# VARIATION IN REPRODUCTIVITY WITH AGE IN THE BROWN PELICAN

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ABSTRACT.—About 10% of the Brown Pelicans breeding in South Carolina are in immature plumage. In comparison to adult breeders, immatures nested later, laid a smaller clutch, nested more frequently in low ground that was flooded, lost a larger proportion of nestlings, and produced fewer downy young per nest. Factors such as experience in breeding and fishing success probably influence reproductive success of pelicans of various ages.—*U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20811 and 85 Silverwood Road, Atlanta, Georgia 30342*. Accepted 10 August 1976.

IN common with many other long-lived seabirds that exhibit deferred breeding (Fisher 1975), the Brown Pelican (*Pelecanus occidentalis*) breeds initially when several years old (Williams and Joanen 1974). Most Brown Pelicans apparently do not breed before acquiring adult plumage. In this study of a population of Brown Pelicans in South Carolina, we found a relatively high incidence of breeding birds in immature plumage. We describe the reproductive success and characteristics of the immature-plumaged cohort in comparison to the adult-plumaged cohort, and discuss briefly the factors influencing breeding of immature-plumaged pelicans.

## METHODS

This study was conducted from 1969 through 1975 on Marsh Island, Cape Romain National Wildlife Refuge, South Carolina. Most of the data concerning nesting of immatures was obtained in 1975. The Marsh Island nesting colony is divided into two sections by a salt marsh containing salt-water cord-grass (*Spartina alterniflora*). Marsh Island encompasses nearly 12 ha, but the pelicans use only about 1.5 ha of it for nesting. Except for a few nests in small shrubs, pelicans built their nests on the ground. Visits to each of the two sections of Marsh Island in 1975 were limited to one or two 1-hour periods each week from April through mid-August.

Nests of pelicans were marked with an aluminum stake with plastic tape or plastic flagging attached. Most nests were marked when they contained freshly laid eggs, but some were marked when incubation was well advanced. A few nests were initially marked when young were present, and one egg was collected from several marked nests; data from these nests from the 1975 study and all marked nests from previous years were used for comparative purposes but were excluded from the statistical analysis for clutch size and reproductive success. This was deemed necessary as reproductive success of the colony varied markedly from year to year, and inclusion of the nests marked initially with young present would unduly increase our estimate of reproductive success.

Fate of marked nests was determined by periodic observations. A nest was successful if one or more downy young survived to leave the nest (usually 4–5 weeks); these are referred to as downy young produced. We also color-banded 28 nestlings to obtain a valid measurement of reproductive success relative to number of young that fledged from ground nests. In addition to marked nests, a complete census of all nests (plus contents) in the colony was made several times during the season. As the season progressed, we counted young out of the nest and recorded mortality. Thus we were able to determine, with little error, the number of young, both color-banded and unbanded, that fledged.

We tried to identify plumage characteristics of each incubating parent at marked nests (Fig. 1). Basically we identified three plumage types of breeding pelicans, although the characteristics of immature-plumaged birds intergraded greatly. Adult breeding plumage has a brownish-black venter, gray dorsum, white head (yellow at start of breeding season), and a chestnut neck and a white stripe (Fig. 1A). Adult Brown Pelicans exhibit no sexual dimorphism in plumage, and no evidence suggests sexual differences in the immature plumages. The second plumage type was essentially that of the adult except the venter was white; important variations included a gray or light brown neck, indistinct neck stripe, and a mottled head or venter (Figs. 1B and 1C). The third plumage type included a white venter and a brown head, neck, and

