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PLUMAGE AND BEHAVIORAL DEVELOPMENT OF NESTLING WHITE IBISES

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ABSTRACT.—We describe the physical characteristics and behavioral development oi 17 hand-reared and more than 400 parent-reared nestling White Ibises (*Eudocimus albus*) hatched in 1985 through 1988 at Pumpkinseed Island, a large colony site in coastal South Carolina. Hatchling ibises are covered with a Pale Neutral Gray to Jet Black natal plumage. About 30% of the hatchlings possess a tuft of white feathers on their crown, and this pattern persists throughout the nestling period. Juvenal plumage, which is complete by 60 days, is mainly Vandyke Brown and Blackish Neutral Gray dorsally and creamy white ventrally. The bill, which is straight at hatching, begins to curve downward at about 14 days. Nestling White Ibises exhibit considerable individual variation in bill markings from approximately 10 days of age through fledging. Increasingly persistent begging vocalizations begin within hours of hatching. Nestlings walk on partially extended legs at eight days of age, pirate food from other nestlings and form creches at 21 days of age, and fledge and join all juvenile and mixed-age feeding flocks at 45–55 days of age. We suggest that the phenotypic variability in plumage, bill coloration, and begging calls we describe enables parental ibises to identify more easily their offspring at the colony site. *Received 27 Feb. 1989, accepted 12 Nov. 1989.*

Although the plumage and behavioral development of several species of wading birds has been studied in considerable detail (e.g., Hammerkops [*Scopus umbretta*], Wilson et al. 1988; storks, Kahl 1962, 1966; Thomas 1984; herons, Gross 1923; Gavino and Dickerman 1972; Juarez and Dickerman 1972; Mc Vaugh 1972, 1975; Snow 1974; Merritt 1981), there are few detailed studies of juvenile ibises. Michelmore and Oliver (1982) describe the plumage and behavioral development of 10 hand-reared and a number of parent-reared Northern Bald Ibises (*Geronticus eremita*) raised at the Jersey Wildlife Preservation Trust. Rudegeair (1975) describes interactions between free-ranging nestling White Ibises (*Eudocimus albus*) and their parents at a colony site in north central Florida. Kushlan provides information on the behavior of free-ranging White Ibises in south Florida (Kushlan 1974), as well as information on growth of body parts of five hand-reared birds (Kushlan 1977a). Beebe (1914) provides a description of changes in behavior, as well as in plumage and soft body parts, of two parent-reared White Ibises maintained at the Bronx

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Zoo and a number of nestlings raised by free-ranging adults in the wild. He also noted variation in bill markings in young ibises. ffrench and Haverschmidt (1970) outline changes in the plumage and soft parts of developing nestling Scarlet Ibises (*E. ruber*), noting that some nestlings have a "white tuft on the crown." Luthin (1983) compares the appearances of nestling Bare-faced (*Phimosus infuscatus*), Green (*Mesembrinibis cayennensis*), and Scarlet ibises.

White Ibises typically breed in large colonies. Colonies vary considerably in size, but ibises usually nest in the company of at least 10 pairs of conspecifics, and many colony sites exceed several thousand pairs (Kushlan 1977b). Nestling ibises are ambulatory at about eight days of age, and they spend several weeks in large creches at breeding colonies being fed by adult ibises before becoming independent at six to seven weeks of age (Rudegeair 1975). Studies of other colonial species where the young intermingle reveal considerable phenotypic variability in nestling plumage and voice, presumably in response to selection for parental recognition of offspring (cf. Buckley and Buckley 1970, Berry 1975, Stoddard and Beecher 1983). Here we: (1) detail extensive observations of 17 hand-reared captive White Ibises together with incidental observations of more than 400 parent-reared nestlings, (2) compare development in White Ibises with that of other species of wading birds, and (3) discuss our observations of phenotypic variability among nestlings in terms of selection for parental recognition.

