

Selection for Sexual Bill Dimorphism in Ibises: An Evaluation of Hypotheses

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Abstract.—Male Scarlet Ibises (*Eudocimus ruber*) and White Ibises (*Eudocimus albus*) have bills that are on average 22% longer than females, yet only half of this difference can be attributed to body-size differences. In this work it is suggested that the sexual dimorphism in bill length and bill shape is based in large part upon the role of bill length in determining the outcome of male bill-sparring contests. Sexual differences in bill morphology and behavior were investigated in a captive flock of 350 Scarlet Ibises. In 29 instances of males sparring with males in contests prior to breeding and in 11 instances of nest take-over during breeding, no significant differences in age, body size, or body condition between winning and losing males were found. 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 in captivity. 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. In addition, among 16 of 23 ibis species for which information was available, sexual dimorphism in bill length was positively associated with colonial nesting but was not associated with group foraging. This result supports the theory that close proximity during nesting is one feature that may facilitate bill sparring between males, resulting in selection for longer bills. Received 19 July 2006, accepted 18 December 2006.

Key words.—sexual dimorphism, bill length, sexual selection, bill sparring, male-male competition.

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In sexual contests over mating opportunities, success is often dependent upon relative rather than absolute trait size. This often leads to evolutionary escalation in size of body, weapons or displays (Andersson 1994). Therefore, when sexual selection is present, small relative differences among males become very important in driving evolution of size dimorphism. This often affects the distribution of the relative sizes of traits among a population. Green (2000) demonstrates that bill dimorphism often exhibits positive allometry when caused by sexual rather than natural selection (i.e., relatively larger traits in larger individuals).

The degree of sexual dimorphism in bill length in birds often exceeds sexual dimorphism in body size (Coulter 1986; Bond *et al.* 1991; Lauro and Nol 1995), and is probably influenced by multiple selective forces surrounding feeding and fighting. Among species, sexual dimorphism of the bill is often 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). Lauro and Nol (1995) offer three non-exclusive hypotheses to explain sexual dimorphism in bill morphology in birds. Sexual dimorphism in bill length may have arisen to reduce sexual competition over limited resources (usually food), to increase the partitioning of reproductive roles, or may have resulted from sexual selection and male-male competition.

Empirical studies have suggested that niche divergence in feeding habits is not a factor in bill dimorphism in gulls (Ingolfsson 1969), Greater Shearwater (*Chionis alba*) (Shaw 1986) or other Charadrii (Szekely *et al.* 2000). However, Radford and Du Plessis (2004) conclude that ecological niche divergence, not sexual selection, is responsible for maintaining a 36% longer bill in the male Green Woodhoopoe (*Phoeniculus purpureus*). This suggests that there is no single reason for bill dimorphism in different groups of birds.

As a group, ibises (subfamily Threskiornithinae 23 species, 14 genera) differ widely with respect to social feeding and mainte-

nance of breeding territory. They also exhibit a wide range of sexual dimorphism in both body and relative bill size. Approximately half of these species exhibit almost no sexual dimorphism. The colonially nesting White/Scarlet Ibis (genus *Eudocimus*) demonstrate the most pronounced sexual dimorphism. Male Scarlet Ibises (*Eudocimus ruber*) have bills that are on average 22% longer than those of females (Hancock *et al.* 1992). Yet only about half of this inter-sexual difference in bills is represented in tarsal length and therefore, sexual bill dimorphism does not seem to be attributable to a body size scaling effect alone.

In White Ibises (*Eudocimus albus*), sexual size dimorphism in the body and bill has been attributed to both natural and sexual selection. Kushlan (1977) proposed that larger male White Ibises were better able to defend the nest from conspecifics or predators than smaller males and were also able to dominate extra-pair females in mating interactions. However, later research showed that male extra-pair mating success was not based on the ability of males to dominate females (Frederick 1987). Bildstein (1987) 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, or be a sexually selected trait.

