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REPRODUCTIVE PERFORMANCE OF THE EASTERN BROWN PELICAN, *PELECANUS OCCIDENTALIS*

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REPRODUCTIVE PERFORMANCE OF THE EASTERN BROWN PELICAN, *PELECANUS OCCIDENTALIS*

By Ralph W. Schreiber[2]

ABSTRACT: Data collected during eight breeding seasons, 1969—1976, on the reproductive biology of the Brown Pelicans *(Pelecanus occidentalis)* nesting on Tarpon Key, Pinellas County, west coast of Florida are presented. Human disturbance bias is discussed in relation to clutch size, hatching success, and fledging success, and data are presented showing that visits by scientific investigators can influence the results obtained. Seasonal differences in reproductive parameters are considered and late nests are shown to be less successful than earlier attempts. Year to year fluctuations in productivity characterize this colony, and by comparison to the published literature, are shown to be usual for this species. Data on production calculated by five different monitoring methods are compared. The prospect of deriving a precise figure for reproductive performance is discussed and a recruitment standard, based on extensive field data, of 0.9–1.0 young per breeding pair is suggested for this species.

INTRODUCTION

The goal of breeding biology studies of birds should be to precisely determine the reproductive parameters necessary for accurate prediction of the status of the wild population. J.J. Hickey (1955) sagely pointed out that "bird populations have a field reality and a paper existence." Startlingly few students have heeded Hickey's intended warning in the intervening years to pay strict attention to the methodologies involved in carrying out studies of avian reproductive biology. However, Ricklefs (1973) thoroughly reviewed this subject and noted that "the data required to construct a life table are straightforward in their meaning and interrelationships, but their estimation is almost always difficult." He further noted that some parameters, "particularly clutch size and nesting success are relatively easy to obtain." R.J. Robel (1973) noted that ". . . life tables are constructed by people not directly involved in the collection of the field data, who may therefore incorporate some major biases in their preparation . . . the mere appearance of data in a life table is impressive and data contained in them are often accepted without close scrutiny of how, where, and when they were collected." Woolfenden and Rohwer (1969) and Ricklefs (1969) discussed calculation methods and Mayfield (1975) noted that calculations of reproductive success contain "not only hard facts but elements of judgment, none of this difficulty is apparent in published tables or figures, which convey an air of indisputable finality."

Unfortunately, all of these biases in scientific study have occurred relevant to the reproductive biology of the Brown Pelican *(Pelecanus occidentalis)* during the past decade of intense interest in the species. In this paper I present data gathered on clutch size, hatching success, and fledging success during a study of this species from 1969 through 1976 in Florida. I further relate some of my difficulties in deriving these "relatively simple" figures. I hope to elucidate the problems involved in calculating reproductive success from extensive field data and the difficulties in obtaining a precise figure that can be used in a modeling equation.

I stress that for comparative purposes, we must pay strict attention to the methodologies used in obtaining data to calculate productivity, especially as regards investigator bias on the results. Only through long term studies done in a consistent manner can accurate, useful data be obtained.

METHODS

From January 1969 through August 1976 I studied the Brown Pelican population of Tampa Bay, specifically Boca Ciega Bay in Pinellas County, centering on Tarpon Key, Pinellas National Wildlife Refuge (27° 40′N, 82° 40′W), on the Gulf of Mexico coast of mid-peninsula Florida. During the nesting seasons (roughly January through September) of these eight consecutive

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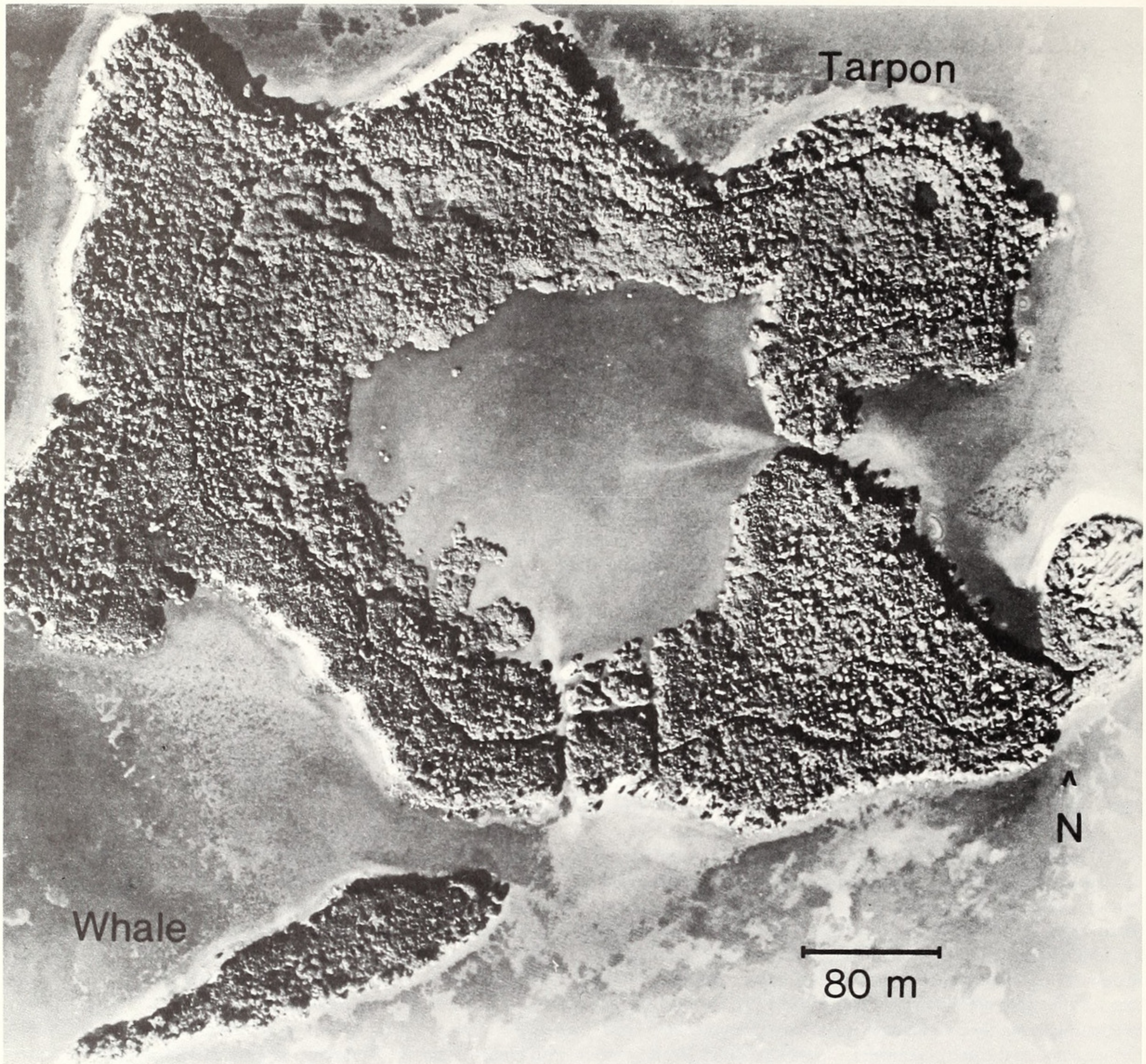

FIGURE 1. Tarpon and Whale Keys, Pinellas National Wildlife Refuge, Boca Ciega Bay, Pinellas County, Florida (27°40′N, 82° 40′W).

years I visited Tarpon and Whale Keys essentially weekly and occasionally three to five times per week. Only on five occasions did more than ten days, but never more than 18 days, separate visits, and then only once each session.

These Keys (Fig. 1) provided a good situation for studying various aspects of the biology of Brown Pelicans. The pelicans nest in Black Mangrove *(Avicennia germinans)*, the majority along the edges of the central lagoon, and are quite undisturbed by humans. The total colony naturally divided into eight units, each of which could be studied discretely without disturbing other units.

In one of these units I measured growth and development of nestlings (Schreiber 1976a); at another I carried out behavior observations (Schreiber 1977); and each year nestlings were banded in the whole colony (Schreiber 1976b). As noted in Schreiber and Risebrough (1972) two other units were checked in 1969 and 1970, one visited weekly and one more frequently. In subsequent years (1971–1976) the weekly visit schedule was continued on the former unit. In addition, on each visit to the colony, all adults, nests, subadults, immatures (by plumages, Palmer 1962; Schreiber *unpublished data*), nestlings, and later fledglings were counted in all units from a consistent location in the center of the lagoon. Data on timing of the nesting season and population structure will be presented in detail elsewhere (Schreiber *in preparation*) but I use the seasonal data on nests, eggs, and young to calculate reproductive success here.

I began visits to units on the week following the first sighting of a nest strucutre on which an adult was sitting. I marked each nest with a numbered plastic streamer hanging below the nest. I used a small mirror attached on a 2.5 m aluminum pole to check contents of nests which were too high for me to reach. Nest contents were recorded directly onto nest record cards. Visits were made on the high tide, to facilitate access across the lagoon by boat, unless the high tide occurred between 11.00 and 16.00 hours during late May through August. At those times, to avoid excessive heat stress to both the pelicans and myself, I visited the colony prior to 11.00. I use the following definitions: NEST, a structure with adults, eggs, or young present; NESTLING, a young bird prior to making its first sustained flight (at 10 to 12 weeks of age) which takes it away from its nest permanently. (Nestlings may move some distance from their nests but usually return to the site to be fed by their parents, and frequently the nests are destroyed by the nestlings within five to seven weeks of age. I prefer to call these birds nestlings, rather than young or pulli, even though they may not actually be in a nest); FLEDGLING, a nestling which has permanently flown from its nest but which has not yet departed from the immediate vicinity of the colony; SUCCESSFUL NEST, one from which one or more nestling has fledged; PRODUCTIVITY, the number of fledglings per total nesting attempts in the colony, or sample of the colony.

RESULTS AND DISCUSSION

Effects of Human Disturbance

Since I am concerned about the effects of human disturbance on measurement of reproductive success, and especially in this case that of the "scientific" investigator, in 1969 and 1970 I compared productivity figures for two units in the colony, one disturbed once weekly and one more frequently. I believe it valid to assume that the adult pelicans in the two units of the colony used for this "experiment" were uniform in age and breeding experience.

The data in Table 1 confirm that in this species disturbance can bias the results, especially with increased number of visits to a colony. Not only were fewer eggs laid in more frequently disturbed nests, but hatching success (Schreiber and Risebrough 1972) and productivity were also reduced ($P<0.01$, t test). Interestingly, the percentage of eggs hatched that produced fledged young and fledglings per successful nest were not affected, indicating that the effects of human disturbance are more pronounced during the pre-egg and incubation periods.

To examine further whether lower reproduction is a matter of the type of human disturbance or of the number of visits, I compared reproductive success between two units of the colony. One was the same unit visited weekly in 1969 through 1976 and the other was the unit used to measure growth and development of nestlings from 1969–1972 (Schreiber 1976a). I checked nests in one unit (60 nests) for presence and number of eggs and young which required about 15–30 minutes. I measured all eggs and nestlings in another unit (26 nests) which required up to an hour and a half. During the incubation period I handled most eggs in the latter unit at least twice and each nestling was handled on each weekly visit. In 1972, no significant differences existed between the units in any of the parameters measured (Table 2). Similar results were obtained in 1969–1971. In fact, for the nests near which I spent more time, a tendency existed to hatch more eggs, more nests were successful, and fledgling success was higher.

Discussion of Human Disturbance Factors

Few studies have directly examined the effects of human disturbance relative to productivity parameters in birds. A recent increased awareness of the investigator bias is occurring (Gottfried and Thompson 1978; and especially Ellison and Cleary 1978). Skutch (1966) noted that any human activity at nests "increased to an inassessible degree the incidence of predation" in Central American land bird species. Fyfe and Olendorff (1976) briefly but thoroughly discussed the problems involved and offered solutions to scientific and amateur disturbance at raptor nests specifically. Their information undoubtedly holds for most avian species. Studies of Bald Eagles *(Haliaeetus leucocephalus)* showed that the timing and kinds of human activities reduce the occupation and productivity of nests of that species (Newman, et al. 1977). Burger and Hahn (1977) examined crow predation on Black-crowned Night Herons *(Nycticorax nycticorax)* but they say nothing about human disturbance facilitating the predation although that is implied since the authors disturbed the heron nests to check their contents. Werschkul, et al. (1976) found a lower fledging rate in a Great Blue Heron *(Ardea herodias)* colony near logging operations in Oregon than in colonies further away.

Robert and Ralph (1975) conducted a detailed controlled study on the effects of human disturbance in a colony of Western Gulls *(Larus occidentalis)* and demonstrated that frequent human visits reduced productivity by increasing loss of eggs. Also, hatching failure was directly proportional to the amount of disturbance, as Western Gulls destroy eggs in neighboring unattended nests. However, chicks survived better in more frequently disturbed nests, apparently because less frequent human visitation resulted in a more intensely "frightened" chick which ran further from its territory and thus encountered a greater risk of being killed. Overall mortality was higher in disturbed than undisturbed areas. These studies indicate that predation is the most usual cause of decreased production that accompanies human disturbance.

However, in a purely experimental approach to predation effects on reproduction in an "old field habitat" situation, Gottfried and Thompson (1978) found that visits to nests by investigators did not affect success or failure. Schreiber, et al. *(in preparation)* found in one colony of Laughing Gulls *(Larus atricilla)* that human visits had no effect on productivity. Gillett, et al. (1975) found human visits decreased mortality of young by only 3–5 percent, primarily in the young chick stage, and did not affect hatching success in the Glaucous-winged Gull *(Larus glaucescens)*. Willis (1973) found that survival rates at visited and unvisited nests were similar in the Bi-colored Antbird *(Gymnopithys bicolor)*. Nisbet and Drury (1972) found that daily visits to tern colonies *(Sterna hirundo* and *S. dougallii)* apparently caused some desertions of nests early in incubation. They did not detect significant differences in productivity related to frequence of visits.

The above data indicate that species differences do exist in response to human intrusion. However, in all the pelecaniformes that have been examined specifically for the problem, human visits to colonies have caused severe problems and Nesbit (1978) believes that "human disturbance by biologists is one of the

TABLE 1

Reproductive success of the Brown Pelican in relation to frequency of human disturbance. Tarpon Key, Pinellas County, Florida 1969 and 1970. Does not include nests in which re-laying occurred or "nests" that did not receive eggs.