MATERIALS AND METHODS

Seventeen 8- to 72-h-old newly hatched White Ibises were taken from a large breeding colony on Pumpkinseed Island in Winyah Bay, Georgetown County, South Carolina, in July 1986 (eight young from eight nests) and 1987 (nine young from six nests). (See Frederick 1987 for a description of the colony site.) Chicks were individually marked with colored pipe cleaner leg bands and transported to rearing facilities at the Savannah River Ecology Laboratory near Aiken, South Carolina. Initially, chicks were maintained in small (14.5 × 24 × 6 cm) plastic baskets lined with crumpled paper. Two of these small baskets, containing two or three chicks each, were placed in larger baskets (60 × 45 × 40 cm). Infrared lamps were used to maintain an ambient temperature of approximately 30°C, and insect netting was draped over the larger baskets each evening to protect nestlings from mosquitos. When chicks became ambulatory at about two weeks of age, they were transferred to a 3 × 4 × 2.5 m indoor-outdoor aviary equipped with branches, plastic boxes for roosting, and a wading pool. Chicks were moved to the indoor portion of the enclosure each evening, where a heat lamp maintained the temperature at approximately 25°C. When they were approximately six weeks of age, the birds were placed in a 9.5 × 14.5 × 4.8 m outdoor flight aviary equipped with flow-through wading pools and natural vegetation.

During the first 35 days, the birds were fed a ground mixture of 65% beef heart, 24% hard-boiled egg, and 11% crayfish (Cambaridae) and fish, fortified with calcium carbonate (0.88%), dicalcium phosphate (0.41%), vitamin premix (0.25%), trace minerals (0.05%), and selenium premix (0.005%) (See Bolden and Jensen 1985). Water was added to the mixture

to create a slurry for feeding. Young chicks were stimulated to gape by applying light pressure on the gonys with the base of the index and middle fingers. We then poured the food slurry into the mouths of the chicks using a narrow spoon. During the first week, chicks were fed every 2 h from 07:00 h to 21:00 h. Beginning on Day 8, chicks were fed every 2 h from 09:00 to 19:00 h. On Day 15, we stopped feeding the chicks the diet in slurry form and began offering the same dietary components cut into 1.3-cm cubes five times a day at 3-h intervals. At this age we began to encourage the chicks to feed independently by "pecking" at food items with the index finger; however, most of the food was still being fed by hand. Throughout the period of hand feeding, birds were fed only until intense begging had ceased, and care was taken not to overfeed the chicks (cf. Archibald et al. 1980). Beginning on Day 22, chicks were provided with food in a feeding tray four times a day at 3-h intervals. At the same time, a commercially prepared diet consisting of horse meat, horse-meat by-products, corn, soy, barley, fish meal, eggs, yeast, and a vitamin and mineral supplement (Bird of Prey Diet, Central Nebraska Packing Inc., North Platte, Nebraska) was gradually introduced in place of the beef heart. Birds were fed twice daily during the sixth week. At 12 weeks of age, the birds were gradually switched to a diet of 67% Bird of Prey Diet, 17% fish or shrimp meal, and 17% dog meal. Water was provided ad libitum once the chicks were ambulatory.

Birds were weighed on a triple-beam balance to the nearest 0.5 g on alternate days through six weeks of age, and then twice monthly until they reached asymptotic mass. Changes in plumage and behavior were recorded daily until the birds were six weeks old. Color descriptions of plumage and hard and soft body parts were made according to Smithe (1975), except where noted. In 1986, we photographed each bird at least once a week throughout the study period. Facial patterns and coloration of the 1987 nestlings were documented with photographs taken when the chicks were 24–31 days old. We recorded the begging calls of the nine chicks raised in 1987 on a cassette tape recorder between Days 9 and 36. Begging calls were analyzed using a Kay Elemetrics Corp. Sona-Graph.

Observations of more than 400 parent-reared nestlings were made at the colony site in 1985, 1986, 1987, and 1988 during regular visits to the colony to measure developing young, band fledglings, and collect regurgitant samples. We attached backpack radio telemetry units weighing 16–22 g (approximately 3% of their body mass at the time of attachment) to eight 25–31-day-old juveniles (two birds in 1987 and six birds in 1988) to determine when fledglings begin to leave the colony site to forage on their own.

