FACTORS AFFECTING NESTING SUCCESS OF THE GLOSSY IBIS

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ABSTRACT.—We studied Glossy Ibis nesting success in New York during 1974 and New Jersey during 1975. The clutch size in New York (2.56) was significantly smaller than in New Jersey (2.93). Fewer eggs hatched in New York, due to higher rates of predation, nest abandonment, and perhaps egg infertility. Including only nests in which at least one egg hatched, however, the same number of eggs hatched in New York and New Jersey, but significantly fewer chicks fledged in New York. The third egg in a nest hatched at a significantly longer interval from the first egg in New York than in New Jersey. In New York, no third chicks fledged, while in New Jersey 37% fledged. Starvation and predation on all chicks were highest in New York. The daily weight of chicks up to 10 days of age was significantly lower on most days in New York, but the rate or length of feeding bouts did not differ from that in New Jersey. This suggests a lower food supply in New York, which may explain the lower clutch size, greater hatching asynchrony, and greater chick starvation in New York, but colder temperatures and rainfall on more days in New York undoubtedly also contributed. Feeding behavior appears not to be as adjustable to prevailing conditions as clutch size and asynchronous hatching. *Received 14 September 1976, accepted 3 July 1977.*

THE northward expansion of the breeding range of the Glossy Ibis (*Plegadis falcinellus*) from Florida since 1940 is well documented (Steward 1957, Hailman 1959, Bull 1974). Factors such as colony and nest site selection (Burger and Miller 1977) and colony success should be examined to help understand this rapid expansion. There are no detailed studies of the nesting success of the Glossy Ibis in North America. The success of some Ardeids that nest with ibises, however, has been investigated (e.g. Meanley 1955; Teal 1965; Dusi and Dusi 1968, 1970; Jenni 1969; Pratt 1970, 1972; Taylor and Michael 1971). Except for Pratt's studies, these authors studied nesting success during only one breeding season in only one area. Yet for many avian species, success varies between years and sites (see Klomp 1970). In this study, we compare the nesting success of the Glossy Ibis in two mixed colonies in New York during 1974 with that in two mixed colonies in New Jersey in 1975. Ibises have been breeding near Brigantine, New Jersey since 1957 (Potter and Murray 1957), which was their northern breeding limit until 1961, when they began breeding on Long Island, New York (Post 1962). In 1973 they began breeding in Maine (Finch 1973). We were especially interested in the overall success of the colonies and in the nature, timing, and causes of nesting failure as possible contributing factors to the northward expansion of Glossy Ibis.

STUDY AREAS AND METHODS

The four colonies studied were similar with respect to vegetation and nest placement. The predominant vegetation was common reedgrass *Phragmites australis*, bayberry *Myrica pennsylvanica*, and poison ivy *Rhus toxicodendron*. All ibis nests were on the ground, except for the reuse of several nests of Snowy Egrets *Egretta thula* in New York (Burger and Miller 1977).

The two New York colonies were in Jones Beach State Park on Long Island, New York. The Meadowbrook colony, behind parking field #1, contained 113 nesting pairs: 71 pairs of Glossy Ibis and 42 pairs of Black-crowned Night Herons (*Nycticorax nycticorax*). The Loop colony, 3.2 km northwest of Meadow-

