

MORPHOLOGIC, BEHAVIORAL AND ENERGETIC  
ASPECTS OF REPRODUCTION AND SEXUAL SELECTION  
IN COLONIAL IBISES, *Threskiornithinae*

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL OF THE UNIVERSITY OF  
FLORIDA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2000

## ABSTRACT

Male Scarlet Ibises, *Eudicimus ruber* and White Ibises, *Eudocimus albus* have bills that are on average 22% longer than females. Only about half of this difference can be attributed to a sexual difference in body size. Sexual dimorphism in bill and body size in White Ibises has been variously attributed to reduction of inter-sexual competition during foraging, increased female clutch size, or natural/sexual selection upon males. In chapter 1, I suggest that the sexual dimorphism in bill length and bill shape is based upon the role of bill length in determining the outcome of male bill-sparring contests. I investigated sexual differences in bill morphology of 133 males and 91 females in a captive flock of 350 Scarlet Ibises at Disney's Discovery Island, a bird park in Orlando, Florida. In 29 instances of males sparring with males in contests prior to breeding and 11 instances of nest take-over during breeding. I found no significant differences in age, body size, or body condition between winning and losing males. However, males winning bill-sparring contests and nest take-overs had significantly longer bills than losing males. Longer billed males also bred significantly earlier than shorter billed males. Sexual differences in the relationship between bill curvature, bill chord and bill length suggest that male Scarlet and White Ibises are under selection for increased bill length. I also show that among ibis species, sexual dimorphism in bill length is positively associated with colonial nesting but not with group foraging. I suggest that close proximity during nesting may facilitate bill sparring between males, resulting in selection for longer billed males.

In chapter 2, I investigated the reproductive energetics of a captive group of Scarlet Ibises. Since Jones and Ward's (1976) study of reproductive energetic and protein requirements of the Red-billed Quelea, *Quelea quelea*, no other study has since investigated the reproductive energetics of a nomadic, colonial breeder that is subject to large scale temporal and spatial unpredictability in food supply. Jonsson (1997) portrays fat storage as a means by which animals can cope with unpredictable resource abundance or availability. Yet, Quelea rely almost completely upon increased rates of feeding rather than fat reserves in order to cover the energetic cost of reproducing. This energetic strategy may be favored by colonial living, which also allows animals to cope with unpredictability in resource distribution and availability. So we might expect Scarlet

Ibises, which are also a nomadic, colonial breeder subject to large-scale unpredictability in food supply, to have evolved a strategy similar to *Quelea*.

Fitzpatrick et al. (1995) demonstrated that organisms reliant directly upon the abundance of food in their environment to cover the cost of reproduction may be able to invest more energy into sexually selected traits without incurring a reproductive cost than can organisms that draw upon a fixed amount of energy stored for reproduction. Within *Threskiornithinae*, colonial forms do appear to be subject to stronger sexual selection (on male bill length) than do non-colonial forms. If income breeding is associated with colonial living and increased sexual selection, then as a group, ibises may support Fitzpatrick's model of relaxed reproductive costs upon sexual selection within colonial forms. So we might predict that colonial ibises rely largely upon food supply and not body reserves to cover reproductive costs. In this chapter, I tested whether body reserves were necessary for the reproductive effort of captive Scarlet Ibises in which a large variation in body condition was present. I found that in Scarlet Ibises, pre-season body condition was moderately but significantly higher in breeding than in non-breeding males and females. I compared the reproductive energetics of the Scarlet Ibis to other species that do and do not rely upon body reserves to support reproduction. I found that both male and female Scarlet Ibises peak in body condition during courtship. This is relevant to colonial nesting because courtship represents a time when males and perhaps also females may not be able to leave the colony to feed without risk of losing potential social partners and nest sites.

## **Chapter 1.**

# **WHEN DO MALE IBISES HAVE LONGER BILLS THAN FEMALES?**

## **INTRODUCTION**

### **SEXUAL DIMORPHISM IN BILL SIZE IN BIRDS**

The degree of sexual dimorphism in bill length often exceeds sexual dimorphism in body size in birds. A few examples are Common Terns, *Sterna hirundo* (Coulter 1986), large gulls, *Larus sp.* (Ingolfsson 1969), Keas, *Nestor notabilis* (Bond et al. 1991) and Oystercatchers, *Haematopus fuliginosus* and *H. longirostris* (Lauro and Nol 1995).

The degree of sexual dimorphism in bill size within and among avian species can be influenced by many different selective forces. Within a species, sexual dimorphism of the bill is often more pronounced in situations where inter-specific competition is reduced and niche breadth is wide, or where niche partitioning has evolved between the sexes (Selander 1966, Aulen and Lundberg, 1991). Ingolfsson (1969) suggested that due to its remarkable constancy from species to species, sexual dimorphism of bill length in gulls is probably related primarily to sex recognition or defense of territory rather than to feeding habits. Sexual differences in bill length have also been related to dominance contests in Greater Sheathbills (Shaw 1986). However, the effects of age and sex were not controlled for in this study and may have played a role in dominance as well.

Sexual bill dimorphism has been discussed far less in the literature than sexual dimorphism in body size. Size dimorphism is most pronounced in polygynous or lekking species where sex roles often differ more than in monogamous species. There is currently little consensus as to whether variation in sexual size dimorphism in birds is

mostly or only partly the product of sexual selection (Andersson 1994). This lack of consensus extends equally well to the origins of sexual dimorphism in bill length in birds.

#### SEXUAL DIMORPHISM IN IBISES

As a group ibises (subfamily Threskionithinae 23 species, 14 genera) show relatively little sexual dimorphism compared to some other avian groups. The sexual dimorphism they exhibit pertains mostly to bill length and varies widely between species. Ibis species also differ widely with respect to social feeding and social breeding habits.

Scarlet (*Eudocimus ruber*) and White Ibises (*Eudocimus albus*) are either close congeners or color morphs of the same species (Ramo and Busto 1987, Hancock et al. 1992). These highly social birds exhibit the largest sexual difference in bill length of any of the ibis species. Male Scarlet Ibises have bills that are on average 22% longer than females (Hancock et. al. 1992). Yet only about half of this inter-sexual difference is represented in tarsal length and therefore, sexual bill dimorphism does not seem to be attributable to a size scaling effect alone.

#### WHAT CAUSES SEXUAL DIMORPHISM IN BILL SIZE?

In White Ibises, sexual size dimorphism in the body and bill has been attributed to both sexual and natural selection. Kushlan (1977) proposed that larger male White Ibises were better able to defend the nest from conspecifics or predators than smaller males and could dominate females in mating interactions. Bildstein (1986) suggested that differences in body and bill size in White Ibises may reduce inter-sexual competition over food, lead to increased clutch size in females (where females could shunt more resources into egg production if they needed less energy to maintain their smaller bodies), or be a sexually selected trait. Although Bildstein (1993) showed experimentally that the longer bill offered male White Ibis access to fiddler crabs that were out of reach for females, bill length did not restrict males to feeding only from deeper burrows, and therefore, reduction of inter-sexual competition was not demonstrated.

Lauro and Nol (1995) offered three non-exclusive hypotheses to explain sexual dimorphism in bill morphology in birds generally. First, sexual dimorphism in bill length

may have arisen in order to reduce sexual competition over limited resources (usually food). Second, sexual bill dimorphism may have arisen to increase the partitioning of reproductive roles, i.e. males and females evolved different bills in order to perform different jobs at the nest. Lastly, sexual bill dimorphism may have resulted from sexual selection and male-male competition. We can make direct predictions about sexual bill dimorphism in ibises that address Lauro and Nol's three hypotheses. If sexual bill dimorphism in ibises has evolved largely in response to reduced sexual competition at foraging sites, then we might expect more dimorphism within those species that tend to forage in large social groups. Very little is known about the partitioning of sex roles in most species of ibises, so we have no data with which to perform a cross-species comparison in order to test Lauro and Nol's second hypothesis. However, if we expect that male bill length might help determine the outcome of competition over nesting sites within a colony, then the longer bill of the male might have evolved primarily for nest acquisition or defense against conspecifics. If true, we would expect longer billed males to win nest-takeovers against shorter billed males and perhaps also to nest earlier within a large colony if nest sites were to be limited. Lastly, if sexual bill dimorphism is largely the product of sexual selection (Lauro and Nol's third hypothesis), then we might expect individual bill length to influence the outcome of male competition or female choice. Also, both sexual selection and sex role partitioning predict that within ibises as a taxonomic group, sexual bill dimorphism might be more pronounced within colonial nesting species where the simple proximity of nests would facilitate bill-sparring behavior and nest take-over.

In this study, I assess the role of potential selection pressures related to colonial breeding in maintaining sexual dimorphism in bill length in colonial ibises. I collected data that specifically address predictions derived from Lauro and Nol's hypotheses. First, by using a morphometric analysis, I describe sexual variation in bill and body size and shape within a group of over 400 captive Scarlet Ibises. Then I quantitatively describe and compare size and shape differences of the body and bill and their association with body size within each sex. Also, I present a discriminant function for sexing Scarlet Ibises that is based upon morphologic measurements from a subset of individuals of known behavioral sex. Second, I evaluated the hypothesis that bill length affects the

outcome of male contests by observing bill sparring behavior, timing of nesting and instances of nest piracy or take-over among captive male Scarlet Ibises of known body size, body condition, bill characteristics and age. Third, I performed cross-species comparisons of the degree of sexual dimorphism in bill length to the incidence of both colonial nesting and group foraging in ibises.

## METHODS

Morphologic and behavioral studies were conducted during the nesting seasons of 1998 and 1999 upon a captive flock of approximately 450 full-flighted birds held in a 3085 m<sup>2</sup> aviary at Disney's Discovery Island in Orlando, FL. The aviary contained mature trees allowing the ibises to nest as high above the ground. Nests were constructed by the birds from bamboo clippings supplied by Disney employees and researchers. Cross-species comparative morphologic data was taken from Hancock et al. (1992).

## SEX DETERMINATION

I extracted a sample subset of the aviary consisting of 114 birds whose sex had been determined through observations of copulation at the nest, and whose eggs hatched during the 1999 nesting season. I conducted a canonical discriminant analysis based upon mass, tarsometatarsus length, straight bill length (bill chord), curved bill length (bill length), bill depth and wing chord and then compared the accuracy of these assignments with the behaviorally derived sex assignments. By using only those birds whose eggs hatched, I was probably able to eliminate from the sample any male-male single sex pairs. Female-female pairs were not as easily controlled for in this manner due to the high level of extra-pair copulation that occurred in the aviary. Twenty four percent of all copulation occurred outside of established social pairs. However, I assume that females that appeared to be males behaviorally were probably very few in number.