Previous hypotheses explaining bill dimorphism in ibises have assumed foraging niche separation is selectively favored by greater inter-sexual competition in socially foraging species like the White Ibis (Bildstein 1987, 1993). Alternatively, if sexual differences in bill length have evolved at least partly in response to nest defense against conspecifics, we might predict that longer-billed males would be more likely to win aggressive contests at nests than shorter-billed males. Additionally, if nest sites or mates are limiting and long bills confer dominance, then longer-billed males would be more likely to nest and might also be expected to nest earlier in the season. And unlike niche separation, male competition and sex role partitioning could create a trend among ibis species where sexual bill dimorphism is associated with sociality. In this study, we investigate the role of potential selection pressures in

maintaining sexual dimorphism in bill length in colonial ibises by testing the predictions of these hypotheses. First, we describe sexual variation in bill and body size and shape in a group of 454 captive Scarlet Ibis (*Eudocimus ruber*). Second, we evaluate the hypothesis that bill length affects the outcome of male contests by analyzing 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, we present interspecific comparisons of sexual dimorphism in bill length and incidence of both colonial nesting and group foraging in 16 species of ibises.

METHODS

Study Area

Morphometric and behavioral studies were conducted during February-June of 1998 and 1999 with a captive flock of 454 full-flighted Scarlet Ibises held in a 3,085 m² aviary at a large theme park (Disney World, Orlando, Florida). All individuals older than one year of age ($\approx 90\%$) were identifiable by numbered and colored leg bands easily visible with binoculars. The aviary contained mature trees allowing the ibises to nest roughly 15-20 m above the ground. All interspecific comparisons were based upon measurements and descriptions in Hancock *et al.* (1992).

Sex Determination

The study included 114 Scarlet Ibises whose sex had been determined through observations of copulation position, and whose eggs also later hatched during the 1999 nesting season. A canonical discriminant function analysis was conducted on the rest of the aviary 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, any male-male single sex pairs were probably eliminated from the sample. Female-female pairs were not as easily controlled for in this manner since extra-pair copulation did occur in the aviary. Twenty four percent of all copulation occurred outside of established social pairs, as may be typical in a non-captive situation (Frederick 1987).

Morphometrics

In February and March of 1998 and 1999, 378 adults were weighed and measured. Measurements included log 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). Measurement error estimated from a subsample of 144 birds

was 3.8% log mass, 1.7% bill chord, 1.8% bill length, 3.7% bill depth, and 7.5% tarsal length (wing chord is unknown). The components of sexual size and shape variation were separated using a correlation-based principal components analysis (PCA) (Manly 1994). Size and shape variation were also analyzed in a similar fashion within both sexes to compare the degree of male and female variation in morphology. Body condition index was taken as the residual (observed minus expected log body mass) around the reduced major axis regression of log body mass upon a body size index (Green 2001; Hammer 2001). The body size index was the first principle component score derived from the PCA as it exhibited strong positive loadings (correlations) on all of the measured variables that were input into the analysis. Degree of allometry of bill length, wing chord and tarsal length were compared to test the idea that sexually selected traits (i.e., bill length) exhibit positive allometry as opposed to isometry in naturally selected traits.

Male Bill-Sparring and Nest Take-Over

Two hundred and nineteen bill sparring bouts between pairs of male Scarlet Ibises were observed during the month of February 1998 just prior to the start of the breeding season. A bill-sparring bout began when two birds faced each other and attempted to strike each other at least once with the bill while facing each other. Bouts were recorded opportunistically and only during the early morning hours (07.00-11.00 h) and occurred mostly on the ground. Bill-sparring events were only recorded more than ten feet away from feeding stations and nests in order to standardize for confounding factors (e.g., hunger, territoriality, occupying nest site advantage etc.) that might have affected the outcome. Males often flew into the air during conflicts that began on the ground, with intensely rapid bouts of opened bill sparring ("Supplanting Flight", see Hancock *et al.* 1992). When bill-sparring bouts occurred on the ground, the losing male was defined as the bird that first retreated. If the contest went into the air, the loser was the bird landing farthest from the spot where the contest began. Twenty three instances of nest take-over in the aviary were recorded 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 (see Frederick 1986). In eleven cases, morphometric measurements of both the displacing and displaced male from each pair involved in a nest take-over were obtained. Comparison of overall size, age, body condition, tarsal length, wing length, bill depth and straight and curved bill length of males winning and losing both Supplanting Flights and nest take-overs was performed using paired t-tests.