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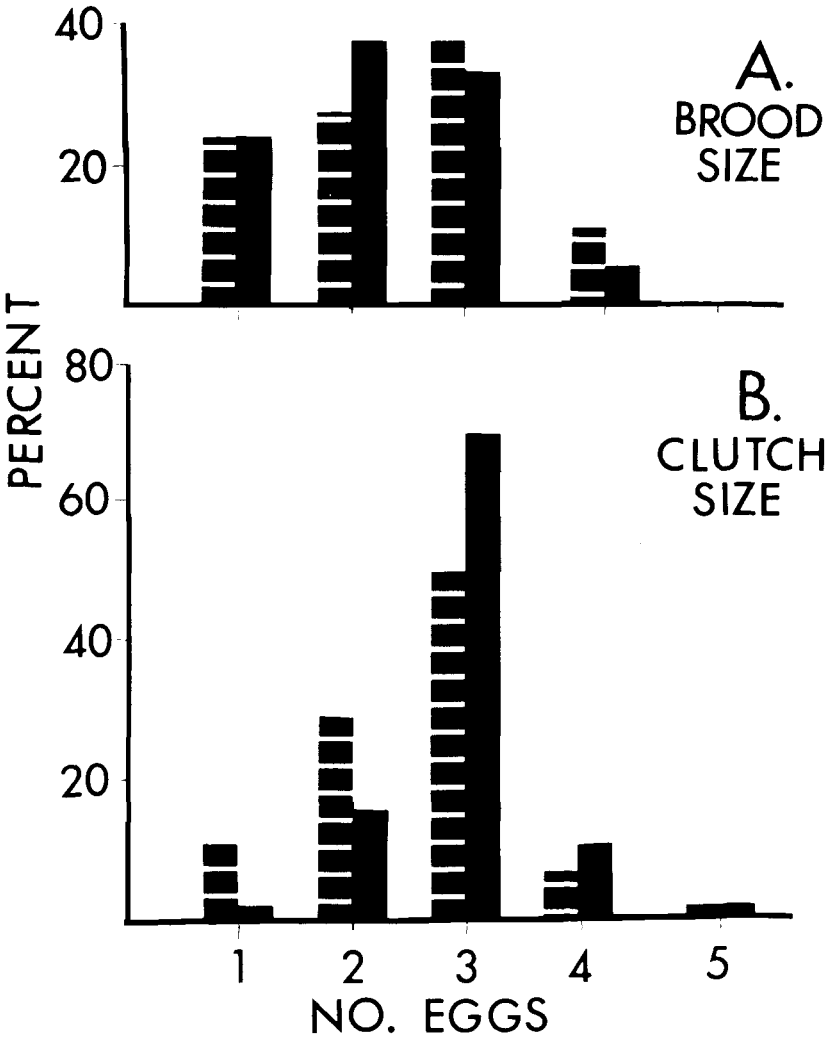

Fig. 1. Brood and clutch size of Glossy Ibis as a function of locality. New York = broken bar; New Jersey = solid bar. **A.** N.Y., N = 37 nests; N.J., N = 58 nests. **B.** N.Y., N = 95 nests; N.J., N = 76 nests.

brook, off the Loop Parkway, contained 152 pairs: 64 pairs of Glossy Ibis, 12 pairs of Black-crowned Night Herons, and 76 pairs of Snowy Egrets. Two hundred to 250 pairs of Herring Gulls (*Larus argentatus*) nested on the open sand and beach grass surrounding each colony.

The two New Jersey colonies studied were each located on a small island in Absecon Bay, north of Atlantic City. Island I (at channel marker 71) contained 1,225 nesting pairs: 300 pairs of Glossy Ibis, 335 pairs of Snowy Egrets, 330 pairs of Little Blue Herons (*Florida caerulea*), 125 pairs of Louisiana Herons (*Hydranassa tricolor*), 25 pairs of Great Egrets (*Casmerodius albus*), and 60 pairs of Cattle Egrets (*Bubulcus ibis*). Island II (at channel marker 61) contained 800 nesting pairs: 175 pairs of Glossy Ibis, 80 pairs of Black-crowned Night Herons, 200 pairs of Snowy Egrets, 208 pairs of Little Blue Herons, 65 pairs of Louisiana Herons, 48 pairs of Great Egrets, and 24 pairs of Cattle Egrets. Sixty to 120 pairs of Herring Gulls nested in *Spartina* around each colony.