## MORPHOMETRICS

In February and March of 1998 and 1999, I weighed and measured 378 individuals. Measurements on live birds included body mass, tarsometatarsus length, curved bill

length (from distal edge of skin on forehead along the top of the upper mandible to the bill tip), bill chord (straight measure of mandible joint to bill tip), bill depth (at top of the nares) and curved wing chord (1999 only). Because size differences strongly dominated the variation in all measurements between the sexes, I chose to separate the components of sexual size and shape variation using a covariance-based principal components analysis on log-transformed body measurements (Manly 1994). I also analyzed the size and shape variation in a similar fashion within both sexes in order to compare male and female variation in morphology. To represent body mass comparably to the other linear measurements, its cube root was taken prior to log-transformation. Body condition was expressed as the ratio of observed to expected mass where expected mass was the linear regression of body mass upon a body size factor score. The body size factor score was determined to be the first principle component score derived from the analysis because it exhibited strong positive loadings (correlations) upon all of the measured variables that were input into the analysis. Intra-sexual variation was described by performing another principal components analysis within each sex. The size dependency of the most significant shape variables was investigated by linear regression of each shape factor score against the body size factor score.

#### MALE BILL-SPARRING AND NEST TAKE-OVER

I observed and recorded 219 bill sparring bouts between pairs of birds during the month of February prior to the breeding season. A bill-sparring bout was defined when two birds faced each other and attempted to strike each other at least once with the bill. Bouts were only recorded during the early morning hours (0700-1100) and occurred mostly on the ground. I only recorded bill-sparring away from feeding stations and nests in order to standardize for confounding factors (e.g. hunger or ownership) that may predispose one bird to winning a bout. Males often flew into the air during conflicts that began on the ground, with intensely rapid bouts of open bill sparring. This behavior has been previously described as Supplanting Flight by Hancock et al (1992). When bill-sparring bouts occurred on the ground, the losing male was determined as the bird that first turned to flee. If the contest went into the air, the outcome was determined by the distances each



bird moved from where the contest began. The winner of Supplanting Flights typically would land very near to the spot on the ground where the altercation began while the loser would land somewhere farther away.

I recorded 23 instances of nest take-over in the aviary during 1999. Nest take-over was defined in this study as a nesting pair losing their nest to another pair during courtship, incubation, or early nestling stages. Nest-takeovers that may have occurred in the later stages of nesting were difficult to discern from nest re-use by incoming pairs after fledging events. In 11 cases, I had measured the displacing and displaced male from each pair involved in a nest take-over. I compared age, body condition, tarsal length, wing length, bill depth and straight and curved bill length of males winning and losing both Supplanting Flights and nests to take-overs using paired t-tests.

#### MALE BILL LENGTH AND REPRODUCTIVE SUCCESS

During 1998 and 1999, I recorded the stage of nesting achieved by all nesting pairs within the aviary. I categorized the ultimate fate of all nesting attempts by each individual during each season by recording the last nesting stage at which individuals were observed. I compared the bill lengths of males between these categories in order to determine if nesting success was affected by male bill length. I also recorded the date on which eggs hatched in order to determine if a male's bill length affected the timing of his nesting within the colony.

#### TAXANOMIC COMPARISON OF SEXUAL DIMORPHISM, GROUP FORAGING AND COLONIAL NESTING IN IBISES

I computed mean male and female bill and wing lengths, and male to female bill length and wing length ratios for all ibis species for which data were available (Hancock et. al. 1992). Species were classified using information in Hancock et al. 1992 as colonial, loosely colonial (breeding both solitarily or in small groups), or non-colonial breeders. The degree of sexual difference in proportional bill length (bill length divided by body size as estimated by wing length) for a given species was calculated by dividing the male to female bill length ratio by the male to female wing length ratio. Thus if the sexes

differed equally with respect to each ratio, wing and bill, then the result would be equal to 1.00 (i.e. non-dimorphic)(Table 1). Cross-species comparisons of group foraging, colonial breeding and degree of sexual bill dimorphism were assigned according to Harvey and Pagel's (1995) evolutionary covariance regression method for working with unresolved phylogenies. This method solved the non-independence problem of using individual species as sampling units by evaluating each possible contrast between adjacent branches on a phylogenetic tree as the sampling units. In essence, the difference between the variables of interest on adjacent branches or clades were calculated. These differences were then treated statistically as independently sampled units. When multi-branch nodes arose due to unresolved parts of the phylogeny, the variables of interest were treated as weighted contrasts within each node, thus they were summed and then divided by the number of branches in the node.

I used the phylogeny from Sibley and Ahlquist (1990) as portrayed in Sheldon and Slikas (1997). I added *Geronticus* aligned with *Boystrichia* as suggested by Fry et al.(1985) and aligned *Eudocimus* with *Plegadis* as suggested by Mayr and Short (1970) and Olsen(1981). I also added congeners within *Threskiornis* and *Boystrichia* to Sibley and Ahlquist's tree creating two multi-branch nodes (Fig 1, Table 2). All branch lengths were considered equal in the analysis. Dummy variables were used for coding group foraging and colonial breeding. Values of 1.0 and 0.5 and 0.0 were used for "yes", "intermediate" and "no". Moller and Birkhead (1993) used this method similarly when dealing with the issue of comparing sociality and extra-pair copulation rates across species. The Hadada Ibis, *Boystrichia hagedash* and Buff-necked Ibis, *Theristicus caudatus* were classified as intermediate group foragers because, according to Hancock et al.(1992), they forage often singly or in pairs or in groups of less than 50 individuals. The other species either always feed exclusively in singles or pairs or else they are typically always found feeding in groups. The Bare-faced Ibis, *Phimosus infuscatus* and Buff-necked Ibis, *Theristicus caudatus* were classified as intermediate colonial breeders because they may nest solitarily or in loose groups of up to 20 pairs. Values for the degree of sexual bill dimorphism were determined by dividing the average male to female bill length ratio by the average male to female wing length ratio as described above.

Table 1. Reported colonial nesting, group foraging and mean values and male to female ratios for bill, wing, and proportional bill length in the ibises. NA = sample size not available. Barefaced and Buffnecked Ibis are loosely colonial, nesting solitarily or in small groups (Data are from Hancock et.al.1992)

<b>Species</b>	<b>N</b>	<b>Mean male bill length (mm)</b>	<b>Mean male wing length (mm)</b>	<b>Mean female bill length (mm)</b>	<b>Mean female wing length (mm)</b>	<b>M/F Bill Length Ratio</b>	<b>M/F Wing Length Ratio</b>
Scarlet/White Ibis	12	163.2	282.3	125.6	265	1.30	1.06
Barefaced Ibis	16	120.2	281.3	108.8	265.2	1.10	1.06
Glossy Ibis	18	131	288.3	104.2	262.2	1.26	1.10
Whitefaced Ibis	19	133.9	269.6	103.6	243.5	1.29	1.11
Puna Ibis	17	117.4	298.4	92	276.8	1.28	1.08
Sharptailed Ibis	13	161.6	399.7	152.7	394.2	1.06	1.01
Plumbeous Ibis	20	153.8	413.4	134.6	384.8	1.14	1.07
Buffnecked Ibis	20	149	402.7	138.8	389.8	1.07	1.03
Green Ibis	9	112.6	280	108.5	283	1.04	0.99
Hadada Ibis	17	134	353	134	353	1.00	1.00
Olive Ibis	NA	95	328	90	313	1.05	1.05
Spotbreasted Ibis	10	126.5	278	126.5	264	1.00	1.05
Sacred Ibis	13	170	383	146	362	1.16	1.06
Australian White Ibis	7	188.6	380.6	153.7	363.7	1.23	1.05
Strawnecked Ibis	NA	169	389.5	137.8	363	1.23	1.07
Waldrapp Ibis	NA	140	411.5	123	399	1.14	1.03

