

STATUS OF A NORTHERN POPULATION OF CALIFORNIA BROWN PELICANS

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ABSTRACT.—In the Southern California Bight (SCB), Brown Pelican (*Pelecanus occidentalis californicus*) breeding populations were apparently historically stable. They are again increasing after pollution-related declines in the late 1960's and early 1970's. This increase has been bolstered by recruitment into the breeding population of pelicans fledged outside the SCB area, but populations did not increase significantly until after improvements in reproduction of the SCB population itself. Nesting chronology is apparently related to food availability. Early-nesting, whether at Anacapa Island or Islas Los Coronados, usually confers a reproductive advantage. This advantage varies at each location; breeding populations reassort each year, apparently in response to variable food supplies. Shifting between two major breeding colonies in the SCB is apparently a response to a changing food supply distribution. Annual variations in normal (as opposed to pollution-affected) breeding population size result partly from changing proportions of the available adult population that actually breeds.

Ornithologists continue to study the factors associated with reproduction and survival in different bird species, in different environments and at different times (see Ricklefs 1977). When populations are declining, improvements in reproduction, survival, or both, can be adequate for population recovery (see Goodman 1980). Although variations in mortality need to be understood, maximum production of young is still critical for population maintenance or increase, especially in environments where the food supply is highly mobile and varies somewhat unpredictably in availability (Cody 1971).

Pollutant-related reproductive problems for California Brown Pelicans (*Pelecanus occidentalis californicus*) in the Southern California Bight (SCB) (reviewed below) and elsewhere in the Brown Pelican range (see Schreiber and Risebrough 1972, Schreiber 1980a), in the decade of the early-1960's to early-1970's, have clouded the understanding of changes of status in SCB pelican populations. However, unnatural catastrophes can provide a setting whereby the processes of population change and maintenance might be examined in different parts of a species' range.

Here, our objectives are threefold: (1) to briefly review recent status changes of SCB pelican populations, (2) to present more detailed information on Brown Pelican demography (and as a comparison, similar data on Double-crested Cormorants, *Phalacrocorax auritus*) over the most recent decade or so (1969–1980), and (3) to evaluate changes in

numbers and distribution and their dynamics in the SCB.

STUDY SITES AND METHODS

Data we discuss here were accumulated over 12 years of field work on breeding populations in the northern part of the breeding range of the California Brown Pelican. The major breeding colonies (after the definition of "colony" by Gochfeld 1980) of this population occurred on West Anacapa Island and Isla Coronado Norte located in the Southern California Bight (see Southern California Coastal Water Research Project 1973 for a definition of the SCB) (Fig. 1). Other islands in the SCB area were surveyed each year, or their status reported to us by cooperators, so that we are certain no colonies were omitted from our analysis.

Breeding pelicans were observed by D.W.A. or F.G. on four to six visits per breeding season, each visit lasting from one to seven days. At the conclusion of each breeding effort for synchronous units within each colony, or at the termination of breeding for the entire colony, samples of young were banded and color-marked, addled eggs and broken eggshells collected for pollutant analyses, conditions of young determined, carcasses counted and sometimes collected, and regurgitations examined and sometimes collected. Aerial population surveys were conducted in 1972 by D.W.A. and 1979–1980 by F.G. Statistical tests used here are described by Sokal and Rohlf (1969).

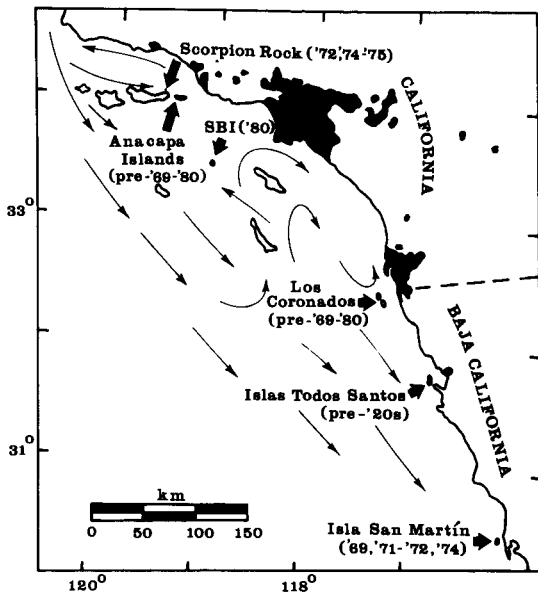


FIGURE 1. Map of Brown Pelican breeding colonies in the Southern California Bight off southern California and northwestern Baja California, showing all colonies known to have recently contained nests (thick, short arrows). Pelicans did not nest at Santa Barbara Island (SBI) since at least the 1960's, but they did so again in 1980 (Gress et al., unpubl. data). Pelicans have not nested at Islas Todos Santos since about the 1920's (Jehl 1973); the colony at Isla San Martín has recently been extirpated (Anderson and Keith 1980). Only Isla Coronado Norte (there was also a small colony at Isla Coronado Sur in 1969 only, Jehl 1973), and West Anacapa Island have consistently had colonies since 1969. Years below each location indicate when pelicans nested. The generalized California Current patterns (Oceanic Period) are only shown crudely (thin arrows) since they vary considerably. Later in the season, north-moving currents become stronger along the coast (Davidson Current). The patterns shown here were determined from Ried et al. (1958), Jones (1971), and Briggs et al. (1981). Black shapes denote urban areas.

Human disturbances can drastically affect reproduction (Schreiber 1979, Anderson and Keith 1980); therefore we took care to avoid disturbing nesting pelicans. Observations were conducted from a boat or from various vantage points near the pelican colonies. Colonies were never entered until they were abandoned or until the smallest young present were at least three weeks of age. Occasionally, while large young were present, a few nests contained eggs, but these "late eggs" were usually found to be addled. The actual breeding places changed considerably on West Anacapa Island and less so on Isla Coronado Norte from year-to-year; observation points and survey techniques were shifted accordingly.