RESULTS

All 17 hand-reared chicks readily accepted the prepared diet and became accustomed to hand feeding. All eight chicks reared in 1986 survived; however, in 1987, two chicks were euthanized (one on Day 17 and one on Day 34) after they developed slipped leg tendons despite the precautions we took to prevent this condition (cf. Archibald et al. 1980). These two chicks appeared healthy in all other respects, and data collected on them prior to the onset of this condition are included below.

Physical Development

Bill and face.—Newly hatched White Ibises have a straight, Flesh Colored (Smithe Color 5) bill, with a Dark Neutral Gray (Color 83) tip. A white egg tooth, which is sloughed at 5–9 days, is located on the distal tip of the upper mandible. The skin surrounding the eyes and on the face is bare, loose-fitting, and Flesh Colored.

This coloration of the bill and face persists for three days. Afterwards, the facial skin and orbital area darken to Light Neutral Gray (Color 85), except in some individuals where a narrow Salmon Color (Color 6) band persists at the base of the upper mandible. The color change proceeds distally until the upper third of both mandibles is Dark Neutral Gray. The remaining portions of the bill change to Salmon Color.

A faint, Light Neutral Gray band appears on the upper mandible immediately distal to the nares between 7 and 10 days. This band gradually becomes Dark Neutral Gray and encircles both upper and lower mandibles by the end of the second week. Gradual downward curving of the bill begins at Day 14. Dark Neutral Gray areas on the proximal, central, and distal portions of the bill gradually increase in size until most of the bill is dark by the beginning of Week 5 (Fig. 1). The pied-bill, which persists at least through Day 24, varies considerably in pattern, even among chicks of the same age (Fig. 2). The dark areas of the bill are glossy in some chicks and dull in others. By six weeks the entire bill is Light Neutral Gray. Over the next three weeks, the base of the bill and the orbital area become Pale Pinkish Buff (Color 121 D), while the remainder of the bill becomes Salmon Color.

Legs and feet.—The legs, feet, and nails of newly hatched chicks are Flesh Colored. The nails and legs change to Neutral Gray between 2 and 7 days of age, followed by a darkening of the feet between 4 and 9 days. The coloration of the nails, legs, and feet gradually becomes Medium Neutral Gray (Color 84) or Dark Neutral Gray by Day 11. By the fifth month, the feet and legs change to one of four shades of gray or grayish brown (Pale Neutral Gray [Color 86], Glaucous [Color 80], Light Neutral Gray, or Light Drab [Color 119 C]).

Body skin.—The skin of hatchlings, which is Light Flesh Color, becomes Light Neutral Gray around Day 2 and bluish gray (nearly Plumbeous [Color 78]) by Day 3. By Day 35, the skin is Deep Vinaceous (Color 4).

Eyes.—The eyes begin to open 1–3 days after hatching and are completely open and alert by Day 9. The irises are Raw Umber (Color 223) through the first month. At five months, the outer ring of the iris changes to Medium Plumbeous (Color 87), while the inner portion becomes Pratt's Payne's Gray (Color 88).

Plumage.—The heads and necks of hatchlings are covered with dense, shiny Jet Black (Color 89) down which, on the crown, projects caudally. Several white feathers form a spot on the crown of approximately 31% of the hatchlings (31.4% of 162 nestlings in 1987, 30.2% of 262 nestlings in 1988). The size of this crown spot, which is randomly distributed among nestlings (Table 1), ranges from 1 to 5 mm in diameter. The remainder of the body is sparsely covered with Pale Neutral Gray down on the underparts and rump, and Dark Neutral Gray down on the shoulders and