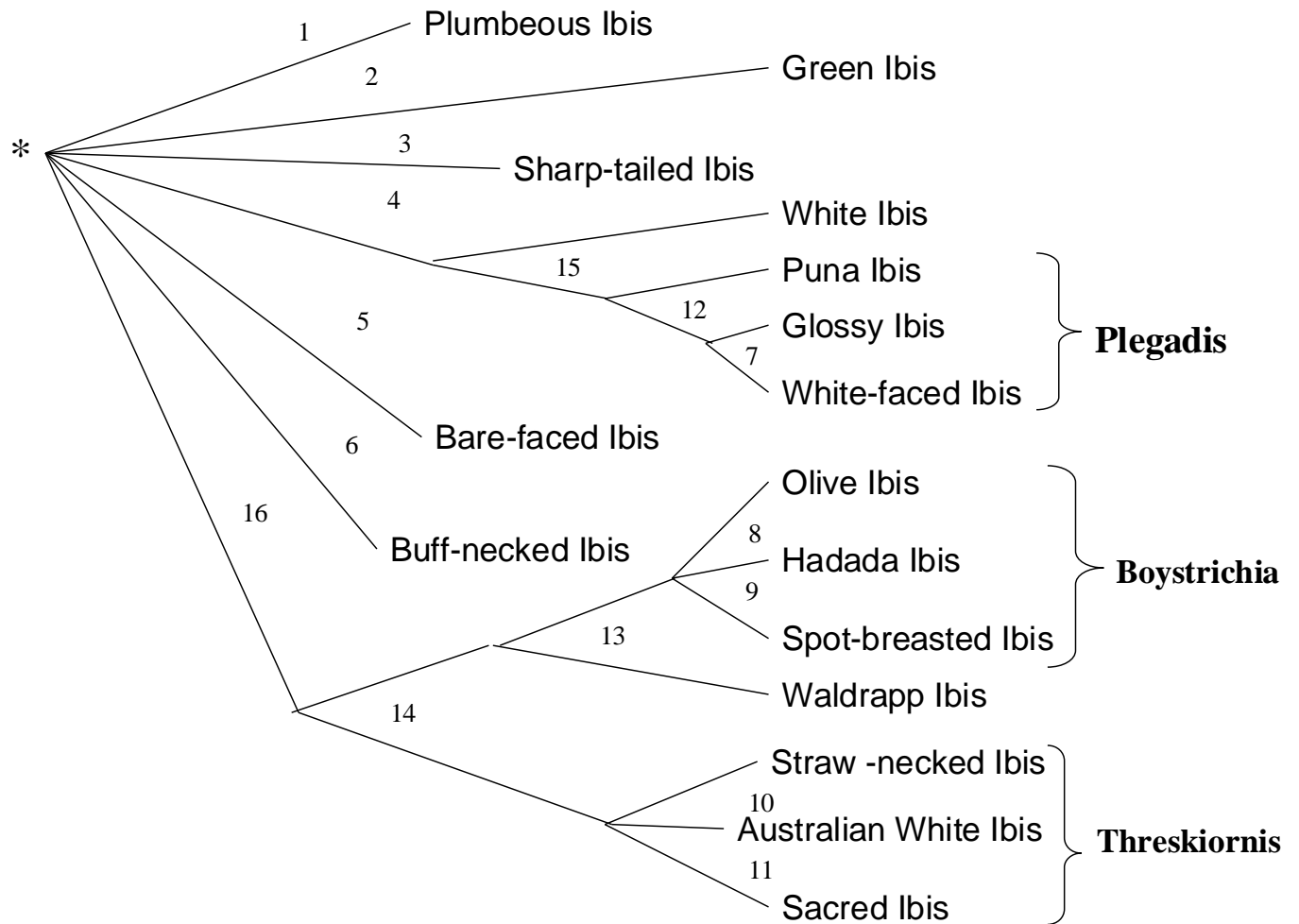


Figure 1. A phylogeny for ibises derived from Sheldon and Slikas (1997). Phylogenetic contrasts are numbered as they appear on Table 2.

Table 2. Values of phylogenetic contrasts calculated for the incidence of colonial nesting, group foraging and degree of sexual bill dimorphism in ibises.

Phylogenetic Node Contrast	Sexual Bill Dimorphism Contrast	Colonial Breeding Contrast	Group Foraging Contrast
1	0.02	0.42	0.500
2	0.01	0.42	0.500
3	0.02	0.42	0.500
4	0.13	0.74	0.666
5	0.04	0.42	0.666
6	0.04	0.07	0.083
7	0.03	0.00	0.000

8	0.04	0.00	0.500
9	0.06	0.00	0.500
10	0.02	0.00	0.000
11	0.06	0.00	0.000
12	0.03	0.00	0.000
13	0.11	1.00	0.166
14	0.10	0.75	0.916
15	0.06	0.00	0.000
16	0.02	0.29	0.083

## RESULTS

### SEX DETERMINATION

The canonical discriminant function using the body and bill measurements of Scarlet ibises proved to be an accurate method of assigning sex when tested against birds of known behavioral sex (Figure 2) (Wilk's lambda = 0.206,  $p < 0.001$  for all birds; mean probability correct in males = 98.11 % and in females = 96.4%).

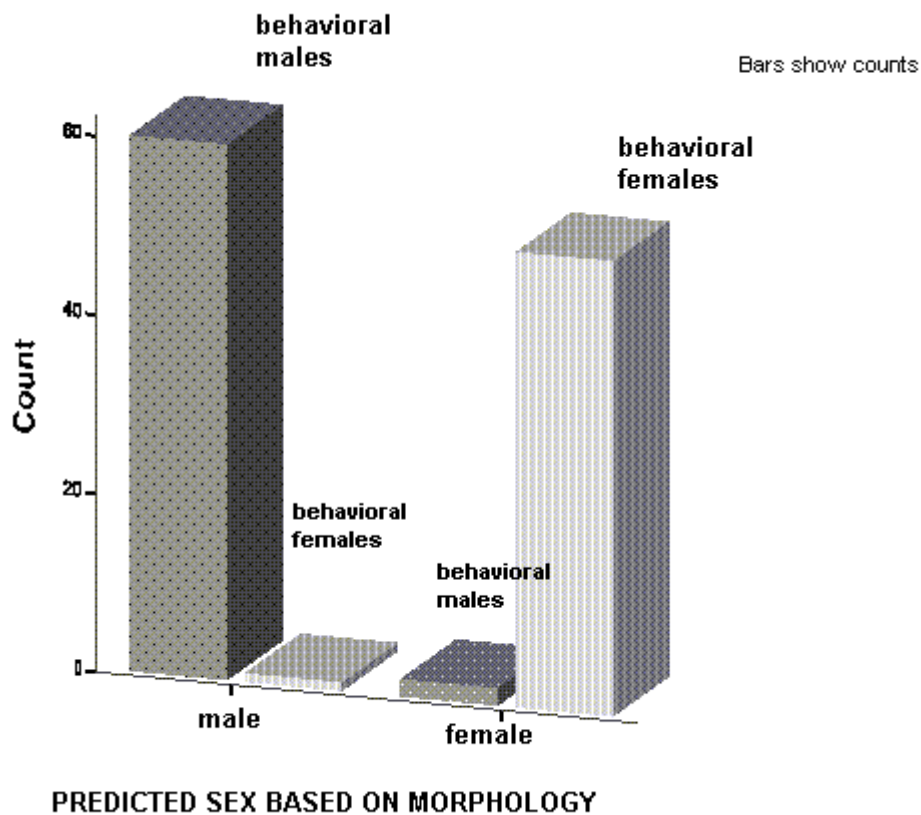


Figure 2. Sex predicted by a discriminant function analysis based upon six body and bill measurements shown for a subset of 114 behaviorally sexed Scarlet Ibises.

# MORPHOMETRICS

Most of the total variance in size and shape between the sexes in this group of Scarlet Ibises was due to a significant difference in body size (88.97% of variance,  $t = 47.2$ ,  $p < 0.001$ , Table 3). The remaining 11.03% variation not due to body size was due to differences in body shape. Most (60.7%) of this variation in shape between both sexes involved differences regarding proportional bill length and depth (PC 2 & 3). These bill characteristics were more dimorphic than body measurements (Figure 3). Proportional bill length (PC 2) component scores differed with marginal significance between sexes ( $t = -1.706$ ,  $p = 0.089$ ). The remaining proportion (24%) of the shape variation between sexes involved differences in relative fatness (body mass contrasted to wing chord length) and bill curvature. Component scores on all the principle component axes reflect nearly identically about zero indicating very similar patterns of size and shape variation within each sex (Figure 4). Males exhibited significantly more variance in bill and mass measurements than did females. ( $F = 1.335$ ,  $p < 0.001$  for mass;  $F = 1.2786$ ,  $p < 0.001$  for bill chord;  $F = 1.575$ ,  $p < 0.001$  for bill length;  $F = 1.159$ ,  $p = 0.02$  for bill depth) There was no significant sexual difference in variance of tarsus and wing chord measurements.

Table 3. A principle component analysis of 3 body and 3 bill measurements in a captive group of 378 unsexed Scarlet Ibises.

COMPONENT	INITIAL EIGENVALUES		
	TOTAL	% OF VARIANCE EXPLAINED	CUMULATIVE %
1	0.008801	88.972	88.972
2	0.000353	3.569	92.541
3	0.0003143	3.178	95.719
4	0.0002634	2.663	98.382
5	0.0001203	1.216	99.598
6	0.00003974	0.402	100

	RESCALED COMPONENT MATRIX					
	1	2	3	4	5	6
LOG BILL CHORD	0.989	-0.072	-0.102	0.021	-0.004	-0.083
LOG BILL LENGTH	0.985	-0.078	-0.127	0.013	-0.010	0.081
LOG BILL DEPTH	0.822	-0.336	0.421	-0.184	-0.020	0.005
LOG BODY MASS	0.858	0.101	0.183	0.236	0.404	0.011
LOG TARSAL LENGTH	0.930	0.320	0.076	-0.160	-0.025	0.002
LOG WING CHORD	0.764	0.131	0.283	0.519	-0.221	0.007

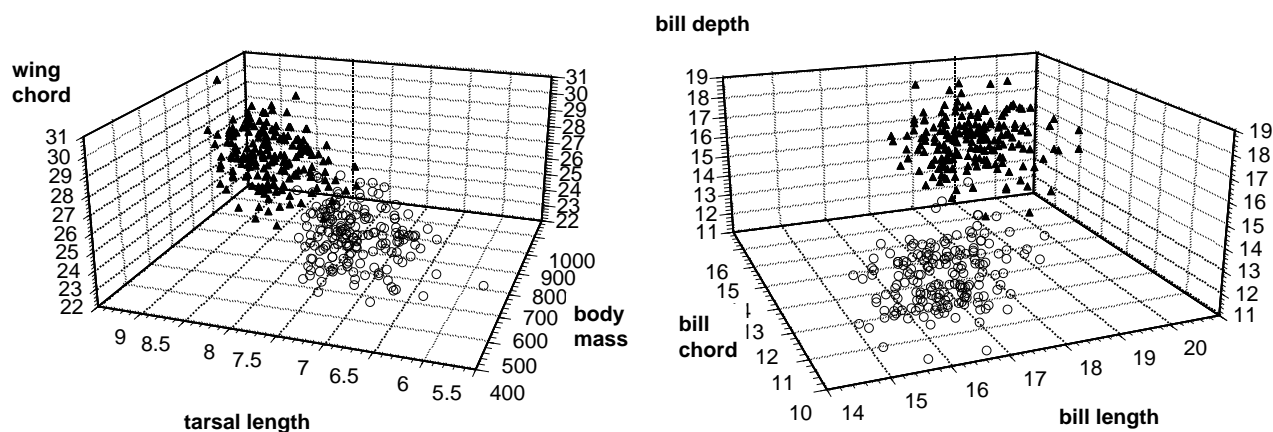


Figure 3. Sexual dimorphism in 378 Scarlet Ibises according to three measures of body size (left) compared to three measures of bill size (right).