Data were collected from mid-April through early August in 1974 and from mid-April through late June in 1975. To determine nesting success, 95 nests in New York (57 at Meadowbrook and 35 at the Loop) and 76 in New Jersey (31 on Island I and 45 on Island II) were followed from egg-laying through 25 days after hatching. Nests were sampled from at least two different areas within each colony. Study sites were

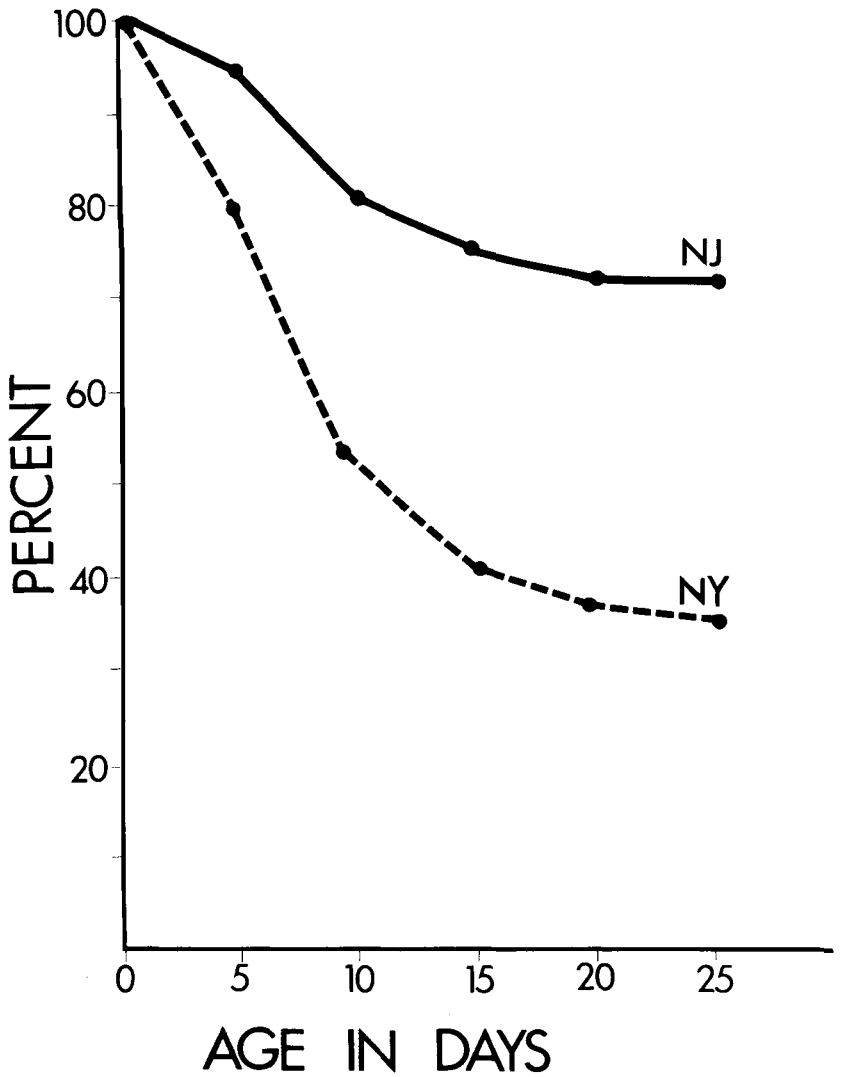

Fig. 2. Survival of Glossy Ibis chicks with age as a function of locality. N.Y., N = 87 chicks from 37 nests; N.J., N = 112 chicks from 58 nests.

sufficiently far apart so that only birds from the area being censused would flush. Adults incubated all sample nests for at least 3 days. Nests were checked every 2–4 days during incubation and every 1–2 days after hatching. The area around the nests was searched for preyed upon eggs and dead chicks. Temperature and precipitation data were taken from monthly reports issued by the National Oceanic and Atmospheric Administration.

