have show long-term declines in nesting trends similar to white ibis, there are several species (e.g., snowy egret, wood stork [*Mycteria americana*]) that have demonstrated similar nesting trends (Crozier and Gawlik 2003). One important similarity between these species that have demonstrated long-term declines in nest effort is that they are all searcher foraging species (Gawlik 2002). Searcher species locate high quality patches, forage at that site until the patch declines to a critical level of food density, the giving up density, at which point the species will move on and search for a more profitable patch (Gawlik 2002). Further food provisioning research may determine if other searchers species are also food limited and if they respond similarly to years with poor prey availability as white ibis.

Pre-breeding adult physiology research suggested that in a year with high prey densities both great egrets and white ibises were in good physiological condition (low levels of stress proteins and fecal corticosterone; Chapter 5). During a year with poor habitat conditions, (2007), ibis physiological condition declined compared to 2006; stress protein 60 and fecal corticosterone were higher during the 2007 pre-breeding period in ibis. However, great egret stress levels remained stable between the two years.

During the below average food year, male egrets and ibises had higher masses than during 2006. Counterintuitive to what landscape level prey availability might suggest, this result fits with foraging theory (see McNamara and Houston 1987, Anholt

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and Werner 1998) and recent experimental research. During poor years, birds prepare for low food availability (see Gosler et al. 1995, Rogers and Reed 2003), unpredictable food (see Pravosudov and Grubb 1997, Cuthill et al. 2000) by increasing mass, or lipid reserves. During good years, both male and female great egrets and white ibises may not need to maximize their physiological condition leading up to breeding, to successfully fledge multiple chicks and increase their long-term fitness because prey availability is high and predictable (McNamara and Houston 1987, Anholt and Werner 1998).

This strategy would be suited to the Everglades ecosystem in its natural state, when short hydroperiod wetlands were abundant, increasing predictability of locating food. These wetlands would have been well matched to a strategy of acquiring food on a regular basis and not increasing reserve levels in preparation for breeding, this response assumes those high quality patches were more common and predictable in the Everglades than they are now (Gawlik 2002). Females had similar or slightly lower masses to 2006 and likely fueled their energy demands on a daily basis. The advantage might be that females may not have to expend as much energy acquiring large amounts of prey when food may be less predictable, instead reserving nutrient reserves for egg production and nesting. Ultimately, this strategy might benefit females because if the nesting season fails, the long-term female costs are reduced, increasing the likelihood of potential future reproductive success for this long-lived species (Drent and Daan 1980).

Nesting results suggest that white ibises modify their clutch size during years with poor habitat conditions in accordance with the life history traits of a long-lived species, whereas great egrets maintained similar clutch sizes during years with poor and good habitat conditions (Chapter 6). The strategy of the great egret is advantageous in years

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with poor habitat if birds are more likely to experience brood reduction rather than total nest failure, or if habitat conditions improve rapidly during the nesting period, allowing for the third egg to hatch and or chick to fledge (Bet Hedging). This bet hedging approach appears to allow great egrets to produce successful nests in poor years and may maximize their reproductive efforts during average to above average years. The strategy of white ibises favors a searcher foraging strategy for wading birds with short legs. These species have less ability to withstand change in hydrological conditions (e.g., depth) and require more numerous high quality foraging patches. Poor prey availability may be a cue for this species to lower its clutch size in preparation for increased costs of locating suitable high quality foraging patches to provision chicks.

This study determined that pre-breeding female ibis had higher levels of circulating corticosterone and fecal corticosterone metabolites during 2007, the year with lower daily survival rates for nests and lower nest success (Chapter 5). I propose that elevated levels of corticosterone may have played an active role in lower white ibis nest success. However, elevated levels of corticosterone in female ibis may not be the ultimate cause of lower nest success, rather just one aspect within a suite of factors that ultimately influenced white ibis nest success during 2007. Future research might examine the relationship between maternal corticosterone levels and those in their eggs to understand how stress associated with landscape habitat conditions might influence nesting in white ibis and possible differences with exploiter species like great egrets.

Corresponding chick physiology results found white ibis chicks to be in poorer physiological condition in 2007 than in 2006 based on measures of long-term stress (SP60) and growth rates (mass). Great egret chicks, however, had increased levels of

fecal corticosterone but no response in the growth rates (mass) of A and B-hatched chicks during the poor year with lower prey biomass. Great egrets were also more likely to have hatched a third chick and provisioned that C-hatched chick for at least 8-10 days before it failed during the below average year. While both great egret chicks and white ibis chicks were influenced by year and the age of chicks, only white ibis chick physiology was influenced by both 1 and 2 week recession rate estimates, and both estimates of the CV for 1 and 2 weeks prior to estimates of chick physiological condition.