During 1998 and 1999, the latest stage of nesting achieved by all nesting pairs within the aviary was recorded. The morphology of males among these categories was compared to determine if nesting success was primarily affected by bill length. The date on which eggs hatched was also recorded to determine if a male's morphology affected the timing of his nesting within the colony.

Taxonomic Comparison of Sexual Dimorphism, Group Foraging and Colonial Nesting in Ibises

Mean male and female bill and wing lengths were obtained from Hancock *et al.* (1992), and male to female bill length and wing length ratios for all ibis spe-

cies were computed for which data were available. Species were classified as colonial, loosely colonial (breeding both solitarily or in small groups), or strictly solitary breeders. The degree of sexual bill dimorphism relative to overall size dimorphism in a given species was calculated by dividing the average male to female bill length ratio by the average 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). 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. When multi-branch nodes arose due to unresolved parts of the phylogeny, the variables of interest were treated as weighted contrasts within each node, and thus were summed and then divided by the number of branches in the node.

We used the phylogeny from Sibley and Ahlquist (1990) as portrayed in Sheldon and Slikas (1997) and added the genus *Geronticus* (Waldrapp Ibis) paired with the genus *Boystrichia* (Olive, Hadada, and Spotbreasted Ibises) as suggested by Fry *et al.* (1985). We also paired the genus *Eudocimus* (Scarlet and White Ibis) with *Plegadis* (Puna, Glossy and White-faced Ibises) as suggested by Mayr and Short (1970) and Olsen (1981) and combined congeners within *Threskiornis* (Straw-necked, Australian White and Sacred Ibises) and *Boystrichia* (Olive, Hadada, and Spotbreasted Ibises) adding them to Sibley and Ahlquist's tree by creating two multi-branch nodes (Fig. 1, Table 1). All branch lengths were considered equal in the analysis. Dummy variables were used for coding group foraging and coloniality. Values of 1.0 and 0.5 and 0.0 were used for "yes", "intermediate" and "no" respectively. Scarlet and White Ibises were (*Eudocimus* spp.) considered conspecific (Ramo and Busto 1987).

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 categorizing individuals of known behavioral sex (Wilk's lamda = 0.21, $P < 0.001$ for all birds; mean probability correct in males = 98.1% and in females = 96.4%). Our function was:

$$\begin{aligned} \text{score} = & -0.002 \cdot (\text{mass}) + 0.204 \cdot (\text{billchord}) \\ & + 0.598 \cdot (\text{billlength}) + 0.292 \cdot (\text{billchord}) \\ & + 0.683 \cdot (\text{tarsuslength}) + 0.227 \cdot (\text{wingchord}) \\ & - 26.808 \end{aligned}$$

A positive score indicated male, a negative, score female.

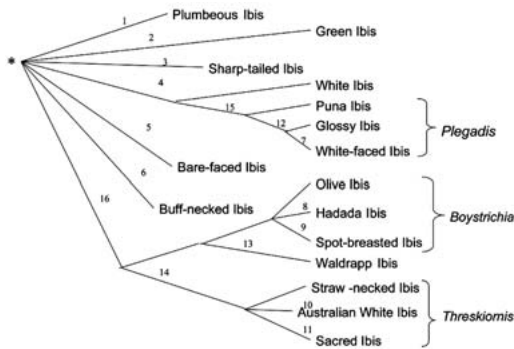


Figure 1. A phylogeny for ibises derived from Sheldon and Slikas (1997). Phylogenetic contrasts are numbered as in Table 4. For example, contrast 16 is the difference in the average value of the *Boystrichia/Threskiornis* clade and the weighted sum of the *Plegadis* group, green ibis, plumbeous ibis, sharp-tailed ibis, bare-faced ibis and the buff-necked ibis.