Young chicks were marked with a small spot of acrylic paint on the head, and chicks older than 10 days were banded with U.S. Fish and Wildlife Service aluminum bands and color bands. Chicks up to 14 days of age were weighed to the nearest 1.0 g on Pesola field scales. Chicks 11–15 days old leave the nest when approached, but they can be identified by the color bands since they remain within about 7 m. Chicks older than 15 days, which spend increasingly less time at the nest, were censused by observations from a small portable blind. Chicks older than 25 days could not be adequately censused.

Since human disturbance is known to cause some nesting failure in Cattle Egret colonies (Blaker 1969), we minimized disturbance by checking nests rapidly and quietly, checking only in the morning when temperatures were lowest, and not checking during heavy rain. By sampling nests in several widely

TABLE 1. Glossy Ibis success differences in New York and New Jersey for (A) all original sample nests and (B) only nests in which at least one egg hatched. Means, the 95% confidence limit (under each mean), and the tests of significance are based on square root transformations of the raw data ($X' = \sqrt{X + 0.5}$)

	N	$\bar{X}$ Eggs laid/nest	$\bar{X}$ Eggs hatch/nest	$\bar{X}$ Chicks fledge/nest
A. All nests				
New York	95	2.56 (2.49–2.63)	0.67 (0.45–0.89)	0.43 (0.16–0.73)
New Jersey	76	2.93 (2.78–3.07)	1.46 (1.19–1.75)	1.09 (0.62–1.63)
Test of significance		$t = 4.54$; $P < .001$	$t = 4.40$; $P < .001$	$t = 5.22$; $P < .001$
B. Viable nests				
New York	37		2.26 (2.22–2.59)	0.85 (0.46–1.30)
New Jersey	58		2.13 (1.93–2.32)	1.28 (1.04–1.72)
Test of significance			$t = 0.70$; N.S.	$t = 3.72$; $P < .001$

separated areas, adults were kept off the nest only a short time. Since the amounts of disturbance in New Jersey and New York were equal, we assume its effect on success was similar.

RESULTS

Egg-laying.—In New York, egg-laying extended for 23 days at Meadowbrook (8–30 May 1974) and for 37 days at the Loop (13 May–18 June 1974). The ibises laid later than other species in the colony. At Meadowbrook the first ibis egg was laid 20 days after the first Black-crowned Night Heron egg. At the Loop, Black-crowned Night Herons and Snowy Egrets began laying at least 12 days earlier than ibises.

In New Jersey, egg-laying extended for 21 days on Island II (1–24 May 1975) and for 24 days at Island I (6–29 May 1975). All species initiated laying within 5 days of each other.

Clutch size and overall success did not differ significantly between the two colonies in each state, so the means were pooled for each state. One to 5 eggs were laid per nest. The most frequent clutch was 3 in both states (Fig. 1).

The mean clutch size in New York (2.56) was significantly smaller than the mean clutch in New Jersey (2.93) (Table 1A). These clutch sizes are within reported ranges: 2.93 in Virginia (Williams 1975); 2.62 in New York (Bull 1974); 1–5 in Europe (Ali and Ripley 1968); 1–3 in Georgia (Shanholtzer 1970).

Egg survival.—In New York, 64% of all eggs (N = 243) never hatched whereas 44% of all eggs (N = 225) never hatched in New Jersey. The greatest egg loss was to predators: 41% in New York and 33% in New Jersey. An egg was considered preyed upon if it was punctured and its contents at least partly eaten, or if it disappeared.

Predators in both areas were Herring Gulls, Fish Crows (*Corvus ossifragus*), and possibly Norway Rats (*Rattus norvegicus*) and Black-crowned Night Herons. Herring Gulls nested in large numbers on the periphery of all colonies. Once we saw a gull land near an incubated nest, causing the ibis to fly, and the gull removed one egg. Four partly-eaten ibis chicks were discovered near gull nests. At least one pair of crows nested within each colony. They were frequently observed entering the colony. Norway Rats were seen and Black-crowned Night Herons nested in all colonies, but their effect is unknown.