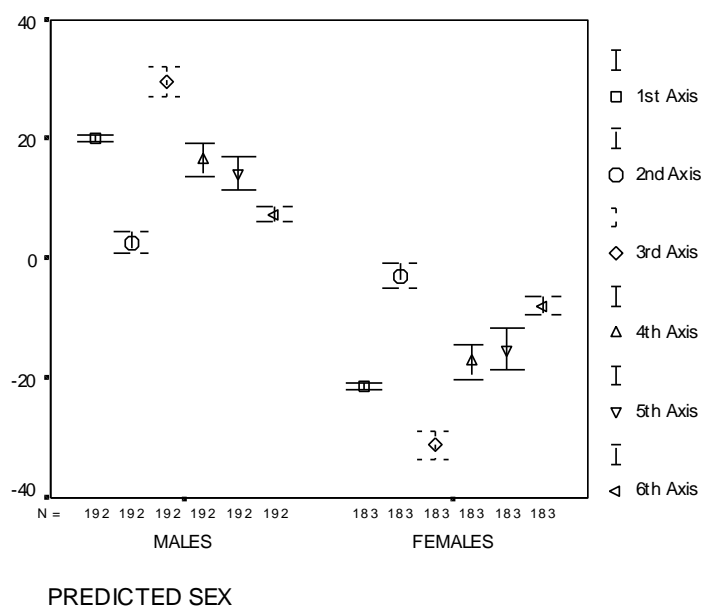


Figure 4. Distribution of principle component scores from Table 3 in relation to predicted sex of 378 Scarlet Ibises.



Most (50.2%) of the variation among males was due to body size (Table 4). Of the remaining shape variation (49.8%), 33.7% was attributed to proportional bill length (PC2), 30.9% was attributed to proportional bill size (PC3) and 22% was attributed to a skeletal shape difference contrasting wing and leg length. Within females, 50.3% of the total variation was attributed to body size (Table 5). Of the remaining variation in shape (49.7%), 35.4% and 25.1% was attributable to proportional bill size and proportional bill length respectively (PC 2&3). Almost all inter-sexual variation in shape in Scarlet Ibis was size dependent. Bill curvature (PC 6) varied independently of size.

Table 4. A principle components analysis of 3 body and 3 bill measurements in 227 male Scarlet Ibises

COMPONENT	<i>INITIAL EIGENVALUES</i>		
	TOTAL	% OF VARIANCE EXPLAINED	CUMULATIVE %
1	0.00101	50.161	50.161
2	0.0003383	16.791	66.952
3	0.0003095	15.365	82.317
4	0.0002344	11.637	93.955
5	0.00009288	4.611	98.565
6	0.0000289	1.435	100

	<i>RESCALED COMPONENT MATRIX</i>					
	1	2	3	4	5	6
LOG BILL CHORD	0.911	-0.255	-0.223	0.105	-0.050	0.206
LOG BILL LENGTH	0.901	-0.313	-0.216	0.113	0.007	-0.176
LOG BILL DEPTH	0.346	0.772	-0.526	-0.075	-0.029	-0.013
LOG BODY MASS	0.532	0.259	0.275	0.201	0.730	0.031
LOG TARSAL LENGTH	0.722	0.130	0.429	-0.524	-0.052	-0.005
LOG WING LENGTH	0.437	0.385	0.533	0.584	-0.189	-0.012

Table 5. A principle components analysis of 3 body and 3 bill measurements in 151 female Scarlet Ibises.

COMPONENT	<i>INITIAL EIGENVALUES</i>		
	TOTAL	% OF VARIANCE EXPLAINED	CUMULATIVE %
1	0.00119	50.341	50.341
2	0.0004169	17.595	67.936
3	0.0002959	12.490	80.427
4	0.0002788	11.766	92.193
5	0.0001366	5.766	97.959
6	0.00004837	2.041	100

	<i>RESCALED COMPONENT MATRIX</i>					
	1	2	3	4	5	6
LOG BILL CHORD	0.905	0.237	-0.220	0.149	-0.007	-0.233
LOG BILL LENGTH	0.890	0.257	-0.285	0.093	0.039	0.225
LOG BILL DEPTH	0.472	0.469	0.440	-0.602	0.026	-0.005
LOG BODY MASS	0.538	-0.085	0.524	0.365	-0.542	0.041
LOG TARSAL LENGTH	0.685	-0.693	0.020	-0.217	0.050	-0.001
LOG WING LENGTH	0.324	-0.002	0.617	0.525	0.488	0.009

I found a sexual difference in how bill curvature relates to bill length. Bill curvature was positively correlated to curved bill length in males but not females (males;  $r = 0.263$ ,  $P = 0.002$ ,  $n = 133$  and females;  $r = 0.021$ ,  $P = 0.844$ ,  $n = 91$ ), though the strength of the association in males was weak. Bill curvature was negatively correlated to straight bill length (bill chord) in females but not males (males;  $r = -0.108$ ,  $P = 0.215$  and females;  $r = -0.287$ ,  $P = 0.006$ ), though the strength of the correlation for females was low. So in males, degree of curvature tended to increase with the curved length of the bill while in females it tended to decrease with straight length.

#### BILL LENGTH AND BILL-SPARRING INTERACTION IN SCARLET IBIS

In 29 instances of males bill-sparring with males, age, bill size, tarsus length, and body condition in both contestants were known. Using paired t-tests, I found no significant differences in mass, age, tarsal length, body condition or bill curvature between male winners and losers. Perhaps this was because males of similar size and condition were those most likely to fight, and were more inclined to test each other in bill-sparring contests. However, winning males had significantly greater straight and curved bill lengths than did losing males ( $n = 28$ ,  $t = 2.698$ ,  $P = 0.012$  for curved bill length), suggesting that longer billed males are more likely to win bouts of bill-sparring regardless of body size or age (Figure 5). The mean difference in bill length between winning and losing males was 0.3667 cm with a standard deviation of 0.7546 cm.

Females engaged in far fewer bill-sparring contests than males and in only 7 instances were complete morphologies and conditions known for both female contestants. Female bill-sparring contests seemed never to escalate to the point of male bill-sparring contests and were usually over after one or two jabs. In females, I found no significant differences between winning and losing birds, but the sample in which both birds were measured was very small.

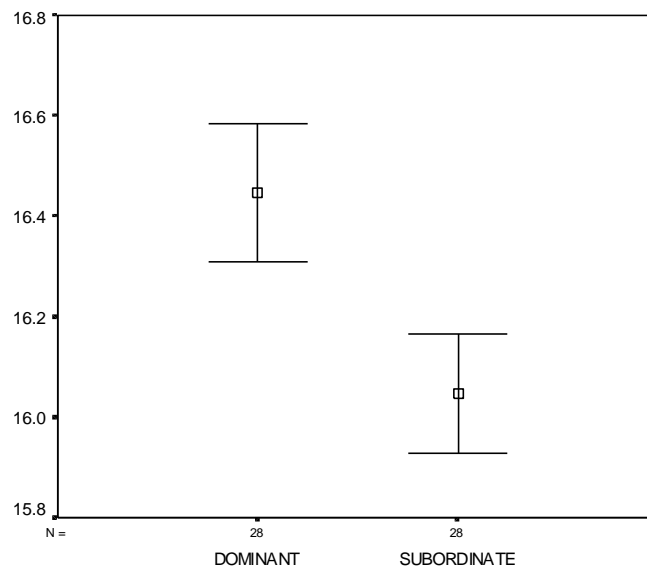


Figure 5. Mean curved bill length of captive male Scarlet Ibises during 29 contests.

## MALE BILL LENGTH AND REPRODUCTIVE SUCCESS

Male bill length (both years) was significantly correlated with hatch date (1998:  $r = -0.395$ ,  $p = 0.036$ ; 1999:  $r = -0.485$ ,  $p = 0.049$ ), indicating that longer-billed males nested earlier. Males of courting pairs were observed often bill-sparring with nest building birds. This result may have been due to the limited amount of nesting material supplied by caretakers and available in the aviary. However, wild White Ibises also do this despite an unlimited amount of nest material. I found no significant relationship between male bill length and the ultimate fate of the nesting attempts.

## BILL LENGTH IN RELATION TO NEST TAKE-OVER

In 11 cases in which bill and skeletal morphology of both males belonging to pairs gaining and losing nests were known, I found significantly longer straight bill lengths in displacing males ( $n = 11$ ,  $t = 2.347$ ,  $P = 0.039$ ). I also found no significant differences between male contestants in tarsal and wing lengths ( $n = 11$ ), or age ( $n = 6$ ).

## TAXANOMIC COMPARISON OF SEXUAL DIMORPHISM, GROUP FORAGING AND COLONIAL NESTING IN IBISES

Using all 16 species for which sufficient data were available, I found degree of sexual dimorphism in proportional bill length to be strongly positively associated with the incidence of colonial breeding ( $n = 15$ ,  $r = 0.683$ ,  $p = 0.005$ , Fig 6). This analysis was most heavily influenced by comparisons between the colonial Waldrapp Ibis *Geronticus* and the non-colonial *Boystrichia* group; the two main Old World branchings (*Boystrichia*/*Geronticus* group against colonial *Threskiornis*); and the *Plegadis*/*Eudocimus* group against the all other ibises. These were nodes 13, 14 and 4 in Figure 1. The degree of sexual dimorphism in proportional bill length was not significantly associated with the incidence of group foraging ( $n = 15$ ,  $r = 0.364$ ,  $p = 0.182$  Figure 6). The incidence of colonial nesting and group foraging were correlated ( $n = 15$ ,  $r$

= 0.554,  $p = 0.032$ ) to each other, but not as strongly as the degree of sexual bill length dimorphism and colonial breeding.

