NESTING CHRONOLOGY OF THE EASTERN BROWN PELICAN

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ABSTRACT.—Nesting of Eastern Brown Pelicans (*Pelecanus occidentalis*) between 10–20°N is irregular and occurs over prolonged periods, usually beginning in the late fall and lasting through June but occasionally lasting throughout the year. Nesting between 20–30°N is on a winter-spring cycle, with only some irregularity. Colonies in the 30–35°N region exhibit a definite annual periodicity, nesting in spring-summer. The time required by adults to nest successfully, and then to undergo molt, plus daylength fluctuations only partially explain the controls on the breeding seasons. Data for the most extensively studied colony of the species on Tarpon Key, Florida west coast indicate that freezing temperatures may control the timing of nesting, because earlier nesting occurs in the absence of cold temperatures. Selection against nesting during the hurricane season may have been an important factor determining the nesting chronology in this species. *Received 14 August 1979, accepted 10 January 1980.*

I SUMMARIZE here the available data on chronology of nesting by Eastern Brown Pelicans (*Pelecanus occidentalis occidentalis* and *carolinensis*). This subject received some note in the past (Bent 1922, Howell 1932, Palmer 1962), and detailed study of the Florida west coast population plus more cursory observations throughout the state between 1969 and 1979 permit interpretation of the nesting seasons of this coastal marine species as related to controls on breeding in birds (Immelmann 1973, Murton and Westwood 1977).

METHODS

My studies concentrated on Tarpon Key in Tampa Bay, Florida west coast (27°40'N, 82°40'W, Fig. 1), which I visited weekly from January 1969 through June 1976 and briefly in March, May, and/or June of 1977, 1978, and 1979. I also visited most other pelican colonies throughout Florida during these years. Data in the literature are summarized for chronology in other colonies.

For this study, counts of adults, nests, and nestlings were made as described in Schreiber (1979), and the tables and appendices of that paper contain the detailed counts used in this analysis.

RESULTS

FLORIDA WEST COAST

Tarpon Key.—In most years at Tarpon Key no adults were present in November, December, and January, and the similar patterns of population build-up in 1969, 1970, 1971, and 1973 were different from later years (Fig. 2). First adults arrived at the island during the last week of February, and numbers increased from count to count or on a weekly basis until the first or second week of April, when peak numbers were present. The peak population lasted for various periods of time; then a gradual decline in numbers occurred through June–August, and the island was deserted by mid-October in 1969 and 1970. During the fall of 1971, the island was never deserted, and numbers of birds increased dramatically during the last week of December, remained high through January 1972, then declined slightly, though noticeably, through February. The population peaked in late March, and the decline in numbers through the summer and fall of 1972 was similar to that in earlier years.

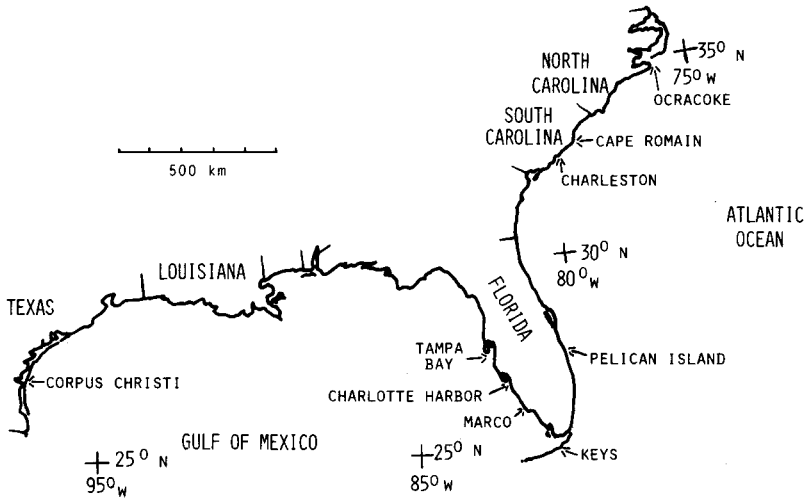

Fig. 1. Southeast United States noting locations relevant to Brown Pelican colonies.

The island was deserted by early November 1972. No adults were present until the last week of February 1973. During this week and the first 2 weeks of March, the most rapid build-up in numbers that I recorded occurred, followed by a precipitous drop and then a slow increase, with the peak not reached until mid-May. This early initial build-up, followed by a decline in numbers, was exhibited by this population in early March 1970 and 1971, in mid- to late February 1974 and 1975, in early February 1976, but most dramatically in March 1973. During 1973 the population again declined through June–September, and no adults were present from late October 1973 until mid-February 1974.

The nesting seasons of 1974, 1976, and especially 1975 showed similar build-up, peak, and decline in the population as in earlier years, but the timing was earlier, and the build-up started in early February or mid-January 1975, with the peak reached in March rather than April as in 1969, 1970, and 1971.

The major events of the nesting cycle are compared in Table 1. First nests occurred from 4 January (1972) to 19 March (1970), with earlier dates occurring in the later years. First nestlings could be heard from 22 February (1972) to 4 May (1969), again with earlier dates occurring in the later years. First nestlings could be seen 1–2 weeks after they could be heard. First fledging occurred from 25 April (1972) to 9 July (1973), 16–18 weeks after the first nests were seen in the colony. The colony was deserted in all years, except the fall of 1971, from mid-October to mid-November, with no apparent trend over the years.

Data for the number and accumulated percentage of nests in a subunit of this colony that was used to study individually marked nests and to measure productivity (Schreiber 1979) clearly indicate the trend of nesting earlier in 1974–1976 than in 1969–1971, although the peak of nesting occurred in this unit of the colony in late April–early May in all years (Table 2). The very early nesting in 1972 is also obvious. Considerable variation occurred in the timing of nesting between specific units of the Tarpon Key colony, but first nesting always occurred in the northern portion of the island, with later arrivals occupying the western and southern mangrove areas.