It was difficult to determine other causes of egg loss; infertile, abandoned, cracked,

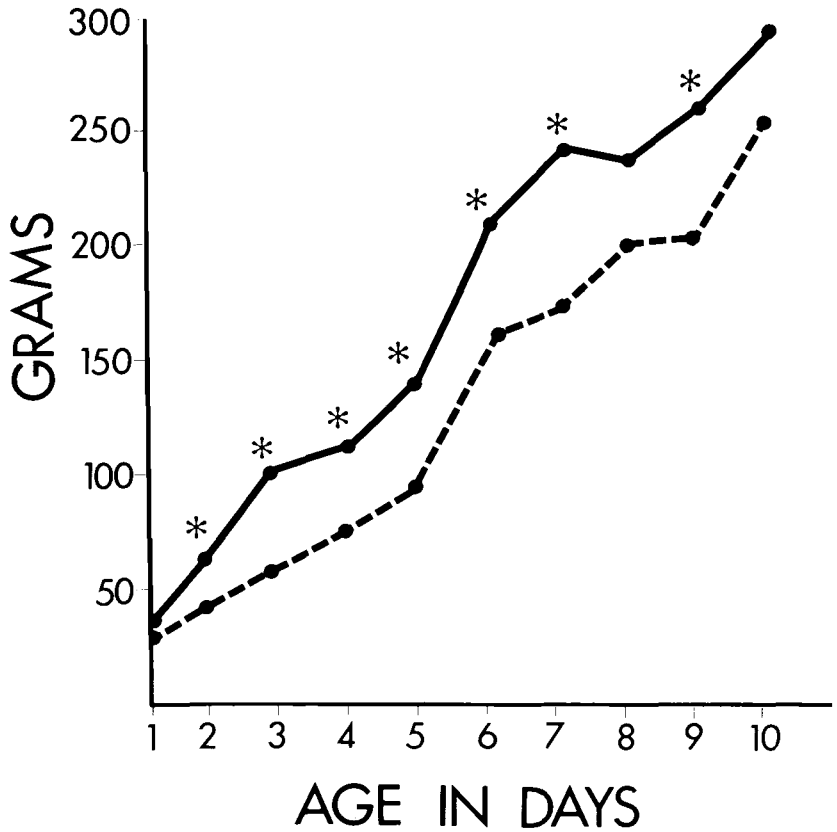

Fig. 3. Weight of Glossy Ibis chicks as a function of locality. New York = broken line (N = 29 chicks); New Jersey = solid line (N = 21 chicks). Differences between states are statistically significant ($P < .05$; based on t-test) for starred days.

or eggs found outside of nests accounted for 23% of all eggs in New York and 11% in New Jersey.

Egg hatching.—Thirty-six percent of all eggs hatched in New York and 56% hatched in New Jersey. Including all original nests, significantly fewer eggs hatched per nest in New York compared to New Jersey (Table 1A). However, including nests in which at least one egg hatched ("viable nests"), the same number of eggs hatched in New York and New Jersey (Table 1B).

In both states, the second chick hatched about 1 day after the first chick. The third chick in New York, however, hatched at a significantly longer interval from the first chick than in New Jersey (Table 2). In both states, incubation began after the first egg was laid, so delayed hatching reflected delayed laying. In New York, the mean

TABLE 2. Hatching interval ($\bar{X} \pm 1$ SD days) for Glossary Ibis chicks in New York and New Jersey when the initial brood size was three

	1^{st}–2^{nd} Chick	1^{st}–3^{rd} Chick
New York	1.1 ± 0.79	4.3 ± 2.53
New Jersey	1.1 ± 0.87	2.3 ± 0.85
Test of significance	t = 0.31, d.f. = 55, N.S.	t = 2.69, d.f. = 31, $P < .01$

temperature (at a station 18 km NW) during egg-laying was 15.5°C, which was 1.06°C below normal for that period, and 9.7 cm of rain fell. During egg-laying in New Jersey, the mean temperature (at a station 7 km SW) was 16.3°C, and only 6.8 cm of rain fell.

