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SPATIAL AND TEMPORAL ASPECTS OF COLONIAL NESTING OF WHITE PELICANS

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Since Darling's (1938) early observations of gulls, many studies have focused on spatial and temporal patterns of reproduction in seabird colonies. Reproductive success of birds differs among colonies at different sites (Hunt 1972, Harris 1973), among habitats within a colony (Brown 1967, Nettleship 1972), between nests positioned centrally or peripherally in a colony (Patterson 1965, Coulson 1966, Tenaza 1971, Dexheimer and Southern 1974), with the relative timing of breeding (Patterson 1965, Vermeer 1970, Parsons 1975, Hunt and Hunt 1976), and between successive seasons (Fordham 1970).

At traditional nesting sites, nests of White Pelicans (*Pelecanus erythrorhynchos*) are grouped into many spatially and temporally separate colonies (Hall 1925, Low et al. 1950, Behle 1958). Since many colonies occur on a single island, climatic factors influencing reproduction affect all birds similarly. At Gunnison Island, Utah, food is equally available to pelicans from different colonies (see discussion by Orians 1961) at the limited foraging areas along the eastern shore of Great Salt Lake (Behle 1958). Patterns of reproductive success in pelicans at Gunnison Island, show basic aspects of the colony-nesting habit better than at many other places. In 1973 and 1974 I studied colonial nesting of White Pelicans at Gunnison Island. I report here the spatial and temporal distribution of their nesting efforts, how the distribution was established, and variations in reproductive success.

STUDY AREA AND METHODS

Gunnison Island lies in the northwest arm of Great Salt Lake about 12 km from the western shoreline (Knopf 1974). The island, 1.6 km long, reaches a maximum width of 0.8 km and rises 85 m above lake level. Its 66 ha include a series of large hills with connecting ridges that separate four low, sandy areas. Vegetation is typical of the cold desert community (Oosting 1956). Prominent forms include *Bromus tectorum*, *Atriplex* spp., *Sarcobatus vermiculatus*, *Suaeda intermedia*, *Bassia hyssopifolia*, *Salsola kali*, *Opuntia fragilis*, and *Chrysothamnus* spp. As many as 6,600 pelicans nest on the flatter, lower elevations of the island each season. Behle (1958) provided details of the study area and its historical use by White Pelicans.

Male pelicans are larger than females (Palmer 1962), and I was able to visually distinguish the sexes (as verified during copulations) by differences in bill lengths. In addition, pelicans undergo a presupplemental molt during incubation (Knopf 1975a). The resulting supplemental plumage of the crown varies greatly among individuals as does the structure of the maxillary "horn." I was able to recognize individuals by using these features.

I surveyed pelican colonies weekly from 1 April to 31 July in 1973 and 1974, using binoculars, from higher elevations of the island. (A colony was defined after Penny [1968] as a geographically continuous group of breeding birds with contiguous territories.) During surveys I recorded reproductive stage and total number of nests for each colony. For each new colony I noted date of establishment and spatial location relative to nature of substrate, angle and direction of ground slope, associated vegetation, and proximity of other colonies. I measured distance-to-nearest-neighbor (nest rim to nest rim) for individual nests after chicks fledged.

To aid in the description of how colonies were formed, I observed individual (n = 25) and paired (n = 42) birds for 30-min periods. I supplemented these observations with telephoto, time-lapse photography of localized aggregations of courting birds.

I surveyed contents of pelican nests periodically using a 20× spotting scope from vantage points overlooking colonies. I recorded numbers of eggs and chicks as pelicans stood to stretch, turn the eggs, or feed a chick. I observed nests in specific colonies daily to define incidence of egg and chick mortality and internest synchronization of hatching.

I photographed each pelican colony weekly at distances of 30 to 60 m from a hill or cliff above a colony. With these photographs I prepared weekly histories of each colony and determined the timing and location of nest abandonments. I also used photographs to census numbers of young surviving the nestling period in larger colonies.

Late in the nestling period (21–28 days of age), I banded 300 pelican chicks in 1973 and 699 chicks in 1974. Plastic leg bands of different colors were applied to 64 of those chicks to aid in recognition of individuals after the nestling period. After all chicks fledged, I searched the island for banded chicks that died during the postnestling, prefledging (4–12 weeks of age) period.

RESULTS

NESTING

The first White Pelicans were sighted at Bear River Migratory Bird Refuge in northern Utah 9–10 March 1973 and 1974. Egg laying at nearby Gunnison Island commenced 30 March–1 April both years. Pelicans laid 2,605 and 2,674 clutches on the island in 1973 and 1974, respectively.

Spatial patterns. White Pelicans nested in 18 colonies in 1973 and 33 colonies in 1974 (Fig. 1). Colonies were widely dispersed on flat areas within 3 m (vertical) of the water level. Extensive flat terrain did not occur at higher elevations.

