COLONY AND NEST SITE SELECTION IN WHITE-FACED AND GLOSSY IBISES

JOANNA BURGER AND LYNNE M. MILLER

ABSTRACT.—The factors determining colony and nest site selection in the White-faced and Glossy Ibises (*Plegadis*) were examined from 1972 through 1975. White-faced Ibises were studied in Texas and Argentina, Glossy Ibises in New Jersey and New York.

White-faced Ibises generally nest in tule marshes, infrequently on dry land. In selecting a dry land site, White-faced Ibises preferred to nest on the ground among low shrubs and in mixed forbs rather than in habitats containing grass and cactus.

Glossy Ibises' habitat varies from *Phragmites*, *Iva*, and *Smilax* to other low shrubs. They did not always nest on the ground.

White-faced Ibises nested next to conspecifics, whereas in Glossy Ibises the choice of nearest neighbor was random with respect to the species present. The mean distance to the nearest neighbor was generally less for Glossy Ibis when compared to White-faced Ibis. The space around nests that was devoid of any other nest was examined graphically. Nearest neighbors were farther away when they were on the same level than when the nearest neighbor was above the nest being examined for both species.

The visibility index from the nests of Glossy and White-faced Ibises was low, and was less than the mean visibility index for heron and egret species nesting in the same colonies. Visibility was less in the direction of the closest nest compared to that in other directions for all colonies examined. In some colonies, the visibility index in the direction of the closest nest was directly related to the distance to the closest nest. Glossy Ibises nested in denser habitats than did White-faced Ibis, and this was reflected in lower visibility indices for Glossy Ibis.

Possible reasons for the recent range changes in the two *Plegadis* species are discussed.—*Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903.* Accepted 15 January 1976.

MOST studies of the breeding biology, behavior, and ecology of the family Threskiornithidae have only mentioned or described the nesting habitat briefly. We know of no study of the factors determining colony and nest site selection in any of the ibises or spoonbills. And, with the exception of Jenni's (1969) study on four species of herons during the breeding season, little work had been done on nesting preferences of herons and egrets, which often nest with ibises and spoonbills.

We studied the factors determining colony and nest site selection in 2 colonies of White-faced Ibises (*Plegadis chihi*) and 5 colonies of Glossy Ibises (*P. falcinellus*), with a view to comparing and contrasting colony and nest site selection in these 2 closely related species, which may help explain the causes of recent range changes.

Until recently in the Western Hemisphere the Glossy Ibis bred in the Eastern United States and White-faced Ibis bred in the Western United States, Mexico, and southern South America (Palmer 1962, A.O.U. Checklist 1957). Both species have been reported to breed in Florida (Brewster 1886) and in Louisiana (Ryder 1967). Historically the White-faced Ibis has had a more extensive, although discontinuous range in the New World (Ryder 1967). Until fairly recently, the breeding range of Glossy Ibis in the United States was limited primarily to Florida (Bull 1974), and the total breeding population was estimated to be 400 pairs (Palmer 1962). Oberholser (1974) attributed the restricted range of Glossy Ibis to the fact that its marsh habitat niche was already occupied by White-faced Ibises. The extension of the breeding range of Glossy Ibis was first noted in the 1940's and 50's (Pearson 1942, Stewart 1957, Stepney and Power 1973). Hailman (1959) summarized the breeding expan-

sion, which reached north to Brigantine National Wildlife Refuge in New Jersey by 1957. Post et al. (1970) recorded the first breeding in New York at Jamaica Bay in 1961. By 1973 they had increased to 711 breeding pairs on Long Island (Buckley and Davis 1973). In 1973 Glossy Ibises' breeding range jumped to Maine (Finch 1972, Bull 1974), and in 1975 they spread into Massachusetts (Finch pers. comm.). Sight records of stragglers have been reported as far north as St. Pierre off Newfoundland (Finch 1973) and at Bradley's Marsh near Brandon, Ontario (Goodwin and Bollinger 1972). Glossy Ibises have also undergone a breeding range expansion into the West Indies and northern South America (Gochfeld 1970, 1973).

The White-faced Ibis, on the other hand, seems to be contracting its breeding range, though such range contractions are poorly documented in the literature. Ryder (1967) summarized the breeding colonies in the United States and estimated that in 1965 there were 10,000 breeding pairs. He reported a decline in breeding numbers in California and attributed it to loss of habitat. Further decline in the numbers breeding in California was noted by Small (1975). White-faced Ibis are also declining in Nevada (Zimmerman 1975) and Utah (Ryder 1967, Zimmerman 1975). A decline in Texas was due to pesticides (Kirke King pers. comm.). Of the Ibis colonies Ryder (1967) lists west of the 89th meridian, 27% were no longer active in 1965.

Study Areas and Methods

We selected study areas to include varied habitats in different geographical locations. Colonies ranged from tules (*Scirpus*) to small shrubs. In general, colonies were homogeneous physiognomically. The vegetation either consisted of all one species (e.g. tules or *Phragmites*) or contained several species of vegetation intermixed so as to appear similar in structure. Thus the latter type did not contain large patches of one plant species surrounded by tracts of other species. Two heterogeneous colonies (Danger Island, Aransas Pass, Texas for the White-faced Ibis, and Meadowbrook on Long Island, New York for the Glossy Ibis) were selected for an examination of general habitat preferences, whereas the homogeneous colonies were selected to study specific nest site selection preferences. Colonies examined were:

1. Laguna de Burgos, Azul, Province of Buenos Aires, Argentina. This colony, located in a pure stand of *Scirpus* sp. (maximum height 3 m) contained 1,500 pairs: 3% Great Egret *Casmerodius albus*, 8% Roseate Spoonbill *Ajaia ajaia*, 45% Snowy Egret *Egretta thula*, 18% White-faced Ibis, and 26% Brown-hooded Gull *Larus maculipennis*. Eggs were laid in November.

2. Danger Island, Aransas Pass, Texas. The colony, in *Borrichia frutescens*, mixed forbs, and *Opuntia* cactus (maximum height 1.12 m) contained 1,500 pairs: 6% Great Blue Heron *Ardea herodias*, 2% Reddish Egret *Dichromanassa rufescens* and Little Blue Heron *Florida caerulea*, 37% Louisiana Heron *Hydranassa tricolor*, 30% Snowy Egret, and 25% White-faced Ibis. Mixed forbs on Danger Island included *Oenothera drummondii, Ambrosia artemisiifolia, Gaillardia pulchella, Thelesperma filifolium, Machaeranthera phyllocephala, Gavra* spp. *Helianthus debilis* (Jones et al. 1961). Laughing Gulls *Larus atricilla* nested nearby. Egg-laying extended from February to April.