Chick survival.—The greatest period of chick loss was between hatching and 10 days of age (Fig. 2). In New York only 52% of the chicks survived to 10 days and 36% survived until day 25 ("fledging"). In New Jersey, 80% survived to 10 days and 71% survived until day 25.

Weights of chicks up to 10 days of age were taken daily in all colonies. There were no significant differences in weights on any day for the two colonies in each state, so the data were pooled. Comparably-aged chicks weighed significantly more in New Jersey than in New York on most days (Fig. 3). Differences in weights could be due to differences in feeding rates, length of feeding sequences, or quantity and quality of food given at the nest by the adults. We were able to measure the first two variables using blinds. Ninety-nine feeding bouts of chicks aged 1–10 days were observed in both states. There was no significant difference between the number of times chicks were fed per hour in New York and New Jersey ($t = 0.56$, N.S.) or between the length of feeding bouts ($t = 1.7$, N.S.).

The exact cause of individual chick loss was difficult to ascertain. Chicks that disappeared before 10 days of age were presumed to have been preyed upon, since they normally do not leave the nest before that age. No dead chicks up to 10 days were found during daily searches of the vegetation; perhaps they were scavenged by rats or gulls. It is not likely that adults removed dead chicks from their nests since in three nests observed from blinds, remaining chicks were brooded with a corpse in the nest. Chicks found partly eaten or bloody were also assumed to be preyed upon. As with egg loss, predation on chicks was higher in New York (31%, $N = 27$) than in New Jersey (10%, $N = 13$).

In New Jersey, six (5%) chick deaths were the direct result of a heavy rainfall (2.6 cm) accompanied by low temperatures (5.6°C below the daily mean) on 12 June. There was less total rain during the period of chick development in New York (6.4 cm) than in New Jersey (9.4 cm), but rain fell on 17 of those days in New York compared to 8 days in New Jersey. Perhaps some chick deaths were caused by exposure in New York. Williams (1975) reported a 27% loss of Glossy Ibis chicks during one hurricane in Virginia.

Twenty-eight chick deaths (32%) in New York and 18 (14%) in New Jersey were not accounted for by predation or adverse weather. These chicks were found dead in or near their nests. Most of these chicks, especially the third chick in a nest, probably died of starvation. No third chicks in broods of 3 survived in New York and only 37% of third chicks survived in New Jersey. The third chicks in New York were consistently below the mean weight at any age. By the time the third egg hatched in New York, the first chicks weighed 70–261 g ($N = 7$ nests). Smaller chicks were unable to compete with the older, larger chicks for food. In 20 feeding bouts of chicks up to 15 days old in New York and New Jersey, the oldest chick was fed 66 times, the middle chick was fed 39 times, and the youngest fed only 18 times ($\chi^2 = 30.7$, $P < .001$).

In New York, there was no significant difference between the number of chicks raised per nest when the initial brood was 1, 2, or 3 ($F = 0.92$, N.S.). A pooled value gives 0.85 chicks raised per nest. In New Jersey, significantly more young were raised in broods of 2 and 3 than in single broods ($F = 6.66$, $P < .005$), but the same

number of young was riased per nest when the initial brood was two or three chicks (1.48, Table 1).

Overall nest success.—Of the nests originally incubated in New York, only 0.43 chicks fledged per nest. This is significantly fewer than in New Jersey, where 1.09 chicks fledged per nest (Table 1A). Because of predation and unsuccessful eggs, only 40% of the original nests in New York had at least one egg hatch. Due to predation, starvation, and inclement weather, only 20% of the original nests in New York and 59% in New Jersey had at least one chick fledge.