	1969		1970	
	Visited weekly	Visited frequently	Visited weekly	Visited frequently
Number of nests	13	63	25	37
Number of eggs laid	37	142	64	77
Clutch size	2.85	2.25**	2.56	2.08**
Number of eggs that hatched	31	80	45	22
Eggs hatched per nest	2.38	1.27**	1.80	0.59**
Hatching success	84%	56%	70%	29%
Number of young that fledged	22	53	26	13
Percentage of eggs laid from which young fledged	59%	37%	41%	17%
Percentage of eggs hatched from which young fledged	71%	66%	58%	59%
Number of successful nests (fledged one or more young)	13	44	21	10
Percentage of successful nests	100%	70%	84%	27%
Fledglings per successful nests	1.7	1.2	1.2	1.3
Productivity (fledglings per total nests)	1.7	0.8	1.0	0.4

** = highly significant difference at 0.01 level, t statistic.

major threats to seabirds." Kury and Gochfeld (1975) reported greatest loss early in the nesting season in gull and cormorant colonies. Johnson and Sloan (1976) summarized the published literature on the intolerance of White Pelicans *(Pelecanus erythrorhynchos)* to human disturbance during the nesting season and noted that gull predation and physical stress on the young were the major causes of mortality. Vestjens (1977) noted the extreme susceptibility of *P. conspicillatus* in Australia. Brown and Urban (1969) and Schreiber *(in preparation)* noted that *P. onocrotalus* in Ethiopia and South West Africa are also extremely sensitive to even the slightest human presence, and especially during the courtship and egg stage of the nesting cycle. Nelson (1966) found that egg loss was proportional to the amount of human disturbance in the Gannet *(Sula bassana)* on Bass Rock, Scotland, and noted that many earlier studies had not taken into account the artifacts introduced into productivity figures by human disturbance. He recently reiterates and emphasizes this point (Nelson 1978). Snow (1960) noted that Ravens *(Corvus corax)*, Herring and Great Black-backed Gulls *(Larus argentatus* and *marinus)* took eggs of the Shag *(Phalacrocorax aristotelis)* after she disturbed some adults. They were slow in returning to their nests and she stated that "normally the eggs would not be open to predation, never being left uncovered unless the bird is put off by human activity." Ellison and Cleary (1978) found that frequent visits caused nest abandonment, allowed gull predation, discouraged late nesters from settling in disturbed colonies, and delayed clutch commencement in Double-crested Cormorants *(Phalacrocorax auritus)*.

Anderson and Keith (1979) and Keith (1978) have thoroughly reviewed the effects of human disturbance, including investigator bias, in marine bird colonies in west Mexico. They showed that human visits, both by "scientists" and "tourists," significantly decreased productivity in Brown Pelican colonies. They demonstrated dramatic effects of this disturbance on Heermann's Gulls *(Larus heermanni)* and populations of Brown Pelicans, especially on Isla San Martín (see also Jehl 1973). These effects were manifested primarily through predation of eggs by Western Gulls. Abandonment of nests (eggs and small young) by adult pelicans for even a brief period of time resulted in predation of contents of unattended nests. They found total abandonment if colonies were visited early in the nesting season, with a 50 to 100 percent decrease in productivity between "disturbed" and control colonies.

However, Blus and his coworkers (Blus, et al. 1974, and references therein) have published a series of overlapping papers documenting the effects of DDE on egg shell thickness and have purported to relate such effects to the reproductive success of Brown Pelicans in South Carolina since 1969. Most of that work entailed collecting eggs for organochlorine residue analysis but some field studies were also carried out. Blus, et al (cited) have suggested that depressed productivity has occurred in those colonies. However, their papers do not indicate how the figures for productivity were derived other than from annual counts of nests and young and no mention is made of the possibility of human disturbance affecting production. They do state that in 1971 the nesting colony was visited on seven occasions and in 1972 it was

TABLE 2

Comparison of reproductive parameters in colony units with different quality of disturbance, 1972. Does not include nests in which re-laying occurred or "nests" that did not receive eggs.

	Nests checked only	Nestlings measured
Number of nests	60	26
Number of eggs laid	156	68
Clutch Size	2.6	2.6
Number of eggs that hatched	103	49
Eggs hatched per total nests	1.7	1.9
Number of nests in which eggs hatched	49	24
Hatching success	66%	72%
Number of young that fledged	69	40
Percentage of eggs laid from which young fledged	44%	59%
Percentage of eggs hatched from which young fledged	67%	82%
Number of successful nests (fledged one or more young)	44	23
Percentage of successful nests	73%	88%
Fledglings per successful nest	1.6	1.7
Productivity (fledglings per total nests)	1.2	1.5

visited on 16 occasions. In Blus and Keahey (1978) they note that in 1975 "visits . . . were limited to ONE OR TWO (emphasis mine) one-hour periods each week from April through mid-August" and, lacking evidence to the contrary, presumably a similar irregular schedule of visits was used in earlier years.

In the study reported here, during a controlled experiment in this colony in 1969 and 1970, human disturbance significantly decreased clutch size, hatching success, and total fledging success; but the number of eggs that hatched that fledged a young and fledglings per successful nest were not affected. The duration of each visit and the handling of eggs and nestlings were not significant factors affecting reproductive success. The total number of visits was the determining factor, more visits producing lowered reproductive success. Prolonged stays in the colony could have disastrous effects during hot, sunny weather since the eggs and small young are highly susceptible to elevated temperatures (Bartholomew and Dawson 1954; Schreiber *unpublished data*).

These data indicate that only colonies which have been visited with a consistent visitation pattern may/should be used to compare productivity within years and between years. Thus, while general comparisons between or within colonies by a different or the same workers *may* be possible, unless similar patterns of nest checking have been utilized, precise comparisons should not be made (Nelson 1966, 1978; Robert and Ralph 1975). This is especially true since significant differences in natural productivity exist between years even in one colony and human disturbance probably compounds these natural fluctuations.

Brown Pelican Behavioral Reactions to Human Disturbance

During my weekly nest-checking in 1972–1976, Elizabeth Anne Schreiber observed the reaction of adult Brown Pelicans in the colony. This information revealed that they become habituated to human intrusion, if it was carried out in a routine manner and pattern. Following is a generalized description of the pelican's reaction to human disturbance in the colony. On the first few seasonal disturbances the adults simultaneously flew from nests or perches while I was approaching at 40–60 m away, although they individually had stood up, assumed an alert posture, and wing-flapped (Schreiber 1977) when I was still 50–80 m away. This early take-off seemed to involve considerable "panic." Most adults circled back and forth over the nest sites during these disturbances but a few landed on the lagoon 30–50 m from the colony unit. If I left the unit and waved my arms or shouted loudly to flush the adults off the water, they flew and circled over the nests and most landed again on their nests within three to five minutes. If not flushed from the water, as much as 15 minutes ensued before all adults returned to their nests, or potential nest sites. Early in the season, adults occupying the colony without a nest structure often abandoned the area when disturbed. This was evident as adults flew out of the colony entirely and did not return during the hour or so after disturbance. By the fourth or fifth weekly visit to the colony the adults stood up and wing-flapped as I approached but few flew from their nests until I was 15–30 m from the nests. Some did not fly until I was in the mangrove and actually underneath the nests. Most of the adults flew directly to and landed on the water but a few continued to circle over the colony throughout my presence there. By the fifth or sixth weekly visit they did not fly from nests until I was essentially in the colony and then they either circled or sat on the water. When flushed from the water they all returned directly to their nests, usually within two minutes. The return to the nest always entailed one or two passes over the nest sities, but the number of these passes decreased from several early in the season, probably as the birds learned the precise location of their nests or became habituated to the disturbance. Early departure from nests upon approach was a good sign that additional birds had moved into the colony and had commenced nesting activities. These early flushers were usually not yet associated with nest structures or nests containing eggs.

This general pattern of reaction to my disturbance took place each year. It was our impression in 1975 and especially 1976 that birds reacted less to my disturbance early in the year than in previous years. The presence of banded birds, as many as six to eight in this unit in 1976, indicated that they probably had been banded as nestlings in this colony in previous years. Brown Pelicans readily learn to beg for fish at boats and fish piers in Florida and it seems likely that they also learn to accommodate to some extent to disturbances in the nesting colony when activities are undertaken in a regular and consistent manner. This same pattern can be seen in the behavior of birds in a colony situation near considerable human activity (i.e. Port Orange, Florida) compared to one which routinely received little disturbance or amount of human activity.

Different levels of disturbance were caused by walking across the lagoon and by approaching the colony in a boat, either rowing or motoring. The upright human figure considerably increased the flight distance (Hediger 1950), especially early in the season. Additionally, a direct approach toward the birds caused a higher level of disturbance than an indirect approach. I have observed fishermen moving within 5 m, but parallel to, the edge of the mangrove colony without causing any birds to take flight, although the birds always assumed the alert standing posture while the fishermen were near. If nests were disturbed on an infrequent or occasional basis, the birds did not seem to habituate, but always departed nests in a "panic."

Comparison of these data with the reaction of the pelicans nesting on the ground in California and Mexico (Anderson and Keith 1979; Keith 1978; Schreiber *unpublished data*) and in South Carolina (Schreiber *unpublished data*) clearly indicates that mangrove-bush nesting birds are far less susceptible to disturbance. Apparently, the substrate is an important mitigator to the panic reaction. Young on the ground wander, walk, or in "panic," run away from nests much more readily than young in bushes. In Mexico almost all adult pelicans fly from nests, either casually if they have seen the observer for some time, or in panic if suddenly surprised (Keith *personal communication*). In mangrove, young birds up to four to six weeks old tend to remain in their nests but older nestlings will either attempt to defend the nest (or themselves) or will attempt to run or take-off, often falling to the ground below the nests. In the mangrove, most young are unable to climb back to their nests if displaced more than a few meters laterally.

I have observed an adult feeding a pre-fledgling away from its nest on only three occasions and if the young do not return to their nests they undoubtedly will starve. It thus seems that strong selection exists for young in bushes to remain in their nests, while in ground colonies pods do form and young birds wander considerably.

I have the definite impression that flight distance (Hediger 1950) in Mexico and California pelicans is much greater than in Florida. Perhaps this resulted from the close proximity of the Florida colonies to man's activities and the lower level of predatory type behavior there than in the western colonies. Predation in colonies, originally by mammalian predators and snakes, undoubtedly caused all pelicans to nest on islands, thus avoiding the high predation rates that would occur on mainland nesting colonies. I have noted two colonies on mangrove islands that have been destroyed and abandoned in Florida after raccoons *(Procyon lotor)* gained access to those islands (Schreiber, *unpublished data*).

Human disturbance in the pelican colonies in Florida allows Fish Crow *(Corvus ossifragus)* predation (Schreiber and Risebrough 1972). I know from observations that no predation occurred in the Tarpon Key colony behavior study units unless adults were flushed from their nests (Schreiber 1977). Also, in three years of this study, and many two to three-week periods during other years, I know that no predation occurred in these study units. The crow problem noted as severe in 1969 and 1970 (Schreiber and Risebrough 1972) was much reduced or nonexistent in later years due to the removal of some crows from the population early in the nesting season. Thus, losses of eggs and small young must occur from other causes such as: adults abandoning nests, either permanently or for so long that incubation temperatures were allowed to fluctuate and the developing embryo died; breakage of eggs or displacement from nests when adults fly from the nests; adults shaking eggs so violently when taking-off that embryological development ceases.

If visits to a colony are necessary, as in many cases they are (see below), nests should be approached slowly and in full view of the birds to prevent undue disturbance effects. When approached in this manner the birds can stand up and remove their feet from the eggs before take-off, rather than flushing from an incubating position with their totipalmate toes wrapped around the clutch. Nests should not be visited during the heat of the day. When the investigator leaves the colony, adults sitting on the water should be flushed so they will return to their nests more quickly than if left sitting on the water to go back "in their own time." Early season visits to colonies should be avoided since they appear to cause greater disturbance than visits made after incubation is well along.

Further study of egg loss and nestling mortality for this and all marine bird species is clearly indicated.

Seasonal Fluctuations in Reproductive Success

In the previous section I demonstrated that only colonies visited on a consistent schedule can be used to compare reproductive success. In this section I discuss the seasonal data on reproductive success in the unit of the colony visited weekly each year 1969–1976. These seasonal data then form the basis for annual comparisons. These annual differences will also be obvious in Tables 3–11, with details presented in Appendices 1–8.

In order to compare seasonal parameters of early, middle, and late nests for all years I combined data for each season by two week or one month periods, depending on the span of laying (vertical divisions in Tables 3–10). These data do not include any nests in which re-laying may have occurred or "nests" that were constructed but never received eggs. The same unit in the northwest portion of the colony was used for checking reproductive success during 1970 through 1976; in 1969 an isolated unit about 50 m to the north away from the lagoon was used. The 328 clutches in this sample from eight years were thus broken down into 104 early, 189 middle, and 35 late initiations. The number of nests in the unit varied considerably between years and the small sample sizes for any one part of a year did not allow complete statistical comparisons. Still, general seasonal trends were apparent.

CLUTCH SIZE (Table 3): Was smaller later in the season and especially so if laying continued beyond mid to late April (see especially 1971, 1972, 1974, and 1976). Clutch size early in the season was nearly as high as in those nests started during the middle of the season. Mean clutch size was 2.5 and 2.6 for the early and middle periods but 2.2 for the late period. The latter is highly significantly different from the earlier periods ($P<0.01$, t test). This general pattern of lower clutch size holds for all years except 1969 (with a small sample) when an increase in clutch size occurred through the year, and in 1971 and 1972 which had higher clutch sizes in mid-season. Major annual differences in the seasonal pattern of clutch size are not obvious.

HATCHING SUCCESS (Table 4): A distinct, but not statistically significant, decrease in hatching success occurs between early and mid-laying periods (84% and 70%), but a highly significant difference ($P<0.01$, t test) exists between both the early and mid-season and the late period (43%); 1973 differs from this general pattern in that the eggs laid in early May (10 clutches) were more successful in hatching than were earlier clutches that year.

The percentage of nests in which one or more eggs hatched (Table 5) are essentially similar between periods (81%, 82%, and 77% of nests). The latest nest I recorded in all eight years (a nest started in late June 1973) did successfully hatch one egg. However, in four of the six years in which laying extended longer than two months, late nests were usually unsuccessful at completing incubation. The differences of the three unusual years (1973, 1974, and 1976) will be discussed more fully below, but I note here that the usual seasonal pattern of egg success shown above does not occur in the two years in which total nesting success was lowest, 1974 and 1976.

FLEDGING SUCCESS: Has been variously defined in the literature so I present my data on this parameter in several methods. Seasonal differences existed in the percentage of eggs laid that actually produced a fledged young (Table 6), with middle eggs producing slightly more than early eggs (41% vs. 33%), and both more than late eggs (28%). Statistically significant differences occurred only between the middle and late nests ($P<0.05$, t test). However, a different pattern of seasonal differences existed in the percentage of eggs which hatched that produced a fledged young (Table 7), with late eggs producing more young than both early and middle period eggs (64% vs. 39% and 59%). Sixty-five percent of early nests were successful (Table 8), 69% of middle nests were successful, while only 43% of late nests were successful. No statistical differences existed between early and middle nests, but late nests were highly significantly less successful than both early and middle ones ($P<0.01$, t test).

Comparing the number of young fledged per nest in nests that

TABLE 3

Clutch size by date of clutch initiation, presented as the mean for two week periods and number of clutches in ( ).

