SEXUAL DIMORPHISM IN THE WHITE IBIS

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Sexual dimorphism in body size has been variously accounted for in different species of birds (Selander 1972), though the phenomenon has been little studied in ciconiiforms. In this paper I analyze dimorphism in the White Ibis (*Eudocimus albus*), suggested by the few measurements in Palmer (1962) and briefly noted by Rudegeair (1975). I also discuss the potential significance of this dimorphism, especially related to food use, feeding behavior, and nesting. The morphological analysis is based on a sample of 36 specimens collected from a single population.

METHODS

All White Ibis specimens were collected in the Everglades and Big Cypress Swamp of southern Florida during the 1972 and 1973 nesting seasons. Standard measurements were made of tarsus, middle toe, wing arc, 8th primary, and central rectrix on the left side. Bill was measured as straight line distance (chord) from tip to anterior edge of nares. Body weight was taken after removal of stomach contents. Stomach contents were identified, separated, dried, and expressed as percentage of total dry weight.

RESULTS AND DISCUSSION

Both juvenile and adult males averaged significantly larger than females in all characteristics for which I have adequate samples (Tables 1, 2). Adults were most dimorphic in weight, females averaging 74% the weight of males, and most similar in measurements of the flight structures, females averaging 91% of males. Juveniles differed significantly from adults in several characteristics because of slow post-fledging growth, but sexual dimorphism was still apparent in these as well as adults.

Bills of females averaged 78% as long as bills of males, and also differed in shape and massiveness (Fig. 1). Bill dimorphism is probably the easiest sexual difference to detect in wild birds and is apparent to experienced observers when the sexes are together and in many cases when they are not. The ratio of male to female bill length is 1.25. Such a pronounced difference suggests that the sexes are using different food resources (Schoener 1965, Selander 1966). Differences in leg length, and weight (Hespenheide 1971) have also been related to differential food consumption. Hutchinson (1959) showed that ratios of trophic appendages of different species exhibiting character displacement were about 1.28, while Schoener (1965) found smaller character difference ratios, about 1.14, among species of congeneric sympatric birds and suggested (Schoener 1970) that for animals of similar morphology

TABLE 1

MEAN SIZE (G OR MM), STANDARD ERROR OF THE MEAN, RANGE, AND COEFFICIENT OF VARIATION OF MERISTIC CHARACTERISTICS OF ADULT (MORE THAN 2 YEARS OLD) AND JUVENILE (SECOND YEAR) WHITE IBIS FROM SOUTHERN FLORIDA

	Adult Males				Adult Females			
	n	x̄ ± SE	Range	cv	n	x̄ ± SE	Range	cv
Weight*	12	1036.4 ± 30.3	872.9–1261.0	10.14	16	764.5 ± 17.1	592.7–864.3	8.93
Bill	12	142 ± 1	136–148	3.12	16	111 ± 1	102–121	5.25
Tarsus	12	102 ± 3	91–110	11.81	16	87 ± 1	79–97	5.43
Middle Toe	12	70 ± 1	64–73	5.26	16	61 ± 1	56–68	5.76
Wing arc	12	302 ± 2	295–315	2.00	12	277 ± 3	262–288	3.14
Primary 8	8	216 ± 3	206–225	3.38	13	196 ± 1	188–208	2.12
Tail	11	108 ± 1	104–115	3.28	17	98 ± 1	92–105	2.75
	Juvenile Males				Juvenile Females			
	n	x̄ ± SE	Range	cv	n	x̄ ± SE	Range	cv
Weight	4	905 ± 23.7	854.8–969.1	5.24	1	771.9	–	–
Bill	4	140 ± 23	137–145	2.82	3	110 ± 2	107–113	2.86
Tarsus	3	102 ± 8	99–106	3.57	3	88 ± 1	86–91	2.63
Middle Toe	4	68 ± 1	65–71	3.86	3	56 ± 2	53–59	5.15
Wing arc	4	298 ± 3	292–304	1.90	3	260 ± 6	258–277	3.69
Primary 8	4	201 ± 1	207–212	1.12	3	188 ± 2	185–192	1.92
Tail	4	104 ± 1	103–106	1.10	3	92 ± 1	89–95	3.05

* Weights are minus stomach contents.