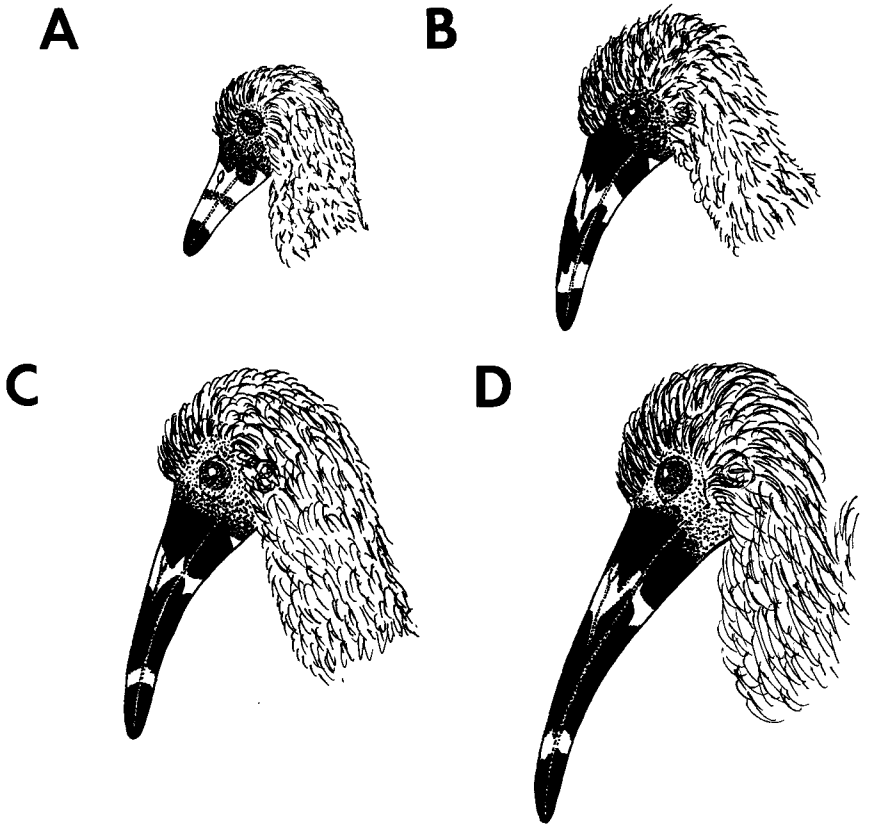

FIG. 1. Bill and facial markings at 7(A), 15(B), 26(C), and 32(D) days-of-age of a single juvenile White Ibis hand-reared in 1986.

wings. For a detailed description of the structure of down feathers of nestling White Ibises see Beebe (1914).

There is no visible feather growth until Day 4 or 5, when primaries begin to emerge. Feathers in the humeral and alular tracts, as well as secondaries and tertiaries, appear between 6 and 10 days. The spinal tract,

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FIG. 2. Bill and facial markings of four 27–31-day-old, hand-reared White Ibises taken from four different nests in July 1987, along with two begging calls recorded on separate days when the birds were between 23 and 30 days old. Note the similarity in calls within individuals compared with differences among individuals. Horizontal marks on the ordinal axis represent 1 and 5 kHz.