YEAR	MEAN	FEBRUARY 1-15	FEBRUARY 16-29	MARCH 1-15	MARCH 16-31	APRIL 1-15	APRIL 16-30	MAY 1-15	MAY 16-31	JUNE 1-15	JUNE 16-30
1969	2.8	—	—	—	2.8 (4)	2.9 (7)	3.0 (2)	—	—	—	—
1970	2.5	—	—	3.0 (4)	2.6 (5)	2.4 (11)	2.4 (5)	—	—	—	—
1971	2.5	—	—	2.0 (2)	2.9 (8)	2.5 (19)	2.6 (8)	1.5 (2)	—	—	—
1972	2.6	2.4 (5)	2.6 (7)	2.8 (23)	2.7 (35)	2.2 (12)	1.8 (4)	—	—	—	—
1973	2.6	—	—	—	2.6 (7)	2.5 (2)	2.5 (2)	2.6 (10)	3.0 (1)	—	2.0 (1)
1974	2.7	—	3.0 (11)	2.8 (18)	2.8 (20)	2.2 (10)	2.0 (1)	1.0 (1)	—	—	—
1975	2.6	3.0 (9)	2.6 (19)	2.9 (8)	—	2.5 (8)	2.2 (4)	2.2 (4)	—	—	—
1976	2.6	—	3.0 (3)	2.8 (13)	2.5 (4)	2.6 (6)	2.0 (2)	2.0 (1)	—	—	—

Means: EARLY = 2.5; MIDDLE = 2.6; LATE = 2.2

TABLE 4

Hatching success (eggs hatched per eggs laid) by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN %	FEBRUARY 1-15 %	FEBRUARY 16-29 %	MARCH 1-15 %	MARCH 16-31 %	APRIL 1-15 %	APRIL 16-30 %	MAY 1-15 %	MAY 16-31 %	JUNE 1-15 %	JUNE 16-30 %
1969	89	—	—	—	73	95	67	—	—	—	—
1970	70	—	—	67	77	67	75	—	—	—	—
1971	62	—	—	75	74	58	62	0	—	—	—
1972	68	66	61	83	68	52	0	—	—	—	—
1973	53	—	—	—	22	40	40	85	0	—	50
1974	78	—	91	88	73	59	0	0	—	—	—
1975	83	96	96	83	—	75	33	44	—	—	—
1976	64	—	100	62	50	64	0	100	—	—	—

Means: EARLY = 84%; MIDDLE = 70%; LATE = 43%

were successful (Table 9), early nests fledged 1.3 young per nest, middle period nests fledged 1.6 young, and late nests fledged 1.5 young per nest. No statistical differences exist between any of these three nest periods.

Comparing the number of young fledged per all nests in the study area (Table 10), early nests fledged 0.8 young per nest, middle period nests fledged 1.1 young, and late nests fledged only 0.6 young per nest. No statistical differences exist between early and middle period nests, or early and late period nests, but the late nests fledged statistically fewer young than the middle period nests ($P<0.02$, t test).

SUMMARY: To summarize the general patterns of seasonal

TABLE 5

Percentage of nests in which one or more eggs hatched by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	100	—	—	—	100	100	100	—	—	—	—
1970	76	—	—	100	100	91	100	—	—	—	—
1971	74	—	—	100	100	68	75	0	—	—	—
1972	85	80	100	100	91	58	0	—	—	—	—
1973	61	—	—	—	28	50	50	90	0	—	100
1974	85	—	100	100	85	60	0	0	—	—	—
1975	94	100	100	100	—	100	50	75	—	—	—
1976	76	—	66	38	50	33	0	100	—	—	—

	EARLY	MIDDLE	LATE
Means	= 81%	= 82%	= 77%

TABLE 6

Percentage of eggs laid from which a young fledged, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	59	—	—	—	45	70	50	—	—	—	—
1970	41	—	—	50	38	41	33	—	—	—	—
1971	47	—	—	50	65	42	48	0	—	—	—
1972	49	50	44	51	55	37	0	—	—	—	—
1973	27	—	—	—	11	20	20	42	0	—	50
1974	12	—	21	16	5	9	0	0	—	—	—
1975	49	41	51	70	—	55	22	22	—	—	—
1976	14	—	22	14	20	14	0	0	—	—	—

	EARLY	MIDDLE	LATE
Means	= 33%	= 41%	= 28%

TABLE 7

Percentage of eggs hatched from which a young fledged, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	67	—	—	—	63	74	75	—	—	—	—
1970	58	—	—	75	50	61	44	—	—	—	—
1971	77	—	—	67	88	71	77	0	—	—	—
1972	72	75	73	61	80	71	0	—	—	—	—
1973	52	—	—	—	50	50	50	50	0	—	100
1974	16	—	23	18	7	15	0	0	—	—	—
1975	59	42	53	84	—	73	66	50	—	—	—
1976	23	—	22	22	40	22	0	0	—	—	—

	EARLY	MIDDLE	LATE
Means	= 39%	= 59%	= 64%

TABLE 8

Percentage of successful nests, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
	%	%	%	%	%	%	%	%	%	%	%
1969	100	—	—	—	100	100	100	—	—	—	—
1970	84	—	—	100	80	82	80	—	—	—	—
1971	69	—	—	100	100	63	62	0	—	—	—
1972	78	80	86	83	88	58	0	—	—	—	—
1973	56	—	—	—	28	50	50	80	0	—	100
1974	33	—	64	44	15	20	0	0	—	—	—
1975	83	88	84	100	—	100	25	50	—	—	—
1976	34	—	67	31	50	33	0	0	—	—	—

	EARLY	MIDDLE	LATE
Means	= 65%	= 69%	= 43%

TABLE 9

Fledging success measured as young fledged per successful nest, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
1969	1.7	—	—	—	1.2	2.0	1.5	—	—	—	—
1970	1.2	—	—	1.5	1.2	1.2	1.0	—	—	—	—
1971	1.7	—	—	1.0	1.9	1.7	2.0	0	—	—	—
1972	1.6	1.5	1.3	1.7	1.7	1.4	0	—	—	—	—
1973	1.2	—	—	—	1.0	1.0	1.0	1.4	0	—	1.0
1974	1.0	—	1.0	1.0	1.0	1.0	0	0	—	—	—
1975	1.6	1.4	1.6	2.0	—	1.4	2.0	1.0	—	—	—
1976	1.1	—	1.0	1.2	1.0	1.0	0	0	—	—	—

	EARLY	MIDDLE	LATE
Means	= 1.3	= 1.6	= 1.5

TABLE 10

Fledging success measured as young fledged per total nests, by date of clutch initiation, presented as the means for two week periods.

YEAR	MEAN	FEBRUARY		MARCH		APRIL		MAY		JUNE	
		1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30
1969	1.7	—	—	—	1.2	2.0	1.5	—	—	—	—
1970	1.0	—	—	1.5	1.0	1.0	0.8	—	—	—	—
1971	1.2	—	—	1.0	1.9	1.0	1.2	0	—	—	—
1972	1.3	1.2	1.1	1.4	1.5	0.8	0	—	0	—	1.0
1973	0.7	—	—	—	0.3	0.5	0.5	1.1	0	—	1.0
1974	0.3	—	0.6	0.4	0.2	0.2	0	0	—	—	—
1975	1.3	1.2	1.3	2.0	—	1.4	0.5	0.5	—	—	—
1976	0.4	—	0.7	0.4	0.5	0.3	0	0	—	—	—

	EARLY	MIDDLE	LATE
Means	= 0.8	= 1.1	= 0.6

TABLE 11

Summary of seasonal parameters of reproductive success in the Brown Pelican.

	Early nests	Middle nests	Late Nests
Number of nests	104	189	35
Number of eggs laid	265	497	78
Clutch size	2.5	2.6	2.2
Number of eggs that hatched	223	351	34
Number of nests in which eggs hatched	84	155	27
Hatching success	84%	70%	43%
Number of young that fledged	88	208	22
Percentage of eggs laid that produced a fledged young	33%	41%	28%
Percentage of eggs hatched that produced a fledged young	39%	59%	64%
Number of successful nests	68	131	15
Percentage of successful nests	65%	69%	43%
Fledglings per successful nest	1.3	1.6	1.5
Productivity (fledglings per total nests)	0.8	1.1	0.6

fluctuations in clutch size, hatching success, and fledgling success for all eight years (Table 11 and Fig. 2): with the exception of the percentage of eggs hatched that produced a fledged young, all parameters are highest in the middle or early portions of the nesting season. Clutch size was essentially similar between early and middle nests but was lower in late nests. Hatching success was highest early in the season and then declined through the year, being much lower in the late nests. The percentage of eggs that produced a young varied between those laid and hatched. Of those laid, most produce a young in the middle period, with late nests being less successful than early nests. However, of the eggs that hatched, the late nests were the most successful with the early eggs being least successful. The middle period had the highest percentage of successful nests, but only somewhat more so than the early nests, with late nests being statistically less successful. Fledglings produced per successful nest was similar between late and middle period nests with early nests producing fewer but not significantly so. However, in fledglings per total nests, early and middle period nests were most successful with the late nests significantly less so.

Discussion of Seasonal Patterns in Reproductive Success

Perrins (1970), reviewed the available avian literature and indicated that young hatched earliest in the season have the greatest chance of surviving to breed. He discussed the selective factors involved in this seasonal phenomenon. In recent years many studies have clearly demonstrated seasonal changes in clutch size and reproductive success, especially in gulls and terns (Laridae). The Herring Gull *(Larus argentatus)* has received the most attention and showed a decline in nest success through the season (Parsons, et al. 1976; for summary) although early and late layers produced fewer fledged young than those nesting at the peak of the season (Parsons 1975). Haycock and Threlfall (1975) showed decreasing clutch size through the season in the Herring Gull, except in late nests when replacement clutches were involved. They did not measure seasonal nesting success and only presented a figure for total nesting success. Morris, et al. (1976) reported higher hatching success in early than middle or late nests of Common Terns *(Sterna hirundo)*. They also did not report seasonal reproductive success but did find that fledging success was not related to clutch size. Coulson and his students demonstrated these seasonal effects are related to the age of individual Kittiwakes *(Rissa tridactyla)*, with older or experienced birds nesting early or at the peak of the nesting season (Coulson 1966; Coulson 1978; Coulson, et al. 1969; Parsons 1976) with age and previous experience perhaps overriding any seasonal effect.

Nelson (1966) found in the Gannet *(Sula bassana)* that experienced breeders nested earlier than inexperienced individuals but that no difference existed between nesting success rate throughout the whole laying period. He related this to an abundant, reliable food supply near Bass Rock, Scotland. Snow (1960) showed that the Shag *(Phalacrocorax aristotelis)* on Lundy, Great Britain, exhibited a slight decrease in clutch size through the season with a well marked decrease in breeding success as the season advanced. She related this decrease to later nesting by younger birds and also to reduced availability of food at the end of the season. Keith (1978) found differences between early and late cohorts of Brown Pelicans in Baja California with later breeders less successful than the early birds. He indicated that food became scarce in August and the late nesters lost their young through starvation. Knopf (1975) found a significant decrease in young fledged with later nest establishment, and a decrease in

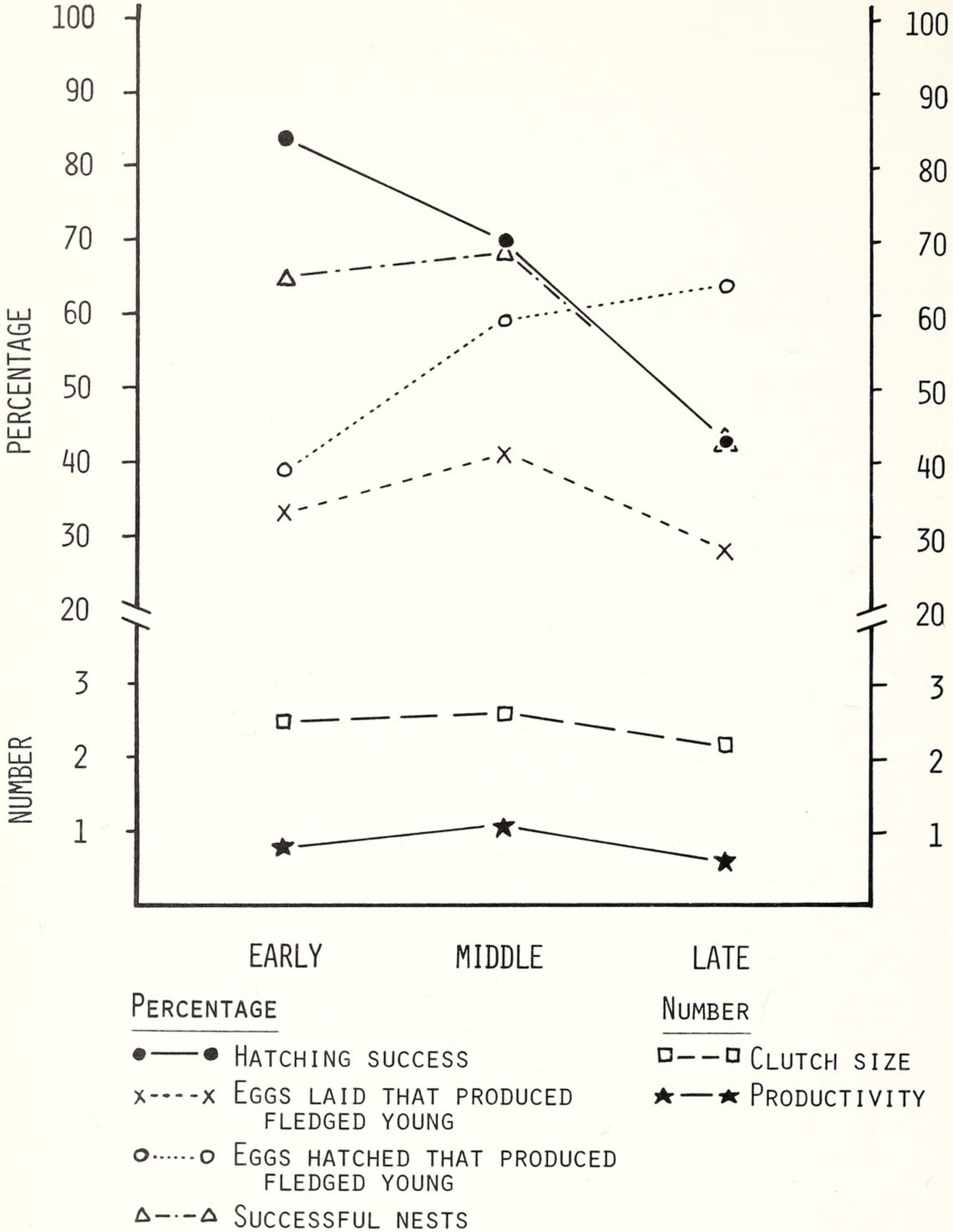

FIGURE 2. Seasonal pattern in clutch size, hatching success, and productivity.

clutch size through the season in the White Pelican *(Pelecanus erythrorhynchos)*. He suggested that late breeders were younger birds (Knopf and Street 1974).

Conventional ornithological thought indicates seasonal changes in reproductive success. However, other than the seasonal effects on clutch size, with larger clutches formed early and at the peak of laying, seasonal changes in reproductive success have actually been demonstrated in few species. In those species for which data are available, indications are that these seasonal changes are related to the age or experience of the nesting birds. Clearly, more data are needed on the subject.

A seasonal pattern of late nests being less successful than early and middle period nests is well established in this colony of Brown Pelicans. Nesters at the peak of laying were the most successful. Early and middle period nesting birds not only have larger clutches, but they are also most successful in producing fledglings.