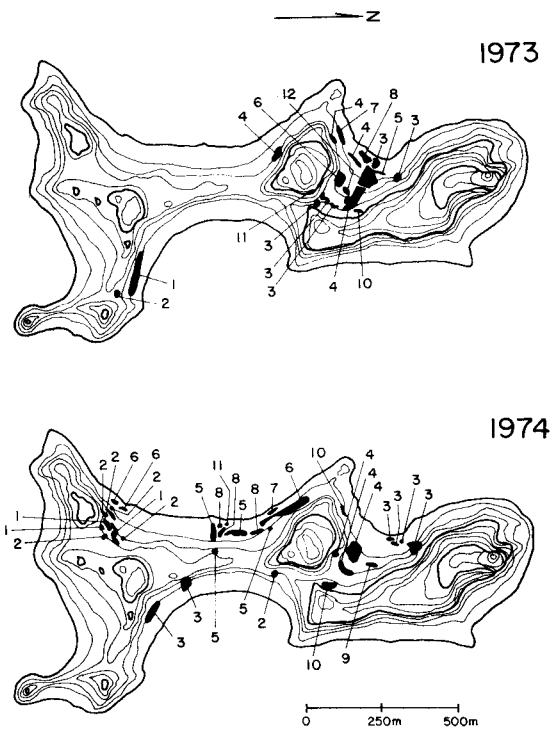

FIGURE 1. Spatial distribution of White Pelican colonies on Gunnison Island in 1973 and 1974. The numeral associated with each colony represents the week (beginning 1 April) during which the colony was established.

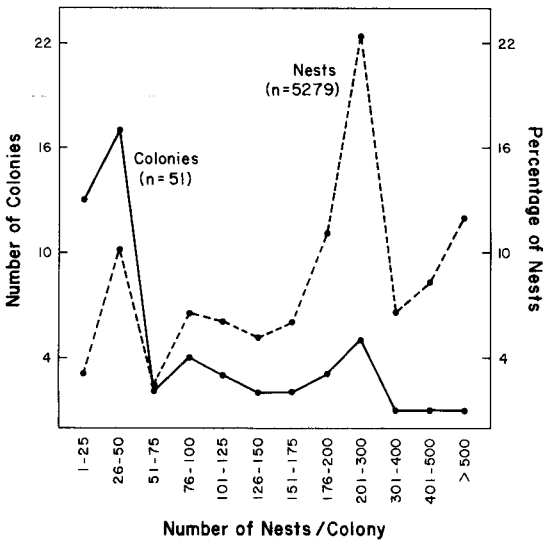

FIGURE 2. Number of White Pelican colonies (left scale) according to number of nests in a colony, and percentage of all nests occurring in those colony sizes (right scale).

Pelican colonies occurred on substrates of loose soil (n = 35), sod (7), sand (6), or fine gravel (3). Thirteen (25.5%) colonies were also among driftwood (railroad ties, telephone and telegraph poles). In all, 28 colonies (54.9%) were located near physical masses (woody vegetation, driftwood, large rocks). The shape of a colony often reflected the presence of these features. For example, colonies in driftwood lines were usually linear: 2–3 nests wide and up to 60 nests long.

Pelican colonies occurred in open areas of annual grasses and forbs (n = 35), shrubs (9), or on nonvegetated sites (7). Nest mounds were best developed in sod areas. Colonies only occurred in sand and gravel substrates where stands of woody vegetation (primarily *Sarcobatus* and *Chrysothamnus*) reached heights exceeding 1 m. Pelicans avoided areas containing large mats of cactus (*Opuntia fragilis*).

The 51 colonies ranged in size from 2 to 633 nests (Fig. 2). Mean colony size was 144.7 ± SD of 146.40 nests in 1973 and 81.0 ± 103.01 nests in 1974. Although 30 colonies (57.7%) contained 50 or fewer nests, 60.4% of all nests were in the 11 colonies exceeding 175 nests. The many small colonies resulted in 1,114 nests (42.7%) being located on the edge (not surrounded by contiguous territories) of a colony in 1973. In 1974, 1,278 nests (47.8%) were on the edge of a colony.

Within colonies, the distance between nearest-neighbor nests ranged from 0.25–1.63 m at the termination of the nestling period. The mean internest distance for 153 pairs of adjacent nests was 0.59 ± 0.16 m.

A small group of pelicans sometimes nested beside a colony established earlier. Such additions to colonies usually occurred where woody vegetation or rock outcrops provided a barrier between colony nests and new nests closest to the colony. Pelicans simultaneously appended one group of 10 nests to the edge of a colony in 1973, and four groups totaling 44 nests to four different colonies in 1974.

Temporal patterns. Pelicans laid eggs from late March through June annually (Fig. 3). Nesting activity was most intense from 9 April to 6 May during which time 1,917 (73.6%) and 1,928 (72.1%) of the nests were initiated in 1973 and 1974, respectively. Up to six separate colonies were established each week, often at widely separated sites on the island (e.g., Fig. 1; 1974, week 3).

Reproductive events of pelicans within a colony were synchronized within the 13-week breeding season. In 16 colonies, the first egg hatched in 90% of the nests within an interval of two to nine ($\bar{x} = 6.2 \pm 2.41$) days. Hatch duration was independent of colony size (Fig. 4; $r = 0.24$, $P > 0.05$).

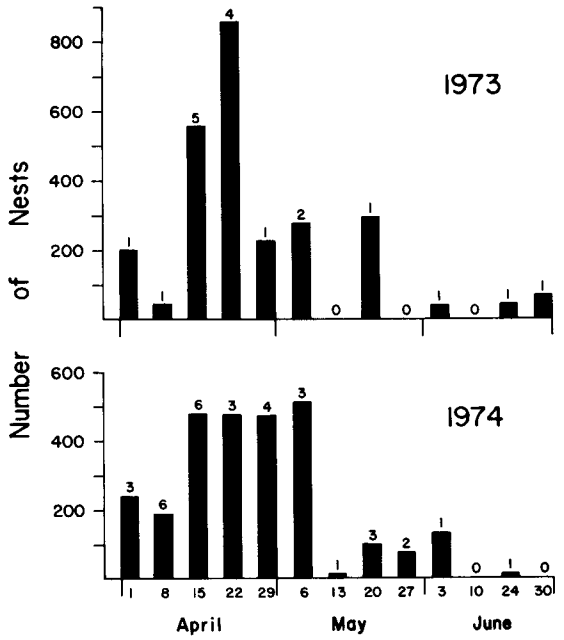

FIGURE 3. Number of White Pelican nests initiated each week on Gunnison Island, 1973 and 1974. The numeral above each bar corresponds to the number of colonies initiated during that week.