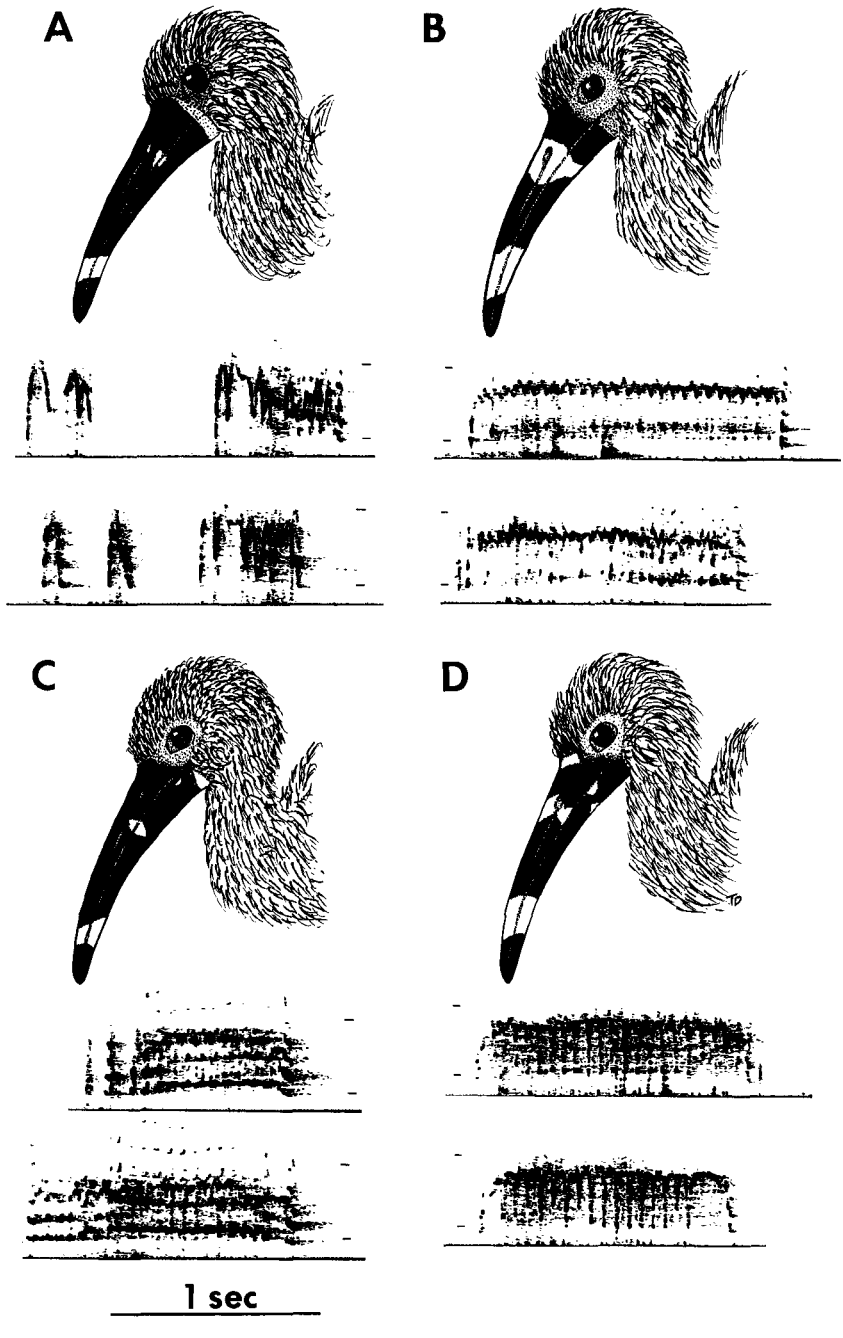
A
B
C
D
1 sec

TABLE 1

DISTRIBUTION OF JUVENILE WHITE IBISES WITH AND WITHOUT WHITE FEATHERS ON THEIR CROWN AMONG 201 NESTS AT THE PUMPKINSEED ISLAND COLONY SITE IN 1987 AND 1988

	Nestlings with white spots : nestlings without white spots	Observed	Expected[a]	*P*[b]
One-nestling nests (34)[c]	Nestling with spot	10	10.4	
	Nestling without spot	24	23.6	>0.10
Two-nestling nests (108)	0:2	57	52.0	
	1:1	39	45.9	
	2:0	12	10.1	>0.10
Three-nestling nests (55)	0:3	22	18.4	
	1:2	18	24.3	
	2:1	11	10.7	
	3:0	4	1.6	>0.10
Four-nestling nests (3)	0:4	1	0.7	
	1:3	0	1.2	
	2:2	0	0.8	
	3:1	1	0.2	
	4:0	1	0.03	NT[d]

[a] Assuming a random distribution of nestlings with and without spots among all nests. (Because there was no indication of a difference between years in the relative frequencies of nestlings with and without spots [χ^2 test for heterogeneity, $\chi^2 = 0.071$, $P > 0.90$], we pooled data from the two years to increase our sample sizes for this analysis.)

[b] Chi-square tests for goodness-of-fit.