At each visit to the islands and at various times of the day, age-classes were identified for nesting and nearby-roosting pelicans. Pelican age-classes are generally identifiable through

plumage characteristics; five such age-classes are describable (Anderson, unpubl. data). For purposes of our discussion here, these are combined into three categories: fledged young-of-the-year (YY) (three to six months of age), sub-adult plumages (variable but retained for up to four years), and full adult plumage (attained between three to five years of age). Often the young that had fledged from the Gulf of California colonies were present at West Anacapa or Coronado Norte long before any locally-produced young were ready to fledge (determined from sightings of young pelicans color-marked in the Gulf of California, see Anderson et al. 1977a). More detail on our field techniques and activities can be obtained from Gress (1970), Anderson et al. (1975), Anderson et al. (1977b), and Anderson et al. (1982).

RESULTS

HISTORICAL ACCOUNTS OF POPULATIONS

Historical accounts of Brown Pelican breeding at Anacapa Island (Grinnell and Miller 1944, Gress 1970, Anderson and Hickey 1970, Gress and Anderson 1982) suggest long-term oscillations in breeding efforts (a phenomenon not unusual even within the center of the range of the California Brown Pelican; Anderson 1973, Keith 1978, Anderson and Keith 1980). Pelican breeding populations at Islas Los Coronados probably also fluctuated similarly, but fewer historical data are available (Jehl 1973, 1977).

Pelicans have certainly bred for a long time at Anacapa Island (and most probably at Los Coronados), for the Native American Chumash named the island chain "Pí awa phew" (= "house of the pelican"; Applegate 1975). Although pelican remains are fairly common at midden sites, there is no evidence that young pelicans and other seabirds were harvested for food (see Guthrie 1980). Brown Pelicans formerly bred as far north as Carmel Bay, California, but apparently only during oscillating periods of oceanic warm-up (Baldrige 1974, Anderson and Anderson 1976). On a long-term (decadal-plus) basis, West Anacapa Island and Isla Coronado Norte remain the "traditional" sites for Brown Pelican breeding colonies in the SCB area.

Historical data (i.e., before 1969) are scant and imprecise, but maximum historical populations were higher previously than they have been recently. Numbers at the Anacapa Islands were perhaps 2,500 pairs (see Anderson and Anderson 1976) and around 1,500 pairs at Los Coronados (Anderson and Hickey 1970, Jehl 1973). Several other islands off southern California have also had nesting Brown Pelicans in the past (see Gress 1970, Gress and Ander-

TABLE 1. Yearly mean population data for Brown Pelicans nesting in the Anacapa Island area and on Isla Coronado Norte, and for Double-crested Cormorants nesting on West Anacapa Island, 1969 through 1980.

Year	Brown Pelicans						Doubled-crested Cormorants		
	Anacapa area			Coronado Norte			Anacapa area only		
	Est. no. pairs (E) ^a	No. yng. fledged (YY)	Productivity (F) ^b	Est. no. pairs (E) ^a	No. yng. fledged (YY)	Productivity (F) ^b	Est. no. pairs (E)	No. yng. fledged (YY)	Productivity (F) ^{b,c}
1969	750	4	0.005	375 ^d	0	0	76	0	0
1970	552	1	0.002	175	4	0.02	50	3	0.06
1971	540	7	0.013	110	35	0.32	48	0	0
1972 ^c	261	57	0.22	250	150	0.60	26	9	0.35
1973	247	34	0.14	350	100	0.29	16	3 ^{+c}	0.19 ⁺
1974 ^c	416	305	0.73	870	880	1.01	29	1 ^{+c}	0.03 ⁺
1975 ^c	292	256	0.88	339	407	1.20	3	3	1.00
1976	417	279	0.67	473	487	1.01	7	2 ^{+c}	0.29 ⁺
1977 ^f	76	39	0.51	263	216	0.82	15	18 ^{+c}	1.20 ⁺
1978 ^f	210	37	0.18	265	62	0.23	34	49	1.44
1979 ^f	1,258	980	0.78	960	920	0.96	66	38	0.58
1980 ^f	2,244	1,515	0.68	758	350	0.46	78	36	0.46

^a Our estimates here represent a compromise between maximum numbers present, numbers of nests constructed, reproductive behavior, and appearances of secondary sexual characteristics.

^b These data are expressed as number of young fledged per pair (= F). Data for 1969–1974 are from Anderson et al. (1975) and Anderson and Anderson (1976).

^c Data from 1969–1972 are from Gress et al. (1973). After 1972, to avoid disturbances, one to three nests were not examined. Therefore, F-values in those years are minimal, but nearly accurate.

^d Includes Coronado Sur (Jehl 1973).

^e Nesting at Scorpion Rock is included: 1972 (112 nests, 31 young), 1974 (105 nests, 75 young), and 1975 (80 nests, 74 young).

^f From Gress et al. (unpubl.); 1980 data include nesting on Santa Barbara Island (97 nests, 77 young).

son 1982; Fig. 1), but during the study period reported here we have seen colonies at only two other places: Scorpion Rock (1972–1973, 1975) and Santa Barbara Island (1980). Scorpion Rock is near Scorpion Anchorage, Santa Cruz Island, about 10 km from West Anacapa and Santa Barbara Island is about 70 km southeast. A more detailed historical review is given by Gress and Anderson (in press).

PERTURBATIONS FROM POLLUTION

After about 1968 (earlier data are not available, see Anderson and Risebrough 1976), DDE contamination of the SCB became great enough to disrupt natural population variation of Brown Pelicans; a population decline resulted mainly through reductions in fledging rates (F) (Jehl 1973, Anderson et al. 1975, Anderson and Anderson 1976). The decline in the late 1960's may also have involved some increases in adult mortality rates from direct poisoning (see data in Keith et al. 1971). The effects of pollution, however, were not a species-specific phenomenon involving only pelicans; other wildlife species were also affected (see Anderson and Risebrough 1976). Double-crested Cormorants (often nesting among pelicans at both West Anacapa and Coronado Norte), in particular, declined as a result of pollution (Gress et al. 1973). Certainly in the mid-1960's and early 1970's natural ecological relationships in the SCB were seriously disrupted (see Table 1 for the resultant poor fledging rates of Brown Pelicans). After a decline in DDT-related pollution by 1972, both pelicans and cormorants improved in fledging rates

(see Anderson et al. 1975, 1977b, Gress et al. 1973), peaking for Brown Pelicans in 1975 at both islands, and highest for cormorants on West Anacapa in 1978. Since 1972 both species have assumed independent patterns in fledging rates (Table 1; $r = -0.210$, $P > 0.10$, comparable data from Los Coronados regarding cormorants are not available). Brown Pelican fledging rates in the SCB have been closely associated with stocks of northern anchovies (*Engraulis mordax*) since about 1974 (Anderson et al. 1980, 1982).