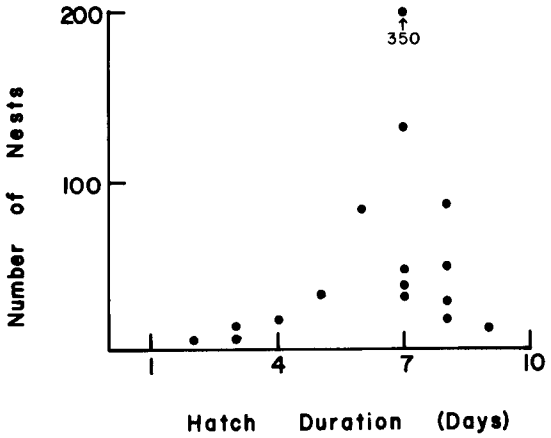

FIGURE 4. Relationship between colony size and synchronization of hatching in 16 White Pelican colonies. Hatching duration is the number of days required for the first egg to hatch in 90% of the nests in a colony.

Where pelicans appended nests to an established colony, they did so during May and June only. Pelicans added nests to a colony where birds were incubating eggs (four groups, 46 nests) or after eggs hatched in the colony (one group, eight nests).

NEST ESTABLISHMENT

Courtship. Schaller (1964) and van Tets (1965) described some social displays of White Pelicans. Courtship has not been described to my knowledge.

Courtship activities appeared restricted to Gunnison Island. They were not observed when birds in the alternate (nuptial) plumage flocked together at surrounding marshlands. Unmated pelicans formed large soaring flocks over the island (Knopf 1975b). From such a flock, groups of two to ten pelicans occasionally stooped, raptor fashion, with half-open wings. Stoops created loud whooshing sounds and terminated 25 to 50 m above the island. Stoops were rare, being observed only 23 times on six days, suggesting that they were not essential components of courtship.

Small groups of pelicans often left the soaring flock and landed on the island or near the shoreline. Upon first arrival on the island, pelicans loitered near established colonies or courting birds. "Newly-arrived" pelicans often stood on driftwood or rocks and were conspicuous in their alert, wary surveillance of the surroundings.

Sometime after arrival, pelicans joined dense flocks on lower elevations of the island. These flocks preceded the establishment of a colony at the site. Birds in these flocks were spatially segregated according to whether they were laying eggs, defending a potential nest site, or courting (Fig. 5). Courting birds occurred on the outer edges of the flock.

When entering the flock, pelicans aggressively jabbed at and received jabs from other pelicans. In response to jabbing from flock birds, females ceased walking and bowed. The bow involved raising the breast, elevating the folded wings at the shoulders, stiffly arching the neck, and bringing the bill against the breast with the tip pointing at the feet. The nearest male responded by moving alongside the female, expanding his pouch, extending his neck over her head and moving his head back and forth displaying the sides of his pouch. The male grunted during these displays. Movements associated with the interaction elicited jabbing from nearby birds to which the male and female responded by jabbing back.

Following the female's bow, the female and male often surveyed their surroundings until the female walked rapidly within the flock and bowed again. The male followed the female and responded to the bow as before. Frequently, the male did not keep up with the female and a new male responded to her bow.

Occasionally, a male and female left the precolony flock and moved about the island. The male followed the female in the strut-

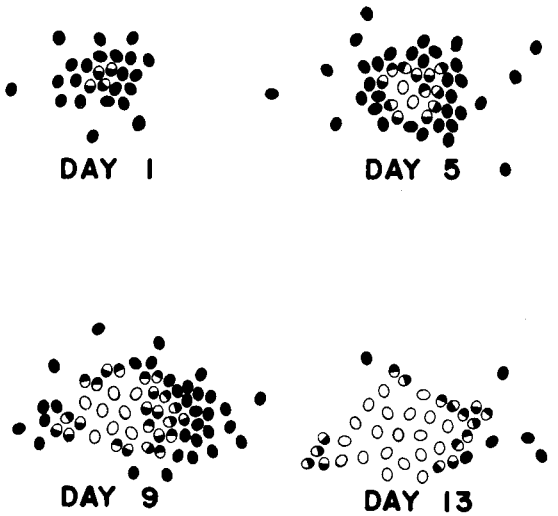

FIGURE 5. Schematic representation of the colony formation process of White Pelicans. Closed ovals indicate spatial locations of unpaired, courting birds; half-open ovals, paired birds; and open ovals, birds laying or incubating eggs.

ting walk (Schaller 1964). The birds often paused during the strutting walk and preened or looked around. Other males sometimes joined birds during the strutting walk, creating a courting party. Males in the courting party often exchanged jabs.