3. Barrel Island, Brigantine National Wildlife Refuge, New Jersey. This colony, in *Iva frutescens* (maximum height 1.15 m), contained 291 pairs: 12% Great Egret, 13% Louisiana Heron, 36% Snowy Egret, 14% Black-crowned Night Heron *Nycticorax nycticorax*, and 25% Glossy Ibis. Herring Gulls *Larus argentatus* nested in *Spartina* around the heronry. Egg-laying was in April–May.

4. Meadowbrook in Jones Beach, New York. This colony, in *Phragmites communis* and *Myrica pensylvanica* (maximum height 3 m) contained 90 pairs: 64% Black-crowned Night Heron and 36% Glossy Ibis. Herring Gulls nested nearby. Egg-laying was April–May in all the New York colonies.

5. Zach's Bay, Jones Beach, New York. This colony, similar in plant species to Meadowbrook, contained 500 pairs: 2% Louisiana Heron and Little Blue Heron, 37% Snowy Egret, 7% Black-crowned Night Heron, and 54% Glossy Ibis.

6. Loop, Jones Beach, New York. This colony, similar to 4 and 5 in vegetation, contained 139 pairs: 52% Snowy Egret, 7% Black-crowned Night Heron, and 41% Glossy Ibis.

7. Seganus Thatch, Long Island, New York. This colony, in *Smilax* sp. and *Iva* (maximum height 3.2 m) contained 300 pairs: 21% Great Egret, 8% Little Blue Heron, 25% Snowy Egret, 19% Black-crowned Night Heron, and 27% Glossy Ibis.

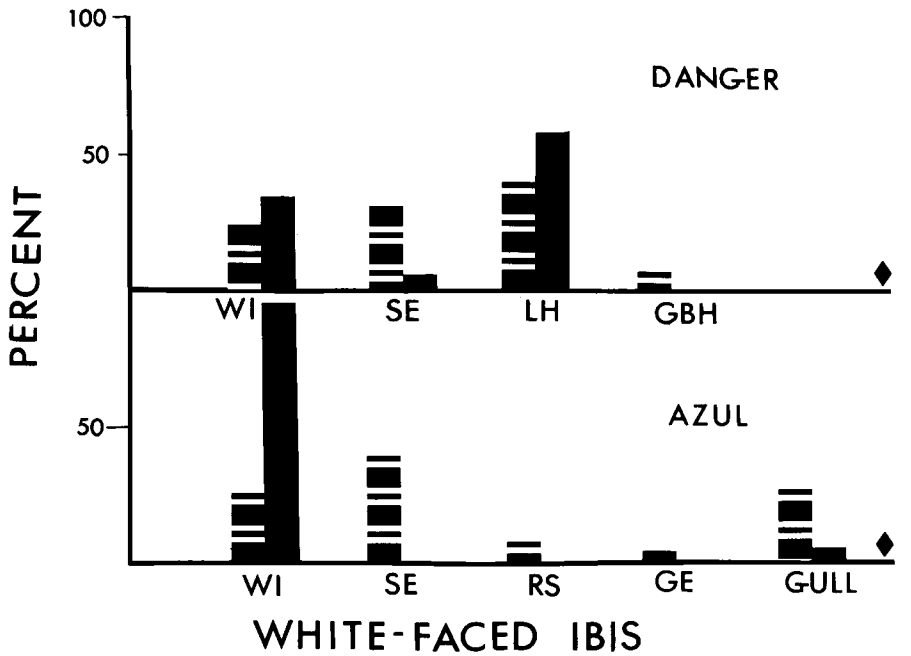

Fig. 1. Nearest neighbors of White-faced Ibises. The broken bar reflects the percent of each species present and the solid bar the percent nearest neighbor. The diamond reflects a significant deviation from random. WI = White-faced Ibis, SE = Snowy Egret, LH = Louisiana Heron, GBH = Great Blue Heron, RS = Roseate Spoonbill, and GE = Great Egret.

Fieldwork was conducted in Argentina in November–December 1972 (JB), in Texas in 1974 (JB), in New Jersey in 1973, 1974, and 1975 (JB and LMM), and in New York in 1974 and 1975 (JB and LMM).

Data collected in all colonies included species of vegetation, height of vegetation, physiognomic characteristics, total number of avian species, and number of individuals breeding, as well as the relative number of each species nesting in the colony. Data collected on 23 to 65 nests in each colony included: species and height of vegetation where each nest was located, rim height of the nest above ground, rim height from the top of the vegetation, nest width and depth, nearest neighbor species, distance to the nearest neighbor, and the distance to the closest conspecific if a nonconspecific was the nearest neighbor. The distance to the nearest neighbor was recorded as the direct linear, horizontal, and vertical distance. We computed the percentage frequency of occurrence as a nearest neighbor in each species present. This was compared to the percentage of the colony comprised by each species. We used a Chi-square test to determine if species of nearest neighbor were random.

Fisheye photographs were taken in two colonies each of Glossy Ibises and White-faced Ibises. A grid placed over each photograph enabled us to determine the visibility index for each quadrat on each photograph (Burger 1972). The total visibility index for a photograph was 160, and any one quadrat had a

TABLE 1

MEASUREMENTS (IN CM) OF WHITE-FACED AND GLOSSY IBIS NESTS

Species	Colony	N	Rim height	Nest width	Cup width	Nest depth	Cup depth
Glossy	Zach's Bay	65	23.6 ± 6.1	41.9 ± 3.8	23.1 ± 3.3	22.6 ± 5.3	2.6 ± 2.0
	Barrel	23	13.1 ± 5.3	35.6 ± 4.8	—	13.7 ± 5.1	—
	Meadowbrook	56	33.8 ± 15.7	40.9 ± 6.4	24.4 ± 2.6	26.6 ± 7.9	2.9 ± 1.9
	Loop	35	31.8 ± 28.4	41.9 ± 8.5	24.9 ± 4.1	26.4 ± 10.7	3.6 ± 3.3
	Seganus	27	54.0 ± 30.3	—	—	—	—
White-faced	Danger	34	19.3 ± 17.5	39.1 ± 7.6	22.9 ± 4.3	15.7 ± 7.4	5.1 ± 2.5
	Azul	60	13.4 ± 8.0	45.6 ± 11.0	26.8 ± 3.9	13.4 ± 8.0	5.0 ± 1.2