Blus and Keahey (1978) noted that the few subadult plumaged Brown Pelicans nesting in South Carolina in 1975 did so later than full adult plumaged birds. Keith (1978) by contrast, found no tendency for subadult plumaged birds to nest late in the season in Baja California. Unfortunately, I know nothing about the precise ages of the breeding birds in this study in Florida. However, no birds in subadult plumage bred in my study units. It is impossible to age the adults that did nest (Schreiber *in preparation*) and few data are available on nesting success related to precise age in this species.

I have demonstrated an investigator bias on reproductive success and distinct seasonal fluctuations in those parameters in this species. With those two factors in mind, I next consider the year to year fluctuations in productivity that are superimposed on the seasonal differences in reproductive success.

Annual Fluctuations in Reproductive Success (based on marked nests)

In Table 12, I present data on various reproductive parameters measured in a consistent manner for 328 nests during eight years in one unit of the colony. The data in this table do not include nests in which relaying occurred or "nests" that did not receive an egg (see Tables 13 and 14).

CLUTCH SIZE: Varied between 2.8 (1969, with few nests) and 2.5 (1971) with a mean for all eight years of 2.6 eggs per nest (Table 12). This figure is lower than the 2.95 mean clutch size given from museum collections by Anderson and Hickey (1970) but that sample includes four egg clutches and is known to be biased toward a larger clutch size (Kiff *personal communication*). Blus and Keahey (1978) reported a clutch size of 2.85 for 89 nests of adults in South Carolina in 1975. They reported the presence of a small percentage of four and five egg clutches in a large sample of nests in that state between 1969 and 1975. I examined over 4,000 nests in Florida between 1969 and 1978 and did not see a four or five egg clutch. Bent (1922) and Palmer (1964) give three and occasionally two as the usual clutch size in this species. I believe that the data available indicate that two or three eggs constitute the normal clutch of the Brown Pelican.

HATCHING SUCCESS: (For individual eggs) varied from 89% (1969) to 53% (1973) with a mean of 71%. The percentage of eggs that produced a fledgling varied between 59% (1969) and 12% (1974) with a mean of 37%. The percentage of eggs hatched that produced a fledgling varied between 77% (1971) and 16% (1974) with a mean of 52%. The percentage of nests that were successful varied between 100% (1969) and 33% (1974) with a mean of 65%. Fledglings per successful nest varied between 1.7 (1971) and 1.0 (1974) with a mean of 1.5. Fledglings per total nest varied between 1.7 (1969) and 0.31 (1974) with a mean of 0.97.

These data clearly indicate that while clutch size and hatching success varied little between years, important differences did occur between years in reproductive success as measured by fledglings produced. Obviously, the figure for fledglings per successful nests will be higher than fledglings per total nests. I consider the figure for fledglings per successful nest as of little value for comparative purposes. The measurement of fledglings per total nests formed in a colony is the only useful measurement of productivity.

In three years (1971, 1972, and 1975) productivity was 1.2 to 1.3 young per nest. In 1969, fledging success in 13 nests was 1.7, a high figure that probably would not have been reached with a larger sample size (see Table 23). In 1970, productivity was one young per total nest. In 1973, 0.6 young fledged per nest. However, in 1974 and 1976 productivity was very low, at 0.3 and 0.4 young per nest.

RE-LAYING: In Table 13, I present an estimate of re-laying in marked nests. This estimate is not based on individually marked birds but on the following information: Several nests were constructed and received one or more eggs. On a later survey the eggs were gone, but the nest was still in undisturbed condition. The adults apparently continued to occupy it and in several instances I observed adults sitting on these empty nests. Unoccupied nests are rapidly destroyed by male pelicans gathering nest material (Schreiber 1977, and *unpublished data*). Thus, I believe it correct to assume that if a nest remained intact, and at a later date had eggs present, the original pair of pelicans had remained together on the site and the female re-layed there.

The amount of re-laying varied considerably between years, with none some years (1970), to as high as in 26% of the nests in 1973. Clutch size in the initial nests was slightly lower than in the re-laying attempt (2.4 vs. 2.5 eggs). Both were somewhat lower than in nests in which only an initial set was laid (2.6). The total number of eggs laid for replacement clutches was considerably greater than in "normal" clutches (4.6 eggs per nest). Only 28% of these eggs hatched (from none to 38% in different years). But of the eggs that hatched, 85% produced a fledgling, a figure significantly greater than for eggs laid in first clutches ($P < 0.01$, t test). Additionally, the 1.2 young fledged per total nest in which re-laying occurred is also higher than in non-replacement nests, although not significantly so.

With a sample of only 30 nests in which re-laying occurred during this eight year study, it is impossible to generalize on its occurrence. Re-laying does occur more in nests initiated early in the season; however, re-laying can occur throughout the season. In 25 of 30 nests in which re-laying occurred, the initial clutch was laid during the first four weeks of the season, probably reflecting the inability of females to recycle later in the nesting season. In my sample, re-laying was not significantly more prevalent in years with longer laying seasons, although more re-laying did occur in 1973 when the season lasted the longest into the summer (see Table 18 and Appendix 14).

Re-laying has occurred in nests from which eggs were lost

TABLE 12

Reproductive success of the Brown Pelican 1969–1976. All nests checked weekly in each year. Does not include nests in which re-laying occurred or "nests" that did not receive eggs.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests	13	25	39	86	23	61	52	29	328
Number of eggs laid	37	64	99	224	59	164	137	76	860
Clutch size	2.85	2.56	2.54	2.60	2.56	2.69	2.63	2.62	2.62
Number of eggs that hatched	31	45	61	152	31	128	114	48	610
Eggs hatched per nest	2.54	1.80	1.56	1.77	1.34	2.10	2.19	1.65	1.86
Percentage of nests in which eggs hatched	100%	76%	74%	85%	61%	85%	94%	76%	82%
Hatching success	89%	70%	62%	68%	53%	78%	83%	63%	71%
Number of young that fledged	22	26	47	109	16	20	67	11	318
Percentage of eggs laid from which young fledged	59%	41%	47%	49%	27%	12%	49%	14%	37%
Percentage of eggs hatched from which young fledged	67%	58%	77%	72%	52%	16%	59%	23%	52%
Number of successful nests (fledged one or more young)	13	21	27	67	13	20	43	10	214
Percentage of successful nests	100%	84%	69%	78%	56%	33%	83%	34%	65%
Fledglings per successful nest	1.69	1.24	1.74	1.63	1.23	1.00	1.56	1.10	1.48
Productivity (fledglings per total nests)	1.69	1.04	1.21	1.26	0.70	0.33	1.29	0.38	0.97

TABLE 13

Re-laying in the Brown Pelican, 1969–1976. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of additional nests in which re-laying occurred	1	0	3	12	6	3	2	3	30
Percentage of nesting attempts in which re-laying occurred	8%	0	8%	14%	26%	5%	4%	10%	9%
In nests in which re-laying occurred:									
Number of eggs laid	5	0	12	59	31	14	11	7	139
First attempt	3	0	6	28	15	8	5	3	68
Second attempt	2	0	6	31	16	6	6	4	71
Number of eggs hatched	1	0	3	23	7	3	2	0	39
Percentage of eggs laid that hatched	20%	0	25%	39%	22%	21%	18%	0	28%
Number of young fledged	1	0	3	19	5	3	2	0	33
Percentage of eggs laid that fledged	20%	0	25%	32%	16%	21%	18%	0	24%
Percentage of eggs hatched that fledged	100%	0	100%	83%	71%	100%	100%	0	85%
Number of young that fledged per total nests in which re-laying occurred	1.0	0	1.0	1.6	0.8	1.0	1.0	0	1.1

either early or late in the incubation period (14 in the first and 10 in the second half of incubation). Re-laying also occurred four times in nests in which one or more nestlings died within ten days of hatching. No re-laying was found in nests in which nestlings died at an older age. With my nest checks occurring only once a week, it was impossible to determine precisely the interval between loss of eggs or small nestlings and re-laying of the first egg of the replacement clutch. However, none was found in less than two or more than four weeks. Replacement after loss of nestlings apparently took no longer than after egg loss, possibly indicating that re-laying is less likely to occur after loss of nestlings. This perhaps also reflects the inability of the female or the pair to recycle once the season has progressed.

No other published data exist on re-laying in Brown Pelicans.

While I have no data on the energy demands of egg production in the Florida Brown Pelicans, individual eggs initially weigh 98

TABLE 14

Aspects of reproductive success in the Brown Pelican: Nests not receiving eggs, fate of eggs that did not hatch, and nestling loss after hatching. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of nests that did not receive an egg	0	0	0	0	6	5	7	0	18
Percentage of nests that did not receive an egg	0	0	0	0	21%	7%	12%	0	5%
Number of nests that failed to hatch any eggs	0	6	10	13	9	9	3	7	57
Percentage of nests that failed to hatch any eggs	0	4%	26%	16%	39%	13%	6%	34%	17%
Number of eggs that did not hatch	6	19	39	72	28	32	22	34	252
Fate and age at which eggs disappeared									
Crushed in nest — Number	0	1	0	1	1	0	0	0	3
Percentage	0	5%	0	1%	4%	0	0	0	1%
Up to 10 days — Number	1	4	10	11	7	2	4	8	47
Percentage	17%	21%	26%	10%	25%	6%	18%	24%	19%
11 to 20 days — Number	1	3	2	9	4	2	2	10	33
Percentage	17%	16%	5%	12%	14%	6%	9%	29%	13%
21 to 30 days — Number	1	1	7	6	8	8	5	5	41
Percentage	17%	5%	18%	8%	29%	25%	23%	15%	16%
30+ days, Unhatched — Number	3	10	17	38	6	9	5	5	93
Percentage	50%	53%	44%	53%	21%	28%	23%	15%	37%
30+ days, Unknown — Number	0	0	3	11	2	11	8	0	35
Percentage	0	0	8%	15%	7%	34%	36%	0	14%
Number of nests that failed to fledge any young after one or more egg hatched	0	3	2	5	1	33	6	9	59
Percentage of nests that failed to fledge any young after one or more egg hatched	0	12%	5%	6%	4%	54%	11%	31%	18%

g (n = 51), less than 3.5% of the female weight of 2900 g (n = 30). Females accumulate massive amounts of subcutaneous and perivisceral fat prior to the onset of the nesting season. I suspect that producing the four to six eggs involved in a first and second laying is not an important energy drain on the female. Since a replacement clutch generally produces a fledgling, and has an even higher probability of doing so than single clutches, it is adaptively significant to produce the replacement clutch.

NESTS NOT RECEIVING EGGS: In Tables 14 and 15, I consider additional data from the nest surveys. Only 5% of all nests judged to be fully constructed did not receive an egg and all these occurred in only three years, 1973, 1974, and 1975 (Table 14). Nests remaining occupied during at least three weekly surveys were included here. Several other structures were started but were present on only one survey, and by the next a well-formed nest was present within a meter of the incomplete structure. I did not consider these structures as nests in which no eggs were laid but rather as the result of preliminary efforts that were later shifted to the actual nest. The number of nests that did not receive any eggs *does* effect computation of total reproductive success of the population (see Table 16).

EGG LOSS AND HATCHING FAILURE: Data on loss of eggs in different stages of incubation are presented in Table 14. Essentially all egg losses reported here resulted from the disappearance of eggs between my visits, except for those listed as "30+ days, unhatched" which were eggs that remained in nests for at least 30, and usually 35 to 40 days. The normal incubation period is 30 days. Only three eggs, one each in 1970, 1972, and 1973, were found crushed in the nest. This was 1% of the total eggs that failed to hatch in the study area and only 0.0035% of the total eggs laid in the study nests.

Egg loss during incubation was essentially equally distributed within 10-day periods of the 30-day incubation period with 19%, 13%, and 16% lost during each interval. Thirty-seven percent (93 of 252) of all egg losses resulted from eggs that did not hatch. Most remained in nests only 32–35 days, but I recorded 27 in nests between 38 and 60 days and one remained in a nest a minimum of 88 days. At least 12 of these eggs were in nests in which one or more eggs had hatched and the unhatched eggs remained in the nest with the chick(s).

I recorded four dead embryos that piped the shell which was somehow then crushed or broken around it. Also, the shells remained intact but the embryo did not break out of the piped shell in eight cases.

During incubation, the whole clutch disappeared from 27 nests between two of my weekly visits; while in 76 nests the eggs were lost one at a time. I believe the loss of the whole clutch represented eggs predated while the others were lost one at a time due to the activity of the adults.

No eggs hatched in 17% of the total nests which received eggs (Table 14). This was highest in 1973 and 1976, years of low productivity. Few nests failed to hatch any eggs in 1974, also a year of low production. No clear relationship exists between productivity and the number of nests that failed to hatch any eggs. In

TABLE 15

Aspects of reproductive success in the Brown Pelican. Numbers of young fledged per nest and age at which nestlings died. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of nests that fledged three young	2	0	2	3	0	0	1	0	8
Percentage of nests that fledged three young	15%	0	7%	4%	0	0	2%	0	4%
Number of nests that fledged two young	5	5	16	36	3	0	22	1	88
Percentage of nests that fledged two young	38%	24%	59%	54%	23%	0	51%	10%	41%
Number of nests that fledged one young	6	16	9	28	10	20	20	9	118
Percentage of nests that fledged one young	46%	76%	33%	42%	77%	100%	47%	90%	55%
Number of successful nests	13	21	27	67	13	20	52	10	214
Number of young that died	9	19	13	42	15	102	46	35	281
Age at which young died									
Up to 10 days old — Number	4	5	10	13	4	24	14	15	89
— Percentage	44%	26%	77%	31%	27%	14%	30%	43%	31%
11 to 20 days old — Number	3	9	1	13	3	24	15	13	81
— Percentage	33%	47%	8%	31%	20%	24%	33%	37%	29%
21 to 30 days old — Number	2	5	2	10	7	38	13	4	81
— Percentage	22%	26%	15%	24%	47%	37%	28%	11%	29%
31 to 40 days old — Number	0	0	0	6	0	16	4	1	27
— Percentage	0	0	0	14%	0	15%	9%	3%	10%
Over 40 days old — Number	0	0	0	0	1	0	0	2	3
— Percentage	0	0	0	0	6%	0	0	6%	1%

years of low productivity, and especially 1974 and 1976, a high number of nests failed to fledge young after successfully hatching eggs (Table 14). In general, loss of young was more important to nesting failure (48%) than loss of eggs (29%).

NESTLING MORTALITY: Mortality of nestlings was essentially equally distributed within the first 30 days of life and 89% of all nestlings that died did so during that period (Table 15). Only 30 of 281 nestlings survived 31 to 40 days and then died and only three nestlings survived over 40 days and subsequently died: one in 1973 and two in 1976. In 1971, the majority of the nestlings that died did so before 10 days of age (77%). In 1974 heavy mortality occurred, being quite low in the first 10 days (14%) and then increasing during the next 20 days (24% and 37% in the ten-day intervals) and continuing through a nestling age of 31–40 days (15%). In 1972 and 1973, several nestlings died at 31–40 days of age.

