

PACIFIC COAST CASPIAN TERNS: DYNAMICS OF AN EXPANDING POPULATION

ROBERT E. GILL, JR.¹ AND L. RICHARD MEWALDT²

¹Marine Bird Section, U.S. Fish and Wildlife Service,
1011 East Tudor Road, Anchorage, Alaska 99503 USA, and

²Avian Biology Laboratory, San Jose State University,
San Jose, California 95192 USA

ABSTRACT.—Nesting distribution, age-related seasonal movements, survivorship, and mechanisms of population expansion in Pacific Coast Caspian Terns (*Sterna caspia*) were examined primarily through analysis of 412 recoveries of birds banded as juveniles between 1935 and 1980. Since the beginning of this century, the population has shifted from nesting in numerous small colonies associated with freshwater marshes in interior California and southern Oregon to nesting primarily in large colonies on human-created habitats along the coast. Colonies at Grays Harbor, Washington and San Francisco and San Diego bays, California account for 77% of the current Pacific Coast population (6,000 pairs), which has breeding and wintering areas separate from those of populations east of the continental divide. There also appears to be some segregation on the wintering grounds by birds from the three major colonies within the Pacific population. Age-related seasonal movements in the Pacific population are characterized by (1) a brief period of northward dispersal by newly fledged birds before migrating to the wintering grounds, (2) a residency on the wintering grounds through their second winter, (3) a return to the breeding grounds the third summer, when most birds are thought to prospect breeding sites and some may breed, and (4) attainment of adulthood the fourth summer, with subsequent annual movements between wintering and breeding grounds.

The Pacific population has increased 70% since 1960, apparently all by intrinsic growth. Over half (57%) of the fledglings reach their fourth year, and they have a subsequent annual survival rate of 89% and a mean breeding life expectancy of 8.6 yr. An average annual fledging rate of 0.64 young per pair was calculated as necessary to have provided the observed growth of the population during its recent expansion. Growth of some of the individual colonies, however, particularly those in Washington, could only have resulted from extensive recruitment of birds from other Pacific Coast colonies. Philopatry is low in this population, and the growth of the northern colonies involved recruitment primarily of first-time breeders but also of some older adults. Factors promoting both first-time breeders and older adults to join new and often distant colonies are discussed. Received 2 August 1982, accepted 2 January 1983.

THE Caspian Tern (*Sterna caspia*) seems to exploit a wider array of nesting habitats and has demonstrated an ability to respond more quickly to changes in these habitats than most other Sturninae. This ability to shift colony sites and the dynamics of population increase and range extension in the species have been studied extensively in Baltic populations (Bergman 1953, 1980; Staav et al. 1972; Väisänen 1973; Staav 1979). In eastern North America, birds have recently responded to changes in nesting habitat and are now colonizing dredge-spoil islands and other human-created habitats in several states (Dunstan 1975, Portnoy 1977, Blokpoel and Fetterolf 1978, Chaney et al. 1978, Scharf 1979, Portnoy et al. 1981); the breeding distribution, however, has remained relatively

fixed. At least one population, that associated with the Great Lakes, has increased since 1960, and birds there have shown considerable movement between colonies (Ludwig 1968, Shugart et al. 1978, Cuthbert 1981). Populations along the Pacific Coast have also shifted in response to habitat changes, and, until recently, nesting has been centered in California (Grinnell and Miller 1944). Since the mid-1960's, however, the Pacific Coast population has increased dramatically, and the largest breeding concentration now occurs along coastal Washington. This study describes (1) shifts in nesting habitat preference and distribution, (2) survivorship, (3) age-related seasonal movements, and (4) dynamics of population expansion in Pacific Coast Caspian Terns.

METHODS

TABLE 1. Bandings of Pacific Coast Caspian Terns, 1955-1980.^a

Years	California										Nevada		Washington		Idaho		Total	
	San Diego	San Francisco Bay	Moss Landing	Humboldt Bay	Clear Lake	Mono Lake	Honey Lake	Pyramid Lake	Grays Harbor	Potholes Reservoir	Pyramid Lake	Grays Harbor	Potholes Reservoir	Pyramid Lake	Grays Harbor	Potholes Reservoir		Pyramid Lake
1955-1960	3,842	518		47			47	2										4,456
1961-1965	2,479	232		186		14		24										2,935
1966-1970	921	433		140	24													1,518
1971-1975	126	743										949	47					1,894
1976-1980	57	314	57									3,493	269					4,190
Total	7,425	2,240	57	373	24	14	47	26				4,442	316					14,993

^a Data from BBL printout (Job 10-4387) and North American Bird Banding Association records. An additional 105 terns banded as adults, subadults, or unknown age were not included in our analysis.

For this report we analyzed 365 recoveries from 14,993 Caspian Terns banded as nestlings or pre-fledged juveniles from 1955 through 1980 in states west of the continental divide, including California, Nevada, Washington, and Idaho (Table 1). We included an additional 47 recoveries from an unknown number of terns banded as nestlings in California between 1935 and 1954. These 412 recoveries (U.S. Fish and Wildlife Service, Bird Banding Laboratory, Job 10-4387, plus recovery data through December 1980) were used to derive patterns of seasonal movement and information on survivorship and colony fidelity. Fifteen of these recoveries were of birds captured and subsequently released. Because these birds were captured at colonies or on the wintering grounds, we assumed that they had settled on these areas and that the data therefore were valid for our analysis of movements and colony fidelity. We did not include these 15 recoveries in our analysis of survival and longevity.