TABLE 2

NEAREST NEIGHBOR DISTANCE IN CM AS A FUNCTION OF SPECIES OF NEAREST NEIGHBOR

Species	Colony	All species	Conspecific	Nonconspecific	t	df	Significance
Glossy	Zach's Bay	94.5 ± 38.2	90.8 ± 35.0	103.0 ± 47.5	1.1	58	NS
	Barrel	88.5 ± 27.0	103.5 ± 32.8	80.0 ± 18.3	3.2	20	$P < 0.01$
	Meadowbrook	112.6 ± 47.4	94.4 ± 48.4	100.7 ± 39.2	0.59	58	NS
	Loop	85.7 ± 58.1	71.1 ± 31.5	96.5 ± 82.8	6.6	42	$P < 0.001$
	Seganus	101.6 ± 42.6	81.7 ± 42.7	111.0 ± 42.5	1.9	32	NS
White-faced	Danger	187.7 ± 60.0	195.8 ± 124.3	155.5 ± 50.0	1.8	44	NS
	Azul	121.7 ± 41.0	111.7 ± 45.0	153.2 ± 37.0	4.3	30	$P < 0.01$

NS = not significant.

maximum visibility index of 40. We were interested in comparing the visibility index within and between the species.

RESULTS

WHITE-FACED IBIS

Physiognomically heterogeneous colony.—White-faced Ibises nested on an island near Aransas Pass, Texas. The colony contained 3 homogeneous areas: *Borrichia*, mixed forbs, and grass; and 2 heterogeneous areas: 90% mixed forbs, 5% *Borrichia*, 5% cactus, and 90% *Borrichia*, 10% cactus. Herons and egrets nested in all of these habitats except in the grass where Laughing Gulls nested. A representative plot in each vegetation type was sampled for colony site selection. Ibises also nested in all except the grass area, but significantly preferred to nest in the homogeneous *Borrichia* and mixed forbs-*Borrichia*-cactus habitat.

The above data were pooled and analyzed for nest site selection determinants. The percent presence of each vegetation species was compared to percent vegetation selected by 60 pairs of ibises. White-faced Ibis built nests only in or on forbs or *Borrichia*, even though this type of vegetation made up only 60% of the total. Great Blue Herons, Snowy Egrets, and Louisiana Herons nested in the same colony. The former two species preferred cactus, and the latter preferred *Borrichia*. Too few Reddish Egrets were present to draw any conclusions about their nesting preferences.

White-faced Ibises built flat nests having a well-formed cup lined with shredded pieces of fine vegetation. Some nests were completely round, others contained a platform on one side. The White-faced Ibis nest characteristics at Danger Island are given in Table 1; 86% of the nests were built on the ground, others were in *Borrichia* branches.

The nearest neighbors of White-faced Ibises were 90% conspecifics or Louisiana Herons. Although this distribution differed significantly from random considering the colony as a whole (Fig. 1), it is important to remember that these species nested in *Borrichia*. The mean distance to the nearest neighbor was 187.7 ± 60 cm, and there was no difference between conspecific and heterospecific nearest neighbor distances (Table 2). Similarly there was no significant difference in the nearest neighbor distance of nests in *Borrichia* and mixed forbs.

Nearest neighbor distance measures the space surrounding an animal (Clark and Evans 1954), but it does not answer the question of space changes as a function of direction from the nest. In other words, are nearest neighbors located at the same distance if they are above, underneath, or horizontal to the nest in question? For 38 White-faced Ibis nests on Danger Island we recorded the horizontal and vertical