RECENT STATUS

Breeding populations (estimated number of pairs) of Brown Pelicans off southern California declined from 1969 through 1973, increased in 1974, continued to decline through 1977, and began increasing again through 1980. Simultaneous trends were apparent at both West Anacapa Island (a) and Isla Coronado Norte (c) (Table 1 presents data through 1980). The numbers of breeding pairs each year at both islands are significantly correlated ($r = 0.590$, $P < 0.05$), and their trends are similar. A chi-square test (=3.6) comparing the two colonies in increases and decreases and assuming equal proportions of all possibilities, was significant at $P = 0.06$. This suggests that whatever controls breeding effort (the numbers of pairs attempting to breed) operates similarly in direction and intensity each year at each of these two colonies (i.e., it represents an imprecise, regional effect). Yet, in any given year, we assume that each colony essentially represents an independent, local response once

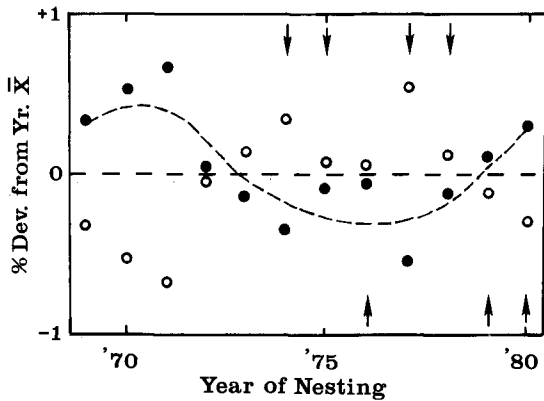


FIGURE 2. Changes between 1969 and 1980 in the relative proportions of breeding pairs of Brown Pelicans at the two major colony areas in the Southern California Bight. Scorpion Rock (1972, 1974–1975) and Santa Barbara Island (1980 only) are included with West Anacapa Island because of their proximity. Data are represented as follows: closed circles = Anacapa area, open circles = Coronados. Arrows mark years of greater abundance and density of anchovies: above the zero-deviation line, near Coronado Norte; below the line, near Anacapa Islands. The line is drawn by eye and smoothed to illustrate the changes at Anacapa Island. A “runs test” at $P = 0.05$ indicated significantly alternating sequences of dominance or periods of “runs” at one colony or the other.

the breeding effort is established, because of limitations in foraging range (the precise distances remain unknown, but see Anderson et al. 1982). The idea that events are not constant near either island is illustrated by: (1) a shifting of breeding effort between the two colonies (Fig. 2), and (2) high overall coefficients of variation (CVs) in numbers of breeders at both colonies ($CV_a = 71\%$; $CV_c = 68\%$). West Anacapa Island had the larger populations from 1969 through 1972 and again in 1979 and 1980 (Fig. 2).

There is little doubt that both Brown Pelican and Double-crested Cormorant populations began to increase about 1973 and later (Table 1, Fig. 3), assuming improved reproduction represents the beginning of such increases. High breeding populations of pelicans in 1979 and 1980 were likely increased by the expected recruitment from improved productivity starting in 1974–1975, reflected through a probable time-lag until breeding maturity (Fig. 3) (see also Blus and Keahey 1978). Data relating breeding populations to total associated adult populations are meager, but they suggest only weak relationships between the two (Table 2); furthermore, the same data suggest that varying proportions of potential breeders present in the SCB actually attempt to breed each year (such data also emphasize the need for adequate, independent population estimates in conjunction with breeding colony censuses to evaluate population status).

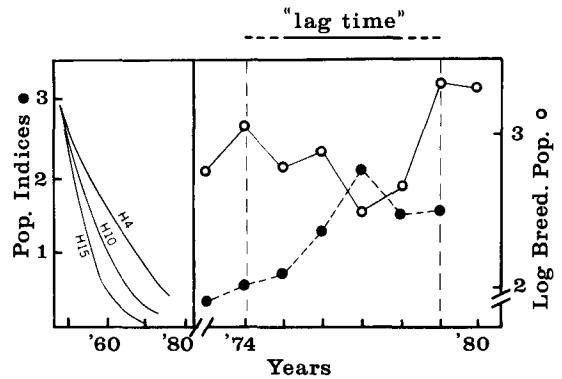


FIGURE 3. Comparisons between breeding adults at Anacapa plus Coronados, from 1973 through 1980 (open circles), and winter population indices (includes young) from Christmas Bird Counts (closed circles) (see Anderson and Anderson 1976). The left side of the graph represents a condensation of time from 1949 through 1974, showing the population decline actually predicted from the population indices (H4) and two hypothetical declines assuming adult mortality rates of 10% (H10) and 15% (H15). All assume zero or near-zero production of young from at least the mid-1960s through the early 1970s, as was generally observed for that period (Anderson et al. 1975). The “lag time” represents the period between first-observed high production of young pelicans (1974–1975) and the increase in the breeding population actually observed. (It may represent the mean age to breeding maturity in this population, with possible variation on either end.)

AGE STRUCTURE IN AND NEAR THE ANACAPA COLONIES

It is difficult to interpret age-ratios, but some patterns were apparent. Early in the breeding season, proportions of younger-than-adult plumaged pelicans varied considerably in and near the colony sites from year-to-year (1–20% younger than adult within the nesting colonies and 2–62% in the peripheral areas nearby) (Table 3). Proportions of younger age pelicans also increased later in the breeding season in the colony area as adults abandoned their nests (Table 3), although some normal increase would be expected (see Knopf 1979). None of those “young” discussed here includes those produced on Anacapa that same year, and proportions of young as high as we observed for several years (Table 3) are unusual for Brown Pelican colonies (see Blus and Keahey 1978 and Schreiber 1979). Younger age-class pelicans tended to be more numerous in and near colony areas just after or when no or few young were actually raised on Anacapa. These are years that followed periods of negligible productivity, at least as early as 1968 (Schreiber and DeLong 1969) and through 1973 (Anderson et al. 1975). Later-season increases of adults and young in the same areas are perhaps more typical and representative of post-breeding increases of non-resident Brown Pelicans (see Anderson and Anderson 1976, Briggs et al.