Intersexual Differences in Body Size and Shape

Most of the total variance in size and shape between the sexes in the Scarlet Ibises was due to a significant difference in body size (82% of variance, $t_{223} = 47.2$, $P < 0.001$, Table 2) with males being significantly larger than females. The remaining 11% variation was due to differences in body shape (i.e., the remaining principal components). Most (67%) of the variation in shape was in proportional bill length and depth (principal components 2 and 3). The small amount of remaining variation in shape between sexes was hard to interpret from the loadings in Table 1. Component scores on all the principal component axes reflected nearly identically about zero indicating very similar pat-

Table 1. A principal component analysis of two body and three bill measurements in a captive group of 378 unsexed Scarlet Ibises At Disney World, Orlando, Florida, 1998-1999.

Principle Component	1	2	3
% variance explained	82	7	5
Bill Chord	0.97	-0.11	-0.14
Bill Length	0.96	-0.13	-0.16
Bill Depth	0.84	-0.33	0.42
Tarsal Length	0.92	-0.05	-0.22
Wing Chord	0.82	0.50	0.20

terns of size and shape distribution within the sexes. However, males exhibited significantly more variance in bill and mass measurements than did females ($N = 223$, $F = 1.3$, $P < 0.001$ for mass; $F = 1.3$, $P < 0.001$ for bill chord; $F = 1.6$, $P < 0.001$ for bill length; $F = 1.2$, $P = 0.02$ for bill depth). There was no significant sexual difference in variance of tarsus and wing chord measurements. Regression of shape variables (PC 2, 3, 4, 5 and 6) upon size (PC 1) showed that none of the inter-sexual variation in shape was size dependent. Scarlet ibises showed large sexual dimorphism in size but little in shape, the only notable shape variation being the relative size of the bill which was longer in males.

Bill curvature was positively correlated with curved bill length in males but not females (males; $r = 0.26$, $P = 0.002$, $N = 133$ and females; $r = 0.02$, $P = 0.84$, $N = 91$), though the strength of the association in males was weak. Bill curvature was negatively correlated with straight bill length (bill chord) in females but not males (males; $r = -0.11$, $P = 0.22$ and females; $r = -0.29$, $P = 0.006$), though the strength of the correlation for females was low. So, in males but not females, degree of curvature tended to increase with bill length. There were no differences in the allometry of male bill length compared to other male or female traits plotted against body size index.

Bill Length in Relation to Dominance and Reproductive Parameters

In the 29 recorded instances of males bill-sparring with males, no significant differences between male winners and losers in log body mass, age, tarsal length, body condition index or body size index were found (Table 2). However, winning males had significantly greater bill length and bill chord than did losing males (Table 2). This suggests that bill length is the only important factor determining the outcome of supplanting flights. Because it is very likely that only males of similar size were most likely to fight and to test each other in bill-sparring contests, we note that other factors such as overall size may still play a role in dominance. Females engaged in far fewer bill-sparring con-

Table 2. Average trait size and size difference between winners and losers of naturally occurring dominance contests (Supplanting flights) in male and female Scarlet Ibises at Disney World, Orlando, Florida, 1998-1999. Mass is gm \pm 1 SE, lengths are in cm \pm 1 SE except bill depth which is mm \pm 1 SE. BSI is body size index and BCI is body condition index.