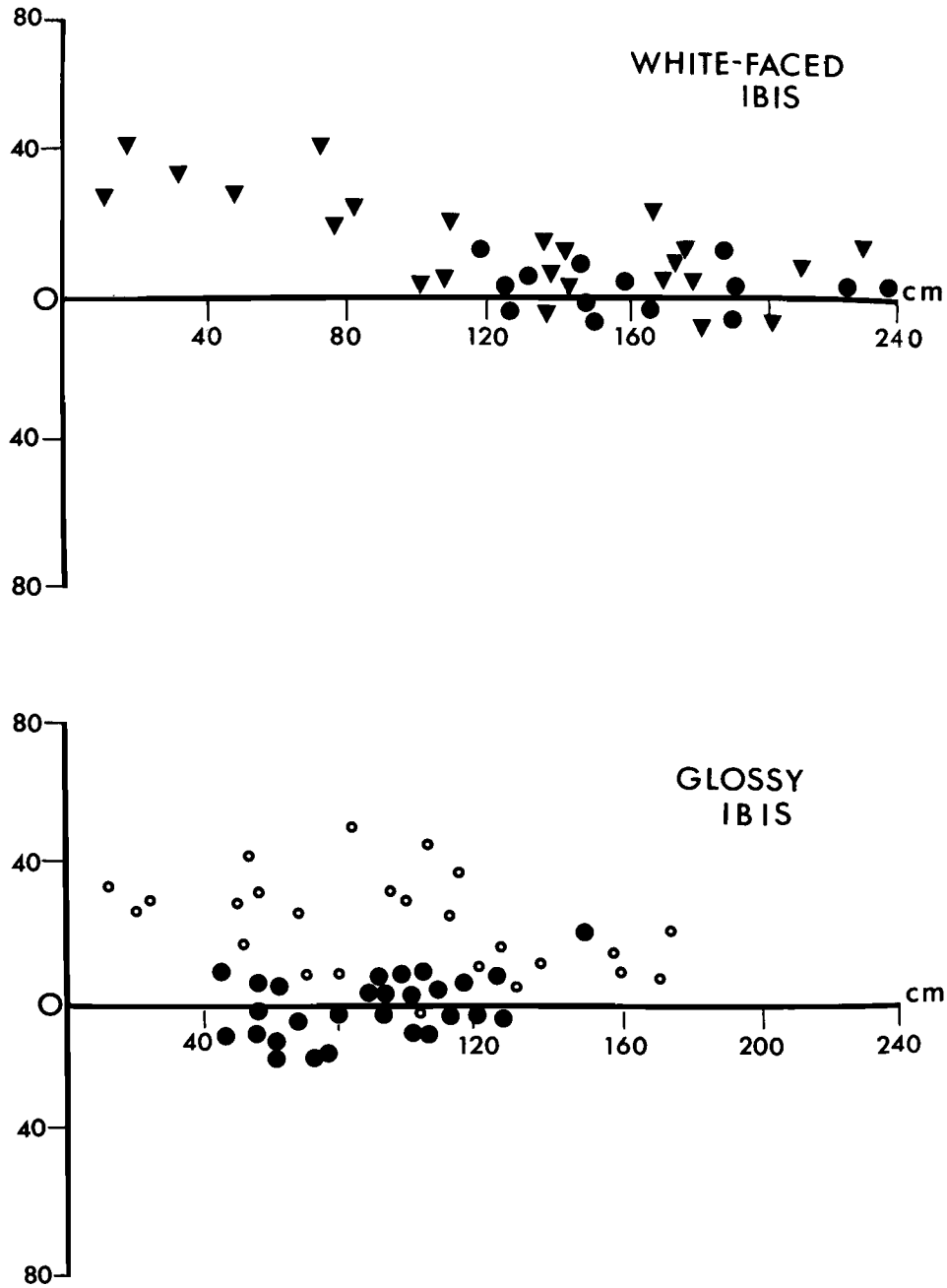

Fig. 2. Nest placement of nearest neighbors to White-faced and Glossy Ibis. Each symbol represents one nearest neighbor from the ibis nests (located at 0). Triangles = Louisiana Herons, closed circles = ibises, and open circles = Black-crowned Night Heron. See text for explanation.

components of the distance to the nearest neighbor. We then graphed these, using zero as the location of each of the 38 nests, and plotting the relative location of their nearest neighbor (Fig. 2), which gives a picture of the space around the nests not occupied by any other nest. As most ibis nests were on the ground, few nearest

neighbors can be closer if they are above the ibis nest than if they are on the same level as the nest.

We took fisheye photographs at 52 nests of White-faced Ibis on Danger Island. One-half of the photographs were taken from nests in *Borrichia*, and half were taken from nests in mixed forbs. As the visibility index for the nests in *Borrichia* was not significantly different from that in the mixed forbs, the data were pooled. Visibility was significantly lower in the direction of the closest neighbor when compared to that in the other directions (Table 3). The correlation between the visibility index in the direction of the closest nest and the distance to the nearest neighbor was also significant, although small ($r = +0.253$).

Physiognomically homogeneous colony.—White-faced Ibises were studied in a tule marsh, their typical habitat (Palmer 1962) near Azul, Argentina. The nests were built floating on the water surface, had a mean rim height of 13.4 ± 8 cm (Table 1), and were wider than those on Danger Island, perhaps to increase standing space.

Of White-faced Ibis nearest neighbors, 95% were conspecifics and 5% were Brown-hooded Gulls. This pattern is not random (Fig. 1) as the colony contained only 33% ibises, though gulls and ibises both built their nests on the water and selected similar nest sites. Mean distance to nearest neighbor was 111.7 ± 41 cm and there was no difference in mean distance to nearest neighbor, whether conspecific or heterospecific (Table 2). The mean nearest neighbor distance at Azul was significantly lower than the mean nearest neighbor distance at Danger Island ($t = 3.73$, $df = 73$, $P < 0.001$).

From fisheye photographs taken at 59 nests at Azul, Argentina, we found no difference in the visibility index in the direction of the closest nest when compared to other directions (Table 3). This may result from ibises building nests in the center of clumps of tules. Similarly there was no correlation between the visibility index in the direction of the closest nest, and the distance to the closest nest. The mean total visibility index in the colony at Azul was not significantly different from that in the colony at Danger Island.

Glossy Ibis

Physiognomically heterogeneous colony.—Glossy Ibises nested at Meadowbrook in a colony with Black-crowned Night Herons, Great Egrets, and Herring Gulls. Vegetation was 50% *Phragmites*-bayberry, 43% grass, and 7% pine. All the ibises and Black-crowned Night Herons nested in the *Phargmites*-bayberry and all of the Great Egrets nested in the pines. The ibises clearly chose to nest in the *Phragmites*-bayberry habitat.

Physiognomically homogeneous colonies.—Four colonies that were physiognomically homogeneous and Meadowbrook were examined for factors determining nest site selection. These colonies will be discussed together with respect to the factors involved. Not all data were recorded at each colony.

Nest characteristics.—Table 1 gives nest characteristics for four colonies. Mean nest rim height in colonies ranged from 13.1 to 33.8 cm. In most colonies Glossy Ibises nested on the ground, but at Seganus Thatch 59% of the 27 nests were on the low *Smilax* bushes. In the Loop Colony the mean rim height of Glossy Ibis nests was 31.8 ± 28.4 cm. These nests were started before mid-June. In mid-June some Glossy Ibises began to use abandoned nests of Snowy Egrets. Of the 85 active Glossy Ibis nests in mid-June, 20% were reused Snowy nests. These reused nests had a mean rim

TABLE 3

VISIBILITY INDICES FROM THE NESTS OF GLOSSY AND WHITE-FACED IBIS

A. The visibility index is compared in the direction of the closest nest with the mean for the other three directions.

Species	Colony	N	Closest nest	Other directions	t	Significance
Glossy	Barrel	23	1.4 ± 2.2	2.6 ± 3.8	2.0	$P < 0.05$
	Zach's Bay	58	1.5 ± 2.9	4.6 ± 4.2	3.9	$P < 0.001$
White-faced	Danger	52	9.2 ± 5.7	12.4 ± 6.7	3.1	$P < 0.01$
	Azul	60	9.9 ± 6.2	10.6 ± 6.6	1.1	NS

B. Comparison of total visibilities from nests between colonies.

Species	Colonies	t	Significance
Glossy:Glossy	Barrel–Zach's	1.64	NS
White-faced:White-faced	Azul–Danger	1.80	NS
Glossy:White-faced	Azul–Barrel	6.40	$P < 0.001$
	Azul–Zach's	4.88	$P < 0.001$
	Danger–Barrel	5.32	$P < 0.001$
	Danger–Zach's	4.93	$P < 0.001$

height of 101.9 ± 40.6 cm, significantly higher than the nests the ibises built. Davis (1967) found some reuse of Snowy Egret nests by Glossy Ibises in another Long Island colony. He also reported that they used nests from the previous year.