FLEDGLINGS PER NEST: During this eight year study, when low production occurred, it was primarily due to losses during the nestling stage and not during the incubation period. Years of low production were years in which a small percent of young survived to fledging (1973, 1974, and 1976; Table 15). In all years, only 4% of all nests fledged three young, from eight total nests distributed in 1969, 1971, 1972, and 1975, the years of highest productivity (Table 15). Forty-one percent of all nests fledged two young; 1969, 1971, 1972, and 1975 had high numbers of these nests while 1974 had none and 1976 had only one. Conversely, in years of low production, such as 1974 and 1976 and to a lesser extent 1973 and 1970, the nests which were successful fledged only one young. In 1974, when productivity was lowest, no nest fledged more than one young, and less than one-third of all nests that received eggs produced one young (Table 14). In 1976, of 29 nests only ten were successful; nine produced one young each, one produced two young.

SUMMARY: To summarize data on reproductive success in this study for all eight years, a total of 376 nests were constructed during 1969 through 1976 (Table 16), including nests which did not receive eggs. Of the 376 nests, 18 (4.8%) did not receive any eggs, which occurred only in 1973, 1974, and 1975. Re-laying occurred in 30 nests (8.0%). One or more were recorded in every year, but the most were found in 1972 (12 = 14%) and in 1973 (6 = 26%). Both 1972 and 1973 were unusual years with long laying periods. The length of the nesting season and the amount of re-laying are undoubtedly related in some manner.

Reproductive success ranged from 1.7 young fledged per total nests in 1969, to 0.33 and 0.34 young per nest in 1974 and 1976, with a calculated mean for all 8 years of 0.93 young per nest (n = 376).

PRODUCTIVITY: This study has clearly demonstrated that: (1) in the Brown Pelican wide differences occur in reproductive success between years; (2) a long-term study is necessary to derive a reasonably accurate figure for productivity; and (3) using different methods of interpreting reproductive success gives different results. Depending on the method of calculation, and the questions being asked in the study, whether from marked nests, whether a nest is defined as simply a structure or a structure that received eggs, and whether re-laying is included in the calculations, important differences will occur in figures derived. In this species, in this colony, re-laying appears to be advantageous since replacement clutches generally produced a fledgling and eggs laid as replacements were significantly more successful at

TABLE 16

Reproductive success of the Brown Pelican, 1969–1976. All nests checked weekly in each year.

	1969	1970	1971	1972	1973	1974	1975	1976	Total
Number of nests that received eggs	13	25	39	86	23	61	52	29	328
Number of nests that did not receive eggs	0	0	0	0	6	5	7	0	18
Number of nests in which re-laying occurred	1	0	3	12	6	3	2	3	30
Total nests	14	25	42	98	35	69	61	32	376
Number of young that fledged from all nests	24	26	50	128	21	23	69	11	351
Productivity (fledglings per total nests)	1.71	1.04	1.19	1.31	0.60	0.33	1.13	0.34	0.93

fledging than were eggs laid in "normal" clutches.

During this study only 5% of the fully formed nests did not receive an egg but this low percentage does represent an important reduction in measuring productivity. Of the nests that received eggs, none hatched in 17%, but the relationship between colony productivity and the number of nests that failed to hatch any eggs is not impressive. Clutch size and hatching success varied little but productivity varied considerably between years. However, years of low productivity were years in which large numbers of nests failed to fledge any young after one or more eggs hatched, indicating that the factors contributing to nesting failure operated on the nestlings rather than during incubation.

Data on fish available to Brown Pelicans during this study do not exist. However, in October through December 1973 fish kills occurred in the Gulf of Mexico in the feeding range of the pelicans nesting in this colony and from January through April and May 1974 fish kills occurred in Boca Ciega Bay and Tampa Bay, surrounding the Tarpon Key area. These fish kills were caused by red tide (*Gymnodinium breve;* Quick and Henderson 1975) and essentially all fish in the region died. These massive fish kills undoubtedly caused the poor reproductive success of Brown Pelicans in this colony in 1974 but no direct data exist on fish for other years. I have examined commercial fish catch records and no relevant data are contained therein that correlate with colony productivity.

One line of evidence indicating that fish availability is related to productivity is the amount of regurgitation that occurred in the colony while I checked nests. In 1969 through 1972, and 1975 (years of high reproductive success), many birds, both adults and nestlings, regurgitated. However, during 1973, 1974, and 1976 (years of relatively low reproductive success) I was unable to gather any food samples from the birds. This is indirect evidence that they were capturing insufficient food, or at least had little in their stomachs or esophagae to stimulate regurgitation as a fright response. Discussion with local fishermen indicated in a general way that "bait fish" were not available in 1973 and 1976 but that information is impossible to quantify. No "bait fish" were available in 1974 during the entire nesting season.

Brown Pelican populations have been decimated by the "crashes" of the Anchovy *(Engraulis gingens)* in Peru for years (Murphy 1936; Schaefer 1970 and references therein) but other than the complete failure of nesting attempts, those studies have not related reproductive success to relative food availability. Keith (1978) after a long term study of Brown Pelicans *(Pelecanus occidentalis californicus)* nesting in the Sea of Cortez, Mexico, documented reproductive success and had good circumstantial evidence that lack of food contributed to low reproductive success in some years but he also had no direct evidence on fish abundance. Blus, et al. (1974), studying Brown Pelicans in South Carolina, showed annual fluctuations in productivity, but also had no evidence for fish availability. Such data are probably impossible to generate since the pelicans feed over such a wide region; eat so many species of fish (40 in Florida: Fogarty, et al. *in press;* Schreiber *unpublished data*); and, most importantly, because it is virtually impossible to quantitatively sample fish stocks in the marine environment. To measure actual fish availability to a surface diving bird is even more difficult. Pelicans probably do not catch fish deeper than a meter and they are probably dependent on predaceous fish (i.e. mackerel, *Scomberomorus sp.*, etc.) and marine animals *(Tursiops sp.)* to drive the fish close to the water surface and thus make them available for capture by the birds (Ashmole 1971; Schreiber, et al. 1975). Thus we must rely on circumstantial evidence for food availability and are unable to adequately describe the ultimate and proximate factors controlling the reproductive success in the species.

I believe the contrast in age at which nestlings died between the years of lowest productivity (1974 and 1976), and the other six years are quite instructive as to these ultimate causes of mortality in pelicans: more old nestlings died in poor reproductive years. In 1974 mortality increased through the first 40 days of nestling life, indicating that the causation probably began and occurred all the way through the nestling period. In 1976, mortality was highest in the early to middle periods, but continued throughout the nestling period, indicating that probably the mortality factor or factors were in effect prior to hatching but were not as severe as during 1974. The high mortality in the 21–30 day period, the middle of nestling life, in 1973 probably indicates the action of the causative agent(s) in the midst of the nestling period. I believe these nestling mortalities reflect the food situation for the adults and the timing of the starvation of the nestlings indicates that the adults were unable to capture sufficient fish to feed them.

In an earlier paper (1976a) I discussed mortality as related to growth of nestlings in this colony and presented data that clearly demonstrated the ability of nestlings to survive long periods of starvation. I also showed that brood size reduction occurs through starvation of nestlings, usually of the third and then second to hatch. The first nestling to hatch has the greatest chance to sur-

TABLE 17

Reproductive success in relation to clutch size of the Brown Pelican, 1969–1976. All nests checked weekly in each year.

	3 Egg Clutch	2 Egg Clutch	1 Egg Clutch
Number of nests	223	87	18
Percentage of total nests	68%	26%	5%
Clutch size	669	173	18
Number of eggs hatched	497	108	5
Number of young fledged	252	61	5
Hatching success	74%	61%	28%
Percentage of eggs laid from which young fledged	38%	35%	28%
Percentage of eggs hatched from which young fledged	51%	57%	100%
Percentage of total nests that fledged one or more young	72%	55%	28%
Fledglings per successful nest	1.58	1.27	1.00
Productivity (fledglings per total nests)	1.14	0.70	0.28

vive, and late hatchlings survive only in years of apparent abundant food. Unfortunately, growth data were collected in this colony only during four years (1969–1972), only one of which (1970) was a relatively low reproductive year. I have no growth data for the less successful years of 1973, 1974, and 1976. However, my impression is that the same pattern existed in those years: the first nestling to hatch was the only one to survive in years when adults apparently were unable to capture sufficient food to adequately feed a full brood.

In this study 89% of all young that died did so during their first 30 days of nestling life. The contrasts between 1974 and 1976 vs. the other six years, and the differences between 1973 and 1974–1976 are most instructive: 1973 was the poorest year in the first consecutive five years of this study and hatching success (53%) was the lowest of all eight years, indicating that for some reason adults abandoned nests early in that year. However, although total fledging success was low, in terms of nests in which eggs hatched, 1973 was a relatively successful year. 1973 was also the year in which the greatest number of "nests" did not receive an egg, again indicating that adults may have abandoned nesting attempts. Also in 1973, a late nest was successful in fledging a young, the only year in which this occurred. In 1974 few nests failed to hatch any eggs but more than half of them failed to fledge young. No nests in 1974 fledged more than one young and few did so in 1973 and 1976, while in the other five years several nests did so.

The sum of these circumstantial data indicate that 1973 but especially 1974 and 1976 were years of decreased food availability that caused lower reproductive success.

PRODUCTIVITY RELATED TO CLUTCH SIZE: With the data collected I was able to examine the relation between reproductive success and clutch size (Table 17). Three egg clutches were the most common and hatching success of individual eggs was significantly higher ($P < 0.01$, t test) in these larger clutches than in one-egg clutches. The percentage of all eggs laid that fledged young declined in smaller clutches (but not significantly so) and the percentage of hatched eggs that fledged young was higher in the one-egg clutches (100%) than in the two or three egg clutches, which were similar (57% and 51%). The chance of a chick surviving from a one-egg nest is greater because it has no siblings to compete with for food. The number of young fledged per clutch increases significantly with increased clutch size. Less than one-third of the one-egg clutches produced one young. In Schreiber (1976a) I presented data from another unit of this colony showing that survival decreased importantly in the second and third eggs in a clutch.

Blus and Keahey (1978) found in the South Carolina Brown Pelicans in 1975 that adults laid larger clutches and had better reproductive success to the "downy young" stage than did "immature" plumaged birds. The only one-egg clutches in their sample were laid by immatures. In my study no immature plumaged birds were involved. However, young or less experienced "adults" could have been involved.

In another study Blus, et al. (1974) attempted to measure success (to the downy young stage) in nests from which one egg was collected to measure pollution levels. Both Skutch (1966) and Mayfield (1961) have strongly made the point that studies of breeding success should be based on nests found for that purpose only, and it is now generally accepted by ornithologists that nest success cannot be measured when eggs have been removed from a clutch. I in no way want to denigrate the Blus, et al. studies of pollution effects, especially of DDE and egg shell thinning in pelicans. However, it is obvious from the data in Table 17 that an unbiased measure of nesting success cannot be obtained using nests from which an egg has been removed, and especially when mortality during the full length of the nestling period is not determined.

Timing of the Nesting Season

In addition to the productivity parameters obtained from marked nests presented above, which I consider the only true measure of productivity obtained during this study, I also counted

TABLE 18

Timing of the nesting season of Brown Pelicans on Tarpon Key, Pinellas County, Florida as determined by observation from mid-lagoon and recorded as first date observed. Events recorded thus happened in the preceding several days, usually not more than one week.

Year	First Nests	First Nestlings Heard	First Nestlings Visible	First Fledglings	Colony Empty
1969	?	4 May	13 May	6 July	11 Oct.
1970	19 March	19 Apr	24 Apr	15 June	?
1971	27 Feb	12 Apr	16 Apr	27 June	12 Sept
1972	4 Jan	22 Feb	11 March	25 April	15 Oct
1973	27 Feb	5 Apr	14 Apr	9 July	18 Nov
1974	23 Feb	3 Apr	20 Apr	28 June	29 Oct
1975	29 Jan	21 Mar	29 Mar	18 May	16 Nov
1976	4 Feb	8 Mar	21 Mar	27 May	24 Oct
Whale Key 1976	10 Feb.	?	30 March	6 June	28 July
Outside Tarpon SE 1976	13 Feb	?	4 Apr	6 June	21 August

nests and young in the colony from a distance without disturbing the adults. These data are useful in further documenting production in a colony, but potential problems occur in this method of calculating reproductive success because of the long interval during which nests are initiated in the colony. I explain here the seasonality of nesting in this colony and then present data obtained from the undisturbed nest counts. This type of information is useful for determining the health of a colony when more detailed studies cannot be carried out.

In Table 18, I present data for 1969–1976 on the timing of the nesting season made on the mid-lagoon counts of the whole colony. The variability between years will be discussed elsewhere (Schreiber *in preparation*). The nesting season of the Brown Pelican for any given pair requires approximately 18 weeks (one to two weeks for courtship and nest building, 30 days incubation period, and 10 to 12 weeks for the nestling stage). In any given year of this study a minimum of three months, and as much as five or six months, separated the time of the first and last fledging from the colony. Thus, during a given season, nestlings were fledging from some nests in the colony at the same time that other pairs of adults were just courting, nest building, or incubating. Therefore, only careful study throughout the whole season with counts of the maximum number of young and the maximum number of nests present resulted in an accurate figure for total production. Counts of the number of young in individual nests on two or three visits should also give a reasonable figure for total production. However, because nestlings in the same nest may fledge with several days separation, it is important for accuracy of the counts of young per nest to make all counts prior to the first fledging. The data given in the following sections are presented as a sample of the type of data that can be generated in this manner over the whole nesting season. They are not meant to describe the annual fluctuations of the population of pelicans nesting on Tarpon Key, which will be done elsewhere (Schreiber *in preparation*). Data summarized in Tables 19–23 are presented in detail for each year in Appendices 9–19.

Colony Production Based on Counts of Undisturbed Nests

COUNTS OF YOUNG PER NEST: Nestling Brown Pelicans can be heard calling on the day they hatch and are sometimes visible from a distance at about a week to ten days of age, when the adults are standing on the nest. An accurate count cannot be made until nestlings are three to four weeks old. Between then and age of seven to eight weeks they are clearly visible and remain essentially in their own nest site (unless disturbed by human intrusion). At age eight to ten weeks old they begin to move around in the tops of the mangroves. Accurate counts of the number of young per nest then become impossible to make although total young present can still be recorded accurately. Counts of young per nest presented in Table 19 were made prior to the time of first fledging.

Counts of young per nest result in a minimum figure of 1.0. This method does not account for any nests that are deserted or in which no eggs are laid, for nests which lose eggs, or in which nestlings die at a young age. Thus, this method only presents a maximum figure for production from individual nests, and as such provides a somewhat useful figure for comparison to other data. For the years in which I have sufficient data to document a seasonal trend, brood size declines through the season. The broad comparisons between 1970–1971–1972–1975 with 1973–1974–1976 are instructive in that the prior years are ones in which productivity was measured by this method as higher than in the later years. The data for 1974 through 1976 provide an illustration of the decline in ratio of three-, two-, and one-chick broods through the season and indicate that in "good" years (1975) the number of three- and two-chick nests remain higher than in "bad" years. Thus, counts of brood size reflect to some degree the productivity in a colony, but these inflated figures must be corrected with data on the ratio of active to "failed" nests to actually derive a figure for productivity.