[c] Number of nests.

[d] No test because of small sample size.

ventral tract, and rectrices emerge between 8 and 12 days. The crural and femoral tracts emerge between 24 and 32 days. The down on the head is replaced by juvenal plumage between 32 and 46 days.

Unsheathing of feathers generally begins 1–2 days after the shafts emerge. Primaries are completely unsheathed by 45 to 60 days, and the juvenal plumage is nearly complete and smooth by the end of the second month. Feather shafts of the developing juvenal plumage are Plumbeous, changing to creamy white (no description in Smithe 1975). Feathers of the shoulders and wings are Blackish Neutral Gray (Color 82). Feathers of the underparts of the trunk, back, legs, rump, and one third of the base of the rectrices and primaries are creamy white. Feathers of the head and neck are Vandyke Brown (Color 121), with narrow (on the head) or broad (on the neck) lacings of creamy white, giving an overall appearance of Glaucous. By three months, the feathers of the shoulders and wings have faded to Vandyke Brown.

Behavioral Development

Week one captive birds.—The period of the most pronounced developmental change occurs during the first week. Newly hatched chicks,

whose eyes are partially or completely closed, are weak and uncoordinated, and they spend most of their time sleeping in a prone position. On Day 1, begging consists of jerky, lateral head movements and soft trilling vocalizations. At this age, begging can be sustained for only about 3 sec at a time. On Day 2, the chicks can support their heads by balancing them on the base on their necks. At this time, begging movements are more controlled, and the wings are held from the body and moved back and forth horizontally, while the chick trills loudly. On Day 3, chicks can hold their necks off the ground by balancing them on their chests and wrist joints. Trilling is louder than on Day 2. At this time, chicks begin to shuffle backwards to the edge of the "nest" to defecate, a behavior that then persists throughout the nestling period.

By Day 4, chicks support their bodies by sitting on retracted legs, and they are able to stand on their tarsometatarsi for up to 10 sec. At this time, chicks, which beg while resting on their tarsometatarsi and moving their wings vertically with their heads and necks fully extended, forcibly probe their bills into the keeper's hand during feedings. Each begging vocalization lasts for about 2 sec. By Day 6, chicks can stand on extended legs for 15 sec and can crawl on their tarsometatarsi.

Week one free-living birds.—The development of locomotion and vocalizations in free-ranging birds are comparable to those observed in captive-reared birds, with a noticeable progression from tentative, uncoordinated begging in newly hatched chicks to the controlled, sustained begging of 7-day-old chicks. Free-living chicks beg continually unless they are being brooded, even when neither parent is near the nest. Although they are capable of crawling by the end of this period, undisturbed chicks remain in the nest.

Week two captive birds.—Chicks begin walking on their partially extended tarsometatarsi by Day 8, and by Day 14 they are walking on fully extended legs, exploring the area within several meters of the nest, and preening their developing juvenal plumage. Chicks continue to beg through this period while resting on their tarsometatarsi. During the second week, chicks begin to flap one or both wings when begging. At this time, chicks beg for food from other chicks by placing their bill around the closed bill of another chick, moving their head laterally, flapping one wing, and trilling loudly. Solicited chicks were not seen disgorging food.

Week two free-living birds.—In the wild, chicks younger than 15-days-old rarely leave the nest except to flee from approaching humans. When approached by a human, nestlings climb from their elevated nests (7–50 cm off the ground in black needle rush [*Juncus roemerianus*], giant cord grass [*Spartina cynosuroides*], and marsh elder [*Iva futescens*]) into the surrounding vegetation. Chicks are less vocal at this age, and they appear to beg only when a parent is near.

Week three captive birds.—At three weeks, chicks beg and feed more persistently, and they pirate food from each other by jabbing their closed bills through the open bill of a nestling being fed by the keeper. If the harassed nestling drops its food, the food is quickly consumed by the other chicks. At this age, chicks beg by rapidly approaching the keeper while flapping their wings and trilling loudly, and they retreat to a corner of the pen after being fed.