At Big Heron Island, Atlantic City, New Jersey, Glossy Ibises used nests left from the previous year. The colony was in *Phragmites* and bayberry. Nests were marked in mid-March before any ibises, egrets, or herons were present, and later, 40% were reused by ibises, Little Blue Herons, and Snowy Egrets; 33% were not used; and 27% had the material completely removed and used in new nests. The ibises' reused ground nests had a mean width of 33.65 cm and a mean depth of 12.25. The nests built on these old nests had mean width of 41.25 cm and a mean depth of 34.18 cm. All nests were of old *Phragmites* stems.

The nest width varied from 35.6 cm (Barrel Island) to 41.9 cm (Zach's Bay and Loop). Nest depths varied from colony to colony, but generally were significantly correlated with rim height, as in the four colonies shown, most nests were on the ground. For example, the correlation between rim height and nest depth was 0.764 for Zach's Bay and 0.955 for Barrel Island.

Nearest neighbor.—The percent of nearest neighbor for Glossy Ibis was compared to the percent presence of each species for all five colonies. In all cases Glossy Ibises' nearest neighbor was random (Fig. 3). The slight preference for conspecifics (in all but Zach's Bay) was not significant. The mean nearest neighbor distance for Glossy Ibis varied from 85.7 cm at the Loop to 112.6 cm at Meadowbrook (Table 2). The distance when the nearest neighbor was a conspecific was less than when it was a different species in four colonies, but was significantly lower in only one colony.

In the Loop colony the distance to the nearest neighbor was computed for all ibis nests. However 20% of the ibises used abandoned Snowy Egret nests. The mean nearest neighbor distance when ibises built a nest ($\bar{x}$ = 81.6 ± 59.7 cm) was significantly more than in the reused Snowy nests ($\bar{x}$ = 42.5 ± 20.2 cm), reflecting the fact that the neighbor ibis had originally built its nest next to a Snowy and not an ibis. The ibis taking over the Snowy nest was left with the ibis neighbor already there. The nearest neighbor distance to a Snowy Egret when the nest was built by an ibis

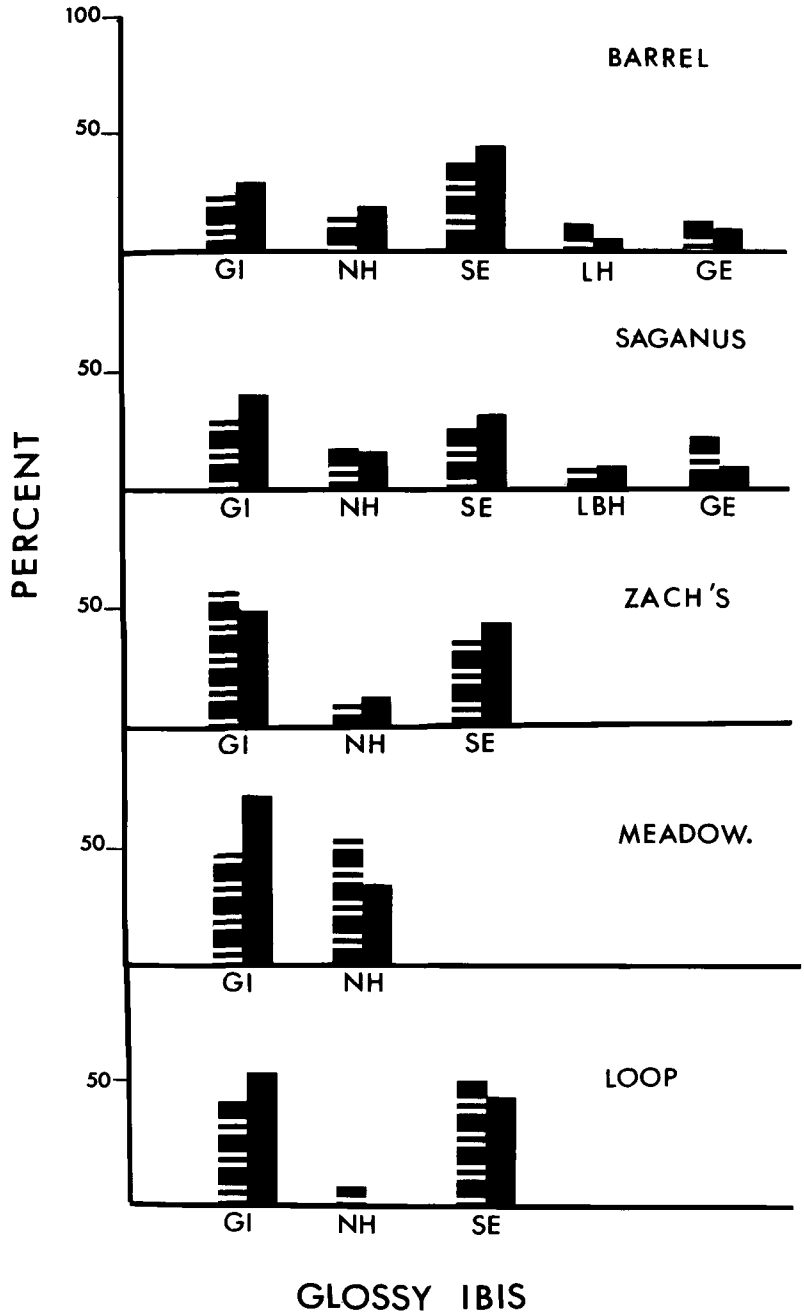

Fig. 3. Nearest neighbors of Glossy Ibis. The broken bar reflects the percent of each species present and the solid bar the percent nearest neighbor. Symbols are the same as in Fig. 1; in addition, GI = Glossy Ibis and NH = Night Heron.

($\bar{x}$ = 70.3 ± 29.8 cm) was significantly less than in the reused Snowy nests ($\bar{x}$ = 136.1 ± 49.8 cm), again the reused nest was built originally by a Snowy, which might defend a greater distance to a conspecific.

As with White-faced Ibises, nearest neighbor distances were also recorded with a

horizontal and vertical component and plotted on a graph to show the open space around Glossy Ibis nests. Only the pattern from Zach's Bay is shown (Fig. 2). As is the case with White-faced Ibis, Glossy Ibis's nearest neighbors were closer if above the nest, and were farther away when on the same level.