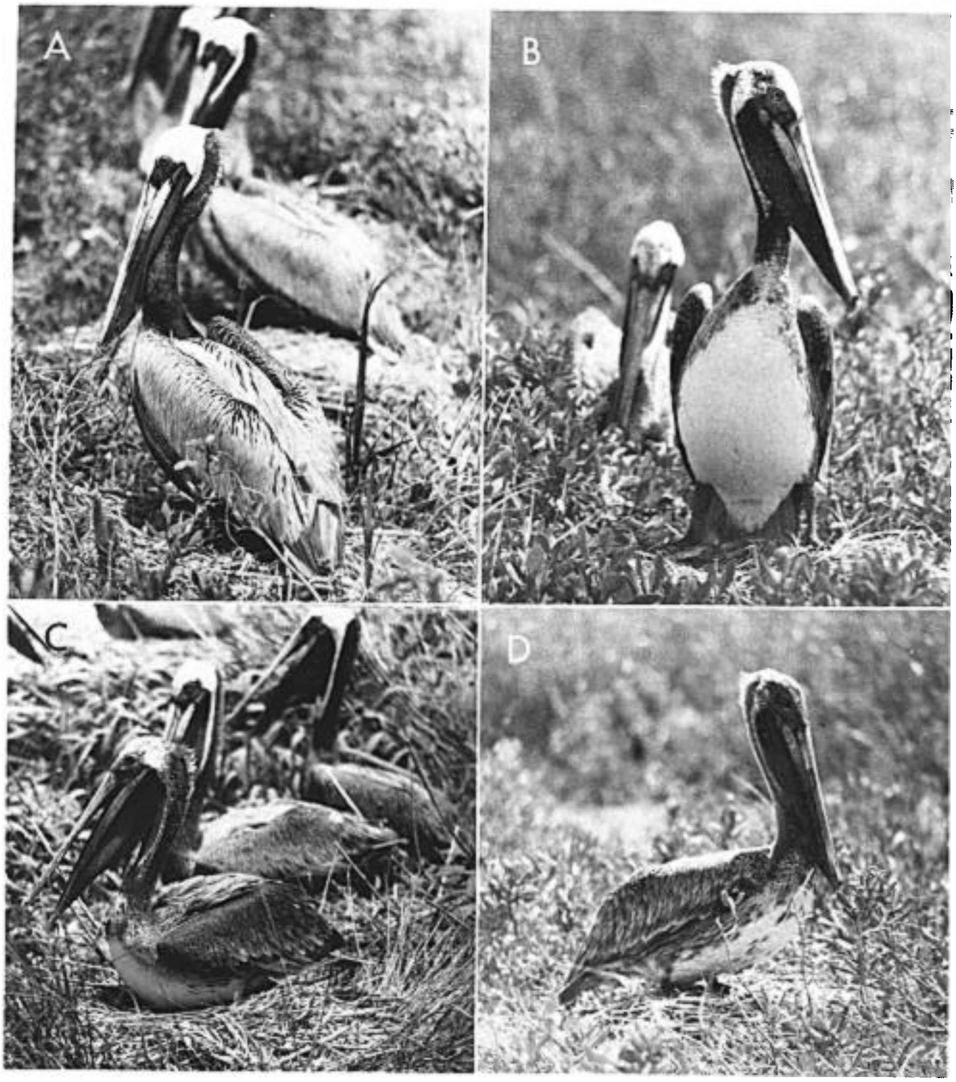


Fig. 1. Plumage characteristics of several nesting Brown Pelicans. A, adults in full breeding plumage with white head. B, C, and D, immature birds. Note proximity of adults to the immature in C.

dorsum; some of these birds have an indistinct neck stripe, a trace of white on the head, and a mottled venter (Fig. 1D). The individuals in the third plumage type are probably the youngest breeding pelicans. For a more detailed description of plumages see Palmer (1962: 271–273). Pettingill (1970: 371) defined an immature as a young bird with teleoptiles that has not acquired its full adult plumage, but it may nevertheless be capable of breeding. Because young pelicans may breed in two types of plumage that show much intergradation, we refer to all breeding pelicans without full adult plumage as immatures.

## Results

*Clutch size.*—The mean clutch size of the adults was significantly larger ($P < 0.001$) than that of immatures (Table 1). The characteristic clutch size for adults was three compared to two for immatures. Clutch size in marked nests ranged from 1 to 3 for immatures and 2 to 4 for adults. Four nests of immatures each contained a single