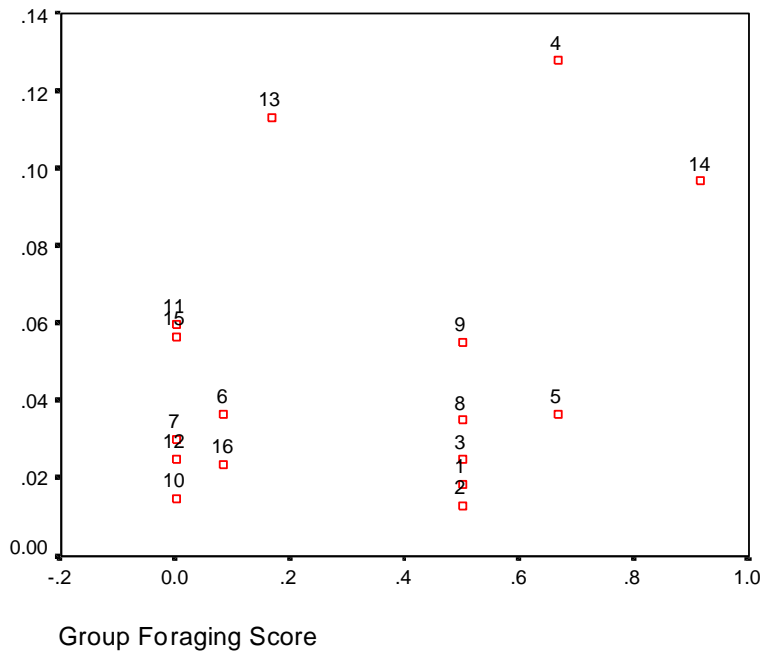
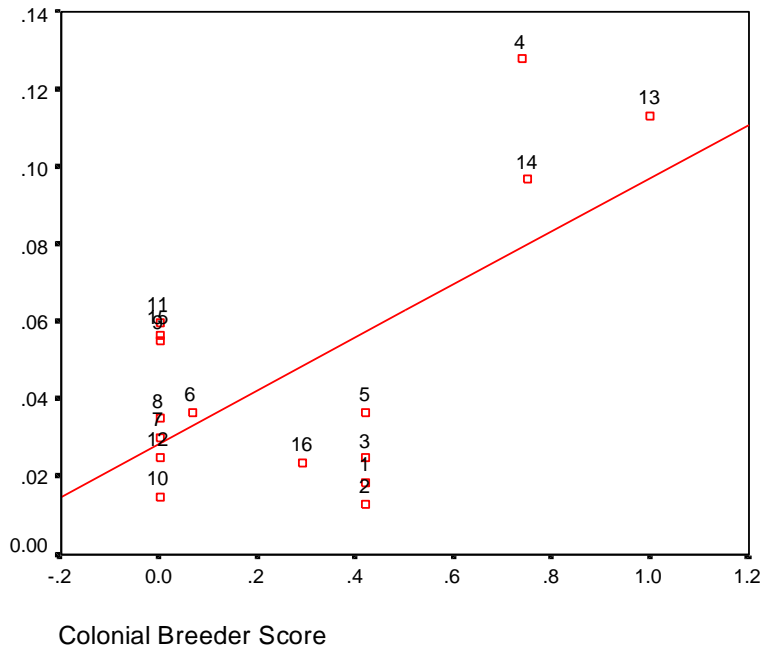


Figure 6. Regressions of phylogenetic contrasts in ibises (labeled in Figure 1) of the incidence of colonial breeding and group foraging against the degree of sexual bill dimorphism

## DISCUSSION

### SIZE AND SHAPE VARIATION IN A SEXUALLY DIMORPHIC IBIS

Marked sexual dimorphism exists in the Scarlet Ibis. Sexual variation between sexes in the Scarlet Ibis is continuous and due mostly to differences in body size rather than body shape. The second most important source of variation both between and within sexes was attributable to proportional bill length and size. Sexual variation was discontinuous upon this trait. Male bills were proportionally longer, but also tended to be proportionally thinner than those of females, suggesting that there may be an upper limit to how massive a male's bill can get and still remain functional. Males may be achieving length while holding the cost of increasing bill mass to a minimum by reducing the bill depth. In males, bill curvature increased with curved length while in females, bill curvature decreased with straight length. Males did not sacrifice bill length for the sake of curvature; females did. My data demonstrated that males with shorter bills tend to have straighter bills, probably in order to maximize reach and thus bill-sparring ability.

The pattern of body size and shape variation in the Scarlet Ibis suggests that selection for sexual dimorphism of bill length is currently strong or has been strong in the past. The division of size and shape variation within each sex also closely resembles the division of variation between the sexes. Males and females share nearly the same pattern of variance in body shape as evidenced by the relationships of the mean principal component scores for each sex in Figure 4. Therefore, dimorphism in this species has evolved to be largely continuous with body size with slight differences in body shape. Proportional bill length was the only body shape variable that differed greatly between sexes and this difference, while large (16.9% in our study), was only a marginally significant one due to the variance among males. The relative separation of the mean principal component scores for each sex in this figure also indicated that proportional bill length (PC 3), while

accounting for less variation than body size (PC 1), is in fact a better qualitative indicator of sex because it separates the sexes more completely.

#### SELECTION FOR BILL DIMORPHISM IN IBISES

The results of behavioral observations pertaining to the role of bill length to fighting in Scarlet Ibises combined with cross-species comparisons of the incidence of bill dimorphism, colonial breeding and group foraging in other species, suggests that sexual bill dimorphism in ibises is related to nesting rather than feeding habits. Although, I was not able to directly test whether sexual bill dimorphism reduced competition over food in any particular species of ibis, the fact that taxonomic comparisons show no significant association between group foraging and sexual dimorphism in bill length suggests that reduction in inter-sexual competition over food may not have been a selective force upon bill length dimorphism in ibises in general.

Evidence that there may be partitioning of sex roles associated with sexual bill dimorphism in colonial ibis species is supported by the fact that shorter-billed male Scarlet Ibises were more susceptible to nest take-overs by longer-billed males. Nest piracy has been reported in the wild in several studies, and so the behavior is not entirely an artifact of captivity (Kushlan 1973, Frederick 1986). Nesting success in the wild is therefore probably partly determined by a male's ability to defend the nest from other males. Males do take a predominant role in nest defense and nest defense (Kushlan and Bildstein 1994) and this is probably facilitated by having a longer bill. In addition to this, the observation that longer billed males bred earlier than shorter billed males lends further weight to this hypothesis. In colonial species, the proximity of nests combined with an increased frequency of nest take-over from conspecifics may favor selection of longer billed males. That sexual bill dimorphism in ibises is associated with colonial breeding supports this hypothesis.

The hypothesis that sexual selection is involved in maintaining and/or creating sexual bill dimorphism is supported by the observation that bill length is a key determinant in the timing of nesting and the outcome of bill-sparring bouts by males. This finding is bolstered by the fact that no other attributes of morphology seemed to contribute to the

outcome of contests in males. The fact that differences in bill length are associated with the outcomes of interactions between male Scarlet Ibises suggests that dominance in this species is partly a function of bill sparring ability which in turn is related directly to the reach or straight length of the bill. A longer bill probably allows a combatant to strike an opponent's face or eyes more easily. Due to the blunt nature of the bill tip and the fact that strikes are usually directed towards the face, eye injury is probably the only substantial physical risk incurred by fighting males.

I should note that in many situations, (perhaps the majority), male dominance might easily be settled without fights, on the basis of size alone. I did not measure all possible types of dominance interaction and therefore bill length might be a deciding factor in only the small proportion of the interactions when males are matched in size and have to bill-spar.

Long-billed males may also be more successful in winning or attracting the few females that are ready to breed early in the season. This is supported by the fact that longer-billed Scarlet Ibis males bred earlier than shorter-billed males. We might also expect that colonial breeding, a form of sociality associated with increased rates of extra-pair copulation in birds (Moller and Birkhead, 1992) which may serve to amplify sexual selection, to therefore be positively associated with degree of sexual bill dimorphism in the cross-species comparison of all ibises. And, indeed this appears to be the case (assuming bill length is in fact, sexually selected).

Because a male's bill length did not determine the ultimate fate of his nesting attempt, we might be tempted to think that reproductive success is relatively unaffected by male bill length and that male bill length in turn, is unaffected by selection. However, the observation that the timing of nesting was negatively correlated to male bill length suggests that longer billed males were more successful in gaining early nesting attempts. Scarlet Ibises have an unusually long nesting season and this combined with a constant supply of food in captivity probably allowed shorter billed males who lost nests early in the season to re-nest again after the longer billed males were already started. However, in many species of birds in the wild, clutch size and therefore potential nesting success tends to decline with hatch date (Rowe et al. 1992), and if this is also true with wild Scarlet Ibises, then male bill length would be associated with reproductive success given



that there was competition over mates or nest sites. While, I have not demonstrated an associated increase in reproductive fitness with male bill length in Scarlet Ibises, the fact that many shorter billed males in the aviary had to re-nest after losing eggs or young implies that they are probably spending more energy to raise fewer offspring over their lifetimes.

## CONCLUSION

I have shown that the degree of sexual difference in bill length, body size and bill length in proportion to body size is greater in colonial than non-colonial species of ibises. I suggest that this result is due to the close proximity of nests in colonial situations, and is associated with frequent bill sparring between males. Based upon the taxonomic analysis of foraging and bill length across ibises, I question the idea that sexual size dimorphism in the body and bill of ibises is only the result of inter-sexual competition during foraging. I suggest that male-male competition over nest sites or mates is probably the most important mechanism in the evolution of bill length in Scarlet Ibises and probably other colonial ibis species as well. I do not, however, suggest that sexual bill dimorphism should be related to colonial breeding in other species, since I believe that the long bills that characterize all ibises, and their bill-sparring behavior are the biological features that allow selection on bill size through competition to occur. And, these features are relatively rare in the avian world.

## **Chapter 2**

### **THE BIOENERGETICS OF REPRODUCTION IN A NOMADIC, COLONIAL BIRD, THE SCARLET IBIS (*Eudocimus ruber*)**

#### **INTRODUCTION**

Breeding birds rely to varying degrees upon endogenous energy reserves, such as stored fat. Reliance upon such reserves has long been considered a hallmark of high latitude, early breeding migrants that are faced with a predictable seasonal food shortage, usually early in the breeding season (Raveling 1979, Ankney and MacInnes, 1978, Drent and Daan 1980). Jonsson (1997) added that reliance upon stored resources for reproduction (often termed “capital breeding”), can also represent a strategy that evolves in animals and plants in response to unpredictable breeding conditions. Attempting to reproduce when food supply is either unpredictable or predictably absent both require that feeding (the acquisition of resources), and reproduction (the use of resources), be de-coupled in time. Jonsson also characterized increased intake of resource from a regional or seasonal abundance of resources (“income breeding”) as a strategy that is most efficient in response to predictable patterns of resource availability. He suggests that reproductive fitness gained through capital breeding must outweigh its energetic inefficiency (cost of production, storage and transport of fat) and other potential fitness costs (e.g. increased risk of predation).

While this dichotomy between income and capital breeders is useful, we should not forget that many energetic strategies other than the storage of fat exist by which individuals can cope with the risk of temporal and spatial uncertainty in finding enough food to support a reproductive effort. For example, some pre- and post-breeding adaptations to temporally unpredictable resources include increased life-span, prolonged or intermittent breeding seasons (Nur and Sydeman 1999, Cam et al. 1998), variable clutch size (Mock and Forbes 1995), facultative brood reduction (Amundsen and Slagsvold 1998, Forbes and Mock 1996), and nomadism (Brown and Hopkins 1996). Colonial breeding and local enhancement through social foraging represent adaptations to spatially unpredictable resources (Brown and Brown 1996, Clark and Mangel 1984, Poysa 1992). Many seabirds are faced with the problem of exploiting a spatially unpredictable but temporally constant food supply.