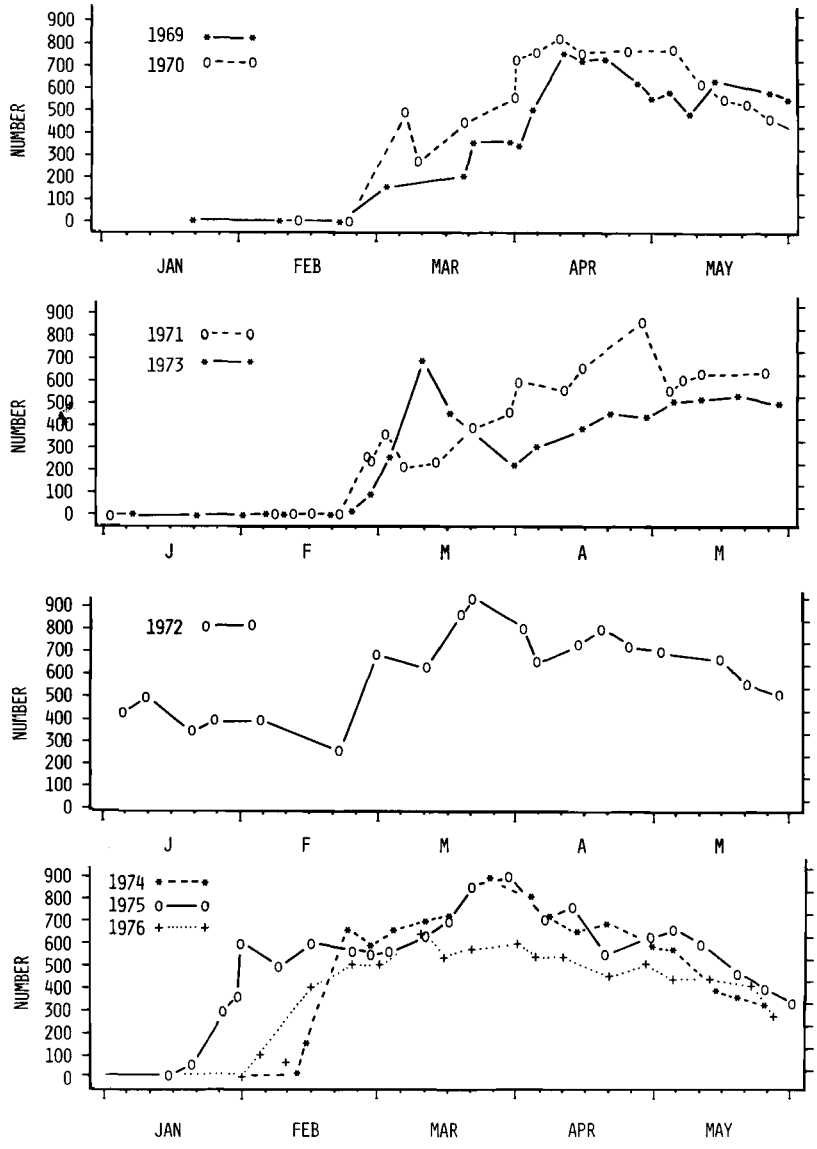

Fig. 2. Number of adult Brown Pelicans present on Tarpon Key, Pinellas County, Florida west coast in Tampa Bay, January–May 1969–1976.

We visited Tarpon Key once or twice in March and May/June 1977, 1978, and 1979, and nesting began in early February in those years.

These data for 8 yr show two long term changes in the general pattern of the onset of breeding in the late winter: initiation of island occupation earlier and the population peaking earlier in 1974–1976 than in 1969–1971. Additionally, the striking contrast between the population changes in 1972 as opposed to the other 7 yr, along with the decline in numbers after initial arrival at the island in all years, provides the basis for my thesis on the controls of breeding in this species.

Nesting records.—Historical records for pelicans nesting on Tarpon (= Bush) Key

TABLE 1. Timing of nesting cycle on Tarpon Key, Pinellas County, Florida, as determined by observation from mid-lagoon and recorded as first date observed. Event thus happened in preceding several days, usually not more than 1 week.

Year	First nests	First nestlings heard	First nestlings visible	First fledglings	Colony deserted
1969	?	4 May	13 May	6 July	11 October
1970	19 March	19 April	24 April	15 June	12 September
1971	27 February	12 April	16 April	27 June	Never
1972	4 January	22 February	11 March	25 April	15 October
1973	27 February	5 April	14 April	9 July	18 November
1974	23 February	3 April	20 April	28 June	29 October
1975	29 January	21 March	29 March	18 May	16 November
1976	4 February	8 March	21 March	27 May	24 October

or nearby Indian (= Bird) Key are available sporadically from 1888. The names of these islands are confusing, but apparently nesting occurred on Indian Key from 1888 through the 1920's (Scott 1888, McPherson 1889, Pearson 1907, Pangburn 1919, Wetmore in litt.; Fargo 1926, 1929; Bent and Copeland 1927, Longstreet 1937) but shifted the 1 km south to Tarpon Key in the early 1930's (Schultz 1936, Mills 1931, 1949), where they have nested since. These records indicate no nesting in the winter, with adults moving to the island in March or April. Egg dates are 27 April 1913, early April 1924–1929, and late April 1925, while only nests were present on 28 April 1888 and 11 April 1906. The earliest nestlings were found on 27 April 1913. June, July, and August found large numbers of adults and nestlings present. While these data are sketchy, many were collected by oologists, and, had eggs been present earlier in the year, they probably would have been noted.