COUNTS OF MAXIMUM NESTS AND MAXIMUM NUMBER OF NESTLINGS PRESENT: Another measure of production obtainable from counts of undisturbed nests is the maximum number of nests present at any one time in the colony, followed by the maximum number of young present as they grow (Table 20). Because of the lack of synchrony in the nesting season this technique necessitates a long series of counts of both numbers of nests and numbers of young throughout the season (see Appendices 9–19). I did not obtain these data in 1969. The years 1970, 1972, and 1975 show a high figure of 1.3 to 1.7 young per nest; 1971 and 1973 show 1.0 young per nest; and both 1974 and 1976 show a figure of less than 1 young per nest. These figures closely parallel the data obtained from counts of brood size and also of productivity described earlier.

In three years small units formed on the outside edges of Tarpon Key, and in 1976 nesting occurred on outlying Whale Key. In these easily visible areas accurate counts of nests and young were possible. In 1971 the figure of 1.2–1.4 young per nest is slightly higher than in the larger sample of nests around the inside lagoon; in 1972 similar figures are derived for both locations; and in 1976 the smaller samples also give similar but slightly higher figures. Thus, in the same years the smaller, more

TABLE 19

Production based on counts of nestlings in each visible nest for Brown Pelicans on Tarpon Key, Pinellas County, Florida. Counts made from mid-lagoon.

DATE	NUMBER OF NESTLINGS PER NEST			TOTAL NESTLINGS TOTAL NESTS	COMPUTED NUMBER OF NESTLINGS PER NEST
	3	2	1		
1970					
15 June	0	33	93	159/126	1.3
1971					
5 June	0	17	13	47/30	1.6
12 June	0	56	48	160/104	1.5
27 June	2	31	27	95/60	1.6
1972					
26 March	0	6	5	17/11	1.5
30 March	0	5	5	15/10	1.5
13 April	0	9	4	22/13	1.7
18 April	0	8	8	24/16	1.5
1973					
3 June	0	6	65	77/71	1.1
10 June	1	6	72	87/79	1.1
9 July	0	0	195	195/195	1.0
1974					
30 April	1	8	13	32/22	1.4
5 May	0	73	67	213/140	1.5
13 May	1	66	129	264/196	1.4
18 May	0	41	172	254/213	1.2
25 May	0	26	229	281/255	1.1
2 June	0	34	238	306/272	1.1
8 June	0	20	284	324/304	1.0
1975					
12 April	11	88	33	242/132	1.8
20 April	7	145	89	400/241	1.7
29 April	3	154	91	408/248	1.6
5 May	0	155	147	457/302	1.5
12 May	2	167	179	513/328	1.6
18 May	0	37	37	111/74	1.5
24 May	1	92	95	282/181	1.5
1976					
11 April	1	10	8	31/19	1.6
22 April	0	15	27	57/42	1.4
29 April	0	29	79	137/108	1.3
4 May	1	34	102	173/137	1.3
13 May	0	24	126	174/150	1.2
22 May	0	25	136	186/161	1.2
27 May	0	25	205	255/230	1.1

TABLE 20

Production based on counts of maximum number of nests and the maximum number of Brown Pelican nestlings visible. Counts made from mid-lagoon.

YEAR	MAXIMUM NUMBER OF NESTS COUNTED (RANGE)	DATES	MAXIMUM NUMBER NESTLINGS COUNTED	DATES	CALCULATED NUMBER OF NESTLINGS PER NEST
1970	200 (194–207)	6–27 May	266	29 June	1.3 – 1.4
1971	inside 250 (236–259)	2–25 May	257	27 June	1.0
	outside 20	13 March – 28 April	24–26	25 May – 10 June	1.2 – 1.4
1972	inside 260 (247–270)	1–18 April	371–417	12–23 June	1.4 – 1.6
	outside 22–24	29 February – 13 April	30–32	27 May – 12 June	1.3 – 1.5
1973	305 (289–320)	19–26 June	310	4 August	1.0
1974	400	13–20 April	304	8 June	0.8
1975	625 (610–636)	21 March – 12 April	675–747	24 May – 28 June	1.4 – 1.7
1976	inside 420 (417–428)	30 March – 11 April	230	27 May	0.6
	Whale 36–38	24 February – 11 April	30–32	22–27 May	0.8
	outside 11–13	2 March – 27 May	11	27 May	1.0 –

easily visible units give similar results to those obtained for the larger sample of nests in the main colony.

These data clearly reflect the differences in production within the colony between years of high and low reproductive success.

COUNTS MADE DURING BEHAVIOR OBSERVATIONS: During 1970 and 1971 I made behavior observations in one unit of the colony from an observation tower ca. 2 m high and 25+ m from the mangrove and the nearest nest (Schreiber 1977). Observations of 19 nests in the unit, from initial courtship activity through fledging of the young, provide a fledging success figure for those years (Table 21). In 1970 all four nests were successful with a total of five fledglings produced, or 1.2 young per nest. In 1971, four of 15 nests were unsuccessful and the 11 others produced 18 young or 1.6 young per successful nest and 1.2 per total nests. These figures are similar to those obtained by other measurements of production in those years.

Reproductive Success Measured During Growth and Development Studies

In 1969 through 1972 I measured growth and development of nestlings in one unit of this colony (Schreiber 1976a). In Table 22, I compile figures on reproductive success from nests in the unit used to carry out these measurements. In this table, for each year the number of nests, the number of fledglings, and a calculated figure for young per nest are presented, with the figures above the dashed line for the nests in which growth and development of nestlings was actually measured (see Table 1, p. 20,

TABLE 21

Productivity based on observations of undisturbed nests.

YEAR	NESTS	YOUNG PRODUCED	PRODUCTIVITY (fledglings per total nests)
1970	4	5	1.2
1971	11 (successful)	18	1.6 (per successful nest)
	4 (unsuccessful)	0	0
	18 (total)	18	1.2

TABLE 22

Productivity based on individually marked nests used to measure growth and development of nestlings. Nests visited on average more than once per week.[1]

YEAR	NESTS	YOUNG PRODUCED	PRODUCTIVITY (fledglings per total nests)
1969	11	18	1.6
	33	43	1.3 (per successful nest)
	53	43	0.8
1970	15	19	1.3
	37	44	1.1 (per successful nest)
	52	44	0.9
1971	17	27	1.6
	26	45	1.7 (per successful nest)
	41	45	1.1
1972	13	17	1.3
	23	40	1.7 (per successful nest)
	26	40	1.5

[1]For each year the data above the dashed line are the nests used for growth and development studies and thus the nestlings were handled on each visit. The data below the line are for all the nests which formed in this study unit.

Schreiber 1976a). The figures below the dashed line include all nests and young in this study unit. This unit was visited essentially weekly and for about 1.5 hours on each visit.

Earlier (Table 2) I indicated that no significant differences existed in the parameters of the 1972 data between the growth and development unit and the weekly nest check unit. Similarly, in 1970 and 1971 no statistical differences existed between units in either young per successful or total nests.

The reproductive success figures obtained during the growth and development studies exhibit annual fluctuations similar to those obtained when nests are disturbed on the same frequency but for a shorter period of time on each visit. I conclude that carrying out these growth studies does not hinder the pelicans. The additional data gathered on growth of nestlings make this a worthwhile effort if colonies are being disturbed to measure productivity.

Comparison of Methods of Measuring Reproductive Performance

In Table 23 I summarize five methods of computing reproductive performance. Four points emerge from these data:

1. Important year to year fluctuations in production occurred in this colony. All five methods reflect these fluctuations. Only a study of several years will generate sufficient data to accurately reflect the reproductive performance in a colony.

2. Important differences exist between calculations of young fledged per successful nest and young fledged per total nests. The former is essentially a useless datum and only data on productivity (young fledged per total nests attempted) are biologically useful.

3. The figures, however, derived from weekly nest checks were similar to the figures derived from observations of the colony from a distance. Thus, the data from counts of nestlings per nest and of the maximum number of nests and nestlings present can be used to assess productivity only if corrected downward with additional data on the number of nests that failed early in the nesting season. These additional data can only be gathered by studying individual nests.

4. A comparison between years (and between studies in different regions) using the figures garnered from any one methodology is valid but comparison between methods (i.e., productivity measured by weekly nest checks vs. production measured by counts of nestlings or maximum nests and nestlings) is invalid. Only data collected in a similar manner can be compared. Only the figures for young per total nest attempts should be used in discussions of population stability.

ESTIMATES OF PRODUCTION: I know of no manipulations that will relate the various production figures obtained from different techniques of data capture and presentation. Years of high and low productivity are easily separable using any one of the data collection methods, however, counts from a distance of nestlings per nest and an estimate of the maximum number of nests

TABLE 23

Comparison of reproductive performance measurements computed from five techniques used to census the colony of Brown Pelicans.

DATE	COUNTS OF[1] NESTLINGS PER NEST	MAXIMUM NESTLINGS[2] / MAXIMUM NESTS	OBSERVATION[3]		GROWTH AND[4] DEVELOPMENT		WEEKLY INDIVIDUAL[5] NEST CHECKS	
			Succ. nests	Total nests	Succ. nests	Total nests	Succ. nests	Total nests (Productivity)
1969	—	—	—	—	1.3	0.8	1.7	1.7
1970	1.3	1.3–1.4	1.2	1.2	1.1	0.9	1.2	1.0
1971	1.5–1.6	1.0	1.2	1.6	1.7	1.1	1.7	1.2
1972	1.5–1.7	1.4–1.6	—	—	1.7	1.5	1.7	1.3
1973	1.0–1.1	1.0	—	—	—	—	1.2	0.6
1974	1.1	0.8–0.9	—	—	—	—	1.0	0.3
1975	1.5	1.4–1.7	—	—	—	—	1.6	1.1
1976	1.0–1.2	0.6–1.0	—	—	—	—	1.1	0.3

[1]Based on counts of nestlings per nest during the nesting season — see Table 19
[2]Based on counts of maximum number of nests and maximum number of nestlings present just prior to first fledging — see Table 20.
[3]Based on nests used for behavioral studies — see Schreiber 1977, and Table 21.
[4]Based on nests used for growth and development studies — see Schreiber 1976a, and Table 22.
[5]Based on individually marked nests checked weekly throughout the nesting season — see Tables 11–16.

formed during a season give the most accurate measure of production in the colony. Obtaining these data requires at least six to eight or more visits to the colony during the nesting season.

The production figures based on two other methods, a) counts of maximum number of nestlings and nests and b) counts of brood size from a distance in the colony, give essentially similar results for all eight years of this study.

PRODUCTIVITY: The only measure of productivity obtained in this study is based on weekly counts of young per individual nest (whether from nests used solely for that or to also measure growth and development). This is the lowest figure obtained by the methods presented here. It is the only one that actually measures productivity since it accounts for nests in which no eggs are laid, in which no eggs hatch or the young die at less than two to three weeks of age, and because of the additional information gained from knowing the details of individual nests. The other methods merely present interesting additional information. Weekly nest checks of individually marked nests requires considerable time and energy to obtain results, but because of the additional data obtainable with that method, it is the most useful type of study to carry out.

CONCLUSION AND SUMMARY

I believe that for this species, *Pelecanus occidentalis*, in these mangrove colonies, a reasonably accurate figure for reproductive performance can be obtained by making weekly surveys of the colony and checking contents of individually marked nests. Years of high and low productivity are easily separable but periodic, frequent visits throughout the nesting season are necessary. Only two or three visits to the colony, even if spaced over a two or three month period, will not yield results comparable between colonies or between years. Comparison of productivity with other colonies of pelicans studied by other workers using different techniques of data collection seem quite futile. I believe it is impossible to generalize on productivity from year to year, but the mean figure derived for young per breeding pair from a reasonably long period of study (six to ten years) is a reasonably accurate measure. However, this mean is of less interest than the year to year variability in productivity and its underlying causes.

Henny (1972) calculated a theoretical recruitment standard of 1.51 to 1.87 young per breeding female necessary to maintain a stable population of Brown Pelicans in North and South Carolina. He noted this standard as too high, based on the clutch size of Brown Pelicans and the productivity of Great White Pelicans *(Pelecanus onocrotalus)* in Africa; and since band loss occurs in the Brown Pelicans the calculated mortality rate estimates for his sample would be inflated. He thus arbitrarily revised downward the recruitment standard as "more closely approximates the range of 1.2 to 1.5 young per breeding pair" but does not indicate how this range was determined. Henny's figures of 1.2 to 1.5 are oft-quoted (Blus, et al. 1977, and references therein) but with serious reservations as to its usefulness (Anderson, et al. 1975).

King, et al. (1977a), recorded 0.87 young per nest in Corpus Christi Bay, Texas, in 1964 through 1973 and noted that this was a "poor" rate "comparable to that of declining populations in South Carolina" (based on Blus, et al. 1974) although that figure is very similar to what Blus found in South Carolina (Blus, et al. 1977). King, et al. (1977b), also noted that nine young fledged from 11 nests in the same area in 1975, or 0.82 young per nest, by birds that may have been renesting late in the season.

Blus, et al. (1977) reported reproductive success in two colonies in South Carolina from 1969 through 1973 as 0.78, 0.85, 0.92, 0.69, and 1.66 although the methods used to derive these figures are not clearly stated and data for independent analysis in that paper or earlier publications are not presented or are difficult to interpret. In 1975 Blus and Keahey (1978) recorded successful nests as those in which one or more downy young survived to leave the nest at four to five weeks of age and recorded 0.89 young per nest for adults and 0.11 young per nest for immature plumaged nesting birds. The colony was visited once or twice a week throughout the season, which probably reduced nesting success to an unknown extent, especially in light of suggested disturbance of up to one hour in the colony, apparently with the adults off of their nests the whole time. In 1976 production of 1.43 fledglings per nest was recorded in this colony (Stickel 1977). While productivity was definitely lower in the 1969–1972 period than in later years, production of 0.92 young per nest from 9370 total nests (8590 young) for those seven years is remarkably close to the mean figure of 0.93 young per nest derived from marked nests in Florida (this study) in the same time span. Blus, et al. (1974 and references therein) note the Florida population as stable. Comparison of Florida and South Carolina data is virtually impossible because of the lack of control on bias caused by human disturbance. However, I would expect the South Carolina birds to exhibit somewhat lower total reproductive success since the large number of young birds breeding in the population would have lower nesting success and because the population is on the northern extreme of the range for the species. Yet even in 1977 reliance by Blus, et al. (1974) on the Henny recruitment standard occurs with the indication that productivity in South Carolina is subnormal. The South Carolina birds spend the winter in Florida (Schreiber 1976b) and the Brown Pelican population of the east coast of Florida has not declined in the past 20 years (Schreiber and Schreiber 1973). It is interesting that Blus, et al. have consistently ignored these Florida Christmas Count data when they claim a population decline in South Carolina. Significant egg shell thinning has occurred in South Carolina but I suggest that the population decline has actually not been as severe as claimed. Production has been erratic and fluctuating in South Carolina but that is characteristic for this species.