Visibility.—Fisheye photographs were taken in only two Glossy Ibis colonies (Barrel Island and Zach's Bay). The mean total visibility from nests at Barrel Island was not significantly different from that at Zach's Bay (Table 3). The visibility index in the direction of the closest nest was significantly lower than the visibility index in the other directions (see Table 3). At Barrel Island the visibility index in the direction of the nearest neighbor was directly related to the distance to that nearest neighbor ($r = + 0.549$), while this was not so at Zach's Bay ($r = + 0.111$).

Preference for bayberry.—The Meadowbrook, Zach's Bay, and Loop colonies contained *Phragmites* and bayberry, and the Glossy Ibises appeared to prefer nesting close to bayberry bushes. For example, the mean distance from the center of Glossy Ibis nests to bayberry ($\bar{x} = 40.9 \pm 53.8$ cm) was significantly less than random ($\bar{x} = 84.4 \pm 60.5$ cm) in the Meadowbrook colony.

Behavioral observations indicated that 96% of all landings (n = 238) of Glossy Ibis adults were on bayberry. Adults then climbed down the bayberry and walked to their nests. Adults left the nest 90% of the time by walking to the bayberry, climbing to the top, and flying. The nests were sufficiently open for the ibises to land either on their nests or on the ground nearby.

DISCUSSION

Colony site selection.—The White-faced Ibises that were studied nested in a tule marsh in Argentina and on a low shrub-forb island in Texas. The dry land colony birds nested on low *Borrichia* shrubs (14%) and on the ground in forbs (86%) rather than in grass or cactus. Eight of the nine colonies that we found described in the literature were in tules. The records from tule colonies date from 1889. Ryder (1967) described the Texas and Louisiana colonies as in costal marshes; the only dry land colony was in Texas in the early 1970's. Thus the use of dry land colonies may be a recent habitat change.

The dry land colony we studied had low success because of fire ants, *Solenopsis* spp. In the 3-week period of observation on that island we saw no young older than about 5 days. The young in almost every nest were dead or dying and were covered with fire ants. In some nests the eggs were pipping and a stream of ants were walking into the egg via the pipped opening. The next day these chicks were dead. This problem occurs because the ibis nests are built on the ground and the ants crawl over the ground and up over the nests. Snowy Egret and Louisiana Heron nests were above ground in the same places, and never contained ants or young killed by ants.

The Glossy Ibis colonies studied ranged from *Phragmites*-bayberry to small shrubs. Most of the colonies described in the literature are on dry land and include *Phragmites*, beach plum, bayberry, elder bushes, willow, black pine, and red cedar (Baynard 1913, Middlemiss 1955, Palmer 1962, Post 1962, Bauer and Glutz von Blotzheim 1966, Davis 1966, Ali 1969, Dement'ev and Gladkow 1951, Post et al. 1970). They nest on the ground and high in trees and have also been reported to nest in reed beds over the waters in South Africa (McLachlan and Liversidge 1969). Apparently the Glossy Ibis is much more versatile with regard to type of nesting habitat than the White-faced Ibis (Post et al. 1970, Palmer 1962, this study). Most colonies of White-faced Ibis are in tules (Davie 1889, Bent 1926, Gabrielson and

Jewett 1970), although some colonies are in low bushes on the ground (Lowery 1974, Flickinger and Meeker 1972). The versatile nesting habits and rapid range expansion in the Eastern United States and South America of Glossy Ibis contrast greatly with the restricted nesting habitat preferences and declining numbers of breeding areas of the White-faced Ibis. Ryder (1967) mentions the decreasing number of breeding White-faced Ibis as a function of decreasing habitat and changing water conditions. Human disturbance and loss of wetlands to agriculture appear to be much more critical for the less versatile nesting behavior of the White-faced Ibis. Although still abundant in Argentina, this species has been rare in Chile with the progressive drainage of suitable habitat (Johnson 1972). The presence of fire ants in the southern regions (e.g. Texas) may prevent the White-faced Ibis nesting successfully on dry ground. Glossy Ibises, on the other hand, are capable of nesting in marshes, on the ground, and above the ground in a variety of habitats. The other notable species undergoing range expansion, the Cattle Egret, may owe its success to the availability of a feeding niche, grazing with large mammals (cows) (Rice 1956).

All the *Plegadis* nest in marshes in tule beds. The Puna Ibis is largely restricted to marshes (Olrog 1959, Koepke 1954), the White-faced Ibis is largely restricted to marshes, and the Glossy Ibis uses marshes infrequently. In Europe the Glossy Ibis nests mostly in reeds (Bauer and Glutz von Blotzheim 1966) which suggests, together with the bulky nest, that the ancestral *Plagadis* was a marsh nester.

The difference in success and relative numbers of the two *Plegadis* species may also be related to an increase in Glossy Ibis habitat by the creation on the Atlantic coast of spoil islands, where most of the heron and ibis colonies on the east coast seem to be found. For example 100% of the herons, egrets, and ibises breeding on Fire Island National Seashore in 1973 nested on dredge spoil islands and not on the natural barrier beaches (Buckley and Buckley 1974). Repeated dredging often maintains spoil islands in an early successional stage, ideal for nesting birds (Soots and Parnell 1974). Thus Glossy Ibises on the east coast have spread north on these spoil islands. Perhaps White-faced Ibis may undergo a similar expansion as the Danger Island colony is on a spoil island. This factor will bear watching in the future.

Nearest neighbor.—White-faced Ibises nested closer to conspecifics than expected by chance, whereas Glossy Ibises appeared to nest randomly with respect to the species of nearest neighbor. This suggests that White-faced Ibises may actively defend the space around their nests from other species and allow conspecifics to nest closer. Glossy Ibises may move in and nest near other species regardless of the species, and may defend the space around the nest less vigorously. The mean neighbor distance is less in the Glossy Ibis than it is in the White-faced Ibis. The mean nearest neighbor distance of White-faced Ibis at Danger Island (187.1 $\pm$ 60.0 cm) is significantly greater than that of Glossy Ibis at Barrel Island (88.5 $\pm$ 27.0 cm, $t = 3.23$, df = 62, $P < 0.001$), and at Zach's Bay (94.5 $\pm$ 38.2 cm, $t = 2.66$, df = 100, $P < 0.01$).