TABLE 1

PARAMETERS OF REPRODUCTIVE SUCCESS FROM MARKED NESTS OF BROWN PELICANS, 1975[1]

| Parameter | Immature | Adult |
|---|---|---|
| Mean clutch size | 2.16[2] (37)[3] | 2.85 (89)[4] |
| % of nests with hatched young | 47.2 (17 of 36) | 68.1 (62 of 91)[5] |
| % of nestlings dying | 85.2 (23 of 27) | 41.6 (57 of 137)[4] |
| % of nests inundated by tidal flooding | 62.9 (22 of 35) | 7.8 (7 of 90)[4] |
| % of nests successful[6] | | |
| Active nests | 11.4 (4 of 35) | 50.0 (45 of 90)[4] |
| Unflooded nests | 30.8 (4 of 13) | 54.2 (45 of 83) |
| % of eggs producing downy young | | |
| Active nests | 5.3 (4 of 75) | 31.5 (80 of 254)[4] |
| Unflooded nests | 16.0 (4 of 25) | 34.0 (80 of 235)[5] |
| Successful nests | 57.1 (4 of 7) | 60.2 (80 of 133) |
| Mean number of downy young produced per | | |
| Active nest | 0.11 (4 from 35) | 0.89 (80 from 90)[4] |
| Unflooded nest | 0.31 (4 from 13) | 0.96 (80 from 83)[4] |
| Successful nest | 1.00 (4 from 4) | 1.78 (80 from 45)[4] |

[1] Procedures in Sokal and Rohlf (1969: 607–610) followed in testing equality of two percentages and determination of required sample size. Student's *t*-test used to determine differences in means for clutch size and downy young per nest.

[2] Frequency of clutch size in marked nests of immatures (I) and adults (A): 1 egg-4I; 2 eggs-23I and 14A; 3 eggs-10I and 74A; and 4 eggs-1A.

[3] Sample size in parentheses. Variation in sample size of nests with parameter is due to incomplete observations.

[4] $P < 0.001$.

[5] Although the statistical test indicated that the percentages were significantly unequal ($P < 0.05$), the test for sample size revealed that, with the sample size available, we could be only 50% certain of detecting a true difference at the 10% level of significance. Tests for required sample size for other percentages exhibiting a significant difference indicated that with the sample size available, we could be 90% certain of detecting a true difference at the 5% level of significance.

[6] A successful nest is one that produces one or more downy young.

egg; these were the only single-egg-clutches verified in this study. A downy young was produced in each of two nests that contained a single egg. Only one marked nest of an adult contained four eggs. Four-egg clutches were rare in South Carolina pelicans; only 5 of 2,400 nests in 1975 contained 4 eggs. The maximum clutch of 5 occurred 3 times in approximately 10,000 South Carolina pelican nests from 1969 through 1975. Coker (1919) reported as many as eight eggs in clutches of the Peruvian Brown Pelican (*P. o. thagus*). The mean clutch size of South Carolina adults in 1975 was 3% less than the mean of 2.95 for 236 Brown Pelican clutches collected in North America from 1879 to 1943 (Anderson and Hickey 1970) and the same as the mean clutch size of pelicans on the Gulf coast of Florida in 1969 and 1970 (Schreiber and Risebrough 1972).

*Reproductive success*.—We determined success of pelicans in relation to plumage type at marked nests. Pairs with 2 adults were much more successful than pairs with at least 1 immature: 45 of 90 adult pairs produced downy young. One of the five pairs containing an adult and an immature was successful. We identified an immature parent at 24 nests but never saw the other parent; only one young was produced. We identified both members of seven pairs as immatures; each of three pairs produced a single young. Most of the marked nests of immatures were initially studied in late May or early June, and many of the nests were destroyed by tidewaters before we identified both incubating parents.

The earliest breeding pelicans each year were adults; these birds usually selected the higher nesting sites. In comparison to adults, immatures nested more frequently in the low-lying periphery of Marsh Island that contained sea-ox-eye (*Borrichia frutescens*) or in still lower places containing salt-water cord-grass; most nests in these peripheral areas were flooded in early June (Table 1). Some of the highest parts of Marsh Island were not used for nesting even though they were secure from the tidal flooding. Thus placement of nests by immatures in low-lying places was apparently not induced by a lack of higher ground. We think the pelicans nested in the low, flooded areas primarily because of poor judgment or lack of experience, but other unidentified factors may be involved. A few pairs of adults and immatures avoided flooding in low-lying ground by building nests as much as 60 cm high. Ryder (1975) reported that immature-plumaged Ring-billed gulls (*Larus delawarensis*) nested more frequently on the periphery of the colony than adult-plumaged gulls; peripheral nesting gulls, like Brown Pelicans, were less successful than those nesting near the center of the colony.