These data are insufficient to draw hard conclusions, but it appears that earlier nesting has occurred in the 1970's than was found from the late 1800's through the 1930's in this population. Clearly, an annual, spring-oriented, nesting cycle exists for Tarpon Key.

Other Florida west coast colonies.—Nesting chronology data are available for the 1970's for a colony of Brown Pelicans on the Alafia Banks, a dredged-material island 35 km northeast of Tarpon Key and in the upper reaches of Tampa Bay, at 27°51'N, 80°25'W. This island was created in the 1930's, and pelicans began nesting there in 1967. During the years for which we have comparative data (Table 3), nesting

TABLE 2. Number and accumulated percentage of nests formed in study area on Tarpon Key. Recorded as date first egg found in marked nests.

	1969		1970		1971		1972		1973		1974		1975		1976	
Date	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
1–15 February	0	—	0	—	0	—	5	6	0	—	0	—	9	17	0	—
16–29 February	0	—	0	—	0	—	7	14	0	—	11	18	19	53	3	10
1–15 March	0	—	4	16	2	5	23	40	0	—	18	48	8	68	13	55
16–31 March	4	31	5	36	8	25	35	81	7	30	20	81	0	68	4	69
1–15 April	7	85	11	80	19	74	12	95	2	39	10	97	8	83	6	90
15–31 April	2	100	5	100	8	94	4	100	2	48	1	99	4	91	2	97
1–15 May		—		—	2	100		—	10	91	1	100	4	100	1	100
16–31 May		—		—		—		—	1	95		—		—		—
1–15 June		—		—		—		—	0	95		—		—		—
16–31 June		—		—		—		—	1	100		—		—		—

TABLE 3. Nesting data for Brown Pelicans on the Alafia Banks, Hillsborough County, Florida west coast.

Year	Courtship	First nest	First hatching	Last hatching	First fledgling	Last fledgling
1969	—	25 March	—	—	—	—
1970	22 March	7 April	7 May	—	25 July	24 August (most gone)
1971	—	—	—	—	23 July	—
1972	—	—	—	—	—	—
1973[a]	—	28 March	11 May (young visible)	late May	late April early May	late August
1974	mid January	—	mid March	late May	late April	—
1975	11 January	27 January	21 March (young visible)	late May	mid April	early September
1976	late December 1975	31 December	early March (young visible)	late May	late April	early September
1977	late December 1976	late January	early March	late May	late April	—

[a] Frank Dunstan became Warden in late March 1973; James Rodgers became Warden in 1977, continuing Dunstan's studies.

commenced in late December or January and proceeded to conclusion 1–2 months earlier than at the Tarpon Key colony. Unfortunately, no data exist for 1972.

Farther south on the west coast of Florida, chronology data exist for two colonies. Data for the first, a large colony on Bird Keys, Charlotte Harbor, Charlotte County, at 26°40′N, 82°14′W and 120 km south of Tarpon Key are for 1974–1977. Adults occupy this island throughout the year, and nesting started in late February 1974–1977, with peak nests present in April and May. First fledlings were recorded in early- to mid-July in 1975 and 1976. The available data indicate that timing of nesting in this colony is consistently on a "spring" regime. Data for the second colony, 45 km south at Marco Island, Collier County, at 25°59′N, 81°44′W are for 1973–1979. They were collected by Theodore H. Below and show no nesting in January but nests present in February (Table 4). The peak of nesting was reached in early July in 1973; in June 1974, 1977, 1978, and 1979; in May 1975; and in April 1976. In 1979, ages of the nestlings indicated that Marco nesting was 2 weeks ahead of that in Charlotte Harbor (Below pers. comm.). The Marco colony thus exhibits an irregular timing of nesting on a somewhat earlier cycle than colonies to the North. This irregularity, however, does not parallel that of other colonies on the west coast of Florida. Historical records indicate that nest building, or only eggs, or eggs and

TABLE 4. Nesting data for Brown Pelicans on Marco Island, Collier County, Florida west coast. Recorded as number of nests and percentage of maximum found that year.

	1973		1974		1975		1976		1977		1978		1979	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
January	0	—	0	—	0	—	0	—	0	—	0	—	0	—
February	0	—	0	—	36	21	58	37	9	6	0	—	7	2
March	47	53	64	34	88	52	140	90	54	34	7	2	63	22
April	41	46	102	55	123	73	156	100	101	63	200	69	177	60
May	75	84	156	84	168	100	130	83	140	88	227	79	241	82
June	87	98	186	100	153	91	93	60	160	100	289	100	293	100
July	89	100	24	13	66	39	45	29	75	47	234	85	265	90
August	42	47	—		46	28	10	6	55	34	—		—	
September	10	11	—		6	3	7	4	25	16	—		—	

TABLE 5. Summary of nesting data for Brown Pelicans on Pelican Island, Brevard County, Florida east coast.

Year	January	February	March	April	May	June	July	August	September	October	November	December
1880	en[a]	en	EN[b]							e	e	en
1891	en	EN									e	en
1894	en	EN										e
1898	en	EN								e	en	en
1900	e	en	en	EN								e
1902	e	en	en	EN								e
1903		e	en	en	EN	N	N					
1904				NONE							e	e
1905	en	EN	EN	EN						e	en	en
1906											e	
1907				E							e	
1908	en	en	EN	EN	EN	N	N	N	N	e	en	en
1909											E	
1910										E[c]	E	
1911						N[d]						
1914	en	EN									e	en
1919	en	EN									e	en
1922								E	EN			
1923								Moved to Brevard Island [see Table 6]				
1970	n	n	n	N								e
1971	e	n	N									e
1972	n	n	N									e
1973										Adults		
1974												e
1975	n	n	n	N						Courtship		Courtship
1976	EN	EN	EN	en	EN							
1977	en	en	en	NF	NF							
1978											e	en
1979	en	en	ENF									

[a] e eggs and n young, calculated as should have been present based on available data, such as estimates of age of nestlings, etc.
[b] E eggs and N young or F fledglings noted as present.
[c] Island occupied continuously from October 1908 to October 1910 when hurricane struck and birds moved.
[d] Activity terminated by mosquitoes and 600 nests abandoned but young had fledged.

small young were present in these areas, but not necessarily the same colonies, in May around the turn of the century (Scott 1887, Jamison 1891, Pearson 1907).