The strutting walk was often interrupted by the female taking flight followed by the male and any bachelor males. The birds flew briefly around the island but did not join flocks of soaring birds at higher altitudes. During the flights, the male maintained a position close to the female and often expanded his pouch (van Tets 1965:54) and grunted while beside her. After one to four trips around the island, courting birds landed and continued the strutting walk. Bachelor males usually abandoned the pair during flight or shortly after returning to the ground.

Nest site selection. Paired birds strut-walked rapidly. The male often jabbed at the back of the female's head causing her to walk faster. The strutting of paired birds always terminated with the female bowing.

Paired females bowed when close to a dense aggregation of pelicans. A female, followed by the male, often approached and bowed beside a colony of incubating pelicans or pelicans with nestlings. The bow was terminated abruptly as the pair responded to aggressive jabs from pelicans on nests. The jabbing usually rebuffed the female and male, but even when the pair defended their position successfully, the female abandoned the location and resumed strutting.

The female and male eventually returned to a precolony flock and walked past the unmated birds to the center near other paired birds. The female bowed and the male responded. Again the bow was interrupted by the jabbing of neighbor birds and the pair jabbed back. Unlike approaches towards birds already on nests, each agonistic encounter in a flock was followed by the female's bowing. The pair continually bowed or retaliated jabs for 30 to 60 min after which jabbing declined. At this time, I considered the nest site successfully defended. Once a site was defended, the bow, performed as before, preceded mounting by the male.

Both the male and female remained at the nest site or in the vicinity of the new colony three to five days after initial defense of the nest site. During that period, the birds built the nest and often exchanged places on it. On the last day the male left the island and presumably went to the feeding grounds. The female remained on the nest until the male returned two to three days later. The first egg appeared four to five days after initial nest site defense and the second after six to seven days.

Paired pelicans continued joining the precolony flock for approximately seven days (range 2–9, n = 12). Decreased recruitment of new pairs at a site occurred simultaneously with increased recruitment to precolony flocks at other sites on the island. Precolony flocks infrequently were located near pelicans on nests resulting in nest additions to a colony.

PRODUCTIVITY

White Pelicans lay two eggs per clutch (Palmer 1962). Incubation requires about 30 days and eggs hatch asynchronously. The altricial chicks develop rapidly and leave the nest during their fourth week. Chicks move freely about the island until they fledge 12 to 13 weeks after hatching.

Egg and chick losses. Four of 550 nests (0.7%) in 1973 and 33 of 1,721 nests (1.9%) in 1974 contained a clutch that did not survive. Pelicans incubated an inviable clutch through the nestling period of neighboring birds before abandoning the nest. Occasionally one egg of a clutch failed to hatch. Only one egg in a two-egg clutch hatched in 5 (1.6%) of 88 nests sampled in 1973 and 15 (0.6%) of 332 nests sampled in 1974. Unhatched eggs contained well-developed embryos.

Eight adult pelicans died on the island during the 1973 nesting season and 12 died

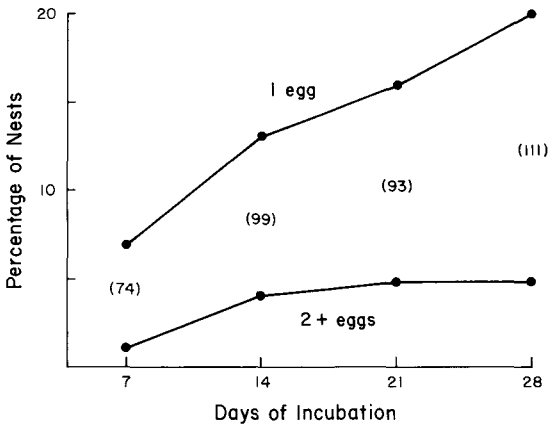

FIGURE 6. Percentage of nests containing either one or more than two eggs relative to date of incubation. The number of nests surveyed is given in parentheses.

in 1974. Since an individual pelican was on the island about half the time, similar numbers may have died at other places during the breeding season. Pelicans are monogamous and the mate of a dead bird probably could not raise the brood. I estimate that 0.6% and 1.0% of the eggs laid in 1973 and 1974, respectively, were lost due to death of a parent.

Two pelican chicks died presumably from bill deformities. A chick with a strongly upcurved bill died at eight weeks of age; one born without a maxilla died at six weeks. Some chicks died of unknown causes (possibly disease) during the postnestling, prefledging period. Two (0.7%) of 300 chicks banded early in the postnestling period died prior to fledging in 1973. Eight (1.1%) of 699 banded chicks died before fledging in 1974.

Twenty (8.3%) of 242 eggs laid in 1973 and 22 (9.9%) of 222 eggs laid in 1974 rolled from nests during incubation. The incidence of nests containing one egg increased steadily through incubation (Fig. 6), indicating that egg losses occurred as a result of general incubation activities.

Many pelicans abandoned nests during incubation and the nestling period (Table 1). Abandonment was most prevalent during the first week of incubation and the week preceding hatching (Table 2). On three occasions I watched pelicans walk off nests and fly away within 30 min after the first egg hatched. The incidence of abandonment was lower ($t = 3.49$, $P < 0.001$, arcsin transformation, Sokal and Rohlf 1969) in 1973 than 1974.

Pelicans occasionally retrieved displaced or abandoned eggs from other nests, increasing their clutches to three to five eggs.

TABLE 1. Nests abandoned by White Pelicans during the incubation and nestling periods in 1973 and 1974 based on 12 and 24 colonies, respectively.