The percentage of Brown Pelican nests that hatched young was greater for adults than for immatures, but the difference was not significant (Table 1). Hatching data are difficult to interpret because nests were checked a maximum of twice a week, and young dying within a few days of hatching may have been missed if they were removed from the nest by the parents or predators. Also, the percentage of eggs flooded by tidewaters was greater for immatures than for adults; thus the eggs were lost before they had a chance to hatch (Table 1).

Only 5% of the eggs laid by immatures produced downy young compared to 32% for adults (Table 1). Excluding clutches that were flooded, only 15% of the eggs of immatures produced downy young compared to 34% for adults. In successful nests, the percentage of eggs that produced downy young was virtually the same for immatures and adults.

The number of downy young produced per nest by adults was significantly greater ($P < 0.01$) than the number produced by immatures (Table 1); this relationship applied to active nests, successful nests, and unflooded nests. The four successful nests of immatures in the analysis (Table 1), produced only one downy young apiece. In 17 other nests, marked when eggs were present but not included in the analysis, 12 produced no young and 5 produced one young. Of 6 additional nests marked initially when young were present, 5 downy young were produced by 4 successful nests. Thus of 13 successful nests of immatures, only 1 produced as many as 2 young. In 1975 adult pairs produced 1 downy young from each of 15 nests, 2 downy young from each of 25 nests, and 3 downy young from each of 5 nests.

The significantly lower nesting success of immature Brown Pelicans in comparison to adults was largely attributable to the higher incidence of flooding of nests of immatures (Table 1). Adults had a higher percentage of successful nests than immatures in nests that were not flooded (Table 1), although the difference was not statistically significant ($10 < P < 20$). Tidal flooding accounted for 19 of the 23 deaths of naked young (<2 weeks of age) in marked nests of immatures. We were not present when nests were flooded, but we could usually determine when this occurred. A heavy rain storm accompanied the high tides that occurred in the second week of June, but the rains apparently killed few young. Of the 22 nests of immatures lost to tidal flooding 10 contained young and 12 contained eggs. The 7 flooded nests of adults included 2 with eggs and 5 with young. The 57 nestlings, 43 naked and 14 downy young (≥2 weeks of age), that died in nests of adults included 10 that were apparently killed by tidal flooding.

The poor reproductivity of immatures in 1975 also seemed partially attributable to their nesting later than most adults. Early-nesting adults whose nests were marked in early April produced 67 downy young from 65 nests compared to 13 downy young from 25 marked nests established after May 1. The 0.52 downy young produced per nest by adults establishing nests after May 1 was greater than the 0.31 downy young immatures with unflooded nests produced per nest.

We regularly found immatures on nests in both South Carolina colonies since our intensive study was initiated in 1971. Complete counts of immatures are lacking, but we identified 50 nests and estimate that at least 100 of the 900 breeding pairs on Marsh Island in 1975 contained at least one immature. Thus pairs with immatures accounted for 10% or more of the breeding population. Our studies on Deveaux Bank show the percentage of breeding pairs with immatures is approximately the same as on Marsh Island. The estimated 300 pairs of immature Brown Pelicans in South Carolina probably produced fewer than 100 fledglings in 1975.

## DISCUSSION

The breeding immatures probably range from 1 to 4 years of age; adults in full breeding plumage are probably over 3 years of age. Marked pelicans in Louisiana bred for the first time when 3 years of age in a newly established colony, but they did not attain full breeding plumage until their 5th year (Williams and Joanen 1974). In contrast, trapping of banded incubating pelicans revealed that some South Carolina birds may attain full adult breeding plumage at 3 years of age (Beckett 1966). In 1972 we found a marked 2-year-old pelican incubating.

Some recruitment of young resulted from the breeding of immatures although they were less successful than adults. Color banding of the 28 nestlings revealed that about 14% of the young died before fledging. Most young fledge when 10–12 weeks of age (Schreiber 1976). Mortality of color banded young of immatures was 25% (1 of 4 died) compared to 12% for banded young of adults (3 of 24 died). While these records of banded young suggest a differential mortality rate, the difference is not statistically significant ($10 > P > 20$). Survival rate of young produced by experienced breeders of such species as the Laysan Albatross (*Diomedea immutabilis*) (Fisher 1975) and Red-billed Gull (*Larus novaehollandiae*) (Mills 1973) was much higher than that of young produced by inexperienced breeders.