FLORIDA KEYS

Kushlan and McEwan (MS) partially summarized nesting by Brown Pelicans in the Florida Keys, where nesting is clearly irregular. Nesting may start in October or November but more usually in December, with a peak in February–April. Generally, colonies are deserted by August, although young have been found through October (Howell 1941, Greene 1945, Moore in litt.), and most nests in April–June contain eggs or young.

On Bush Key, Dry Tortugas, 24°38′N, 82°52′W, Monroe County, however, pelicans nested for the first time in the 20th century in 1974, laying between 8 and 19 June (Schreiber et al. 1975). In 1975 and 1976 laying occurred in early April and through mid-June. In 1977 first laying occurred in early March, some eggs were laid as late as the end of April, and only chicks 5–7 weeks old were present in mid-June. In 1978 available data indicate that eggs were laid between 3 and 7 April but probably continued later through April. In 1979 no nesting had occurred by early

TABLE 6. Summary of nesting data for Brown Pelicans on Brevard Island, Mosquito Lagoon, Florida east coast.[a]

	January	February	March	April	May	June	July	August	September	October	November	December
1924	x	x	x								x	x
1925	x	x									x	x
1926	x	x								e	x n	x n
1927	N										x	x
1928								e	en	EN	EN	x
1929							e	x	e(80%N)	x	x	x
1930						x	x	EN	x	x	x	x
1931	x					E	x	x	x	x	x	x
1932						x	x	x	x	x	x	x
1933					x	x	x	x	x	x	x	x
1934					x	x	x	x	x	x	x	x
1935				x	x	x	x	x	x	x	x	x
1937							E	EN	EN	EN	EN	N
1942					x	x						
1957	x											

[a] Redrawn from Longstreet 1956, who indicated just presence of nesting activity, and supplemented by additional published data; see Table 5 for codes; x indicates merely presence of "nesting activity."

April, but in mid-June 2 nests held downy young, so eggs must have been laid in late April (Robertson and Below in litt.).

To summarize the Florida west coast and Keys data, in southern areas nesting tends to be irregular throughout the year but with most laying occurring in December through June. Farther north, laying becomes more regular and usually is in April and May. Individual colonies seem to exhibit a specific breeding cycle. Historical data are scanty, but all colonies except that on Tarpon Key exhibit similar timing through the 1900's. Tarpon Key is an exception, perhaps because of the detailed data that are available in the 1970's. While the colony is on a late-winter-spring cycle, a shift toward earlier nesting occurred in the mid- to late 1970's, and nesting began at least 2 months earlier than "normal" in 1972.

FLORIDA EAST COAST

Nesting by pelicans on the Florida east coast is much better documented than in the Keys or on the west coast. The most thorough data are for Pelican Island National Wildlife Refuge, Brevard County, 27°49′N, 80°30′W, and Brevard Island, Brevard County, about 25 km to the north, but the specific location of which is now unknown. I have summarized these data in Tables 5 and 6 from the following sources: Gibbs (1891, 1894); Lawrence (1891); Watkins (1894); Chapman (1900, 1901, 1908); Dutcher (1903); Kroegel (1910); Bowdish (1909); Nelson (1911); Wetmore (field notes, 1919); Bent (1922); Hiatt (1931); Mills (1931); Longstreet (1932, 1942, 1956); Harris (1933); Shannon (1933, 1934); Davis (1934); Westfall (1937); Woodhead (1938); Mason (1945); Stevenson (1957); Schreiber (field notes, 1970–1979); they clearly indicate a nesting season beginning occasionally in October, but usually in late November and December. Few eggs were laid after March or April. Only rarely does any nesting occur in June–September, but occasionally nesting has occurred throughout the year (1908–1910). Several authors commented on the contrast between the timing here and on the Gulf Coast of Florida. Between 1924 and 1935, the season shifted so that nesting occurred earlier and lasted longer throughout the year. Characteristic of the Pelican Island National Wildlife Refuge colony were high

tides flooding the ground nests, usually in February (in 1885, 1905, 1906, and 1910 at least) and cold spells apparently causing mass starvation of young and desertion of eggs (in February 1908 and 1979 at least).

Chronology data are available for three other small colonies on the east coast of Florida only for the 1970's: Hall Island, Brevard County, in Cocoa Beach, 28°23'N, 80°37'W; Rio Mar Island, Indian River County, in Vero Beach, 27°38'N, 80°22'W; and Ft. Pierce, Indian River County, at 27°28'N, 80°19'W. These data clearly indicate that pelicans used these islands for nesting occasionally from January but usually from December through September–October, with laying and nestling peaks in April through July in all years for which data are available (Maxwell and Kale 1974; Schreiber, field notes, 1970–1979). These islands are also used for roosting and loafing throughout the year.

SOUTH CAROLINA

In South Carolina nesting has occurred in two locations, the Cape Romain National Wildlife Refuge at 33°57'N, 79°35'W; and on the Deveaux Banks, near Charleston, at 31°33'N, 80°11'W. Data from Baldwin (1946), Sprunt and Chamberlain (1949), Blus (1970), Blus et al. (1977), and Blus and Keahey (1978) and records of the Cape Romain National Wildlife Refuge clearly indicate a regular annual cycle, with adults returning to the state in February and March, with egg laying primarily in April and May, with occasional laying in mid- to late March and in June, but with young rather than eggs present in June and July. Young remain into September, but most are gone in August, and the colonies are abandoned by late September or October.