Discussion

The differences in the nesting success of the Glossy Ibis between the New York colonies in 1974 and the New Jersey colonies in 1975 could reflect intra-area or yearly variation. Fewer (minus 37%) ibises bred on Long Island in 1974 than in 1973 (Buckley and Davis 1973). Numbers of breeding ibises increased in 1975 to the 1973 levels (Buckley et al. 1975). A low food supply in New York during 1974 is indicated by the chick weights, which were less even though feeding frequency and duration were not different from New Jersey. Perhaps this postulated low food supply prevented many ibises from breeding in 1974. Some species lay smaller clutches when food is below normal (see Klomp 1970), which might account for the significantly smaller clutch size in New York.

Hatching was asynchronous in both areas, which is an adaptation to an unpredictable food supply for the young at the time of laying, and will operate through starvation to reduce the brood size to the number the adults can feed (Lack 1947). In poor food years, the last hatched chick(s) will quickly starve, but in good years, all will be raised (Lack 1954). In New York, many chicks probably died of starvation and all third chicks died. In New Jersey, where higher chick weights might indicate a greater food supply, fewer chicks probably died of starvation and 63% of the third chicks died. Starvation has also been reported to be an important factor in chick mortality in other Ciconiiformes, such as the Spoonbill (*Platalea leucorodia*) (Vespremeanu 1968), Louisiana Heron and Snowy Egret (Jenni 1969), Great Blue Heron (*Ardea herodias*) (Pratt 1970), Cattle Egret (Blaker 1969) and the Grey Heron (*Ardea cinerea*) (Owen 1960).

The degree of asynchrony in hatching should indicate the extent of variability in the food supply (Hussell 1972). This would account for the significantly longer interval between the hatching of the first and third eggs in New York. Low temperatures and heavy rains during egg-laying might also have been a factor, since low temperatures are known to delay the laying of the second or third egg in swifts (*Apus apus*) (Weitnauer 1947). Even though adults in New York were unable to deliver adequate amounts of food, the feeding rate and length of feeding bouts were not different from those in New Jersey. These behaviors appear stereotyped and are not modifiable with clutch size and asynchronous hatching to the prevailing conditions.

In both New York and New Jersey most egg and chick loss was due to predators (gulls and crows; possibly rats and night herons). These rates are comparable to predation in other mixed heronries reported by Teal (1965), Baker (1940), and Taylor and Michael (1971). Crows have been reported to be serious predators in heronries (e.g. Baker 1940, Stoner 1942, Dusi and Dusi 1968). There have been no reports of Herring Gulls as predators of Ciconiiform chicks, although they are known to prey upon other species (Harris 1965, Parsons 1971) and upon their own nestlings (Hatch

1970). In the White-faced Ibis (*Plegadis chihi*) in Utah, 22% of all eggs and 15% of all chicks were preyed upon by Franklin's Gulls (*Larus pipixcan*) (Kotter 1970).

It is not known if the nesting success in New York and New Jersey is typical for the edge of the breeding limit for ibises, or at what age ibises first breed; both factors would contribute to understanding the rapid range expansion. Some Glossy Ibises may breed after their first year, for an ibis color banded as a chick in New York was observed building a nest the next year in Maine, the current northern breeding limit. The breeding expansion of the Glossy Ibis has been characterized by the initial appearance of only a few pairs (see Hailman 1959, Post 1962); perhaps ibises from range edges help establish colonies further north. In order for a species to expand, extrinsic factors (e.g. climate, predators, habitat), which usually work against expansion, must exert less of an effect than intrinsic factors (e.g. rate of increase, population density, age structure) (Stepney and Power 1973). Ibises' rate of increase and the early age at which they may breed contribute to making them an expanding species, but the rate of increase in any one colony depends on the factors considered in this paper: food availability, predation and environmental conditions.

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George Lowery, a Past-President of the A.O.U., passed away on 19 January 1978. A **Lowery Memorial Fund** has been established to provide an endowment from which expenses of research and publication by the staff, students, and associates of the LSU Museum of Natural Science may derive support. Persons wishing to contribute to this fund may do so through the **LSU Foundation, 122 Systems Building, Louisiana State University, Baton Rouge, Louisiana 70803**. Indicate that contributions are intended for the Lowery Memorial Fund.