Week three free-living birds.—Chicks spend little time in their nests after they reach 15 days-of-age. Creches of up to at least 30 similar-aged juveniles walk and stand within 20 m of their nests. Food piracy occurs regularly. When solicited, unattended wild chicks disgorge food to both juvenile and adult pirates.

Weeks four and five captive birds.—Chicks now eat from feeding trays most of the time but still solicit food from the keepers. By Week 4, chicks no longer allow the keepers to use their fingers to stimulate gaping, and they accept food without encouragement. At this time, chicks accept less food by hand from the keepers, and body mass stabilizes for 6–10 days until the chicks begin to feed on their own (Fig. 3). Chicks sometimes appear lethargic and subdued during this period. Chicks begin to take short hopping flights between branches, and by the end of Week 5, most birds are able to fly at least 2 m. Chicks increase the number of visits to wading pools, and they begin to exhibit considerable probing behavior.

Weeks four and five free-living birds.—Wild birds spend much time perched on black needle rush and marsh elder, and they take short flights of up to 2 m. They also begin to wade and probe in the shallow water (<10 cm) surrounding the island colony site. Chicks are fed by adults away from their nests while perched on vegetation.

Weeks six and seven.—Captive birds were released a into large flight aviary at this time and continued to beg for food from the keepers. Sustained flights of at least 50 m occurred in free-living ibises at approximately 35–40 days. Young ibises are often seen flying after adults, begging for food. At 45 to 55 days of age, juveniles first leave the island colony site and fly over water for at least 750 m to forage in juvenile or mixed-age flocks of up to 300 individuals. (Eight radio-telemetered chicks left the Pumpkinseed Island colony site between approximately 47 and 56 days of age.)

DISCUSSION

Plumage and behavior appeared to develop in the same manner and at the same rate in hand-reared and parent-reared nestlings, although in our study hand-reared birds achieved the same mass several days later than did parent-reared birds (see also Kushlan 1977c). Even so, several

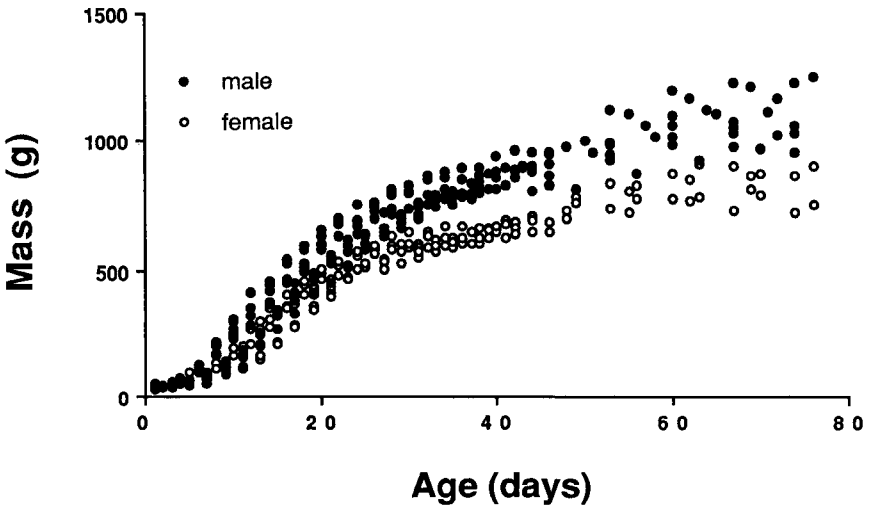

FIG. 3. Body masses of 17 White Ibises hand-reared during 1986 and 1987.

behavioral patterns developed in our hand-reared birds earlier than in parent-reared birds, probably because we tracked the development of hand-reared birds more closely than that of parent-reared birds (cf. Kahl 1966). Overall, there was no indication that the captive birds failed to develop normally (cf. Rudegeair 1975).

The patterns of behavioral and plumage development in nestling White Ibises appear to be nearly identical to that described for the somewhat larger Northern Bald Ibis, although nestling White Ibises develop considerably more rapidly and fledge earlier than do nestling bald ibises (Michelmore and Oliver 1982).