Such life history strategies may allow for less reliance upon stored reserves for breeding even when reproduction is limited by uncertain resource distribution or availability. These adaptations also might allow birds to adopt a more energy efficient “income breeding” strategy where the rate of resource use is increased in order to support increased energetic needs during breeding.

Yet, in the real world, where animals may employ various combinations of strategies of resource acquisition, allocation and use (Boggs 1992), the interaction between limiting factors can create constraints that are greater than those caused by the factors themselves. For example, Rogers and Smith (1993) demonstrate that avian fat storage patterns in winter reflect that populations are more often limited by interacting factors or “trade-offs” (such as predation and food supply) rather than by single (food supply) factors. For instance, ground feeding species need to store enough fat to survive periods of snow cover but not so much that they are too heavy to escape from predators. By extension, we might expect avian reproductive life history to reflect solutions to the interaction between multiple energetic limiting factors, perhaps even many more than affect winter fat storage.

One such potential reproductive energetic trade-off between limiting factors is that between sexual selection and reproduction. Reproduction requires an obvious energetic investment in producing a clutch and maintaining parental behavior. However, in many

species there is the added energetic investment into sexually selected behaviors and physical traits (e.g. songs and plumage). Fitzpatrick et al. (1995) elaborates upon the potential tradeoffs in energy allocation between sexual selection and reproduction. The authors state that under normal circumstances, sexual selection will be self-limiting in females (and the parental investing male) because, all other things being equal, it is in the individual's best interest to select a mate that has a maximum amount of energy to invest towards offspring. Potential mates that have large amounts of energy invested towards sexually selected traits and behavior are wasting energy that could otherwise be put into offspring. So unless they have a considerably greater amount of energy to invest, they should be selected against. Therefore, reproductive costs tend to create selection for efficiency in the indicative nature and discrimination of sexually selected ornamentation or behavior. For e.g. colorful plumage is relatively energetically cheap to create compared to a vigorous dancing display for attracting mates. (On the other hand, behavioral displays can be less costly than pigment in other currencies of fitness. For e.g. predation risk.)

Fitzpatrick et al. (1995) made a key point in that income breeders may be able to allocate energy to sexually selected traits from surplus income during part of the non-breeding season, with no costs to reproduction. In a capital breeder, investment into sexually selected traits at any time will be reflected in reproductive cost. In this way, the reproductive costs of sexually selected traits, as well as their value as indicators, may be become relaxed in income breeders therefore allowing sexual selection to continue unchecked by natural selection more than in species which allocate energy from a fixed pool of resource (e.g. fat). During times of plenty, income breeders may be much more constrained by the time it takes to acquire energy, find a suitable mate and build a nest than by the amount of energy that is available.

Many colonial breeding birds will not attempt to nest unless feeding conditions are optimal (Jones and Ward 1976, Kushlan and Bildstein 1992). Because colonial breeding and social foraging are essentially strategies evolved to enable individuals to capitalize upon resources that are hard to find, but too rich for any one individual to monopolize (Poysa, 1992), we might expect social birds to frequently adopt income breeding strategies. And accordingly, we would expect sexual selection to be less limited

energetically in colonial species. However, because breeding in a colony usually implies that food sources are not at the colony, we might expect fat storage, a capital strategy, to be useful to colonial birds when males or females cannot afford to leave the colony. In some colonial species, the courtship period is a time when sexual selection operates intensely (particularly in males), and may also be a period when birds cannot leave the colony to feed without risking losing a potential nest site or chance to mate. So we might predict that courtship would be a period when fat storage is beneficial.

In order to characterize the importance of body reserves to reproduction for a nomadic, colonial breeder, I chose to investigate the reproductive energetics of the Scarlet Ibis (*Eudocimus ruber*). Since studies of energetics and food consumption in wild populations of Scarlet Ibises are logistically very difficult due to their nomadic nature, I investigated how reproduction was associated with body condition in captive Scarlet Ibises (*Eudocimus ruber*). I studied reproduction and energetics in a captive colony of over 400 Scarlet Ibises at Disney's Discovery Island, a bird park in Orlando, Florida, where the birds exhibit high individual variation in reproductive response in captivity. I hypothesized that internal body reserves prior to or during breeding would predict whether or not individuals initiated breeding. The use of captive birds enabled me to control food type and measure body condition prior to breeding. To test this hypothesis, I used several approaches. First, I manipulated body condition in some birds through a supplemental feeding program and compared their reproduction (initiation rate and success) with non-supplemented birds. Second, I compared body condition indices of successful and unsuccessful breeders. Third, using feeding stations fitted with scales, I observed changes in body condition associated with the various stages of reproduction. Because reproductive performance can often be influenced by other factors such as age (Saether 1990), experience (Ratcliffe et al. 1998), time of season (Wilson and Cooper 1998), and mate quality (Otter et al. 1999), I also monitored these characteristics.

## METHODS

During the breeding seasons of 1998 and 1999, I studied the reproduction of over 400 individually color-banded Scarlet Ibises in a 3082m<sup>2</sup> aviary at Disney's Animal Kingdom

in Orlando, Florida . Built by the park over 20 years ago, the aviary was nearly 20m high at some points and encloses mature trees. The flock was composed of birds predominantly under 6 years of age, with a few individuals as old as 18-20 years. The sex ratio was 59/41% male to female.

The birds were fed twice daily ad libitum on a commercial flamingo diet (19 % protein, 5 % fat), supplemented with approximately 38 gm per bird/day frozen Atlantic Silversides (*Menidia menidia*). This resulted in only a few birds obtaining fish at each feeding, however individuals obtaining fish appeared random due to the intense degree of kleptoparasitism. Although the commercial diet was continuously available, the ibises fed only in small groups, and rarely alone. This nearly obligate social feeding behavior resulted in strong dominance interactions over food. Typical feeding bouts involved subordinate birds feeding only when they were not supplanted by more dominant birds, resulting in very short bouts and decreased food intake for subordinate birds.

Of the >400 birds, 378 (83%) were lured by food and trapped in 6 flight pens measuring 15x15x3 meters, adjacent to the aviary. The birds were held for roughly 5 weeks during February and March 1998 and 1999. This time period varied from several days to 6 weeks for each individual depending upon when it was caught. These birds were weighed and measured once at some time between mid-February and mid-March, prior to the initiation of nesting which began in late March. I measured mass, bill chord, bill length, bill depth at the base of the nares, wing chord (1999 only) and tarsometatarsal length. Body condition was estimated as the difference between observed and expected mass predicted from body size (Brown 1996, Jacob et al. 1996). Expected mass was predicted through a linear regression of body mass upon a body size factor score. The body size factor score was derived through principal components analysis of all the measurements taken prior to nesting. I estimated body condition in 226 birds in 1998 and 378 birds in 1999 once during the two months prior to nesting.

I categorized the ultimate fate of nesting attempts by all individuals for which I estimated body condition. In 1998, nesting attempts were categorized as “no attempt to breed”, “courting or nest building with no egg production”, “nesting with egg production” and “successful hatching”. In 1999, the nesting stage categories were the same, but I split the “courting with no egg production” into three categories: birds that

were observed courting and copulating over several days but not observed nest building, birds that were observed nest building, and birds that were observed copulating but never courting or nest building. I compared pre-season body condition with ultimate outcome of nesting using one-way ANOVA. I used age, nest density, and male morphologic traits (bill length and body size factor score) as other dependent variables in the ANOVA. Nest density was determined as the ratio of the number of other nests present when a pair started nest building to the ground area covered by whole colony during its maximum size. In 1999, I also looked for evidence of any birds re-nesting with the same mate from the previous season in order to account for the effect of prior experience on nesting success. However, I found no re-pairings during the course of the study. In order to track changes in body condition during the breeding season, I weighed individuals repeatedly throughout the 1999 nesting season. I used feeding stations attached to electronic balances that could be read remotely. Ibises were weighed as they fed from a dish.

I measured the importance of body condition experimentally, by manipulating pre-nesting body condition of a random sample of birds from the aviary through supplemental feeding, and compared their breeding success with a control group on the normal diet. I anticipated that this random choice would control for possible effects of dominance status and parasite load, which I was unable to measure directly. Prior to the 1999 season, two groups of 30 birds were held for 54 days in identical 15x15x3 meter adjacent flighted pens. Birds were captured and body mass recorded both before and after treatment. I supplemented the diet of one group of birds, while keeping a control group on the normal aviary diet. The experimental group was fed to satiation once a day on Atlantic silversides to increase availability of fat in these individuals. I compared the timing and ultimate fate of breeding attempts of individuals in these two groups after their return to the aviary on March 19, 1999.

This experiment was conducted concurrently with an annual large-scale trapping effort involving all birds in the aviary (described above). This was conducted by the staff at Disney in order to band juveniles, check records and overall health of the flock. All of these birds were released back into the aviary on March 19 after being held for approximately 1-6 weeks. Nest building behavior was first observed in the aviary by the last week of March in both years of the study.

## RESULTS

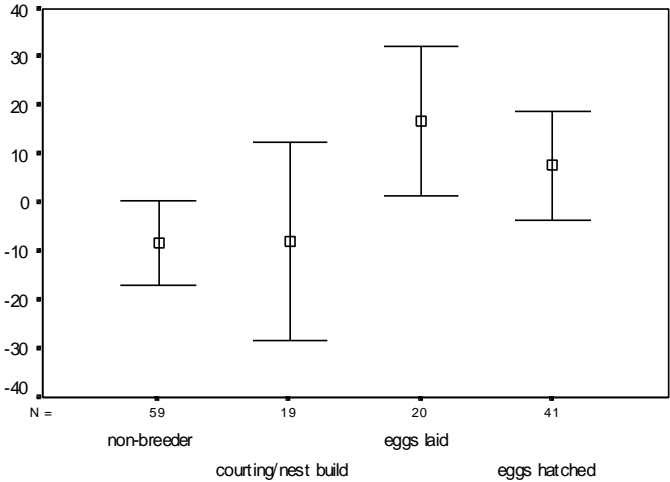
### PRE-BREEDING BODY CONDITION AND REPRODUCTION

The proportion of birds that produced eggs or young in the aviary did not differ significantly between 1998 and 1999 (males,  $\chi^2 = 1.26$ ,  $p = 0.15$ ; females  $\chi^2 = 0.329$ ,  $p = 0.64$ ). 43.3% of the males and 34.4% of the females in the aviary produced eggs or young in 1998 and 33.9% of males and 29.8% of females did so in 1999. In 1998, I found lower levels of pre-breeding body condition in individuals of both sexes who did not attempt to nest or whose nests did not produce eggs, compared to those whose nests did produce eggs (Figure 7). This difference was significant for females but not males (females:  $t = -2.551$ ,  $p=0.023$ ). Courtship was not observed closely in 1998, so during that year, birds that did not progress beyond the courtship phase were categorized either as attempting to nest but not producing eggs, or as making no attempt to nest.