TABLE 2. Comparisons between some estimates of Brown Pelican populations in the Southern California Bight (SCB), where data were available.^a

Year	Estimated populations			Ratios	
	Potential breeders		Totals	N/A	A/T
	Nesting (n)	SCB(A)			
1972	1,220	3,800	5,200	0.32	0.73
1975	1,260	3,840	6,000	0.33	0.64
1976	1,780	4,760	7,000	0.37	0.68
1977	680	3,500	5,000	0.19	0.70
1979	4,440	6,450	7,500	0.69	0.86
CV ^b	79%	27%	18%	—	—

^a "SCB(A)" represents adult-plumaged birds, "SCB(T)" represents total pelicans censused. Data from 1975 through 1977 are from Briggs et al. (1981) and they represent values estimated from their Figures 6 (counts in May and June) and 7 (age ratios in March). 1972 and 1979 data were gathered specifically for Brown Pelican population assessment, and are therefore the most comparable.

^b CV = coefficient of variation.

1981). It is notable that late in the 1976 breeding season pelicans nearly abandoned the Anacapa nesting colony and the entire island (Table 3).

IMMIGRATION AND MORTALITY

Simple calculations suggest that the population levels at breeding colonies in 1979 are not solely attributable to fledging rates since 1974 (Brown Pelicans reach maturity at about three to five years of age, see also Blus and Keahy 1978 and our Fig. 3). We therefore hypothesize that recruitment of breeding populations is augmented by outside sources. Outside recruitment in the SCB is suggested by sightings of marked or banded birds (Anderson, unpubl. data) and by the presence of younger age-class pelicans in and near the Anacapa colonies (previous section) when the colonies were known to have previously failed.

Outside recruitment is expected to be high in a situation of pollution-disruption such as we observed in the late 1960's and early 1970's with such extremely poor fledging rates for a long period of time, coupled with the presence of non-resident pelicans for a substantial period each season (four or more months per year; Briggs et al. 1981). High outside recruitment has also been suggested from banding data of Great Lakes populations of Herring Gulls (*Larus argentatus*), also known to be highly contaminated by organochlorines (see Gilman et al. 1977).

Mortality rates for adult Brown Pelicans are not yet well-documented, although Henny (1972) has attempted estimations (not agreed upon by Schreiber 1979). Until more data become available, we explore two different adult mortality rates: 12% (M1) and 15% (M2). These represent hypothetical but logical and reasonable adult mortality rates. The low value (M1) is not unreasonable in light of low values re-

TABLE 3. Age-ratios of Brown Pelicans on different parts of Anacapa Island during different periods of the breeding season.^a

Year	March through mid-June						Mid-June through September						Total no. present ^b
	In nest areas			Near nest areas			In nest areas			Near nest areas			
	JY	SA	AD	JY	SA	AD	JY	SA	AD	JY	SA	AD	
1971	<1	<1	99 ± 1 (503)	1	1	98 ± 2 (371)	52	14	34 ± 7 (197) ^c	36	6	58 ± 3 (1,386)	1,600
1972	1	<1	99 ± 1 (601)	18	13	69 ± 9 (105)	4	4	92 ± 4 (182)	19	13	68 ± 2 (1,604)	1,800
1973	3	10	87 ± 7 (111)	11	15	74 ± 2 (1,878)	20	35	45 ± 11 (92)	17	23	60 ± 6 (273)	360
1974	ND	ND	87 ± 2 (866)	ND	ND	ND	4	26	70 ± 5 (294)	9	16	75 ± 2 (1,622)	2,100
1975	3	<1	96 ± 3 (167)	57	3	38 ± 8 (141)	6	37	57 ± 18 (35)	20	5	75 ± 4 (427)	450
1976 ^e	7	13	80 ± 3 (691)	11	10	79 ± 4 (357)	0	0	100 ± 2 (22)	0	0	0	30 ^f
1976 ^g	1	2	97 ± 4 (104)										
1977	2	6	92 ± 3 (331)	17	19	64 ± 4 (538)	10	21	69 ± 19 (29)	36	20	45 ± 4 (660)	1,500
1978	1	4	95 ± 3 (302)	18	7	75 ± 8 (124)	ND	ND	ND	ND	ND	ND	ND
1979	1	3	96 ± 2 (696)	5	6	89 ± 5 (173)	ND	ND	ND	ND	ND	ND	ND

^a Three age-classes are defined here with the following symbols: JY = young of previous year plus hatch-year young, but not including young produced on Anacapa Island; SA = subadults (at least two year-classes); AD = full adult-plumaged pelicans; ND = no data available. AD mean percentages are given ± 95% C.L. (Shedden and Cochran 1967:211) followed by sample-sizes in parentheses. "Near nest areas" includes all pelicans within about 1,500 m of the nearest nest.

^b Totals are approximate total number of pelicans associated with the breeding colony and nearby roosts at midday.

^c Nests with incubating pelicans had 100% AD (n = 41).

^d A 1972-marked pelican from the Gulf of California was seen among these birds. Heermann's Gulls (*Larus heermannii*) were also present in greatly-expanded numbers for that time of year around Anacapa Island in 1973, while this gull is normally rare or absent at Anacapa through June.

^e Nesting data for 1976 are divided into early (E) and late (L) cohorts because a larger proportion than usual of immature-plumaged birds attempted to nest in March of 1976 (E); but by May, they had largely failed and abandoned the nesting area.

^f During the latter part of the 1976 nesting season, few pelicans could be found at Anacapa despite the presence of pre-fledging young (mean about six weeks of age) in the nesting area. Many of these young eventually starved in the colony (Anderson, field notes).

ported for many other seabirds (Lack 1954, 1966). Our high value (M2) approaches that estimated by Henny (1972) for Brown Pelicans (16% based on band recoveries). Pre-adult mortality rates are also approximated from Henny (1972). Our estimates here are conservative, and if based only on data from the literature or band recovery data, such estimates would inflate mortality estimates and increase the resulting estimates of immigration rates. The mortality sequence we use here is as follows: first year = 0.50, second year = 0.25, third year = 0.15, fourth year and beyond, M1 = 0.12 and M2 = 0.15. Data for the period 1974–1979 are considered.