Keith (1978), during a detailed study of the largest colonies in North America on the San Lorenzo Island group of the Sea of Cortez, Mexico, in 1970–1977, despite severe difficulties of access and fully cognizant of the sensitivity of the pelicans to human disturbance, noted distinct annual fluctuations in productivity, primarily from starvation of nestlings and desertion of nests by adults during incubation. He also found wide fluctuations in the number of breeding attempts. Using detailed counts of total young produced and total nests present, Keith found low productivity of 0.43 to 0.23 young per total nests with an average of 0.30 young per nest attempt in 1973 through 1976. Keith also discusses the biases in the Henny (1972) recruitment standard, especially as regards non-breeding by adult birds, and finds it not a useful comparison.

I believe that the data are now overwhelming that "normal" nesting success of Brown Pelicans fluctuates, with the mean centering around or slightly below one young fledged per nesting pair per year. It is time to abandon the theoretical recruitment standard of Henny (1972) in favor of productivity based on field data in a stable population. Only further analysis of banding data, utilizing the greatly increased number of recoveries in the past decade, will provide a test of whether banding data can provide an accurate index to mortality rates and production necessary for population maintenance in this species (Schreiber *in preparation*).

The fluctuations in productivity between years noted in all studies thus far carried out on Brown Pelicans (Blus, et al. in South Carolina, Anderson and Keith in Baja California and California, King in Texas, and my data for Florida) clearly indicate that only a long term study, probably on the order of 20 years or the reproductive span of an adult female Brown Pelican, whatever that may be, carried out by the same individuals using precise methods and who are fully cognizant of the effects of human disturbance on measurement of reproductive success, will be adequate to determine the long term population trends of this endangered species.

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APPENDIX 1

1969 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	16-31 March	1-15 April	16-30 April	Total
Number of nests	4	7	2	13
Percentage of total nests	31%	54%	15%	100%
Number of eggs laid	11	20	6	37
Clutch size	2.8	2.9	3.0	2.9
Number of eggs that hatched	8	19	4	31
Eggs hatched per total nests	2.0	2.7	2.0	2.5
Number of nests in which eggs hatched	4	7	2	13
Hatching success	73%	95%	67%	89%
Number of young that fledged	5	14	3	22
Percentage of eggs laid from which young fledged	45%	70%	50%	59%
Percentage of eggs hatched from which young fledged	63%	74%	75%	67%
Number of successful nests (fledged one or more young)	4	7	2	13
Percentage of successful nests	100%	100%	100%	100%
Fledglings per successful nest	1.2	2.0	1.5	1.7
Productivity (fledglings per total nests)	1.2	2.0	1.5	1.7

APPENDIX 2

1970 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	1-15 March	16-31 March	1-15 April	16-30 April	Total
Number of nests	4	5	11	5	25
Percentage of total nests	16%	20%	44%	20%	100%
Number of eggs laid	12	13	27	12	64
Clutch size	3.0	2.6	2.4	2.4	2.6
Number of eggs that hatched	8	10	18	9	45
Eggs hatched per total nests	2.0	2.0	1.6	1.8	1.8
Number of nests in which eggs hatched	4	5	10	5	24
Hatching success	67%	77%	67%	75%	70%
Number of young that fledged	6	5	11	4	26
Percentage of eggs laid from which young fledged	50%	38%	41%	33%	41%
Percentage of eggs hatched from which young fledged	75%	50%	61%	44%	58%
Number of successful nests (fledged one or more young)	4	4	9	4	21
Percentage of successful nests	100%	80%	82%	80%	84%
Fledglings per successful nest	1.5	1.3	1.2	1.0	1.2
Productivity (fledglings per total nests)	1.5	1.0	1.0	0.8	1.0

APPENDIX 3

1971 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	2	8	19	8	2	39
Percentage of total nests	5%	20%	49%	20%	5%	100%
Number of eggs laid	4	23	48	21	3	99
Clutch size	2.0	2.9	2.5	2.6	1.5	2.5
Number of eggs that hatched	3	17	28	13	0	61
Eggs hatched per total nests	1.5	2.1	1.5	1.6	0	1.6
Number of nests in which eggs hatched	2	8	13	6	0	29
Hatching success	75%	74%	58%	62%	0	62%
Number of young that fledged	2	15	20	10	0	47
Percentage of eggs laid from which young fledged	50%	65%	42%	48%	0	47%
Percentage of eggs hatched from which young fledged	67%	88%	71%	77%	0	77%
Number of successful nests (fledged one or more young)	2	8	12	5	0	27
Percentage of successful nests	100%	100%	63%	62%	0	69%
Fledglings per successful nest	1.0	1.9	1.7	2.0	0	1.7
Productivity (fledglings per total nests)	1.0	1.9	1.1	1.2	0	1.2

APPENDIX 4

1972 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	1-15 February	16-19 February	1-15 March	16-31 March	1-15 April	16-30 April	Total
Number of nests	5	7	23	35	12	4	86
Percentage of total nests	6%	8%	26%	41%	14%	5%	100%
Number of eggs laid	12	18	65	95	27	7	224
Clutch size	2.4	2.6	2.8	2.7	2.2	1.8	2.6
Number of eggs that hatched	8	11	54	65	14	0	152
Eggs hatched per total nests	1.6	1.6	2.4	1.9	1.2	0	1.8
Number of nests in which eggs hatched	4	7	23	32	7	0	73
Hatching success	66%	61%	83%	68%	52%	0	68%
Number of young that fledged	6	8	33	52	10	0	109
Percentage of eggs laid from which young fledged	50%	44%	51%	55%	37%	0	49%
Percentage of eggs hatched from which young fledged	75%	73%	61%	80%	71%	0	72%
Number of successful nests (fledged one or more young)	4	6	19	31	7	0	67
Percentage of successful nests	80%	86%	83%	88%	58%	0	78%
Fledglings per successful nest	1.5	1.3	1.7	1.7	1.4	0	1.6
Productivity (fledglings per total nests)	1.2	1.1	1.4	1.5	0.8	0	1.3

APPENDIX 5

1973 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	15-30 March	1-15 April	16-30 April	1-15 May	16-31 May	1-15 June	16-31 June	Total
Number of nests	7	2	2	10	1	0	1	23
Percentage of total nests	30%	9%	9%	43%	4%	—	4%	100%
Number of eggs laid	18	5	5	26	3	—	2	59
Clutch size	2.6	2.5	2.5	2.6	3.0	—	2.0	2.6
Number of eggs that hatched	4	2	2	22	0	—	1	31
Eggs hatched per total nests	0.6	1.0	1.0	2.2	0	—	1.0	1.3
Number of nests in which eggs hatched	2	1	1	9	0	—	1	14
Hatching success	22%	40%	40%	85%	0	—	50%	53%
Number of young that fledged	2	1	1	11	0	—	1	16
Percentage of eggs laid from which young fledged	11%	20%	20%	42%	0	—	50%	27%
Percentage of eggs hatched from which young fledged	50%	50%	50%	50%	0	—	100%	52%
Number of successful nests (fledged one or more young)	2	1	1	8	0	—	1	13
Percentage of successful nests	28%	50%	50%	80%	0	—	100%	56%
Fledglings per successful nest	1.0	1.0	1.0	1.4	0	—	1.0	1.2
Productivity (fledglings per total nests)	0.3	0.5	0.5	1.1	0	—	1.0	0.7

APPENDIX 6

1974 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	16-29 February	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	11	18	20	10	1	1	61
Percentage of total nests	18%	30%	33%	16%	2%	2%	100%
Number of eggs laid	33	50	56	22	2	1	164
Clutch size	3.0	2.8	2.8	2.2	2.0	1.0	2.7
Number of eggs that hatched	30	44	41	13	0	0	128
Eggs hatched per total nests	2.7	2.4	2.0	1.3	0	0	2.1
Number of nests in which eggs hatched	11	18	17	6	0	0	52
Hatching success	91%	88%	73%	59%	0	0	78%
Number of young that fledged	7	8	3	2	0	0	20
Percentage of eggs laid from which young fledged	21%	16%	5%	9%	0	0	12%
Percentage of eggs hatched from which young fledged	23%	18%	7%	15%	0	0	16%
Number of successful nests (fledged one or more young)	7	8	3	2	0	0	20
Percentage of successful nests	64%	44%	15%	20%	0	0	33%
Fledglings per successful nest	1.0	1.0	1.0	1.0	0	0	1.0
Productivity (fledglings per total nests)	0.6	0.4	0.2	0.2	0	0	0.3

APPENDIX 7

1975 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date of first egg laid. Does not include nests in which relaying occurred or "nests" that did not receive any eggs.

	1-15 February	16-29 Feb.	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	9	19	8	0	8	4	4	52
Percentage of total nests	17%	36%	15%	—	15%	8%	8%	100%
Number of eggs laid	27	29	23	—	20	9	9	137
Clutch size	3.0	2.6	2.9	—	2.5	2.2	2.2	2.6
Number of eggs that hatched	26	47	19	—	15	3	4	114
Eggs hatched per total nests	2.9	2.5	2.4	—	1.9	0.8	0.8	2.2
Number of nests in which eggs hatched	9	19	8	—	8	2	3	49
Hatching success	96%	96%	83%	—	75%	33%	44%	83%
Number of young that fledged	11	25	16	—	11	2	2	67
Percentage of eggs laid from which young fledged	41%	51%	70%	—	55%	22%	22%	49%
Percentage of eggs hatched from which young fledged	42%	53%	84%	—	73%	66%	50%	59%
Number of successful nests (fledged one or more young)	8	16	8	—	8	1	2	43
Percentage of successful nests	88%	84%	100%	—	100%	25%	50%	83%
Fledglings per successful nest	1.4	1.6	2.0	—	1.4	2.0	1.0	1.6
Productivity (fledglings per total nests)	1.2	1.3	2.0	—	1.4	0.5	0.5	1.3

APPENDIX 8

1976 Reproductive success of the Brown Pelican, Tarpon Key, Pinellas County, Florida. All nests checked weekly in each year. By date first egg laid. Does not include nests in which re-laying occurred or "nests" that did not receive any eggs.

	25-29 February	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	Total
Number of nests	3	13	4	6	2	1	29
Percentage of total nests	10%	45%	14%	21%	7%	3%	100%
Number of eggs laid	9	37	10	14	4	2	76
Clutch size	3	2.9	2.5	2.7	2.0	2.0	2.6
Number of eggs that hatched	9	23	5	9	0	0	48
Eggs hatched per total nests	3.0	1.8	1.2	1.5	0	2.0	1.6
Number of nests in which eggs hatched	3	10	4	4	0	1	22
Hatching success	100%	62%	50%	65%	0	100%	64%
Number of young that fledged	2	5	2	2	0	0	11
Percentage of eggs laid from which young fledged	22%	14%	20%	14%	0	0	14%
Percentage of eggs hatched from which young fledged	22%	22%	40%	22%	0	0	23%
Number of successful nests (fledged one or more young)	2	4	2	2	0	0	10
Percentage of successful nests	67%	31%	50%	33%	0	0	34%
Fledglings per successful nest	1.0	1.2	1.0	1.0	0	0	1.1
Productivity (fledglings per total nests)	0.7	0.4	0.5	0.3	0	0	0.4

APPENDIX 9

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible from the observation tower.

1970 North Area

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS: ADULTS ONLY	NEST CONTENTS: NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK	TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
13 Feb	0									
7 Mar	193	0								
9 Mar	157	0								
19 Mar	155	24	6.4/1							
30 Mar	257	75	2.4/1							
1 Apr	290	78	2.7/1							
5 Apr	295	88	2.5/1							
7 Apr	340	105	3.2/1							
11 Apr	356	127	2.8/1							
14 Apr	304	—	—							
19 Apr	—	—	—	First nestlings heard						
24 Apr	290	173	1.7/1	First nestlings visible						
6 May	308	194	1.6/1	—	11					
11 May	230	—	—	—	29					
17 May	210	204	1.0/1	—	44 nestlings visible					
22 May	257	207	1.2/1	—	53					
27 May	205	203	1.0/1	—	96 nestlings visible					
3 June	204	—	—	—	132 nestlings visible					
10 June	108	—	—	—	181 nestlings visible					
15 June	84	—	—	First fledglings		0	33	93	159/126 =	1.26
22 June	94	—	—	—	188 nestlings visible					
29 June	62	—	—	—	228 nestlings and 38 young of the year					
2 July	28	—	—	—	281 nestlings and young of the year					
17 July	21	—	—	Major number of young of the year away from Tarpon Key						
30 July	18	—	—	—						

APPENDIX 10

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible from the observation tower.

1971 North Area

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK	TOTAL CHICKS/ NESTS		COMPUTED CHICKS PER NEST
28 Feb	141	—									
2 Mar	172	—									
5 Mar	143	—									
13 Mar	128	—									
24 Mar	224	—									
27 Mar	225	—									
29 Mar	279	—									
31 Mar	264	—									
12 Apr	206	—	—	First nestlings heard							
16 Apr	250	—	—	First nestlings visible							
21 Apr	270	—	—								
2 May	255	259	1/1								
4 May	267	253	1/1								
17 May	245	241	1/1	—	—	—	—	—	85/56	=	1.52
25 May	232	236	1/1	—	118 nestlings visible						
5 June	155	—	—	—	126 nestlings visible						
					a sample =	0	17	13	47/30	=	1.57
12 June	133	—	—	—	—	0	56	48	160/104	=	1.54
27 June	118	—	—	—	257 nestlings visible						
					a sample =	2	31	27	95/60	=	1.58
6 July	—	—	—	First fledglings							
10 Aug	—	—	—	—	52 nestlings visible						
24 Aug	—	—	—	—	15 nestlings visible						
2 Sept	—	—	—	—	3 nestlings visible						

APPENDIX 11

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible in the north outside area of the colony, 1971.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	2 CHICKS	1 CHICK		
16 Feb	0									
27 Feb	45	2	22.5							
2 Mar	43	8	5.3							
5 Mar	36	17	2.1							
13 Mar	21	19	1.1							
27 Mar	13	13	1.0							
29 Mar	29	16	1.8							
31 Mar	22	17	1.3							
12 Apr	20	17	1.2	First nestlings heard (at least in 2 nests)						
16 Apr	27	18	1.5	15	3					
28 Apr	28	20	1.4	10	10					
8 May	19	17	1.1	8	9	3	3	3	18/9 =	2.0
20 May	14	16	0.87	4	12	1	6	5	20/12 =	1.67
25 May	14	18	0.77	4	14	2	8	4	26/14 =	1.86
10 June	14	18	0.77	3	15	1	7	7	24/15 =	1.60
27 June	14	—	—	First fledgings						
3 July	13	—	—	0	2	0	1	1	3/2 =	1.5
8 July	12	—	—	0	2	0	2	0	4/2 =	2.0
23 July	2	—	—	0	0	0	2	0	4/2 =	2.0
17 Aug	0	—	—	0	0					

APPENDIX 12

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1972 Inside, Northeast, West, and Southeast areas.