We determined that approximately 10,000 pelicans fledged from the South Carolina colonies from 1969 through 1975. We estimated that 850 potential breeding pairs of immatures survived to 1975, calculated under the following assumptions: (1) All the pelicans raised in 1970 and preceding years and surviving to 1975 were in adult plumage; (2) all the pelicans raised in 1971–1974 and surviving to 1975 were in immature plumage; and (3) age-specific mortality rates from banding data (Henny 1972) were applicable to this population. If the above estimate is correct, then less than one half of the 850 potential breeding pairs of immatures actually bred in South Carolina. We do not know whether all the immatures return from the wintering grounds to their natal colonies in South Carolina. Also, we do not know whether all of the immatures that return to South Carolina colonies are physiologically capable of breeding; our limited observations suggest that some of the immatures seen near colonies are nonbreeders.

While contemporary Brown Pelicans in South Carolina regularly breed in immature plumage, the senior author failed to find a single nesting immature in Florida in 1974 though he visited a number of colonies and studied hundreds of nesting birds at close range. Williams and Joanen (1974) also noted few breeding immatures in the Florida colonies except in one newly established colony of 13 pairs of immatures; this colony was some distance from the nearest breeding pelicans. Newly established colonies of the Kittiwake (*Rissa tridactyla*) also contained a high proportion of inexperienced breeders (Coulson and White 1958).

The breeding population of Brown Pelicans in North Carolina was discovered in 1929 (Pearson et al. 1942: 16); 36 nests were present on the small nesting island in 1974. We found 70 immatures near the North Carolina colony during the 1974 visit, but saw only adults on nests.

Lack (1968: 197) indicated that birds with deferred breeding may nest at an earlier age with reduced competition; thus breeding of immature Brown Pelicans in South Carolina may be related to conditions associated with a population that declined from approximately 6,000 breeding pairs in the 1950's (Beckett 1966) to slightly over 1,000 pairs by 1969 (Blus et al. 1974a, Blus et al. 1974b). In contrast, few immatures breed in Florida where the population is regarded as stable (Williams and Martin 1970, L. Williams pers. comm.) and apparently none in North Carolina where the breeding population has remained at low stable numbers since the colony was established nearly 50 years ago.

Breeding immature Brown Pelicans were reported near the turn of the century in Peru (Forbes 1914, Coker 1919), and within the past few years in Peru and Baja California, Mexico (D. W. Anderson, pers. comm.). Recently Brown Pelicans in California experienced a low rate of productivity and a population decline (Anderson et al. 1975); studies initiated in 1969, when these problems were first noted, showed that immatures were breeding (D. W. Anderson, pers. comm.).

In common with the Brown Pelican, many deferred breeders nesting for the first time are also less successful than experienced breeders; this relationship was reported for the Red-billed Gull (Mills 1973), Laysan Albatross (Fisher 1975), Kittiwake (Coulson and White 1958), Ring-billed Gull (Ryder 1975), and by Richdale (1949: 14) for the Yellow-eyed Penguin (*Megadyptes antipodes*). Ryder (1975) concluded that adult Ring-billed Gulls attained a higher egg success than immatures largely because adults were more persistent incubators. Coulson and White (1958) found that the parental drive in Kittiwakes tends to be weaker and often more abortive in younger than in older birds. Immature Brown Pelicans are less successful than adults in catching fish (Orians 1969); failure to provide sufficient food for their young may be closely related to the low breeding success of immatures in combination with inexperience in breeding and other factors.

Major theories explaining low reproductive success of inexperienced breeders include: (1) clutch size is adapted to the number of young that can be raised; therefore, small clutches evolved for younger individuals because they were less efficient in feeding young than experienced breeders (Lack 1968: 298); (2) younger birds lay as many eggs as they can produce, but they lay a smaller clutch because they are inexperienced and find less food than experienced breeders (von Haartman 1971: 429–430); and (3) fertility is largely governed by the interplay of social rank and economic conditions with the result that newcomers to the breeding population are likely to be handicapped by their inferior social position (Wynne-Edwards 1962: 566). Colonies of Brown Pelicans containing only immatures such as those noted in Louisiana in 1971 and Florida in 1974 (Williams and Joanen 1974) provide a possible means of studying the validity of at least one of the three theories.

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