Our 1974 starting population estimates were projected back from 1975 aerial survey data of Briggs et al. (1981), as those are the most complete and accurate population censuses available. Confidence intervals on such estimates unfortunately average 30–50% of the mean; nonetheless, the initial population values (corrected backward for one year of mortality) are as follows: M1 = 5450, M2 = 5650.

The estimates based on M1 and M2 predict that outside recruitment is still significant in California, even if one assumes that all capable adults bred in 1979. In 1979 we censused a minimum of 4,440 adults, the highest number found in our studies through that year (Table 1). Predicted adult numbers under M1 and M2 mortality patterns ending in the 1979 breeding period, and including the young produced with similar mortality patterns, would be 3,270 and 2,950 respectively.

REPRODUCTIVE RATES

Both Schreiber (1979) and Anderson (unpubl. data) have noted repeating, maximum fledging rates (here defined as young fledged per nest attempt, F_{\max}) of 1.3 to 1.7 (mean about 1.4) and long-term means of about 1.0 in two separate studies of nearly a decade each outside the SCB area. These are higher in all respects (F_{\max} and long-term means) than any similar data obtained by us in the SCB. There are few historical data for comparison in the northern populations of California Brown Pelicans, but Williams (1931) reported 79 young produced in 55 nests at Point Lobos, Monterey Co., California in 1929 ($F_{\max} = 1.4$).

Rather than use only a mean "recruitment standard" as suggested by Henny (1972), we assume that the F_{\max} -values above represent a "ceiling level" or potential that should be expressed during periods of maximum food abundance in each situation. The level of F at mean 1974–1979 anchovy biomass estimates in the SCB (see Anderson et al. 1982) is about 0.83 and the F_{\max} is 1.04, as represented through

the two-colony mean (1975) (Table 1). At these levels, SCB fledging rates are about 74–83% of comparable values reported for other populations. The mean F -values are about 71–77% of their F_{\max} values. It is not clear, however, whether SCB F -values are at pre-pollutant levels. If reproduction were unimportant as a demographic parameter (see Zwickel 1973), then the Brown Pelican populations of the SCB should not have begun to increase only after improvements in reproduction, although some maintenance of the breeding populations probably occurred in the "pollution years" through immigration (see above section).

Judging from available data, we believe that the reduced reproductive rates of SCB Brown Pelicans still represent unnatural factors rather than inherently lower mean reproductive rates characteristic of a northern population. A greater tendency for r -selection might be predicted nearer the range periphery if food resources were more patchy than in central areas, or roughly equal if patchiness was equal throughout the range (see Horn 1978). Duffy (1980) suggested high reproductive rates for Peruvian Brown Pelicans, but uneven distribution in that case is apparently even more extreme than in the SCB, resulting also in higher adult mortality rates at times of food stress. Greater patchiness and variability of food resources might be expected for the SCB area as compared to the Gulf of California, for example, because the SCB is apparently a varying zone of overlap between warm-temperate and cold-temperate waters (see Hunt et al. 1980, Anderson in press).

NESTING CHRONOLOGY

From 1970 through 1980, the Brown Pelican breeding season (here defined in terms of the period of egg-laying) at both island areas fluctuated considerably from year-to-year, sometimes beginning as early as December and extending into early August (Fig. 4). Egg-laying usually occurred within a two to five-month period (mean = 3 months) with two or three-week peaks. Brown Pelican nesting chronology on the East Coast becomes more seasonal with increasing latitude (Schreiber 1980b). Southern California somewhat resembles these mid- to high-latitude populations in most cases. Schreiber (1980b) speculated that pelicans probably commence breeding when they are sufficiently nourished (proximally related to food supply; see also Verbeek 1979).

DISCUSSION

With decreases in pollution levels (see Anderson et al. 1975, 1977b), breeding populations of Brown Pelicans in the SCB began to in-

crease, thanks largely to improvements in fledging rates (see also Anderson et al. 1982). The substantial breeding population increase in 1979 and 1980 may represent improved fledging rates since about 1972. All available data suggest that pelican populations in the SCB area during the breeding season are continuing to grow (Fig. 3, Table 1, Table 2). Had pelicans continued to decline in the SCB at the rate reported by Anderson and Anderson (1976), they would have been extirpated by the late 1980's. Their breeding populations have now shown a recovery in less than a decade.

If adult mortality has been no less than that estimated in the two mortality patterns used by us (M1 and M2), populations would still be declining if balanced by SCB fledging rates only. Our calculations suggest that an average of about 46 new adults (16% by M1) or 128 adults (34% by M2) immigrated each year during the period 1974–1979. The only way populations might have either maintained equilibrium or increased on the basis of their own reproduction would have been if mortality rates were heavily compensatory, or density-dependent, relative to mortality rates reported for other populations of Brown Pelicans. Yet, adult mortality rates increased during the “pollution years” (see Keith et al. 1971).

From 1972 through 1974, nesting success of pelicans on San Martín Island was poor (Anderson and Keith 1980; Fig. 1), and subsequently not successful at least through 1980 (Anderson, unpubl. data); failure was likely due to disturbances (Anderson and Keith 1980). Although there were no marked pelicans from this island, we suggest that these pelicans could be one source of “new” breeders in the SCB (as well as newly-recruited younger birds, see earlier discussion). The SCB recovery would therefore appear better than it really is. The unusually high proportions of younger age-class pelicans at Anacapa nesting sites and the late-season decreases in proportions of adults in central parts of the main colony areas support the idea that reproductive problems had occurred (with resultant nest abandonments, reported originally by Gress 1970 as symptomatic of DDE-related problems). Such behavioral phenomena seem to have predisposed the SCB breeding units to: (1) weaker adult defense for nest sites as they abandoned for abnormal reasons (loss of nest contents), (2) younger birds produced elsewhere having the opportunity to enter colony areas earlier in their life compared to other colonies, (3) then perhaps gaining early experience, and (4) eventually entering that particular breeding population. If decreased fledging rates were mostly caused by the pres-