TABLE 2
DIFFERENCES OF CHARACTERISTICS OF WHITE IBISES IN SOUTHERN FLORIDA SHOWN IN TABLE 1

	Adult vs Juvenile		Juvenile vs Juvenile	Adult vs Adult	
	♂ vs ♂	♀ vs ♀	♂ vs ♀	♂ vs ♀	DS
Weight	*	*	–	**	73.8
Bill	–	–	**	**	78.3
Tarsus	–	–	**	**	85.8
Middle Toe	–	*	**	**	88.0
Wing arc	–	*	**	*	91.7
Primary 8	–	**	**	**	90.7
Tail	–	–	**	**	91.7

DS = Sexual difference = 100 (mean of females/mean of males), see Selander (1966).
* = Significantly different by t test at $P < 0.05$.
** = Significantly different by t test at $P < 0.01$.
– = Not significantly different.

and feeding behavior, smaller ratios than found by Hutchinson should result in the taking of different foods. The large bill-size ratio of the White Ibis indicates that selection for character dimorphism within this single species has resulted in a difference of similar magnitude to that for competing species.

However, I found little evidence of resource partitioning. In nearly all instances, I observed no discernible difference in the feeding behavior of male and female White Ibis. An alternative method of resource division would be for ibis to forage allopatrically. Because they possess larger bills and legs, males could forage in deeper habitats than females. My limited data show that they do this in only 2 habitats, canal-edge marshes (19 observations of ♂♂, 2 of ♀♀) and offshore on coastal shoals (18 observations of ♂♂, none of ♀♀). However neither habitat is heavily used by ibises. I found no differences between sexes in the mixed species flocks feeding in the Everglades, the primary feeding habitat in southern Florida (70 observations). As feeding site data are somewhat equivocal, I collected males and females feeding in the same locations on 3 occasions in the heavily used fresh water marshes. In no case are large differences in the food taken by the sexes apparent (Table 3). The 2 sets of Everglades samples show overlap between sexes of 98 and 99% and the Cypress Swamp samples have a 75% overlap (Morisita's index of overlap, Horn 1966). Although Earhart and Johnson (1970) suggested that consumption of numerous and relatively small prey items, such as is the case in ibises, results in the lack or reduction of dimorphism, White Ibis appear not to follow this generalization.

It remains possible, of course, that the sexes could be taking different

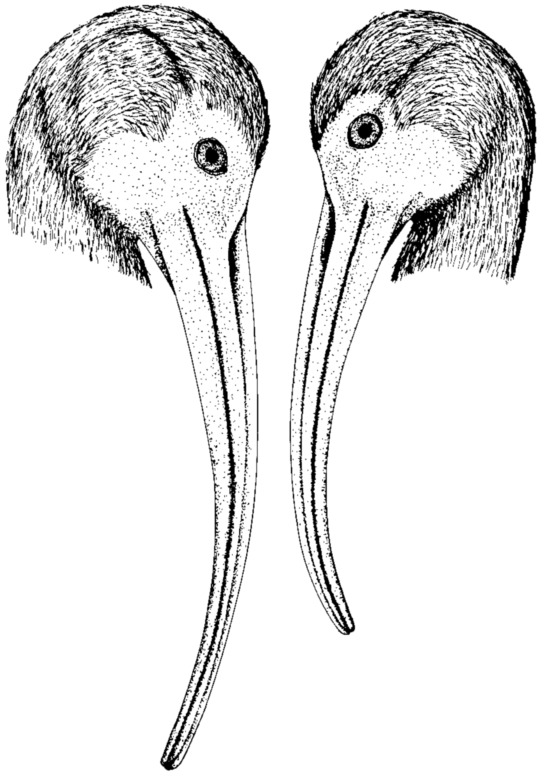

FIG. 1. Sexual dimorphism in the bill length and bill shape of the White Ibis. Male left, female right.

foods, particularly during the non-breeding season when water levels in the interior marshes of southern Florida are deeper and most birds feed along the coast in tidal situations. Male ibises may also take their prey from deeper in the sediment than females and thus take the same prey type without competition.