	Number of nests	Number abandoned (%)	Total percent abandoned
1973			
Incubation	1,052	174 (16.5)	22.4
Nestling	878	62 (7.1)	
1974			
Incubation	1,320	292 (22.2)	28.7
Nestling	1,028	87 (8.5)	

I observed two different pelicans add an egg from nearby abandoned nests. Each of 22 nests with more than two eggs was adjacent either to a nest containing only one egg or to the site of an abandoned nest. The percentage of nests with more than two eggs increased early in the incubation period (Fig. 6), a time when nests were most frequently abandoned (Table 2).

Pelicans incubated two-egg clutches by covering each egg with one foot. Seven (1.5%) of 467 nests in 1973 and 15 (1.9%) of 795 nests in 1974 contained more than two eggs and exhibited complete nest failure. I inspected 26 eggs from those nests—all were addled.

One chick of the two usually died during the nestling period. A chick died during the first (n = 15), second (38), or third (36) week after the first egg hatched. In nests where both eggs hatched, one chick died in 176 (90.3%) of 195 nests in 1973 and 339 (90.6%) of 374 in 1974. These losses represented 515 (29.0%) of 1,776 eggs laid in the colonies.

Spatial patterns. In studies of nesting success, estimates of productivity usually are biased since losses of eggs or nests during early incubation are missed (Mayfield 1975). Accuracy in this study was within three days: first records of each nest occurred three or fewer days after completion of the clutch.

Mean productivity of brooding pelicans was similar for nests located in each vege-

TABLE 2. Nest abandonment during incubation in 34 White Pelican colonies during 1973 and 1974.

Week	Total number of nests	Number of nests abandoned (%)	Percentage of all nests abandoned
1	2,261	265 (11.7)	44.8
2	1,996	87 (4.4)	14.7
3	1,909	92 (4.8)	15.5
4	1,817	148 (8.1)	25.0

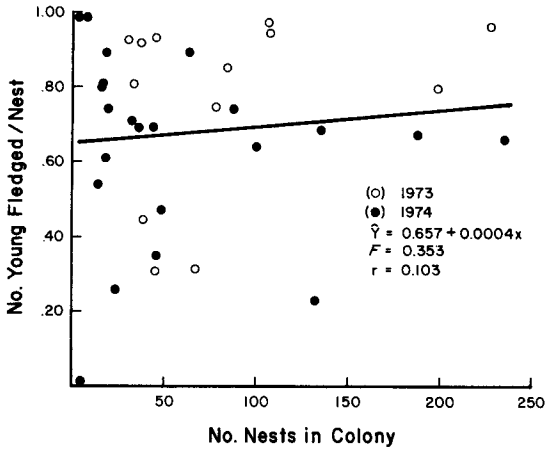

FIGURE 7. Mean nest productivity relative to total number of nests in a colony for 35 White Pelican colonies during 1973 and 1974.

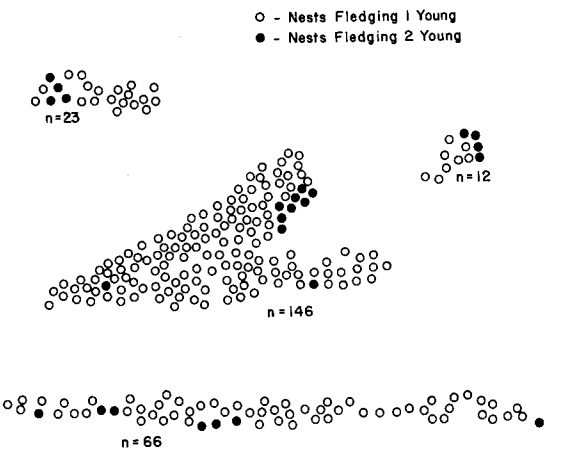

FIGURE 8. Locations of nests (dark circles) from which two chicks fledged in four White Pelican colonies.

tational habitat. Pelicans fledged 0.85 chicks/clutch (n = 1,057) in herbaceous vegetation and bare-ground areas, 0.85 chicks/clutch (n = 144) in shrub areas, and 0.89 chicks/clutch (n = 142) at driftwood sites. Differences in fledging success were not significant between habitats.

Mean nest productivity for 35 pelican colonies (1973 and 1974) ranged from 0.0–1.0 chicks. Productivity was independent of colony size (Fig. 7). Pelicans in small colonies exhibited both the highest and lowest mean production.

Pelicans that appended nests to established colonies generally failed to produce young. Ten nests added to a colony in 1973 were abandoned before the eggs hatched. Only 9 of 44 nests added to four colonies in 1974 resulted in fledged young. The successful nests were among 26 added to a colony of two nests, the only time appended nests outnumbered nests in the original colony.

Within a colony, pelicans abandoned 106 of 432 (24.5%) nests on colony peripheries and 43 of 292 (14.7%) nests centrally located ($t = 3.28$, $P < 0.01$). Nest abandonment was the only source of egg or chick loss that varied significantly between peripheral and central nests. Abandonment was never contagious with the adults of an entire subsection of a colony abandoning nests in a short period of time.

Pelicans raising two chicks to the postnestling stage tended to occur on colony peripheries. Pelicans raised two chicks in 38 of 236 (16.1%) nests on colony peripheries versus 6 of 146 (4.1%) nests centrally located ($t = 3.97$, $P < 0.001$). Pelicans raising two chicks also tended to have nested near to one another (Fig. 8). Thirty-two of 44 (72.7%) nests from which two chicks fledged were neighbor to a nest from which two fledged also ($\chi^2 = 12.7$, $P < 0.001$).