Taken as a whole, this study demonstrated the significant effects of landscape level prey availability and the habitat variables that influence prey availability on pre-breeding physiological condition of great egrets and white ibises and their reproductive responses. The differential responses of the two species suggest that food availability has played an important role in the long-term nesting trends of both species, with ibis responding more acutely to lower prey availability. Results from adult, chicks, and nest survival supported the Prey Availability Hypothesis (Gawlik 2002), that both density and factors that make prey vulnerable to predation (e.g., recession rates, hydrological reversals) are important during all stages of the reproduction. Physiologically, the responses of both adult and chicks for the two species appear to match expectations given nesting trends. Great egrets tended to be more robust, responding less to variation in hydrological conditions during the breeding season, correspondingly, white ibis responded more acutely to those changes, with decreased physiological condition, smaller clutches, and slower growth rates during the year with low prey availability.

Everglades Management Recommendations

The differences between the responses of these two species suggest that they may not respond similarly to management and restoration of the Everglades. One way in which these species may respond differently is when water managers make short-term management/operation decisions that result in increases in water depths and decreases in recession rates. These changes may produce earlier, and larger responses (e.g., nest failure) in white ibis, given the decreases in daily nest survival associated with increasing coefficient of variation of recession rates (hydrological reversals). Results suggest that water depth increases that slow recession rates enough so that prey species are not concentrated may be enough to disrupt the nesting cycle and that water depths do not have to go as deep as to preclude foraging to cause nest failure. Results also demonstrated that this response is apparent in adult and chick physiology as well as nest survival. While the apparent solution to these issues would seem to be simply to avoid increasing water levels in regions that active nesting or wading birds are currently foraging in, predicting the sequence of drying down and concentration of prey in adjacent wetlands areas may be equally important to maintaining the viability of those colonies.

The primary objective of the Comprehensive Everglades Restoration Plan (CERP) is to restore the hydrological conditions within the Everglades to mimic those of the pre-impoundment natural ecosystem (Sklar et al. 2005). Critical to the restoration of the Everglades are the response of indicators species, like wading birds, to those restoration changes. This study suggests that if the hydrological conditions can be changed, such that they are more similar between regions, and then function similarly between regions throughout the wading bird breeding season (e.g., similar recession rates), then we can

expect species like white ibis to respond positively. Such conditions could be expected to bring about more consistent and successful nesting patterns between regions, with less dramatic responses during poor years if water levels are allowed to disperse across larger areas after rainfall events, rather than rising sharply as in the current situation.

Given great egrets responded less acutely to changing hydrological conditions during this study, restoring hydrological conditions across the Everglades should not be expected to produce as large of a response in nesting patterns for egrets, as would be expected in white ibises. This should not be confused with saying great egrets will not respond favorably to restoring hydrological conditions in the Everglades, just that they may not increase their nesting populations in parallel to white ibis because they are already more stable.

LITERATURE CITED

Anholt, B. R., and E. E. Werner. 1998. Predictable changes in predation mortality as a consequence of changes if food availability and predation risk. Evolutionary Ecology 12:729-738.

Crozier, G. E., and D. E. Gawlik. 2003. Wading bird nesting effort as an index of wetland ecosystem integrity. Waterbirds 26:303-324.

Cuthill, I. C., S. A. Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. Behavioral Ecology 11:189-195.

Drent, R. H., and S, Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329-346.

Gosler, A. G., J. J. Greenwood, and C. Perrins. 1995. Predation risk and the cost of being fat. Nature 337:621-623.

McNamara, J. M., and A. I. Houston. 1987. Starvation and predation as factors limiting population size. Ecology 68:1515-1519.

Pravosudov, V. V., and T. C. Grubb, Jr. 1997. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. Behavioral Ecology 8:332-339.

Rogers, C. M., and A. K. Reed. 2003. Does avian winter fat storage integrate

    temperature and resource conditions? A long-term study. Journal of Avian

    Biology 34:112-118.

Sklar, F. H., M. J. Chimney, S. Newman, P. McCormick, D. Gawlik, S. Miao,

    C.,McVoy, W. Said, J. Newman, C. Coronado, G. Crozier, M. Korvela, and K.

    Rutchey. 2005. The ecological-societal underpinnings of Everglades restoration.

    Frontiers in Ecology and the Environment 3:161-169.