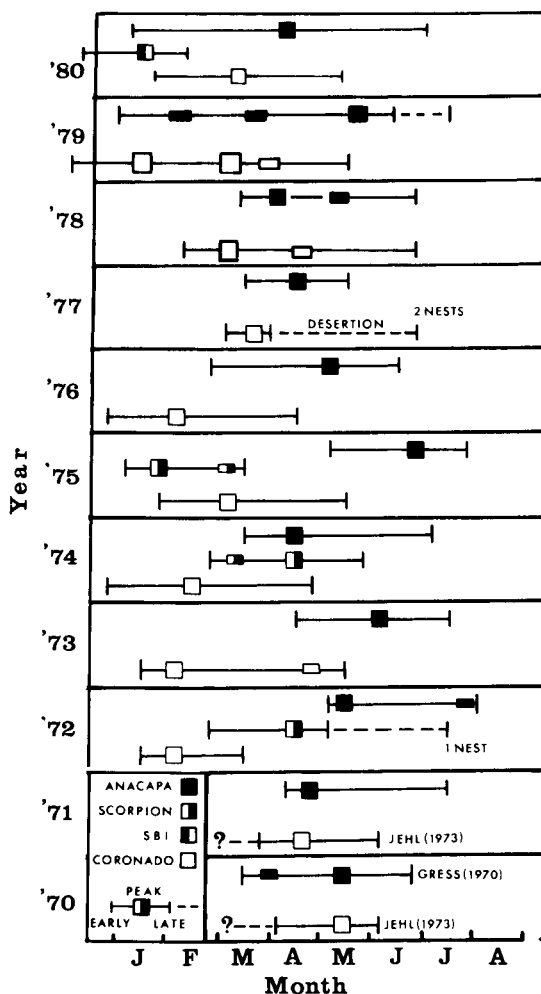


FIGURE 4. Condensed nesting phenology (egg-laying dates) of Brown Pelicans in the Southern California Bight, 1970 through 1980. The large squares represent the peak periods, small rectangles represent minor peaks, and vertical lines represent the entire period. Dashed lines represent one or two unusually late nests. “SBI” (see legend) represents Santa Barbara Island. Because of early potential failures in 1970 and 1971 due to pollution (see text), it remains unknown if peaks actually represent second attempts at nesting after initial failures due to egg breakage (? on graph).

ence of younger, inexperienced adults in the colony areas (see Knopf 1979), however, we should have seen fledging rates gradually improving to eventual F_{max} during years of plentiful food. Undoubtedly, complex natural phenomena related to SCB pelicans have been further complicated by a complex series of unnatural events.

Populations of Double-crested Cormorants have also improved but annual changes are independent from those of Brown Pelicans (Table 1). Pelicans and cormorants are not similarly dependent on the same foods. In 1975–1978, anchovies were not highly impor-

tant in the diet of most Double-crested Cormorants breeding on the Pacific Coast, but samples from the SCB were small (Ainley et al. 1981). Anchovies certainly dominate the food items of SCB Brown Pelicans: over a seven-year period, 92% of the pelican diet during the breeding season consisted of these fish (Gress et al. 1980). Reproductive rates of pelicans are closely tied to anchovy abundance near the breeding colonies (Anderson et al. 1982).

For the 12-year period of our studies, nesting in the first decade began earlier (less than one to about three months) on Isla Coronado Norte (Fig. 4), the more southern colony (Fig. 1). That phenology was consistent with anchovy distribution during that period. Anchovies were abundant as spawners in the more southern area earlier in the year (Pacific Fisheries Management Council 1978). During this period, 1980 was the first year when reproduction was probably not drastically affected by pollution in which we noted a complete shift in breeding effort from Coronados to the Anacapa Island area. Associated with that shift was a pelican reproductive rate that was higher for the Anacapa area (Table 1), as well as earlier nesting at both Anacapa and Santa Barbara Islands (Fig. 4). This was also true in 1981 at Anacapa alone (Gress et al., unpubl. data). The earlier nesters have usually been more successful in productivity, as might be generally predicted from past studies (e.g., Fisher 1975, Knopf 1979, Manuwal 1979, and Hedgren and Linnman 1979), although trends are not consistently related to latitude in the SCB. In any case, proximate timing of the Brown Pelican reproductive season and location of breeding effort may be tied to food supplies before the breeding season, as suggested by Lack (1966: 259–260).

Scorpion Rock and Santa Barbara nesting phenologies deserve added comment here. In 1972 Scorpion Rock was phenologically intermediate between Anacapa and Isla Coronado Norte. In 1974 nesting peaked there at the same time as on nearby Anacapa, but in 1975 peak nesting was the earliest in the SCB area (Fig. 4). A later and smaller peak in 1975 corresponded to the peak at Coronado Norte. Scorpion Rock had nesting Brown Pelicans during the years of increasing and peak SCB anchovy abundance (Anderson et al. 1982), but detailed relationships of Scorpion Rock's nesting pelicans to either Anacapa or Coronado Norte are not as yet entirely clear. Aerial surveys in 1980 (Gress et al., unpubl. data) hint at one important proximate cause of pelican nesting on Santa Barbara Island that year. Pelicans feeding at sea early in the breeding season were

found to be closely associated with anchovy patches; in that year, these patches were closer to Santa Barbara Island than Anacapa (they are more typically north of Anacapa in the Santa Barbara Channel, see Fig. 1) (Gress et al. 1980, Gress et al., unpubl. data).

Age ratios at Scorpion Rock when nesters were present did not support the notion that younger birds comprised that nesting population. In fact, proportions of adult-plumaged pelicans were equal to or greater than those at either Anacapa or Coronado Norte (see Table 3); for example, an aerial survey of Scorpion Rock on 27 April 1972 revealed about 300 adults present with only two pelicans of sub-adult plumage (Anderson, unpubl. data). Nesting at Scorpion Rock and Santa Barbara Island was loosely associated with the shifts of nesting populations discussed earlier. Both islands first had breeders when the highest proportion of the population was either changing from Anacapa to Coronado Norte or vice versa (Fig. 2). We can only speculate, but such observations imply either that individual pelicans shifted breeding locations within the SCB area, or that variable proportions of a larger pool of adults breed at each area each year (if one assumes a constant return of adults to particular nesting sites). Where more data are available, frequent and extensive local shifts at Anacapa (Gress and Anderson 1982) and on islands in the Gulf of California (Anderson, unpubl. data) suggest that the same individuals are generally involved. Without marked birds, however, this remains unclear.