Temporal patterns. The incidence of egg and chick losses increased during the nesting season. Nests containing clutches of two eggs declined while clutches of one or more than two eggs became more frequent through May and June annually (Fig. 9). Pelicans also abandoned a greater proportion of nests later in the nesting season (Fig. 10).

Pelicans fledging two chicks consistently laid eggs prior to 15 May each season (Fig. 11). For nests initiated within a given one-week interval, two chicks fledged from a maximum of 22.2% of all clutches, or 33.0% of those nests from which at least one chick fledged.

As a consequence of increased egg and chick mortality, mean nest productivity within pelican colonies (range 3–235 nests) declined linearly with the number of days after 1 April that eggs were laid (Fig. 12). Production of chicks was greater in 1973 than 1974 ($F\ [b_1 1973 = b_1 1974] = 1.44$, $P > 0.05$; covariance analysis $F = 40.1$, $P < 0.001$). For those colonies for which I had information on hatching synchronization (Fig. 4), mean nest production in a colony was not correlated ($r = 0.254$) with synchronization of reproductive events within a colony.

DISCUSSION

COLONY FORMATION

Many field studies of pelicans describe the behavior of birds at colonies (Schaller 1964,

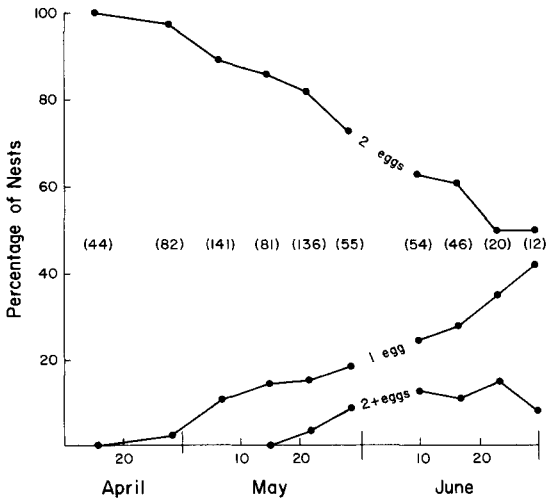

FIGURE 9. Percentage of nests containing one, two, or more than two eggs relative to date in 1974. Number of nests surveyed is given in parentheses.

Burke and Brown 1970, Schreiber 1977, and others). The role of behavior patterns in pair formation and nest site selection is best known for the ground-nesting European White Pelican (*Pelecanus onocrotalus*; Brown and Urban 1969), Australian Pelican (*P. conspicillatus*; Vestjens 1977), and arboreal Pink-backed Pelican (*P. rufescens*; Din and Eltringham 1974).

In my study, unmated female pelicans initiated courtship as they entered flocks of courting birds. Males outnumbered females in precolony flocks, indicating that the number of pairs formed during a given week was determined by the number of females entering these flocks. The number of precolony flocks on the island, in turn, determined how many colonies would be established. Thus, the size of a given colony reflected the number of females breeding that week divided (albeit unevenly) by the number of active flocks on the island.

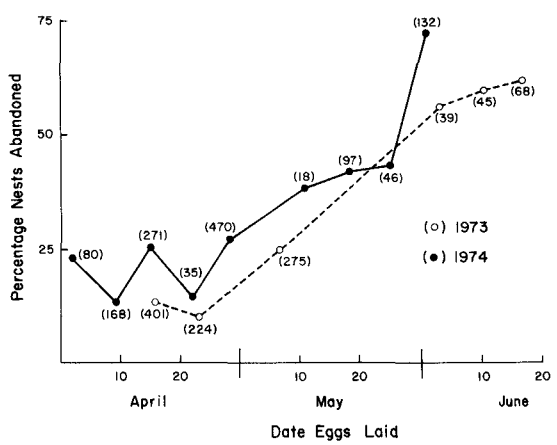

FIGURE 10. Percentage of nests abandoned relative to the date the first eggs were laid in those nests (1973 and 1974). Data are derived from weekly photographic surveys of 12 colonies in 1973 and 24 colonies in 1974. Total number of nests surveyed each week is given in parentheses.

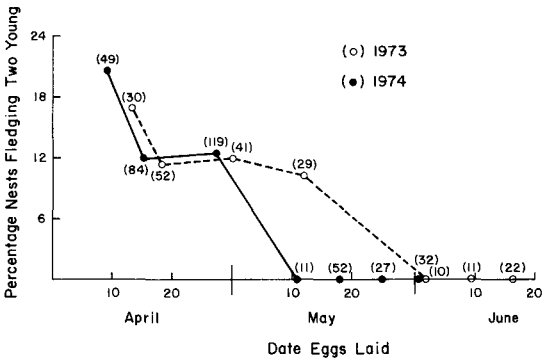

FIGURE 11. Percentage of nests from which two chicks fledged relative to the date that the first eggs were laid in those nests, 1973 and 1974. Data are derived from surveys of 12 colonies in 1973 and 24 colonies in 1974. Total number of nests surveyed is given in parentheses.