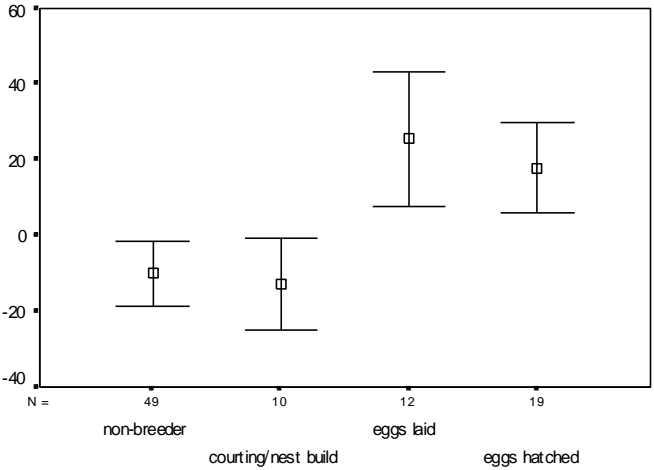


MALES



LAST NESTING STAGE OBSERVED

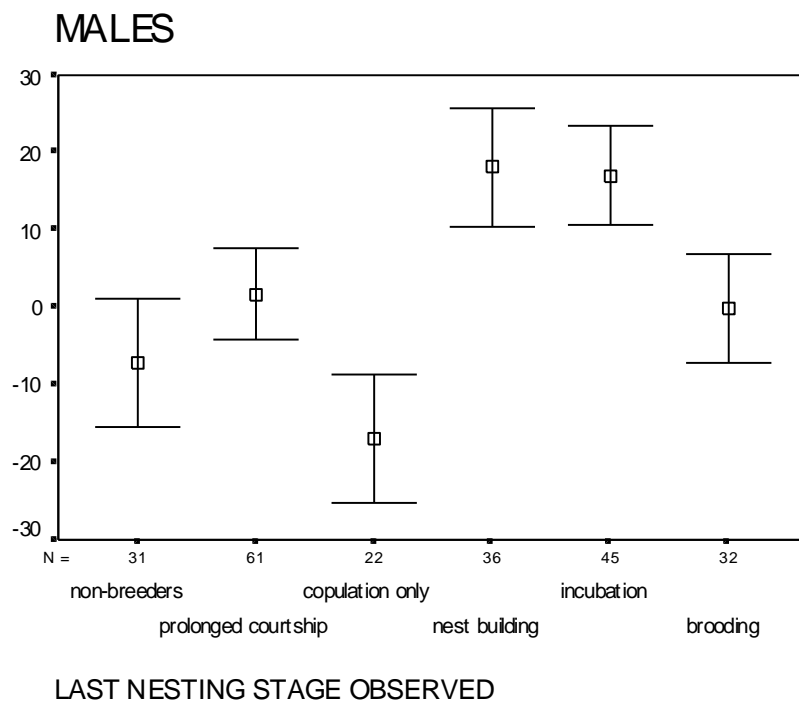
FEMALES



LAST NESTING STAGE OBSERVED

Figure 7. Pre-season body condition in grams over expected mass (mean  $\pm$  1 SE) for last observed nesting stage in a group of 229 captive Scarlet Ibises during the 1998 breeding season.

In 1999, I distinguished between courting and nest building birds, and found a significantly lower pre-season body condition in both males and females observed only courting or never attempting to build a nest, compared to those that built nests or laid eggs (males,  $t = -2.239$ ,  $p = 0.026$ ; females,  $t = -2.34$ ,  $p = 0.021$ , Figure 8). Mean differences in body weight in these contrasts between nesting and non-nesting groups were 18.92 grams (2.0%) for males and 31.42 grams (4.2%) for females in 1998, and 16.81 grams (1.8%) for males and 16.88 grams (2.3%) for females in 1999. In 1999, 22 males and 20 females were observed copulating with each other but were not observed courting as is typical when a pair bond is formed. These non-courting males were on average 16.95 grams below their expected mass, while the females were on average 14.83 grams above their expected mass. Non-breeding males were in significantly better body condition than non-breeding females ( $t = 2.363$ ,  $df = 100$ ,  $p = 0.02$ ).



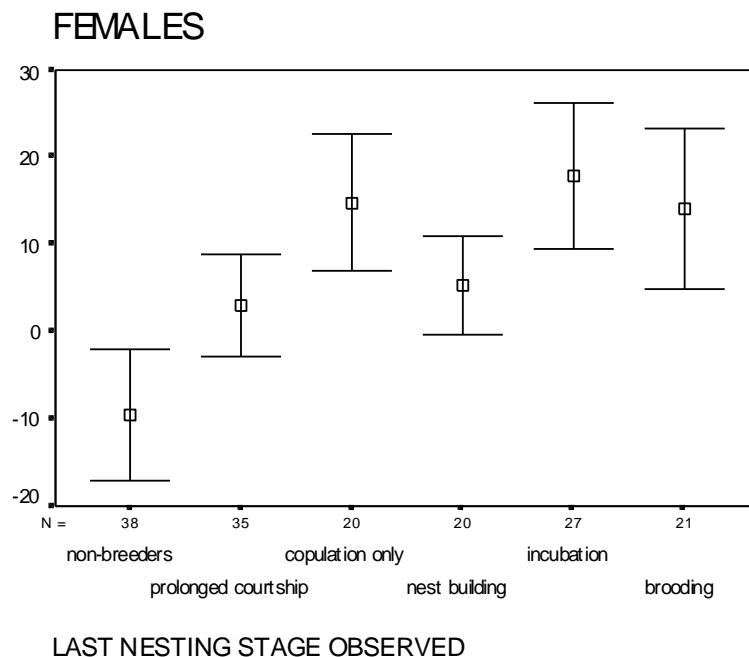
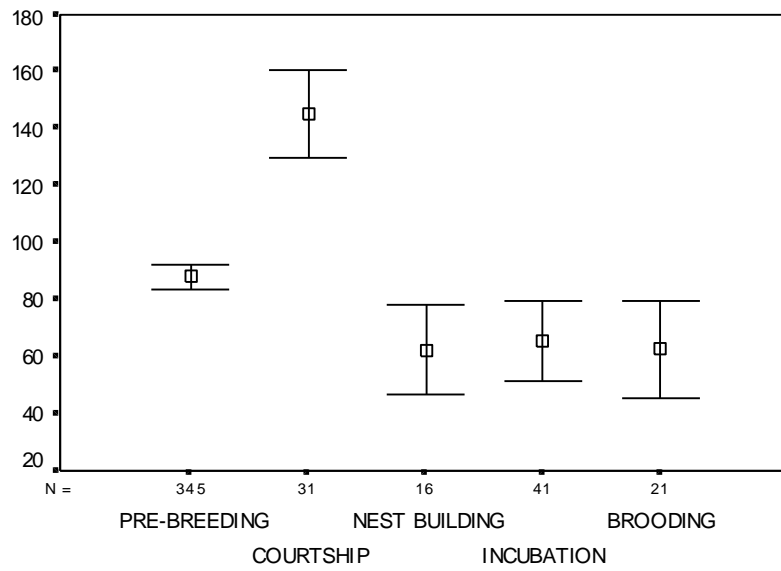


Figure 8. Pre-breeding body condition (mean  $\pm$  1 SE) for last observed nesting stage in 378 captive Scarlet Ibises for the 1999 breeding season.

#### CHANGES IN BODY CONDITION ASSOCIATED WITH REPRODUCTION

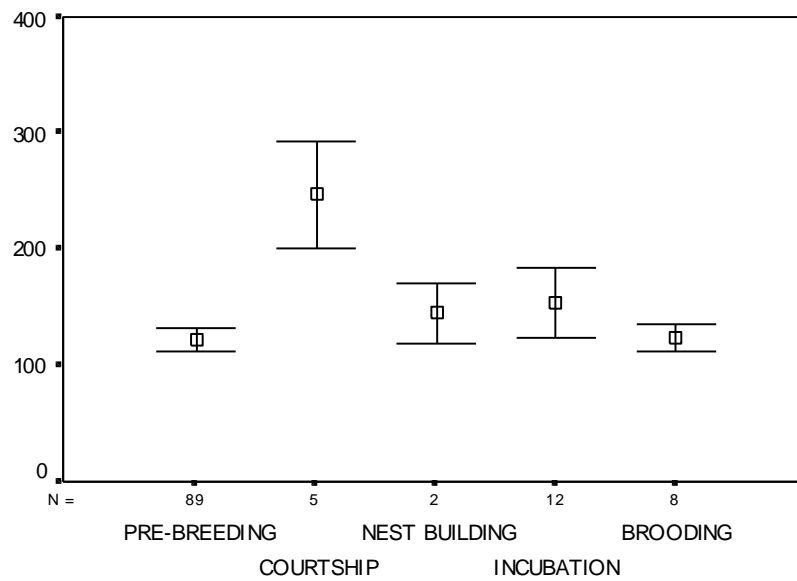
Body mass of all birds monitored on feeder scales increased an average of 107 grams in the period after their release and prior to nesting with no significant differences in the amount of increase between successful (=laid eggs) and unsuccessful breeders. Breeding males increased an average of 67.78 grams (7.1%) from the non-breeding stage (n = 248) to the courtship stage (n = 28)(Figure 9). Breeding females increased an average of 132.29 grams (16.5%) from the non-breeding stage (n = 58) to the courtship stage (n = 6)(Figure 9). During incubation, males lost an average of 43.21 grams (4.6%) (n = 14;) while females lost an average of 21.67 grams (2.9%) (n = 3). Females varied significantly in body condition throughout the nesting stages ( $F = 6.78$ ,  $p < 0.001$ ) while male condition followed a similar trend but did not vary significantly (Figure 9). The most pronounced difference between nesting stages was marked by males and females exhibiting the highest body condition during courtship.