NORTH CAROLINA

In North Carolina, nesting has occurred near Ocracoke in Hyde County either on Shell Castle Island, 35°06'N, 76°04'W, or on nearby North Rock, 35°07'N, 76°04'W, or on Beacon Islands, 35°06'N, 76°03'W, since at least the mid-1940's. Egg laying has begun in recent years in mid-March and usually extends through May and occasionally into late July. The nesting sites are usually abandoned in September (R. Steiner in litt.; Parnell and Soots 1976; Wooten 1977; O. Florschutz, Jr. in litt.; Soots and Parnell MS). In 1978, a colony was established on the lower Cape Fear River between Wilmington and Southport in Brunswick County. This site was on an unnamed dredged-material island, 33°55'N, 77°51'W. In 1979 this site was again used, and a few birds established a second colony about 2 km upriver on a second unnamed dredged-material island, 33°59'N, 77°57'W. Egg laying began in 1978 in the Cape Fear River in late May and continued into June (Soots and Parnell MS).

LOUISIANA AND TEXAS

In Louisiana and Texas, nesting has occurred in many locations between 28° and 29°N, and 89° and 97°W. Useful data on nesting chronology are remarkably scanty. It appears, however, that nesting has never occurred before March; in some years laying occurs in March, but most eggs are laid in April and May, with some laying occurring occasionally in June and only rarely in early July (Job 1915, Pearson 1921, Cahn 1922, Williams 1938, Lowery 1974, Oberholzer 1974, Williams and Joanen 1974, King et al. 1977, Chaney et al. 1978). In the 1970's, nesting has occurred on

three islands in southern San Antonio Bay, Aransas Bay, and Corpus Christi Bay, and similar timing occurred as in the past. But the Corpus Christi Bay colony is always 1–2 months later (incubating in mid-May) than the other colonies, which are only 12 km away (Paul, Blankinship, and Payne in litt.).

Oology

Data from oological collections indicate nesting in September in Cuba; February and March in Panama; April, May, and June in Texas; March through June in Louisiana; December through June in Florida east coast; March through June in Florida west coast; and May, June, and July in South Carolina. Bent (1922) gives the following egg dates: Florida, 34 records from 1 February to 30 June and 17 records from 16 April to 15 May; Texas, 15 records from 4 April to 28 May and 8 records from 16 April to 28 May; South Carolina, 9 records from 8 May to 23 June. These oological data confirm those presented above from field observations.

Caribbean and Gulf of Mexico

Nesting throughout the remainder of the Eastern Brown Pelicans' range in the Caribbean and Gulf of Mexico is poorly documented. Nesting occurs at many small colonies, rarely with more than 100 pairs, and nesting is highly asynchronous within and between colonies. Much between-year variation occurs, but initiation of nesting can occur in any month and then is quite extended, with laying occurring over 4–5 months in most colonies. To summarize egg dates briefly by locale: Aruba, May through August; Venezuelan islands, January through December but most in January through April (Cory 1909); Trinidad and Tobago, annual cycle on Saut d'ear but otherwise February–July (Dinsmore in litt.); Lesser Antilles, much yearly variation but, for Pelican Key off St. Martin, a usual fall and winter cycle, with most eggs in December–March but in some years in the summer and fall; the Virgin Islands, February through September but most in February and March (Robertson 1962); on Saint John in the U. S. Virgins, Robertson and Ogden (1969) found numbers of fledged young and adults still on eggs in late September 1968; Hispaniola, January through October but most in January–February; Jamaica, August (Scott 1891); Cuba, March and April; Puerto Rico, from October through July in 1978 and probably extended in other years (Schreiber et al. MS); in Costa Rica, Stiles and Smith (1977) found many eggs and some young in early January, while most nests held well grown young by late February 1972 on Isla Guayabos at 10°N, 86°W. Murphy (1936) noted "since the nesting season is almost everywhere prolonged, it is usual to find fresh eggs and well grown young at the same time." It is amazing how few additional data are available for this species since Murphy's classic study and summary.

Summary of Nesting Chronology

In Fig. 3 I summarize the available egg dates for the entire breeding range of the eastern Brown Pelican by location and latitude. This figure clearly shows that in the low latitudes around the Caribbean, between 10° and 20°N, nesting is inconsistent and irregular and occurs over a prolonged period, usually beginning in October or November and continuing through May and June and occasionally throughout the year. Nesting colonies in the 20°–30°N latitudes usually do not have any eggs