Courting pelicans selected mates with little attempt to defend a potential nest site, frequently moving their location within the

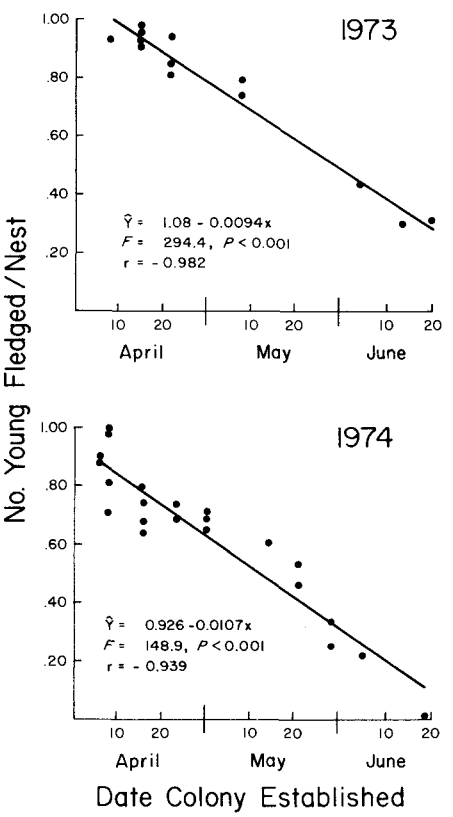

FIGURE 12. Mean number of chicks fledged per nesting attempt in pelican colonies relative to the date the first egg was laid during 1973 and 1974.

precolony flock. Intense agonistic behaviors in flocks appeared to function in defense of birds rather than sites. Components of nesting behavior such as retrieving materials for a nest mound were rare at first and gradually became more frequent.

The spacing of nests appeared to be the outcome of conflicting tendencies towards gregariousness and social intolerance during nest site selection. Paired pelicans were attracted to other pelicans, but were intolerant of birds within striking distance. Pelicans required behavioral reinforcement from other pelicans prior to becoming site tenacious. Paired pelicans persisted in defending a potential nest site only when beside another pair also defending a site.

Colony size reflected the number of pairs joining the courting flock during its presence at a site. After the flock had been active three or four days at a site, male pelicans from the earliest nests began leaving the island to feed while females remained to lay eggs. On each subsequent day additional males left, giving the dense courting flock the increasing appearance of an established colony of dispersed nests. Simultaneously, social interactions within the flock became less intense. The flock came to look like an established colony of incubating birds and ceased to attract new birds. Courting pelicans congregated at other sites with birds behaviorally more in phase with their reproductive cycle.

PRODUCTION

White Pelican numbers in North America declined during the last century due, in part, to human disturbance at breeding sites (Thompson 1933, Lies and Behle 1966). The rugged terrain of Gunnison Island concealed most of my activities from nesting birds and I am convinced that pelican productivity was not influenced by my presence.

Major sources of egg and chick mortality in pelicans were typical of colonial seabirds in general (Ricklefs 1969). Among ground-nesting pelecaniforms, eggs easily roll from the rudimentary nests (Dorward 1962, Snow 1960, this study). Dorward (1962) marked eggs of Brown Boobies (*Sula leucogaster*) and found that an egg laid in one nest commonly was incubated in a different nest, indicating that boobies, like White Pelicans, tend to incorporate eggs from outside the nest into the clutch.

White Pelicans abandoned about one-fourth of their nests each season. The incidence of nest abandonment was similar to the 21.6% reported for the Blue-faced Booby (*Sula dactylatra*), on Kure Atoll (Kepler 1969). Proximate causes of nest abandonment in pelicans were unknown.

Nest abandonment was the only significant source of egg and chick mortality which varied between 1973 and 1974, seasons with significantly different production in the population. Thus, annual differences in production of the pelican population reflected differing rates of nest abandonment.

Behle (1958) noted that the major source of White Pelican chick mortality is death of the smaller chick in nests where two chicks hatch. In my study, 45% of the chicks in two-chick nests died (from starvation or harassment by the larger sibling) during the nestling period.

White Pelicans at Gunnison Island fledged 0.85 chicks per clutch (n = 1,343) or 0.42 chicks per egg. Schaller (1964) reported 117 chicks fledged from 507 eggs for a 0.23 chicks per egg ratio at Yellowstone Lake, Wyoming. Strait and Sloan (1974) estimated 0.62 chicks per nest (n = 26) at Chase Lake, North Dakota, but neither study described the relative timing of surveys within the nesting season. Burke and Brown (1970) reported Pink-backed Pelicans fledging 0.57 chicks per nest (n = 20) in Kenya. Some nests contained chicks when the study began, however, and nest, egg, or chick losses prior to the study were not incorporated into their calculations.

SPATIAL PATTERNS

White Pelicans nested in colonies at high densities while three-fourths of the available habitat remained unused each year. Since mean productivity of chicks was similar between habitat types, habitat differences appeared insignificant to reproduction. Pelicans did not resettle former colony sites on Gunnison Island the subsequent year suggesting that some altered feature (probably vegetative) of the habitat influenced the location of precolony flocks the following spring.

At the time of joining a precolony flock, paired pelicans chose nest sites in the middle of the flock but peripheral to pairs already defending sites. The last pairs to select sites prior to disbanding of the precolony flock had peripheral locations in the colony. Since some colonies grew linearly (along driftwood lines for example) the first pelicans to defend nest sites often remained at peripheral positions within the colony.