Sex	Measurement	Avg. trait size	Avg. size difference	Paired t test	P value
Male vs Male	Mass	851.90 \pm 69.5	1.47 \pm 27.5	0.05	0.96
	Tarsal length	9.01 \pm 0.07	0.05 \pm 0.14	0.39	0.70
	Wing chord	28.30 \pm 0.21	0.13 \pm 0.29	0.45	0.66
	Bill length	16.44 \pm 0.13	0.40 \pm 0.15	2.70	0.012
	Bill chord	15.15 \pm 0.10	0.32 \pm 0.12	2.65	0.013
	Bill depth	18.48 \pm 0.15	0.16 \pm 0.37	0.45	0.66
	BSI	1.05 \pm 0.11	-6.48 \pm 0.16	-0.40	0.70
	BCI	-1.65 \pm 1.14	-1.67 \pm 1.41	-1.18	0.27
Female vs Female	Mass	676.30 \pm 34.0	2.83 \pm 32.2	0.09	0.93
	Tarsal length	7.77 \pm 0.15	0.14 \pm 0.26	0.52	0.62
	Wing chord	25.80 \pm 0.92	-0.35 \pm 0.44	-0.80	0.44
	Bill length	13.40 \pm 0.50	0.26 \pm 0.82	0.31	0.76
	Bill chord	12.41 \pm 0.40	0.24 \pm 0.72	0.34	0.75
	Bill depth	17.64 \pm 0.43	0.08 \pm 0.42	0.20	0.85
	BSI	-0.78 \pm 0.06	-0.08 \pm 0.13	-0.66	0.52
	BCI	-8.64 \pm 0.04	-0.01 \pm 0.01	-0.63	0.54

tests than males. Only ten instances in which complete morphology and body condition were known for both female contestants were recorded. Female bill-sparring contests seemed not to escalate to the degree of male bill-sparring contests and were usually over after one or two jabs. In females, we found no significant differences in any of the parameters between winning and losing birds.

Male bill length and bill chord (both years) were significantly correlated with hatch date (1998: $r = -0.40$, $P = 0.04$; 1999: $r = -0.49$, $P = 0.05$), indicating that longer-billed males nested earlier. No significant relationship between male bill length and the success of the nesting attempts was discovered.

During eleven instances of nest takeover, displacing males had significantly longer bill chord lengths than displaced males ($N = 11$, $t = 2.4$, $P = 0.04$). Also no significant differences between male contestants in tarsal length, wing length ($N = 11$), body mass or age ($N = 6$) were found.

Taxonomic Comparison of Sexual Dimorphism, Group Foraging and Colonial Nesting in Ibises

Using all 16 species for which sufficient data were available (Table 3), it was discovered that the degree of sexual dimorphism

in proportional bill length was positively associated with the incidence of colonial breeding ($r = 0.68$, $P = 0.005$). The degree of sexual dimorphism in proportion to bill length was not significantly associated with the incidence of group foraging ($r = 0.36$, $P = 0.18$). The incidence of colonial nesting and group foraging were correlated ($r = 0.55$, $P = 0.03$) with each other, but not as strongly as the degree of sexual bill length dimorphism and colonial breeding (Table 4).

DISCUSSION

Sexual differences in size in the Scarlet Ibis are due mostly to differences in body size rather than body shape. However, the most important source of shape variation between and within sexes is in proportional bill length. Male bills were proportionally longer, but also tended to be proportionally thinner than those of females, perhaps suggesting that there may be an upper limit to how massive a male's bill can become and still remain functional. Males with shorter bills also tended to have straighter bills, consistent with the idea that males maximize reach and thus bill-sparring ability. This pattern was not seen in female ibises.

The pattern of body size and shape variation in the Scarlet Ibis suggests that selection

Table 3. Colonial nesting, group foraging and mean values and male to female ratios for bill, wing, and relative bill dimorphism 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.