No clear picture emerges within and between species with regard to distances to conspecific versus nonconspecific nearest neighbors (see Table 2). In some cases the differences may reflect different individuals or defendable distances of the nearest neighbor. For example, when the nearest neighbor of the White-faced Ibis at Azul is a conspecific, the mean distance is 111.7 cm; when not conspecific, the mean distance is 153 cm. All of the nonconspecific nearest neighbors were Brown-hooded Gulls and gulls have a mean nearest neighbor distance of 160 cm (Burger 1974a). Thus the White-faced Ibis nearest neighbor distance to a nonconspecific may reflect a charac-

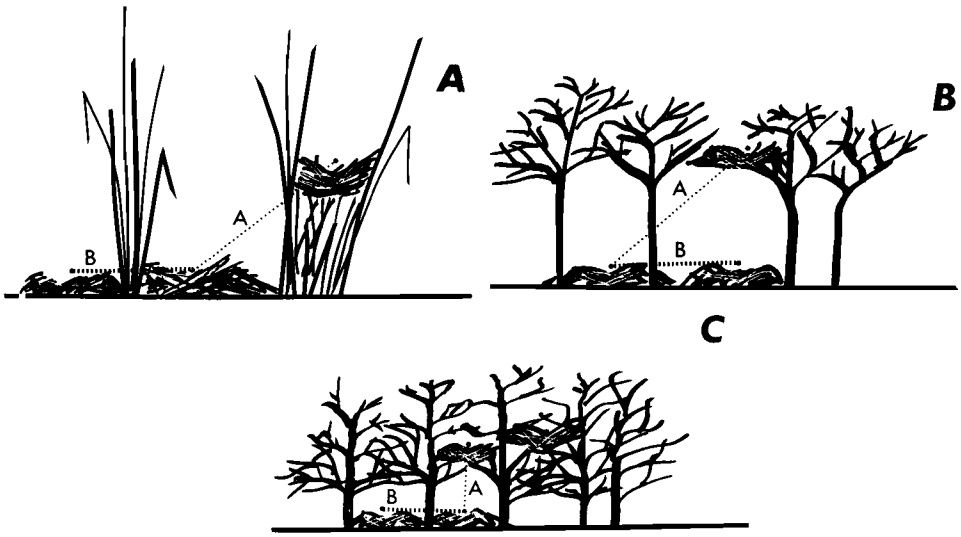

Fig. 4. How the structure of the vegetation determines the smallest nearest neighbor distance. See text for explanation.

teristic of the nearest neighbor and not something about ibises. Structural differences in habitat may also influence the relationship between conspecific and nonconspecific nearest neighbor distances. In the Meadowbrook, Loop, and Zach's Bay colonies, the vertical nature of the vegetation (Fig. 4A) prohibits the building of any nest directly above a Glossy Ibis' nest; it is impossible to build a nest high in *Phragmites* unless several stems are bent over for support. Thus, functionally it is possible to build closer together if nests are on the ground, as they are for ibises. In the Barrel Island colony the reverse situation exists, as the branched nature of the *Iva* bushes makes it possible for nests to be built directly above a Glossy Ibis nest (Fig. 4C). As we have shown that the open distance around ibis nests is not constant and that nests can be closer if they are above, it is expected that the conspecific distances would be greater, as ibis nests are on the same horizontal plane. The Seganus Thatch habitat is similar to that of the Barrel Island colony, so one might predict that the conspecific nearest neighbor distance should be greater than the nonconspecific distance. Over half of the ibis nests at Seganus were in the branches and not on the ground. Thus, spatially, other species could nest anywhere with respect to the Glossy Ibis.

Visibility relationships.—White-faced and Glossy Ibis selected nest sites well covered with vegetation and thus the visibility from the nests was low, lower than that of the other species in the colonies they inhabited. The visibility from both Glossy and White-faced Ibis nests was less in the direction of the closest nest than in all other directions. Similar results were obtained for Franklin's Gull *L. pipixcan* (Burger 1974b), Brown-hooded Gull (Burger 1974a), Black-headed Gull *L. ridibundus* (Burger 1976), and Laughing Gulls (Burger, pers. obs.).

White-faced Ibises nested in more open habitats than did Glossy Ibises. The difference between the total visibility index of the White-faced Ibis colony in Argentina when compared to that of the Glossy Ibis colony was significant at Barrel Island ($t = 6.4$, df = 81, $P < 0.001$) and at Zach's Bay ($t = 4.9$, df = 116, $P < 0.001$). There was also a significant difference in the visibility index from the White-faced Ibis nests at Danger Island when compared to that from Glossy Ibis nests at Barrel

Island ($t = 5.3$, df = 73, $P < 0.001$) and Zach's Bay ($t = 4.9$, df = 108, $P < 0.001$). There was no difference between Glossy Ibis nests in New Jersey and New York colonies.

Nest structure.—The nests of Glossy and White-faced Ibis are very similar. Both make well-built nests with a well-formed cup lined with finely cut pieces of vegetation. White-faced Ibis nests were larger when they were over water. Such construction is adaptive, as young birds are in the nest for at least 4 weeks before fledging. The presence of a well-formed cup is adaptive in preventing eggs from rolling out of the nest. It would be more dangerous for eggs to roll out of a White-faced Ibis nest into the water than onto the ground from a Glossy Ibis nest. The maintenance of the construction of a substantial nest in the Glossy Ibis may suggest an ancestral marsh habitat.

ACKNOWLEDGMENTS

We thank D. Gladstone, M. Gochfeld, C. Hahn, K. Parkes, and W. Vesterman for reading the manuscript. J. C. Ogden provided helpful comments on the role of spoil islands. The following people aided in data collection and analysis: M. Gochfeld, C. Hahn, M. Howe, P. Miles, D. Moch, D. and E. Miller, and we are thankful. G. W. Blackloch identified the plants in the Texas coloines. Special thanks are due D. Moch and M. Gochfeld for their field help, logistical support, discussions, and friendship in the Texas and New York colonies, respectively. We thank R. Brady of the Jones Beach State Park Commission for permission to work in Jones Beach, and the staff of the Brigantine National Wildlife Refuge for permission to use the colonies on Little Beach Island.

Various aspects of this research were supported by grants from the Penrose Fund of the American Philosophical Society (JB), Research Council and Biomedical Sciences Support Grant of Rutgers University (JB), and the Society of Sigma XI (LMM). During the fieldwork the senior author was funded by the American Association of University Women (1972–3) and the Research Council of Rutgers University (1974). Logistic support at Brigantine, New Jersey was provided by USPHS grant MH 16727 to Colin G. Beer, in Texas by the Rob and Bessie Welder Wildlife Foundation, and in Argentina by P. Miles. We thank these organizations and people for making this research possible.