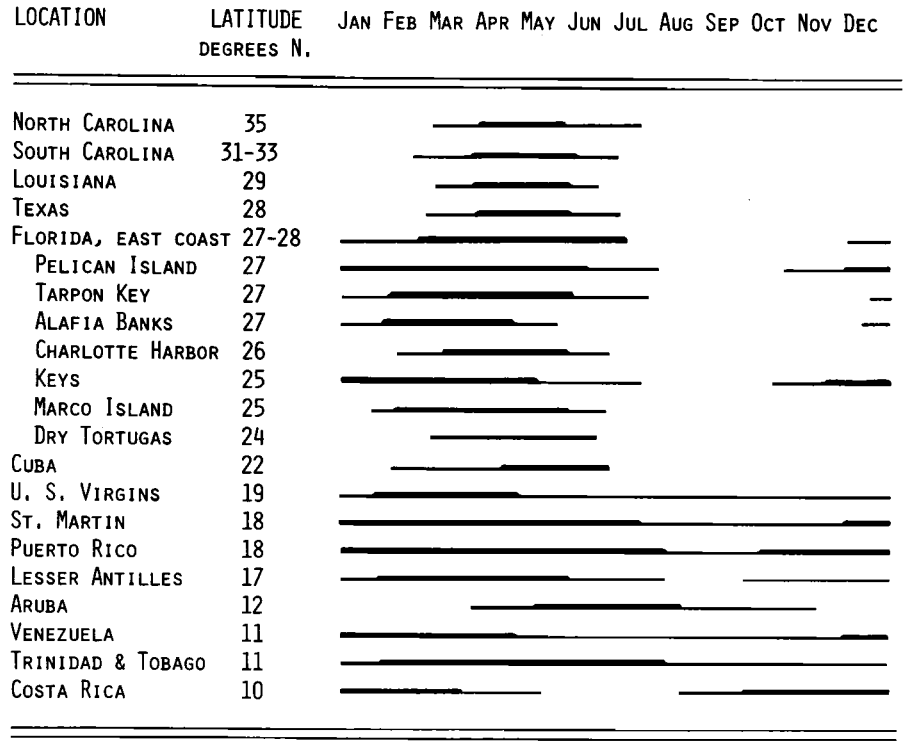

Fig. 3. Summary of egg dates for the Eastern Brown Pelican. Thickness of the line within one location indicates probability of eggs being present.

or young in the fall and are generally on a winter-spring cycle, but some irregularity occurs. Colonies in the 30°–35°N latitude regions in Louisiana, Texas, and North and South Carolina exhibit regular definite annual periodicity, with colony abandonment during the fall and winter and most egg laying from late March through May and occasionally into June. Only rarely does laying occur in early March or as late as July in these regions.

ENVIRONMENTAL DATA.

In the following section I discuss environmental data relevant to the control of these nesting periodicities, discussing the Tarpon Key situation in detail because the best bird data are available for that colony, and then generalizing to other colonies in Florida and throughout the species range.

No variation occurred in the monthly mean, maximum, and minimum temperatures during April through October 1968–1976 that can be related to the bird populations. November through March do show annual differences, however, that can be related to the chronology of nesting. November through March 1968–1971 were consistently colder than 1972–1976 (Table 7). The fall and winter of 1971–1972 were the warmest period recorded, and in fact, the winter of 1971–1972 was the warmest on record to date in Florida. The fall of 1972 was again warm, but February and March were cold. In November 1971 to February 1972 the minimum temperature

TABLE 7. Climatic data, based on 42-yr mean, for Tampa International Airport, Hillsborough County, Florida, Florida west coast (from N.O.A.A. Environmental Data Service).

Year	July	August	September	October	November	December	January	February	March	April	May	June	Total
Monthly departure from normal temperatures[a]													
1968–1969	0	0	–	–	−2	−3	−2	−4	−4	0	0	0	
1969–1970	1	–	0	1	−2	−2	−4	−3	–	1	–	0	
1970–1971	1	1	1	1	−3	0	−1	0	−2	−1	–	0	
1971–1972	0	–	–	2	0	4	3	1	0	0	–	0	
1972–1973	0	0	0	1	1	2	0	−3	−2	−1	0	1	
1973–1974	2	–	1	1	4	−2	11	–	5	−1	1	−1	
1974–1975	−1	0	2	−2	1	0	5	5	2	2	4	2	
1975–1976	1	2	1	3	1	−1	−4	1	5	−1	−1	−2	
Heating degree days[b]													
1968–1969	0	0	0	27	138	264	201	252	220	0	0	0	1,102
1969–1970	0	0	0	0	111	218	343	209	81	0	0	0	962
1970–1971	0	0	0	0	145	115	201	134	139	36	0	0	770
1971–1972	0	0	0	0	41	13	62	139	26	5	0	0	286
1972–1973	0	0	0	0	65	130	166	223	18	21	0	0	623
1973–1974	0	0	0	6	24	200	0	159	17	12	0	0	418
1974–1975	0	0	0	0	39	138	84	64	61	5	0	0	391
1975–1976	0	0	0	0	88	183	268	109	18	2	0	0	668
												42-yr mean =	589
Minimum monthly temperature, °C													
1968–1969	20	22	19	7	2	−3	2	0	3	13	10	19	
1969–1970	22	20	21	18	1	0	−4	0	5	11	12	17	
1970–1971	17	22	20	13	−5	0	−4	0	2	4	9	17	
1971–1972	20	21	19	15	7	10	2	1	7	8	16	16	
1972–1973	20	21	18	14	7	1	−1	0	8	8	12	21	
1973–1974	22	19	22	9	3	−1	14	−1	7	8	14	19	
1974–1975	20	22	22	12	6	2	1	4	3	9	18	21	
1975–1976	22	22	20	14	3	−1	−2	2	6	8	12	20	

[a] (–) indicates minus departure of less than 1°C.
[b] A high number indicates a cooler temperature than a lower number, based on the daily mean temperature.

never reached 0°C (Table 7). In all other years except 1974–1975, such low temperatures were reached in at least 2 months each fall and winter. The December 1971 minimum temperature was only 10°C; in all other Decembers during 1968–1976 the minimum was from +2 to −3°C. I cannot discern any pattern in other climatological parameters, such as precipitation, humidity, cloud cover, thunderstorm activity, or wind direction and velocity, that relate to the nesting of the birds.

Water temperatures recorded at Egmont Key, less than 5 km from Tarpon Key, by the U.S. Coast Guard accurately reflect the water conditions in which this pelican population feeds. They indicate similar patterns during each year, 1968–1976, but do not exhibit as wide fluctuations as did air temperatures. Coolest water temperatures were reached in January and February at 13–15°C, and a clear warming trend does not begin until the second week of March and through April. Water did not go below 20°C in 1971–1972 until the third week of February, although this occurred in late November or early December in all other years.