The classic work on White Ibis nestling ontogeny was by Beebe (1914). Overall, our results agree with his earlier report, as well as those of Kushlan (1974, 1977c), Rudegeair (1975), and ffrench and Haverschmidt (1970). Because we tracked changes with age in the appearance of the bills of individual nestlings, we are able to document that the "good deal of variation" in bill patterns first reported by Beebe (1914) is due not only to differences within individuals as they develop, but also to differences among individuals of the same age. Kushlan (1977a, c) reported that hand-reared nestlings increased their mass more slowly than did parent-reared birds, a phenomenon we also noted, even though in our study we found no difference between these two groups with regard to plumage or behavioral development. The reason for the difference in growth is unclear. Kushlan (1977c) suggested that the growth of his captive birds may have

been "similar to that in the wild under stressful conditions." Because our nestlings were part of a long-term study of among-year variance in the growth of nestling ibises and because we wished to reduce within-year variance in our data set, parent-reared birds measured during the course of our study included only first-hatched chicks (De Santo, Johnston, and Bildstein, unpubl. data). Our hand-reared nestlings, however, included both first- and later-hatched individuals, and it may be that part of the difference in the growth rates of these two groups reflects that situation.

Our results demonstrate that White Ibises are ambulatory several weeks before they begin to fly. This developmental sequence parallels Kushlan's (1977a) findings that in young ibises "structures associated with terrestrial locomotion" grow more rapidly than those "associated with flight."

As in many species of wading birds (for examples see Gross 1923; Kahl 1962; Mc Vaugh 1972, 1975; Gaviño and Dickerman 1972; Luthin 1983; Thomas 1984), bill coloration and markings in nestling White Ibises differ considerably from those found in adults. Furthermore, even though the color and pattern of each ibis nestling's bill changes continuously as the bird develops (Fig. 1), by the end of their second week same-aged nestling White Ibises also exhibit considerable individual variation in these characteristics (Fig. 2). The same appears to be true in at least several other species of colonial nesting wading birds (Little Blue Heron [*Egretta caerulea*], Tri-colored Heron [*E. tricolor*], Mc Vaugh 1972; Least Bittern [*Ixobrychus exilis*], Snowy Egret [*E. thula*], Yellow-crowned Night-Heron [*Nyticorax violaceus*], Mc Vaugh 1975; Green-backed Heron [*Butorides striatus*], Gaviño and Dickerman 1972).

Several researchers have suggested that such individual variation, especially in species where individuals nest close to one another or where creching occurs, helps parents recognize their young (Buckley and Buckley 1970, Skutch 1979, O'Connor 1984, Stoddard and Beecher 1983). Individual variation in the bill markings of the White Ibises we reared was obvious by Day 9 (Fig. 2), just prior to the onset of increased mobility and creche formation in the wild. The white crown that occurred on 31% of the nestlings (Table 1) was obvious by Day 2 and remained so throughout the nestling period. ffrench and Haverschmidt (1970) also report the presence of white crown feathers on some of the nestling Scarlet Ibises they studied. We were able to use these markings alone to recognize our captive birds individually. We propose that this extreme variation in the appearances of nestling White Ibises, together with individual variation in the begging calls of nestlings (Fig. 2), function as highly variable "signature traits" (sensu Stoddard and Beecher 1983) that enable parent ibises to locate and preferentially care for their young in large creches.

Stoddard and Beecher (1983) offer data suggesting that, in swallows,

coloniality selects for conspicuous signature traits similar to those we have described for White Ibises. Incidental observations of Glossy Ibises (*Plegadis falcinellus*), which also nest colonially on Pumpkinseed Island, and whose nestlings often creche, suggest considerable individual variation in the head and facial plumage of nestlings (pers. obs., see also Cramp and Simmons 1977). The extent to which nestlings of other species of colonial and, especially, solitary nesting ibises (e.g., Green Ibises) exhibit individual variation is unknown (cf Luthin 1983).

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