## MALES



## NESTING STAGE

## FEMALES



## NESTING STAGE

Figure 9. Body condition (grams over expected mass) of 332 captive Scarlet ibises during subsequent nesting stages.

#### OTHER CORRELATES TO REPRODUCTIVE SUCCESS

There were no significant differences in mean age of successful and unsuccessful breeders, in either sex. However, failure to progress beyond the courtship stage was common when old males were paired with young females (Figure 10).

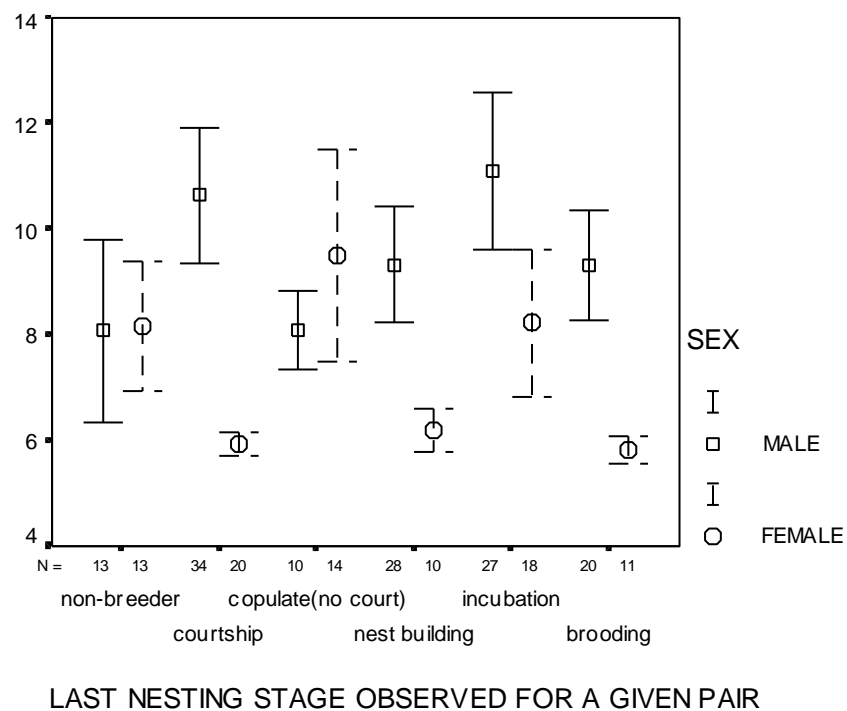


Figure 10. Mean age for last observed nesting stage in a group of 378 captive Scarlet Ibises during the 1999 breeding season.

There were no obvious male morphologic traits, such as size, that were associated with nesting success. Successfully nesting females had significantly larger body size factor scores ( $t = -2.868$ ,  $p = 0.005$  in 1999 and  $t = -2.321$   $p = 0.027$ ) than non-successful females. We found no birds that re-nested in 1999 with the mate they had paired with in 1998. Previous nesting experience with particular individuals therefore was not an important factor contributing to nesting success.

#### SUPPLEMENTAL FEEDING EXPERIMENT

During the 5 weeks that the experimental and control groups were held separately from the rest of the aviary, the supplemented group gained significantly more mass (mean = 108 grams) than the control group (mean = -39 grams) ( $t = -11.5$ ,  $p < 0.001$ ). However, I found no significant differences between supplemented birds and controls in either nesting success, or timing of breeding when returned to the aviary.

#### DISCUSSION

In both years of study, I demonstrated a significant association between pre-breeding body condition and the stage of reproduction achieved. The mean difference in pre-breeding body condition between breeders and non-breeders, (16-18 grams for males and 16-30 grams for females), represents about 44% of the typical estimated fat component in the body of an 800 gram bird based upon allometry given in (Calder 1984). I observed individual variation in pre-breeding size-corrected mass ranging on the order of 30% above and below expected mass for males and females of a given size. In one case, a

nearly starved female was found to be at only 69% of her expected mass. I estimate that the potential energetic value of the body condition differences that I report between breeding and non-breeding birds, to be capable of supporting about 1/5 the energetic cost of foraging flights during one breeding attempt by an ibis at a typical colony during a typical season (assuming two 50km flights per day) (Pennycuick 1989). So, not only is this difference between breeding and non-breeding birds statistically significant, the magnitude of the difference is biologically significant as well.

I was unable to influence breeding status or success by supplemental feeding, even though I was able to achieve marked differences in body condition. This result seems to contradict the evidence (above) that body condition influences breeding success. However, there are several lines of evidence that suggest that the experiment was confounded. First, my experiment was confounded by the fact that body condition within the aviary (non-experimental birds) increased overall in both sexes just prior to nesting. This suggests that birds on the normal aviary diet (including control birds) were able to fatten up in a short period immediately prior to breeding. Both control and experimental birds began nesting on average five weeks after their release into the aviary. In our remote monitoring of body condition in the aviary, I observed some individuals increase in mass by 100 grams in as little as two weeks suggesting that food was not limiting to many individuals. Thus, the differences in body condition I established through supplemental feeding were probably overwhelmed by pre-breeding hyperphagia. This pattern of mass gain suggests that increased body condition is a precursor to breeding, and that mass gain can be accomplished in a short period immediately prior to breeding.

That non-breeding males were in significantly better body condition than non-breeding females is likely related to the male-biased sex ratio (60/40 male to female) and suggests that some males may have not been able to nest due to a lack of potential mates, despite being in good body condition. Alternatively, males may need to be in a higher threshold body condition because they need to endure long periods of fasting.

Captive Scarlet Ibises cannot be readily characterized as only either a capital or an income breeder. The pattern of increases in pre-breeding body condition, while substantial, does not conform to readily known examples in either category. The magnitude and speed of body mass change in both sexes of our ibises is similar to that of



female wood ducks (*Aix sponsa*), an income breeder that relies upon pre-laying hyperphagia to acquire lipids necessary for egg production (Drobney 1980). Income breeders typically only show an increase in body reserves just a few days before egg production. Unlike wood ducks, the ibises in our study peak in body mass during the pre-nesting period rather than just prior to the laying period. Body reserves increase significantly well before the breeding season in high latitude capital breeders. Male and female Cackling Canada Geese (*Branta canadensis minima*) exhibit a peak of a 20-30% increase in mass during the pre-laying period (Raveling 1979). However, Scarlet Ibises exhibit on average an 11.8% increase in mass. And, unlike in the female Lesser Snow Goose (Ankney and MacInnes 1978), another high latitude capital breeder, the mass loss in male and female ibises does not continue steadily throughout the nesting cycle. It only occurs right after courtship. This may be the result of a captive artifact in our study. Unlike a typical ibis colony, our nesting birds could feed readily at the colony site, and their energetic needs were probably considerably reduced by comparison with a natural situation.

Do the reproductive energetics of the Scarlet Ibis show similarity to other nomadic, colonial birds? Jones and Ward (1976) studied the reproductive energetics and nutrition of a tropical colonial passerine, the Red-billed Quelea, *Quelea quelea*. Female Quelea increased in mass only several days prior egg production and then lost a significant amount of their mass during the laying period. When plenty of food was not present directly in the vicinity of the colony, some birds starved to death by the time the third egg was produced. Not all of this mass loss could be attributed to egg formation and the authors suggested that females may either fast during egg production or may be otherwise constrained by their time budget during nesting. Males also lost significant mass, but did this earlier than females during the courtship and nest building period. The authors credited this to the haste in which males must construct nests, sing and court females. Scarlet Ibises show similarities to the Red-billed Quelea in regard to this reliance on body condition for initiation and maintaining the earliest stages of reproduction. In both species, the peak in body reserves observed during courtship is suggestive that energetic demand was greatest at this time.

What causes high energy expenditure in Scarlet Ibises during courtship? Extra-pair copulations and nearly continuous mate guarding were evident in wild populations of White Ibises (Frederick 1987). I observed in our study that 24% of the copulations occurred outside of socially bonded pairs. This was similar to wild populations as well (Frederick 1987). Male ibises may have to rely upon their larger size and greater fasting endurance during courtship in order to mate-guard during the female's most fertile period. Bildstein (1987) demonstrated that male White Ibises do not forage more efficiently in order to make up for the metabolic needs of being larger. Therefore, they must forage longer. So fat reserves were probably very important for enduring the courtship period. This also suggests that perhaps body size was not constrained to be optimal for foraging in males. And, it may have been a sexually selected trait that is supported by surplus income. Females may also expend substantial energy while frequently courting and switching mates during courtship. However, those costs have not been measured and because females are apparently more able to leave the colony to feed during courtship, they may not have the same pressure to fast.

The relevance of my results to wild populations of this species must be gauged cautiously. The captive birds were more crowded and many individuals could feed in much closer proximity to their nests than their wild counterparts. However, the rapid period of fattening that I observed immediately prior to reproduction in this captive group is potentially significant in characterizing the reproductive energetics of this species and other ciconiiform birds. Whether changes in body condition are a cause or a consequence of breeding is much harder to judge. The failure of supplemental feeding to affect reproductive outcome or timing could also be the result of a pseudo-replication problem in that due to lack of aviary back-holding space, I was only able to produce one replicate with this captive group.

However, I conclude that captive Scarlet Ibises, and perhaps also wild populations, rely upon pre-breeding hyperphagia to create the modest amount of body reserve necessary during the pre-nesting/courtship period. This period is relatively close in time to the initiation of breeding (approximately 10 days), and there seems to be the opportunity to elevate body condition rapidly during this time, even for birds in initially poor condition. Reliance upon body reserves during pre-nesting is likely related to the

energetic costs incurred during courtship, particularly when males may refrain temporarily from feeding. After the formation of social pairings, all other duties at the nest appear to be more or less equally shared (Frederick 1987). This allows for individual feeding forays from the colony at least several times a day. And therefore, reproductive costs incurred in the later stages of reproduction can probably be covered by increased feeding rates.

## ACKNOWLEDGEMENTS

I would like to thank Beth Stevens, Mary Healy, and the rest of the staff of Disney's Discovery Island for making this research possible. I also thank Heather Randle for assistance in the collection of data and Dr. Richard Kiltie for instruction and comment on the analyses. This work was supported by a grant from the U.S. Army Corps of Engineers.

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## BIOGRAPHY

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