Thus, the weather data for 1968–1976 clearly show a warm November–February 1971–1972, the year in which the pelicans in the region began nesting the earliest on record. Air temperatures were decidedly warmer during the fall and winter of 1972–1975, the years when nesting commenced sooner, than during 1968–1971, the cool months/years. I believe it is these cold days/nights that inhibit breeding. In the

absence of the cold weather and especially one or more nights of freezing temperatures, the birds nest earlier than when the cold front incursions occur.

Because the climatological data and population data for the Tarpon Key region indicate such a close relationship between low temperatures and the onset of breeding, I compared temperatures for locations throughout the range of the Brown Pelican. In more northern locations (North and South Carolina, Louisiana, and Texas) freezing temperatures occur from October through March or April in all years, but such temperatures never occur in southern Florida, and generally warmer weather occurs on the east than on the west coast of Florida.

Outside of the continental United States, the Brown Pelican breeds in the tropical maritime climate, generally south of the Tropic of Cancer, an area of high humidity and small temperature changes. Data relevant to the controls of the nesting season of pelicans for this region are scanty, and the following is a brief summary of climatological factors. The mean air temperatures for the Caribbean region range from 19 to 29°C, with extremes of only 16°C minimum and 37–38°C maximum. The diurnal temperature range exceeds the annual mean temperature range. The waters are warmest, at 27–28°C, in September, and air temperatures are highest in August and September and lowest in December–February (Portig 1976). Wind direction and speed tend to be easterly trades, with minimum speeds in the fall, but this is also the time of the isolated hurricanes (Beaufort force 12, 115+ kmph) and tropical storms (Beaufort forces 8–11, 60–113 kmph). The breeding range of the Eastern Brown Pelican corresponds with and falls directly within the hurricane belt in the Gulf of Mexico, Caribbean Sea, and Atlantic Ocean. Of all recorded hurricanes, 83% occur in August–September, with only 1.4% occurring outside of June–November (Alaka 1976). The amount of sunshine is affected by rainfall, and the percent of sunshine is least in the fall, when rainfall is generally highest. Summarizing rainfall patterns for the total region is difficult, but maxima tend to occur in the Gulf of Mexico in June–December, minima in March–May. Elsewhere, maxima occur in May–June and September–November, with a minimum in July. Maxima in Cuba, the Bahamas, and Venezuela occur in October, but in November in the Leeward Islands.

DISCUSSION

The controls on breeding in birds have been discussed extensively in recent years. It is now generally accepted that the "ultimate" factor exerting control is food supply, with breeding timed so that young are produced when maximum food is available (Thomson 1950, Lack 1966, Immelmann 1973). Other environmental cues provide the "proximate" factors to which the species or populations respond to insure that breeding begins at a time that is predictive of when food will be most available. Data on these factors and on food, especially, are generally lacking for seabirds and for pelicans in particular, and quantitative data, especially on food availability, probably are impossible to obtain. Species nesting in tropical climes, where variation in climatological factors is small, provide special difficulties for the researcher attempting to determine their control mechanisms. As thoroughly summarized by Immelmann (1973) and Murton and Westwood (1977), food supply will exert evolutionary control on nesting-season chronology at the end of the long sequence of behavioral events leading to feeding nestlings and to fledgling independence. What is needed is a "forewarning" stimulus to set this cycle in motion. Both internal

rhythmic cycles and external environmental stimuli are involved in this predictive process, and the environmental stimuli must be reliable to be adaptive.

Daylength is the major factor regulating gametogenetic cycles, migratory behavior, and fat deposition, and the degrees of dependence vary from species to species and even within forms of the same species (King 1979). Marshall (1970) indicated that external cues other than light may regulate cycles in some species, but Murton and Westwood (1977) have assumed that endogenous periodicities or circannual oscillations are entrained by annual light cycles, and they indicate that the amplitude of this cycle is high in temperate but low in equatorial regions. Photoperiodic entrainment is apparently less critical in the tropics, and the connection between daylength and food supply is imprecise. Thus, daylength appears to be less important in the control of onset of breeding in those locales, which leads to less synchronization in breeding regimes. King (1979) has pointed out, however, that the universality of this annual photocycle is far from proven, and further study on environmental cues is needed.

My experience with the Brown Pelican leads me to focus on the role of temperature in controlling their nesting cycle. Data thus far available for temperature in other species merely indicate that a connection exists between ambient temperatures and reproductive activities (Lack 1950, Immelmann 1973). Temperature is the most important modifier of the gonad cycle, and its effects have been demonstrated experimentally in many species of land birds (Murton and Westwood 1977). The mechanisms are unknown, but cold temperatures inhibit breeding. In many temperate-zone birds, temperature provides a sufficiently accurate timing mechanism to modify the photoperiodic response to bring the breeding cycle into alignment with the season of abundant food.

In tropical regions with weak environmental control and slight seasonal fluctuations in food, timing of nesting may be regulated by individual pairs acquiring sufficient energy reserves for egg production and incubation-shift survival (Ashmole 1971) and/or by sociological factors (Schreiber and Ashmole 1972). The nesting of pelicans in these regions in many small colonies suggests such local synchrony rather than widespread control.

Available data on Brown Pelicans indicate that breeding requires a minimum of 4.5 months (2 weeks courtship and nest building, 1 month incubation, 3 months nestling stage; Schreiber 1976, 1977, 1979). In adults, molt of the body feathers, primaries, secondaries, and rectrices occurs exclusive of the nesting season and requires approximately 2–3 months (Schreiber MS). Circumstantial evidence indicates that this molt does not commence for a few weeks after young fledge. Adults show considerable more variability in tropical regions in the plumage coat worn at any given season outside of the breeding period than individuals in more northern locales. A minimum of 8–9 months is thus required for a successful breeding period by an adult pelican.