Species	n	Mean male bill length (mm)	Mean male wing length (mm)	Mean male bill length (mm)	Mean female wing length (mm)	M/F bill length ratio	M/F wing length ratio	Bill dimorphism relative to size dimorphism (1.00 = non-dimorphic)	Coloniality and group foraging
Scarlet/White Ibis	12	163.2	282.3	125.6	265.0	1.30	1.06	1.22	+/+
Barefaced Ibis	16	120.2	281.3	108.8	265.2	1.10	1.06	1.04	Intermediate/+
Glossy Ibis	18	131.0	288.3	104.2	262.2	1.26	1.10	1.14	+/+
Whitefaced Ibis	19	133.9	269.6	103.6	243.5	1.29	1.11	1.17	+/+
Puna Ibis	17	117.4	298.4	92.0	276.8	1.28	1.08	1.18	+/+
Sharptailed Ibis	13	161.6	399.7	152.7	394.2	1.06	1.01	1.04	-/-
Plumbeous Ibis	20	153.8	413.4	134.6	384.8	1.14	1.07	1.06	-/-
Buffnecked Ibis	20	149.0	402.7	138.8	389.8	1.07	1.03	1.04	Intermediate/ intermediate
Green Ibis	9	112.6	280.0	108.5	283.0	1.04	0.99	1.05	-/-
Hadada Ibis	17	134.0	353.0	134.0	353.0	1.00	1.00	1.00	-/-intermediate
Olive Ibis	NA	95.0	328.0	90.0	313.0	1.05	1.05	1.01	-/-
Spotbreasted Ibis	10	126.5	278.0	126.5	264.0	1.00	1.05	0.95	-/-
Sacred Ibis	13	170.0	383.0	146.0	362.0	1.16	1.06	1.10	+/+
Australian White Ibis	7	188.6	380.6	153.7	363.7	1.23	1.05	1.17	+/+
Strawnecked Ibis	NA	169.0	389.5	137.8	363.0	1.23	1.07	1.15	+/+
Waldrapp Ibis	NA	140.0	411.5	123.0	399.0	1.14	1.03	1.10	+/-

Table 4. 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

for sexual dimorphism of bill length is currently strong or has been strong in the past. Proportional bill length was the only body shape variable that differed greatly between sexes representing a 16.9% difference, and was a better qualitative indicator of sex than body size (i.e., with less overlap). This trait also had high variance among males, a finding that supports the idea that it is a sexually selected trait. In addition to losing bill-sparing contests, one evident cost of shorter bills in males was that it was associated with losing established nest sites. Nest take-over has been reported in the wild in several studies, and so the behavior is not necessarily an artifact of captivity (Kushlan 1973; Frederick 1986) however it is likely that nest sites and nesting material are more limiting in this study than in the wild. While male-male competition may be elevated in captivity, the proximity of males in natural colonies may cause nesting success in the wild to be partially determined by a male's ability to defend the nest from other males (Kushlan and Bildstein 1994). This study indicates that successful defense of the nest is apparently facilitated by having a longer bill. The observation that longer billed males bred earlier than shorter billed males suggests that earlier breeding may be achieved either through dominance (allowing access to mates or nests) or through more

able nest defense. Our finding that colonial species were more likely to have sexual dimorphism in bill length also supports the idea that bill length may become important in nest defense where there are frequent contests among closely-nesting conspecifics over mates and nest sites.

Because no significant association between group foraging and sexual dimorphism was discovered among ibises when controlling for taxonomic relatedness, we believe that selective pressures maintaining sexual bill dimorphism in ibises are related to taxonomically specific nesting behavior rather than general feeding habits. The observation that bill length is a key determinant in the outcome of bill-sparing bouts by captive males is consistent with the hypothesis that sexual selection is involved in maintaining and/or creating sexual bill dimorphism. This idea is also supported by the observation that no other attributes of morphology seemed to contribute to the outcome of contests between males. Among otherwise evenly matched males, a slightly longer bill may allow 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. It is also noted that in many situations

(perhaps the majority), male dominance might easily be settled without fights, on the basis of size alone. It is also noted that all possible types of dominance interaction were not measured here (only bill sparring during Supplanting Flights) 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. Nevertheless, the deciding role that bill length has in determining the outcome of fights that do occur, strongly suggests that sexual dimorphism in bill size in this species is maintained by benefits that accrue to dominant males through sexual selection.

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