Among colonial seabirds, birds nesting in

the colony center produce more young than those on the edge (Patterson 1965, Dexheimer and Southern 1974, and others). Tenaza (1971) proposed that reproductive success of birds should decrease with declining colony size because of an increased proportion of peripheral nests. Nest abandonment is the only source of White Pelican egg or chick mortality which occurred at a higher rate on the edge than in the center of a colony. For the White Pelican, Tenaza's hypothesis at first appears to be supported by a higher incidence of nest abandonment in 1974, a year when mean colony size was smaller and overall productivity lower than 1973. Although more nests were abandoned on the edge of a colony, most of the nests from which two chicks fledged were also on colony edges. These offsetting phenomena resulted in no apparent difference in productivity between central and peripheral nests, and in similar production within small and large colonies.

TEMPORAL PATTERNS

The productivity of White Pelicans decreased as the breeding season progressed. Blus and Keahey (1978) reported that Brown Pelicans (*P. occidentalis*) between one to four years of age nested later and produced fewer young than older adults. I speculate that the negative correlation between productivity and date of egg laying in White Pelicans reflected an increasing percentage of younger birds in colonies. White Pelican eggs laid late in the season contained higher levels of organochlorine residues (Knopf and Street 1974) which may have influenced egg or chick survival.

Within the long breeding season, reproductive events were more synchronous within pelican colonies than among colonies, synchronization being independent of time of year and colony size. Similar independencies were reported for Sandwich Terns (*Sterna sandvicensis*; Langham 1974) and South American grebes (Burger 1974). In both studies, reproductive events also tended to be more synchronous in smaller colonies. Such a tendency was evident for Gunnison Island pelicans and reflected abbreviated activity of a precolony flock at a site.

Hailman (1964) concluded that colony synchrony is socially mediated, the mechanism being either active or passive. The hypothesis of an active mechanism (Darling 1938) maintains that displays of neighboring birds modulate physiological progression of the breeding cycle, promoting synchrony between pairs. Such synchrony is envisioned as being greater in large colonies, enabling birds in those colonies to breed earlier and with greater nesting success (the Darling effect). This hypothesis appears to lack support for some species based upon synchronization of egg laying within colonies (Coulson and White 1956, 1960, Vermeer 1963, Langham 1974). For White Pelicans the Darling effect is unsupported by data taken at the time eggs hatch, when synchronization should be most pronounced. Synchronization, reproductive success, and time of breeding were independent of the number of nests in White Pelican colonies. In addition, synchronization and reproductive success were not correlated.

The passive mechanism of synchronization, as proposed by Orians (1961), maintains simply that courting birds may be attracted to birds already on nests. Synchrony in White Pelican colonies conformed with this idea although the mechanism was behaviorally more refined. Courting pelicans were attracted to other pelicans but required some feedback from the birds approached prior to continuing sexual displays or nest site defense. The density of birds was greater in precolony flocks than in established colonies due to the simultaneous presence of both sexes at many nest sites. Possibly, the sound of bills clapping during aggressive encounters, grunting associated with intrapair interactions, plus movements from these events and copulations were excitatory stimuli for courting and paired birds. These events were absent in established colonies where birds were comparatively sedate.

The lack of synchronization of reproductive events would be detrimental to productivity of pelicans. Pelican nestlings were poorly coordinated and sluggish at the beginning of the prefledging period. A chick that wandered into the territory of an adult who was incubating eggs or brooding small chicks might be killed by the adult. Such mortality was not observed during 1973 or 1974 but was photographed during 1972 in a colony to which 10 nests were added prior to the termination of the nestling period of the original nests. The termination of territoriality at nearby nests appears to favor survival of chicks during early stages of the postnestling period.

SUMMARY

White Pelicans on Gunnison Island, Utah, nested in 18 spatially and temporally finite

colonies in 1973 and 33 colonies in 1974. Within colonies, nests averaged 0.59 m apart and occurred in areas of loose substrate in herbaceous or shrubby vegetation, or along lines of driftwood. Most colonies contained 50 or fewer nests, while most nests were in colonies larger than 175 nests. The numerous small colonies resulted in 42.7% and 47.8% of all nests being located on colony peripheries in 1973 and 1974, respectively.

The first colonies were established during late March with new colonies appearing through late June each year. Over 70% of all nests were constructed 9 April to 6 May, with as many as six colonies established weekly. Reproductive events were highly synchronous within colonies regardless of colony size.

Qualitative observations indicated that pelicans congregated into dense flocks soon after arrival on the island. Courtship and nest site selection were initiated by a female entering such a flock. After pairing, nest sites were selected in the center of the flock, near other pelicans also defending nest sites. Unmated pelicans continued to join the flock up to nine days at a given site.

Of the number of eggs laid each season (potential productivity), approximately 5% were lost due to either addled eggs, death of an adult, morphological deformities of chicks at hatching, or unknown causes during the postnestling, prefledging period. In addition, 9% were lost because an egg rolled from a nest, 1–2% from adults supplementing the normal clutch with additional eggs ultimately causing all eggs to become addled, 25% from nest abandonment, and 29% to death of one chick from sibling harassment or starvation.

Pelicans abandoned nests more frequently on the periphery than in the center of colonies; while mortality from other sources occurred uniformly throughout the colony. Pelicans fledging two chicks per clutch tended to nest in clumped dispersions on colony peripheries. These compensating phenomena in nests on the periphery resulted in similar production in central and peripheral nests. Mean production per clutch was comparable between colonies of different sizes and in different habitats.

The incidence of major sources of egg and chick mortality increased, and reproductive success of pelicans declined, as the season progressed. This trend probably reflected later breeding by younger birds with less reproductive experience. Nest productivity of the population was lower in 1974, reflecting a higher frequency of nest abandonment that year.

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