Adaptive changes have occurred in Brown Pelicans so that pelicans show little response to daylength, but they respond to other local factors such as the immediate food situation, which appears to be the final determinant of their breeding seasons. They commence breeding when sufficient energy reserves are available. Recrudescence of reproductive potential may take a comparatively short period of time so that Brown Pelicans are ready to breed again at the end of a molt and when food is sufficiently available. In latitudes south of 20°N, nesting by Brown Pelicans usually

occurs from October through July, and, while individual colonies appear to exhibit some periodicity, nesting may occur at any time of year. In the absence of strong environmental control in this region, the pelicans may breed as frequently as possible, with breeding commencing immediately postmolting. The high variability in timing of nesting and the prolonged breeding period exhibited by some colonies is thus explained, as individual birds commence nesting on their own cycles. Data from the cycles of individually marked birds throughout the range are badly needed.

While free-running endogenous periodicities may be expressed in some species (*Sterna fuscata* on Ascension Island), this cannot be expressed in the northern range of the Brown Pelican because of the inhibiting effects of cold temperatures. It is tempting, however, to interpret the Brevard Colony timing in 1924–1935 (Table 6) as such a free-running rhythm, with a periodicity of ca. 340 days thus further emphasizing the lack of daylength control. Unfortunately, I can find no weather data for that period to determine if an absence of cold weather occurred in the region. In more southern regions, pelicans, like most tropical marine species, must depend on randomly fluctuating food resources that cannot be predicted; a period of good feeding may induce laying and thus impose some synchrony, as has been found in at least two species of *Sula* (Simmons 1967; Nelson 1969). In the tropics the proximate factors that keep the endogenous rhythms in phase with the changing environment are not necessary or available, and probably an immediate response to food and the social stimulation from other birds in the population serve as both the initiating and adjusting stimuli for breeding. The situation at the Dry Tortugas with the small population of Brown Pelicans nesting at essentially the same time as the Sooty and Noddy terns (*Sterna fuscata* and *Anous stolidus*; Robertson 1964 and pers. comm.) may provide an example of a local population of one species responding to the behavioral stimulation of other species as well as to food availability.

The lack of breeding throughout the Brown Pelican range during August–September perhaps indicates that a gonadal refractory period may occur then. The ability to ovulate may be rapidly regained, however, at least in the low 20°N latitudes and to the south, and breeding can occur in November–December and possibly as early as October. Obviously, variation occurs in the response threshold to environmental stimuli throughout the range of the species.

The distribution of Brown Pelicans is restricted to regions where 5–7 months of freeze-free temperatures occur, or south of about 33°N latitude. The cold air temperatures in the fall and winter north of about 25°N inhibit nesting until the period when temperatures lower than 0°C do not occur. This inhibition occurs in November–December and acts to prevent breeding at a time when the probability of producing young successfully is minimal. The cessation of nesting that is obvious in spring in the Tampa Bay region when cold pulses occur after some nesting has already commenced (Fig. 2) is evidence for the sensitivity of this species to lowered temperatures. Based upon the inhibition of breeding in the fall and the modifying effects of temperature that are seen once the nesting season begins in the spring, I believe that cold may well serve as both a synchronizer and modifier of nesting seasons but at different phases of the annual cycle. Pelicans move into the colony and initiate nesting as warm weather occurs in the spring (February). In most years, however, a "late" cold front moves through the Tampa Bay region, causing birds who are not then on nests to desert the colony. They return after the continuing warming trend later in the season. While this pattern is obvious in 1970, 1971, 1974,

and 1975, it is especially so in 1973, when a warm spell in early March was followed by a severe cold spell at the end of the month. I believe the decline in numbers in January and February 1972 is also a manifestation of this cold inhibition.

The Brown Pelican does not fit the assumption that the reproductive pattern in avian species is "usually precisely defined and of limited duration" (Lofts 1975). I believe the field data suggest that the breeding cycle is not cued to light but rather to some factor such as temperature, and specifically low temperatures, that inhibits breeding. In the absence of these low temperatures, nesting can be initiated at any time of year. Based upon the lack of nesting in August–October, I suggest that the timing of the nesting season throughout the range may have evolved so no nests are occupied during the hurricane season. Breeding must begin in the fall-winter in the hurricane belt so that young have fledged by late summer, thus avoiding nesting during the high winds and heavy rain of hurricanes. Few data exist on this subject but Wayne (1894) noted high mortality of pelicans followed a cyclone in South Carolina.

While experimental data are lacking, on the basis of the field data summarized here and those of Harris (1969) for the Galápagos Islands on the Equator in the Pacific Ocean (which are suggestive but also need documentation for individual birds), I suggest an endogenous breeding-molting rhythm in the Brown Pelican of less than a year, and probably on the order of 8.5–10 months. This rhythm is rarely expressed because of the interference of cold (freezing) temperatures in the northern portions of the species' range. In the southern colonies, individuals may well breed this often, but the fact is masked by the extended period of nesting.

If the Brown Pelican does have a less than annual breeding rhythm, it will be the third family of Pelecaniformes, along with the Phaethontidae and Sulidae (see Harris 1969 and Murton and Westwood 1977 for summaries), that does so. Such a breeding regime should not be considered as unusual for this primarily tropical group of birds.

Study of marked birds throughout the Brown Pelican's range is needed to examine the patterns of individual nesting cycles. Physiological studies are needed to determine how environmental variables influence the neuroendocrine mechanisms regulating gametogenesis. Experimentation would be reasonably easy, because pelicans are simple to maintain in captivity and they breed readily if sufficient numbers are present. Studies of the photoperiodic and temperature interactions on stimulating breeding would be easy on such a large species, because laparotomy would give good data on gonad size, and hormones could readily be sampled. Such studies would contribute importantly to our understanding of the factors regulating the complex nesting seasons exhibited by this popular, obvious species of coastal marine bird, and thus to all ornithology.

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