DATE	ADULTS	NESTS	ADULT/NEST RATIO		
4 Jan	199	courtship activity ongoing			
9 Jan	378	"	"		
19 Jan	267	"	"		
25 Jan	266	102	2.6/1		
4 Feb	284	143	2.0/1		
7 Feb	228	136	1.7/1		
22 Feb	194	90	2.2/1		
29 Feb	293	118	2.5/1	First nestlings heard	
11 Mar	361	148	2.4/1		
18 Mar	365	214	1.7/1	First nestlings visible	
21 Mar	445	229	1.9/1		
1 Apr	338	247	1.4/1		
4 Apr	327	261	1.2/1		
13 Apr	348	270	1.3/1	Nestlings visible in 38 nests	
18 Apr	370	259	1.4/1	Nestlings visible in 41 nests	
25 Apr	336	216	1.6/1	Nestlings visible in 55 nests First fledglings	
2 May	313	231	1.4/1	Nestlings visible in 78 nests	
14 May	312	231	1.3/1	Nestlings visible in 118 nests	
		Adults on nests	Nestlings	Fledglings	
21 May	261	118	207	25	119 nestlings in 69 nests = 1.7 chick/nest
26 May	226	143	240	53	
12 June	232	—	344	45	
23 June	93	—	372 (49 downy)	45	
27 June	93	—	293	114	First influx of birds of the year away from Tarpon Key
8 July	48	—	224	147	
16 July	56	—	226 (33 downy)	149	
22 July	47	—	173 (16 downy)		
30 July	101	—	150		
7 Aug	38	—	64		
13 Aug	23	—	72		
26 Aug	7	—	36		
31 Aug	20	—	22		
8 Sept	13	—	12		
26 Sept	5	—	7		
30 Sept	14	—	2		
7 Oct	4	—	1		
15 Oct	8	—	0		
20 Oct	3	—	0	14 fledglings still present	
12 Nov	0	—	0	No fledglings present	

APPENDIX 13

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1972 Outside Northeast.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS: ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK	TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
4 Jan	26	10	2.6/1							
19 Jan	26	16	1.6/1							
4 Feb	18	17	1.0/1							
22 Feb	22	18	1.2/1			First nestlings heard				
29 Feb	53	22	2.4/1							
11 Mar	34	23	1.5/1	15	8	First nestlings visible				
18 Mar	28	23	1.2/1	14	9	1	6	2	17/9 =	1.9
21 Mar	35	24	1.4/1	13	11	—	—	—		
26 Mar	28	23	1.4/1	12	11	0	6	5	17/11 =	1.5
30 Mar	26	24	1.1/1	14	10	0	5	5	15/10 =	1.5
4 Apr	10	24	0.4/1	11	13	—	—	—	—	
13 Apr	22	23	0.9/1	10	13	0	9	4	22/13 =	1.7
18 Apr	19	27	0.7/1	11	16	0	8	8	24/16 =	1.5
2 May	17	—	—	7	—	—	—	—	27	
14 May	17	—	—	—	—	—	—	—	29 (15 ready to fly)	
27 May	12	—	—	—	—	—	—	—	28 + 4 fledglings	
12 June	5	—	—	—	—	2	10	4	30/16 =	1.9
									+ 8 fledglings	
27 June	2	—	—	—	—	—	—	—	19	
8 July	1	—	—	—	—	—	—	—	18	
22 July	0	—	—	—	—	—	—	—	8	
30 July	0	—	—	—	—	—	—	—	3	
13 Aug	0	—	—	—	—	—	—	—	0	

APPENDIX 14

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1973 Inside.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	
21 Feb	0			
27 Feb	—	Pairs together and active courtship		
17 Mar	442	150	2.9/1	
31 Mar	195	140	1.4/1	
5 Apr	275	143	1.9/1	First nestling heard
14 Apr	380	217	1.7/1	First nestling seen
21 Apr	435	246	1.8/1	
28 Apr	414	235	1.8/1	Nests with chicks visible .
5 May	476	255	1.9/1	7
12 May	491	278	1.8/1	35
19 May	510	320	1.6/1	42 (all 1 chick per nest)
25 May	492	306	1.6/1	40 3 Ch. 2 Ch. 1. Ch.
3 June	487	304	1.6/1	71 0 6 65 = 77ch/71 nests = 1.08 ch/nest
10 June	450	305	1.5/1	79 1 6 72 = 87/79 = 1.10 ch/nest
16 June	377	289	1.3/1	83
23 June	340	290	1.2/1	77
9 July	290	—	—	195 total nestlings, all 1 inch per nest. First fledglings
14 July	255	209	1.2/1	239 total, all 1 chick per nest
21 July	172	—	—	282 total, all 1 chick per nest
4 Aug	97	—	—	310 total, 1 two chick nest, and 51 fledglings
				nestlings + fledglings = total
12 Aug	127	—	—	270+ 95 = 361
19 Aug	122	—	—	242+153 = 365
24 Aug	104	—	—	208+160 = 395
3 Sept	167	—	—	242+127 = 369
9 Sept	93	—	—	123+108 = 231
15 Sept	44	—	—	87+126 = 213
23 Sept	144	—	—	86+ 91 = 177
29 Sept	67	—	—	32+ 78 = 110
25 Oct	51	—	—	10+ 40 = 50
10 Nov	22	—	—	2+ 5 = 7
18 Nov	0	—	—	0 0

APPENDIX 15

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1974 Inside

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS: ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK	TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
14 Feb	143	0								
23 Feb	626	25	25.0/1							
28 Feb	558	76	7.3/1							
3 Mar	631	105	6.0/1							
11 Mar	655	194	3.4/1							
17 Mar	693	—	—							
25 Mar	873	201	4.3/1							
3 Apr	773	343	2.3/1		First nestlings heard					
7 Apr	702	388	1.8/1							
13 Apr	636	403	1.6/1							
20 Apr	666	423	1.6/1		First nestlings visible (two nests with 3 chicks each)					
30 Apr	558	—	—		223	1	8	13	32/22 =	1.45
5 May	542	—	—		140	0	73	67	213/140 =	1.52
13 May	331	322	1.0/1		196	1	66	129	264/196 =	1.35
18 May	315	—	—		213	0	41	172	254/213 =	1.19
25 May	295	328	0.9/1	83	255	0	26	229	281/255 =	1.10
2 June	324	330	0.9/1	70	272	0	34	238	306/272 =	1.13
8 June	227	—	—	18	304	0	20	284	324/304 =	1.06
28 June	89	—	—	—	First fledglings	—	—	—	352+2 fledglings	
9 July	119	—	—	—	—	—	—	—	333+24 fledglings	
19 July	103	—	—	—	—	—	—	—	170+206 fledglings	
27 July	85	—	—	—	—	—	—	—	82+265 fledglings	
3 Aug	40	—	—	—	—	1	2	—	80+196 fledglings	
11 Aug	11	—	—	—	—	0	1	27	29+153 fledglings	
18 Aug	19	—	—	—	—	0	3	24	30+103 fledglings	
31 Aug	11	—	—	—	—	0	4	3	11+28 fledglings	
16 Sept	—	—	—	—	—	0	5	0	10+32 fledglings	
26 Sept	8	—	—	—	—	0	1	3	5+24 fledglings	
29 Oct	1	—	—	—	—	0	0	0	0+0	

APPENDIX 16

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1975 Inside.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS					TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
				ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK		
19 Jan	63	courtship activity								
27 Jan	267									
29 Jan	356	2+								
1 Feb	598	—								
8 Feb	492	111	4.3/1							
16 Feb	591	269	2.2/1							
25 Feb	552	384	1.4/1							
3 Mar	551	400	1.4/1							
11 Mar	631	460	1.4/1							
16 Mar	689	565	1.2/1							
21 Mar	832	610	1.4/1	First nestlings heard						
29 Mar	871	625	1.4/1		11 First nestlings visible					
6 Apr	696	636	1.1/1		108					
12 Apr	733	626	1.2/1	—	132	11	88	33	242/132 =	1.83
20 Apr	526	564	0.9/1	—	241	7	145	89	400/241 =	1.66
29 Apr	608	525	1.2/1	277	248	3	154	91	408/248 =	1.64
5 May	617	540	1.1/1	238	302	0	155	147	457/302 =	1.51
12 May	593	—	—	—	328	2	167	179	513/328 =	1.56
18 May	428	—	First fledglings 588 total nestlings sample=			0	37	37	111/74 =	1.50)
24 May	381	—	—	186	713 nestlings	(1	92	95	282/181 =	1.48)
31 May	329	—	—	176	747 nestlings	—	—	—	816 total young	
7 June	294	—	—	138	675 nestlings	—	—	—	904 (159 downy)	
12 June	245	—	—	—	680 " (69 downy young in 44 nests)				1029 (179 downy)	
28 June	188	—	—	46	688 nestlings				830 (75 downy)	
6 July	140	—	—	—	453 nestlings	—	—	—	606 total young	
10 July	146	—	—	30	373 nestlings	—	—	—	503 total young	
19 July	66	—	—	27	328 nestlings	—	—	—	602 total young	
4 Aug	20	—	—	—	250 nestlings	—	—	—	463 total young	
10 Aug	11	—	—	11	186 nestlings	—	—	—	493 total young	
18 Aug	22	—	—	8	79 nestlings (9 downy)			—	303 total young	
7 Sept	0	—	—	0	35 nestlings		—	—	214 total young	
19 Sept	0	—	—	0	18 nestlings	—	—	—	160 total young	
5 Oct	0	—	—	0	10 nestlings	—	—	—	144 total young	
16 Nov	0	—	—	0	0	—	—	—	0	

APPENDIX 17

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible from mid-lagoon.

1976 total inside colony.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS: ADULTS ONLY	NEST CONTENTS: NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK	TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
4 Feb	96	1	—							
10 Feb	65	21	3/1							
15 Feb	382	36	10/1							
24 Feb	486	152+	46 pairs courting A/N = 3.2/1							
2 Mar	496	226	2.2/1							
8 Mar	607	329	1.8/1	First nestlings heard						
15 Mar	527	332	1.6/1							
21 Mar	586	381	1.5/1	First downy nestlings visible						
30 Mar	586	428	1.4/1							
4 Apr	539	421	1.3/1							
11 Apr	518	417	1.2/1	398	19	1	10	8	31/19 =	1.63
22 Apr	485	374	1.5/1	332	42	0	15	27	57/42 =	1.36
29 Apr	513	337	1.5/1	229	108	0	29	79	137/108 =	1.27
4 May	401	351	1.1/1	214	137	1	34	102	173/137 =	1.26
13 May	407	350	1.2/1	200	150	0	24	126	174/150 =	1.16
22 May	374	309	1.2/1	148	161	0	25	136	186/161 =	1.15
27 May	252	324	0.77/1	94	230	0	25	205	255/230 =	1.11
									(downy young)	
11 June	—	—	—	First fledglings		—	—	—	257 (45)	
18 June	—	—	—	—	—	—	—	—	220 (41)	
26 June	—	—	—	—	—	—	—	—	166 (22)	
7 July	—	—	—	—	—	—	—	—	125 (27)	
13 July	—	—	—	—	140	—	—	—	155/140 =	1.11
21 July	—	—	—	—	—	—	—	—	151 (32)	
28 July	—	—	—	—	—	—	—	—	117 (44 in 23 nests)	
21 Aug	—	—	—	—	—	—	—	—	67 (28 in 15 nests)	
8 Sept	—	—	—	—	—	—	—	—	35 (9)	
25 Sept	—	—	—	—	—	—	—	—	5/3 =	1.67
24 Oct	—	—	—	—	—	—	—	—	0	

APPENDIX 18

Brown Pelicans. Tarpon Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

Outside southeast 1976.

DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS: ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	2 CHICKS	1 CHICK	TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
10 Feb	0									
13 Feb	21	2	10.5/1							
15 Feb	22	8	2.8/1							
24 Feb	24	12	2/1							
28 Feb	18	5	3.6/1							
2 Mar	16	11	1.5/1							
8 Mar	18	13	1.4/1							
15 Mar	16	11	1.5/1							
21 Mar	27	12	2.2/1							
30 Mar	15	11	1.4/1							
4 Apr	16	11	1.5/1	First nestlings visible						
11 Apr	13	11	1.2/1	—	5	1	3	1	10/5 =	2.0
22 Apr	10	11	0.9/1	3	9	0	3	6	12/9 =	1.3
29 Apr	6	10	0.6/1	2	8	0	5	3	13/8 =	1.6
4 May	3	10	—	—	8	0	2	6	10/8 =	1.3
13 May	4	10	—	1	9	0	2	7	11/9 =	1.2
27 May	1	11	—	0	11	0	0	11	11/11=	1.0
6 June	0	9	—	First fledglings		0	0	9	9/9 =	1.0
11 June	0	7	—	0	7	0	0	7	7/7 =	1.0
26 June	0	7	—	0	7	0	0	7	7/7 =	1.0
7 July	0	3	—	0	3	0	0	3	3/3	
13 July	0	2	—	0	2	0	0	2	2/2	
21 July	0	2	—	—	2	0	0	2	2/2	
28 July	0	1	—	—	1	0	0	1	1/1	
21 Aug	0	0	—	—	0	0	0	0		

APPENDIX 19

Brown Pelicans. Whale Key, Pinellas County, Florida. Number of adults, nests, and nestlings visible.

1976 DATE	ADULTS	NESTS	ADULT/NEST RATIO	NEST CONTENTS: ADULTS ONLY	NESTS WITH CHICK(S) VISIBLE	NESTS WITH 3 CHICKS	NESTS WITH 2 CHICKS	NESTS WITH 1 CHICK	TOTAL CHICKS/ NESTS	COMPUTED CHICKS PER NEST
11 Jan	8									
20 Jan	14									
28 Jan	57									
4 Feb	40									
10 Feb	37	15	2.5/1							
13 Feb	65	26	2.5/1							
15 Feb	71	26	2.7/1							
24 Feb	67	36	1.9/1							
28 Feb	50	37	1.4/1							
2 May	55	33	1.3/1							
8 May	76	33	2.3/1							
13 May	63	37	1.5/1							
15 May	44	38	1.3/1							
21 May	49	35	1.4/1							
30 May	36	33	1.1/1	First nestlings visible						
4 Apr	33	36	0.9/1	9	8	1	7	0	17/8 =	2.1
11 Apr	31	37	0.8/1	—	17	1	7	6	23/14 =	1.6
22 Apr	35	—	—	—	19	0	7	8	22/17 =	1.3
29 Apr	29	32	—	—	25	1	7	17	34/25 =	1.4
4 May	13	28	—	—	28	0	8	20	36/28 =	1.1
13 May	6	—	—	—	27	0	3	24	30/27 =	1.1
22 May	15	—	—	—	30	0	3	27	33/30 =	1.1
27 May	10	—	—	—	32	0	3	29	35/32 =	1.1
6 June	—	—	—	First fledglings		—	—	—	36	
11 June	—	—	—	—	—	—	—	—	36 (3 downy)	
18 June	—	—	—	—	—	—	—	—	26 (3 downy)	
26 June	—	—	—	—	—	—	—	—	18	
7 July	—	—	—	—	—	—	—	—	12	
13 July	—	—	—	—	—	—	—	—	12	
21 July	—	—	—	—	—	—	—	—	3	
28 July	—	—	—	—	—	—	—	—	0	