Earlier nesting may give breeders an advantage on the eventual energetic restriction of molt, which is proximately controlled by photoperiod (see Verbeek 1979). Schreiber (1980b) discussed the possible advantages of early nesting in Eastern Brown Pelicans. Colony shifting suggests that SCB breeders may gain the advantage of early nesting by responding to changing food in the SCB. Food supplies do not diminish in a distinct and consistent seasonal manner (see Hedgren and Linnman 1979), however, as related to regular seasonal events. Rather, early nesting probably represents variability in food near either colony on a yearly and seasonal basis as also constrained by physiological responses of the breeders (see Manuwal 1979). Data are needed to specifically relate short-term variations in food supply to short-term behavioral and ecological phenomena.

Control of reproduction might occur both during (Anderson et al. 1982) and outside the breeding seasons. Temperature may be an important proximate mechanism in controlling Eastern Brown Pelican phenology as suggested

by Schreiber (1980b), but this may act indirectly through its effects on food supplies. Southern California is a seasonal environment similar to that of mid-latitudes on the East Coast but few natural catastrophic events (such as hurricanes, see Schreiber 1980b) occur in southern California. In the SCB, sea temperatures are usually lowest early in the breeding season (January through March), and warm up later in the season (see Lynn 1967). In some years, nesting may begin as early as December and January when temperatures are declining.

One could hypothesize that regardless of temperatures, if the food supply is adequate and the molt complete, breeding will begin. Greater food availability should give each individual a better chance of maximizing its reproductive potential within the colony setting (see Anderson et al. 1982), where each pair contributes to the colony's mean reproductive rate and responds to the general message of food. Orians (1971:532) stated: "For any given level of food availability there will be a point at which the flying time and energy expended . . . will exactly offset the energy realizable by foraging. . . ." The most efficient way of responding to this constraint in the SCB, and within the added constraints of nest-site location and physiological state, may be to shift the location of the breeding effort. Later nesters may indeed be limited by physiological events such as molt, since food supply usually increases in the SCB later in the nesting season (July through October), when newly produced young anchovies become large enough to be suitable pelican food items. The large influxes of Brown Pelicans or other seabirds at that time attest to the abundant food supplies in the post-breeding period (Ainley and Lewis 1974, Briggs et al. 1981). Breeding in the SCB occurs when food is abundant near the breeding colonies (Anderson et al. 1982) but not when food is seasonally most abundant; in this period a different food source (young anchovies) exists for newly fledged pelicans to exploit (after Lack 1954, in that fledging occurs at a period of maximal food abundance).

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LITERATURE CITED

- AINLEY, D. G., AND T. J. LEWIS. 1974. The history of Farallon Island marine bird populations, 1854-1972. *Condor* 76:432-446.
- AINLEY, D. G., D. W. ANDERSON, AND P. R. KELLY. 1981. Feeding ecology of marine cormorants in southwestern North America. *Condor*: 83:120-131.
- ANDERSON, D. W. 1973. Gulf of California seabird breeding failure. *Event Notif. Rep.*, Smithson. Inst., 1653.
- ANDERSON, D. W. In press. The sea birds. In T. Case and M. L. Cody [eds.], *Biogeography in the Sea of Cortez*. Univ. California Press, Berkeley.
- ANDERSON, D. W., AND I. T. ANDERSON. 1976. Distribution and status of Brown Pelicans in the California Current. *Am. Birds* 30:3-12.
- ANDERSON, D. W., AND J. J. HICKEY. 1970. Oological data on egg and breeding characteristics of Brown Pelicans. *Wilson Bull.* 82:14-28.
- ANDERSON, D. W., AND J. O. KEITH. 1980. The human influence on seabird nesting success: conservation implications. *Biol. Conserv.* 18:65-80.
- ANDERSON, D. W., AND R. W. RISEBROUGH. 1976. Brown Pelican reproduction: letters to the editor. *Science* 193: 96-97.
- ANDERSON, D. W., L. R. DEWEESE, AND D. V. TILLER. 1977a. Passive dispersal of California Brown Pelicans. *Bird-banding* 48:228-238.
- ANDERSON, D. W., F. GRESS, AND K. F. MAIS. 1982. Brown Pelicans: influence of food supply on reproduction. *Oikos* 39:23-31.
- ANDERSON, D. W., R. M. JUREK, AND J. O. KEITH. 1977b. The status of Brown Pelicans at Anacapa Island in 1975. *Calif. Fish Game* 63:4-10.
- ANDERSON, D. W., F. GRESS, K. F. MAIS, AND P. R. KELLY. 1980. Brown Pelicans as anchovy stock indicators and their relationships to commercial fishing. *Cal. Coop. Oceanic Fish. Invest. Rep.* 21:54-61.
- ANDERSON, D. W., J. R. JEHL, JR., R. W. RISEBROUGH, L. A. WOODS, JR., L. R. DEWEESE, AND W. G. EDGECOMB. 1975. Brown Pelicans: improved reproduction off the southern California coast. *Science* 190: 806-808.
- APPELEGATE, R. 1975. An index to Chumash placenames. San Luis Obispo Co. (Calif.) Arch. Soc. Occas. Papers 9.
- BALDRIDGE, A. 1974. The status of the Brown Pelican in the Monterey Region of California: past and present. *West. Birds* 4:93-100.
- BLUS, L. J., AND J. A. KEAHEY. 1978. Variation in productivity with age in the Brown Pelican. *Auk* 95: 128-134.
- BRIGGS, K. T., D. B. LEWIS, W. B. TYLER, AND G. L. HUNT, JR. 1981. Brown pelicans in southern California: habitat use and environmental fluctuations. *Condor* 83: 1-15.
- CODY, M. L. 1971. Ecological aspects of reproduction, p. 461-512. In D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 1. Academic Press, New York.
- DUFFY, D. 1980. Comparative reproductive behavior and population regulation of seabirds of the Peruvian coastal current. Ph.D. diss., Princeton Univ., Princeton, NJ.
- FISHER, H. I. 1975. The relationship between deferred breeding and mortality in the Laysan Albatross. *Auk* 92:433-441.
- GILMAN, A. P., G. A. FOX, D. B. PEAKALL, S. M. TEEPLE, T. R. CARROLL, AND G. T. HAYMES. 1977. Reproductive parameters and egg contaminant levels of Great Lakes Herring Gulls. *J. Wildl. Manage.* 41:458-468.
- GOCHFELD, M. 1980. Mechanics and adaptive value of