Sexual dimorphism in the White Ibis, as in many species (Selander 1972), is likely adaptive in reproduction. The larger size and aggressiveness of males is important because males spend much of their time defending the nest. In the first 2 weeks after hatching, the male broods during most of the daylight hours (Kushlan 1976) when predators and other colony members are active and thus protects the nestlings until they are large enough to be left alone.

Dimorphism may also be of advantage to females in nesting. A smaller

TABLE 3

FOOD OF MALE AND FEMALE WHITE IBIS COLLECTED AT THE SAME TIME AND LOCATION*

	Everglades 1		Everglades 2						Cypress Swamp			
	♂	♀	♂	♂	♂	♂	♀	♀	♂	♂	♀	♀
Prawn, *Palaemonetes*						0.2						
Crayfish, *Procambarus*	85.0	79.5					5.1		67.2	99.5	72.0	41.7
Dragonfly, Odonata	2.4	13.6	0.2						0.3		1.0	5.1
Water bugs, Hemiptera	0.5						3.0	9.6				
Diving beetles, *Hydrophilus*	0.1	1.6								1.4		
Snails, Mollusca									32.5		27.1	41.0
Fish, Pisces			95.6	100.0	100.0	95.4	91.8	90.4				
Frog, *Rana*		2.5	4.2			4.4						13.9
Newt, *Diemyctylus*	12.0	2.7										
Plant	0.1	0.02	0.06									

* Data expressed as % of dry weight of stomach contents.

female may be better able to enter the male's territory during pair formation. Dimorphic enlargement of the gular sac of the female also functions during pair formation (pers. obs., Rudegeair 1975). A primary pairing behavior consists of intertwining downward head thrusts described by Meyerriecks (*in* Palmer 1962). In early pair formation, the female when bringing her head upward turns it sideways to the male and holds that posture rigidly, thus displaying in profile the small bill, bright red facial skin and enlarged gular pouch. Rudegeair (1975) suggested a similar function during another display. Thus dimorphic development of the pouch and the female's smaller size probably function together in pair formation. During the first 2 weeks after hatching, the burden of food gathering falls primarily on the female. This is similar to the situation in some raptors in which the male (which is smaller) is the major food provider through the early stages of nesting. It has been argued (e.g., Reynolds 1972) that smaller size is adaptive in increasing foraging efficiency on numerous and agile smaller prey. Such reasoning is not transferable from actively pursuing predators to searching predators, such as White Ibis, that eat passive food items as they are encountered. However, the smaller size of the female ibis does suggest that the amount of food needed for her own metabolism may be less than that of the male (Mosher and Matray 1974) and so a greater percentage of the foraging effort can be allotted to obtaining food for the young. This may be a selective force maintaining the smaller size of the female.

Body size differences may also permit the promiscuous mating behavior that characterizes this species (Kushlan 1973). Irrespective of the adaptiveness or maladaptiveness of promiscuity, the smaller size of the female may make it advantageous for her to permit promiscuous copulation rather than ineffectually attempt defense. The larger size of the male confers advantage in both dominance and mating interactions, much as the case in polygynous systems.

Thus sexual dimorphism in size is a recognizable characteristic of the White Ibis that probably serves several functions within the adaptive complex of the species. My field observations, examination of small numbers of museum specimens of known sex, and comments in the literature suggest that other ciconiiforms including the Roseate Spoonbill (*Ajaia ajaja*), Glossy Ibis (*Plegadis falcinellus*), White-faced Ibis (*Plegadis chihi*), Scarlet Ibis (*Eudocimus ruber*), Sacred Ibis (*Threskiornis aethiopica*), American Wood Stork (*Mycteria americana*), and the Marabou (*Leptoptilos crumeniferus*) are also sexually dimorphic in body size. Herons appear to be less obviously dimorphic, if at all, although statistical differences exist in some species (Browder 1973). For species in which dimorphism is recognizable in the field, body size difference becomes a promising tool in behavioral and ecological study. Because of this, comparative study of character dimorphism in other ciconiiforms is desirable.

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