LITERATURE CITED

ALI, S. 1969. Birds of Kerala. Oxford, Oxford Univ. Press.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.

BAUER, K. M., AND U. GLUTZ VON BLOTZHEIM. 1966. Handbuch der Vogel Mitteleuropas, vol. 1. Frandfurt am Main, Akademische Verlagsgesellschaft.

BAYNARD, O. E. 1913. Home life of the Glossy Ibis (*Plegadis autumnolis* [sic] *Linn.*). Wilson Bull. 20: 103–117.

BENT, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135: 1–490.

BREWSTER, W. 1886. Breeding of the White-faced Glossy Ibis in Florida. Auk 3: 481–482.

BUCKLEY, P. A., AND T. H. DAVIS. 1973. The nesting season June 1–July 31, 1973: Hudson-St. Lawrence region. Amer. Birds 27: 846–853.

BUCKLEY, P. S., AND F. G. BUCKLEY. 1974. The significance of dredge spoil islands to colonially nesting waterbirds in certain national parks. *In* Proc. conf. mgmt. dredge islands in North Carolina estuaries. Chapel Hill, North Carolina.

BULL, J. 1974. Birds of New York State. Garden City, Doubleday.

BURGER, J. 1972. The use of a fish-eye lens to study nest placement in Franklin's Gulls. Ecology 53: 362–364.

———. 1974a. Breeding biology and ecology of the Brown-hooded Gull in Argentina. Auk 91: 601–613.

———. 1974b. Breeding adaptations of Franklin's Gull (*Larus pipixcan*) to a marsh habitat. Anim. Behav. 22: 521–567.

———. 1976. Nest density of the Black-headed Gull in relation to vegetation. Bird Study 23: 27–32.

CLARK, P. J., AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445–453.

DAVIE, O. 1889. Nests and eggs of North American birds. Columbus, Hann and Adair.

DAVIS, T. H. (Compiler). 1966. Breeding bird census #73—heron colony. Audubon Field Notes 10: 662–664.

———. 1967. Breeding bird census #84—heron colony. Audubon Field Notes 21: 666–667.

DEMENT'EV, G. P., AND N. A. GLADKOW (Eds.). 1951. Ptitsy Swvetskogo Soyuza, vol. 2. Jerusalem, Israel Program for Sci. Transl.

FINCH, D. W. 1972. The nesting season June 1, 1972–August 15, 1972: Northeastern maritime region. Amer. Birds 26: 832–837.

———. 1973. The spring migration April 1–May 31, 1973: Northeastern maritime region. Amer. Birds 27: 748–751.

FLICKINGER, E. L., AND D. L. MEEKER. 1972. Pesticide mortality of young White-faced Ibis in Texas. Bull. Environmental Contamination and Toxicology 8: 165–168.

GABRIELSON, I., AND S. JEWETT. 1970. Birds of the Pacific Northwest with special reference to Oregon. New York, Dover Publishing Co.

GOCHFELD, M. 1970. What is the Jamaican Glossy Ibis? Broadsheet Gosse Bird Club 15: 9–10.

———. 1973. Observations on new or unusual birds from Trinidad, West Indies, and comments on the genus *Plegadis* in Venezuela. Condor 75: 474–478.

GOODWIN, C. E., AND R. C. BOLLINGER. 1972. The spring migration April 1–May 31, 1972: Ontario-western New York region. Amer. Birds 26: 754–758.

HAILMAN, J. 1959. Consolidation of the northward extension of the Glossy Ibis' breeding range. Bird-Banding 30: 231–232.

JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida, Ecol. Monogr. 39: 245–270.

JOHNSON, A. W. 1972. Supplement to the birds of Chile and adjacent regions of Argentina, Bolivia and Peru, Buenos Aires. Platt Establecemientas Graficas, South America.

JONES, F. B., C. M. ROWELL, JR., AND M. C. JOHNSTON. 1961. Flowering plants and ferns of the Texas coastal bend counties. Sinton, Texas, Rob and Bessie Wilder Found.

KOEPCKE, MARIA. 1954. Corte ecologico trasversal on los Andes del Peru central con especial consideracion do las aves. 1. Costa, vertientes occidentales y region altoandina. Mem. Mus. de Hist. Nat. "Javier Prado" no. 3.

LOWERY, G. H., JR. 1974. Louisiana birds. Baton Rouge, Louisiana State Univ. Press.

MCLACHLAN, G. M., AND R. LIVERSIDGE. 1969. Roberts Birds of South Africa. Cape Town, Cape and Transvalla Printers, Ltd.

MIDDLEMISS, E. 1955. Nest of Glossy Ibis at Rondevlei. Ostrich 26: 137.

OBERHOLSER, H. C. 1974. The bird life of Texas, vol. 1. Austin, Univ. of Texas Press.

OLROG, C. C. 1959. Las Aves Argentinas: una guia de campo. Tucuman, Univ. Nacional de Tucuman.

PALMER, R. S. 1962. Handbook of North American birds, vol. 1. New Haven, Yale Univ. Press.

PEARSON, T. G. 1942. Birds of North Carolina. Raleigh, Bynum Printing Company.

POST, P. W. 1962. Glossy Ibis breeding in New York. Auk 79: 120–121.

POST, W., F. ENDERS, AND T. H. DAVIS, JR. 1970. The breeding status of the Glossy Ibis in New York. Kingbird 20: 2–6.

RICE, D. W. 1956. Dynamics of range expansion of Cattle Egrets in Florida. Auk 73: 259–266.

RYDER, R. A. 1967. Distribution, migration, and mortality of the White-faced Ibis (*Plegadis chihi*) in North America. Bird-Banding 38: 257–277.

SMALL, A. 1975. The birds of California. New York, Winchester Press.

SOOTS, R. F., AND J. F. PARNELL. 1974. Introduction to the nature of dredge islands and their wildlife in North Carolina and recommendations for management. *In* Proc. conf. mgmt. dredge islands in North Carolina estuaries. Chapel Hill, Univ. North Carolina.

STEPNEY, P. H. R., AND D. M. POWER. 1973. Analysis of the eastward breeding expansion of Brewer's Blackbird plus general aspects of avian expansions. Wilson Bull. 85: 452–464.

STEWART, R. E. 1957. Eastern Glossy Ibis nesting in Southeastern Maryland. Auk 74: 509.

ZIMMERMAN, D. A. 1975. The changing seasons. Amer. Birds 29: 23–28.