- reproductive synchrony in colonial seabirds, p. 207–270. *In* J. Burger, B. L. Olla, and H. E. Winn [eds.], *Behavior of marine animals*. Vol. 4. Plenum Press, New York.
- GOODMAN, D. 1980. Demographic intervention for closely managed populations, p. 171–195. *In* M. E. Soule and B. A. Wilcox [eds.], *Conservation biology: an evolutionary-ecological perspective*. Sinauer Assoc., Sunderland, MA.
- GRESS, F. 1970. Reproductive status of the California Brown Pelican in 1970, with notes on breeding biology and natural history. Calif. Dep. Fish Game, Wildl. Manage. Br. Admin. Rep. 70-6.
- GRESS, F., R. W. RISEBROUGH, D. W. ANDERSON, L. F. KIFF, AND J. R. JEHL, JR. 1973. Reproductive failures of Double-crested Cormorants in southern California and Baja California. *Wilson Bull.* 85:197–208.
- GRESS, F., P. R. KELLY, D. B. LEWIS, AND D. W. ANDERSON. 1980. Feeding activities and prey preference of Brown Pelicans breeding in the Southern California Bight. Calif. Dep. Fish Game Annu. Rep.
- GRESS, F., AND D. W. ANDERSON. *In press*. The California Brown Pelican recovery plan. U.S. Fish and Wildlife Service, Region 1, Portland, OR.
- GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. *Pac. Coast Avifauna* 27:1–608.
- GUTHRIE, D. A. 1980. Analysis of avifaunal and bat remains from midden sites on San Miguel Island, p. 689–702. *In* D. M. Power [ed.], *The California islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- HEDGREN, S., AND A. LINNMAN. 1979. Growth of guillemot *Uria aalge* chicks in relation to time of hatching. *Ornis Scand.* 10:29–36.
- HENNY, C. J. 1972. An analysis of the population dynamics of selected avian species: with special reference to changes during the modern pesticide era. U.S. Fish Wildl. Serv. Res. Rep. 1:1–99.
- HORN, H. S. 1978. Optimal tactics of reproduction and life-history, p. 411–429. *In* J. R. Krebs and N. B. Davies [eds.], *Behavioral ecology: an evolutionary approach*. Sinauer Assoc., Sunderland, MA.
- HUNT, G. L., JR., R. L. PITMAN, AND H. L. JONES. 1980. Distribution and abundance of seabirds breeding on the California Channel Islands, p. 443–459. *In* D. M. Power [ed.], *The California islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- JEHL, J. R., JR. 1973. Studies of a declining population of Brown Pelicans in northwestern Baja California. *Condor* 75:69–79.
- JEHL, J. R., JR. 1977. An annotated list of birds of Islas Los Coronados, Baja California, and adjacent waters. *West. Birds* 8:91–101.
- JONES, J. R. 1971. General circulation and water characteristics in the Southern California Bight. Southern California Coastal Water Res. Proj., Tech. Rep. 101., El Segundo, CA.
- KEITH, J. O., L. A. WOODS, JR., AND E. G. HUNT. 1971. Reproductive failure in Brown Pelicans on the Pacific Coast. *Trans. N. Am. Wildl. Nat. Res. Conf.* 35:56–63.
- KEITH, J. O. 1978. Synergistic effects of DDE and food stress on reproduction in Brown Pelicans and Ring-billed Gulls. Ph.D. diss., Ohio State Univ., Columbus.
- KNOFF, F. I. 1979. Spatial and temporal aspects of colonial nesting of White Pelicans. *Condor* 81:353–363.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford Univ. Press, London.
- LACK, D. 1966. *Population studies of birds*. Clarendon, Oxford.
- LYNN, R. J. 1967. Seasonal variation of temperature and salinity at 10 meters in the California Current. *Cal. Coop. Oceanic Fish. Invest. Rep.* 11:151–186.
- MANUWAL, D. A. 1979. Reproductive commitment and success of Cassin's Auklet. *Condor* 81:111–121.
- ORIANI, G. 1971. Ecological aspects of behavior, p. 513–546. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 1. Academic Press, New York.
- PACIFIC FISHERIES MANAGEMENT COUNCIL. 1978. Implementation of northern anchovy fishery management plan: solicitation of public comments. *Fed. Register* 43:31651–31879.
- REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE. 1958. Studies of the California Current System. *Cal. Coop. Oceanic Fish. Invest. Rep.* (1958):29–57.
- RICKLEFS, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *Am. Nat.* 111:453–478.
- SCHREIBER, R. W. 1979. Reproductive performance of the eastern Brown Pelican. *Los Ang. Cty. Mus. Contrib. Sci.* 317:1–43.
- SCHREIBER, R. W. 1980a. The Brown Pelican: an endangered species? *BioScience* 30:742–747.
- SCHREIBER, R. W. 1980b. Nesting chronology of the eastern Brown Pelican. *Auk* 97:491–508.
- SCHREIBER, R. W., AND R. L. DELONG. 1969. Brown Pelican status in California. *Audubon Field Notes* 23:57–59.
- SCHREIBER, R. W., AND R. W. RISEBROUGH. 1972. Studies of the Brown Pelican. *Wilson Bull.* 84:119–135.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1967. *Statistical methods*. Iowa State Univ. Press, Ames.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman Co., San Francisco.
- SOUTHERN CALIFORNIA COASTAL WATER RESEARCH PROJECT. 1973. The ecology of the Southern California Bight: implications for water quality management. Southern California Coastal Water Res. Proj. Tech. Rep. 104, El Segundo, CA.
- VERBEEK, N. A. M. 1979. Timing of primary molt and egg-laying in Glaucous-winged Gulls. *Wilson Bull.* 91:420–425.
- WILLIAMS, L. 1931. Further notes on California Brown Pelicans at Point Lobos, California. *Condor* 33:66–69.
- ZWICKEL, F. C. 1973. Discussion, p. 107–110. *In* D. S. Farner [ed.], *Breeding biology of birds*. National Academy of Science, Washington, DC.

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