Recovery distances were calculated as direct heading distances from the natal colony. For most recoveries from Mexico, we fixed the location of recovery at the geographic center of a particular state; the exceptions were those recoveries from Baja California for which we had more specific information obtained from copies of the original correspondence reporting the recovery. Those recoveries north and south of Mexico were plotted to within a 10-min block of latitude and longitude. The direction of a recovery was defined by its bearing from the bird's natal colony: north (300-070°), east (071-100°), or south (101-220°). Natal area was considered an area within a 100-km radius of the natal colony and was based on the probable maximum foraging distance of breeding terns (Soikkeli 1973b, Koli and Soikkeli 1974, Gill 1976). Birds recovered beyond 100 km of their natal colony and not within 100 km of another colony were generally considered to have been in migration or dispersal. We have defined the breeding season as April-August, inclusive, and the nonbreeding season as September-March, inclusive. We realize that, given the range of latitude over which Caspian Terns breed along the Pacific Coast, the timing of nesting and the onset of fall migration vary among colonies. Birds generally arrive at breeding areas throughout their range during April, however, and are moving south to wintering grounds by September.

Age at recovery was based on the calendar year following hatch. For our analysis of age-related movements we used four age categories: Hatching Year (HY), Second Year (SY), Third Year (TY), and After Third Year (ATY) (U.S. Fish and Wildlife Service 1976). Because we found a significant difference ($\chi^2 = 4.86$, $df = 1$, $P < 0.05$) in the portions of recoveries at and away from colonies between TY and ATY birds, but not between Fourth Year (FY) and all

older birds and as Ludwig (1965) suspected that most Caspian Terns in the Great Lakes population did not breed until their fourth summer, we combined all FY and older birds into one age class (ATY), which we considered adults. Because survival rates of immature birds are often considerably lower than survival rates of adults, we used Cormack's (1970) ratio method, as suggested by Seber (1972), to derive survival rates for each age class of immature birds and Haldane's (1955) methods to calculate the survival rate of adults (all ATY birds) and the standard error of this estimate. An important assumption in calculating survival rates by these methods is that reporting rates are constant among the various age groups (Brownie et al. 1978). Birds reported during their first year of life were considered to have fledged and were included in these calculations only if their bands were recovered outside of the 10-min latitude and longitude block of banding; thus, reporting rates of young birds would not be expected to have been biased by being higher than that of adults near the site of banding. As the reporting rate on the breeding grounds may have differed from that on the wintering grounds, however, survival rates calculated for young birds may have been biased, because they spent a greater proportion of the year away from breeding areas than did adults. For example, the actual survival rate of SY birds would have been lower than estimated if the reporting rate were lower in Mexico than in the United States, as SY birds spent more time in Mexico than birds of other age groups (see results). In turn, the actual survival rate of HY birds would have been higher than estimated, as it was calculated by a ratio method from the survival rate of SY birds. Because we had no way of estimating the extent of these biases, these calculations were used as the best available approximations of actual survival rates.

Ludwig's (1981) study of the Great Lakes Caspian Tern population showed that band loss may significantly affect calculations of survivorship. When we applied his correction factors to our sample of recovered birds, however, we found no change in our survivorship data. The average life expectancy of birds once they reached adulthood (ATY birds) was calculated according to Soikkeli (1970) as $100 \cdot m^{-1} - 0.5$, where m is the percentage average adult mortality rate or 100 minus the percentage average survival rate.

To determine whether the growth of colonies was intrinsic or required immigration of birds from other colonies, we calculated the number of fledglings per breeding pair required to sustain the observed growth. For this we assumed that (1) annual survival of adults was constant and equal to that calculated according to Haldane's (1955) method for the entire population; (2) all females that survived through their first adult breeding season (August of their fourth year) bred; (3) the average number of young fledged

did not vary with age of the breeding females; and (4) the sex ratio of young produced was 50:50, male:female. The proportion of fledglings that survived to their first adult breeding season (S_{FB}) was calculated as: $S_{HY} \cdot S_{SY} \cdot S_{TY} \cdot (S_{ATY}^{0.67}) = S_{FB}$, where S_{HY} , S_{SY} , S_{TY} , and S_{ATY} are the annual survival rates for HY, SY, TY, and ATY birds, respectively, of the population. The exponent for survival of ATY birds equals the portion of the year that FY birds had to survive to reach the end of their first breeding season as adults.

If there has been no immigration or emigration, the number of females (number of pairs) at a colony after a given number of years should be equal to: (1) the number of females originally at the colony that survived through the period, plus (2) all female progeny (produced by the original females and by their progeny) that survived to the end of the period. The number in the first group is simply $N_o \cdot (S_{ATY})^x$, where N_o = original number of females (pairs), S_{ATY} = annual survival rate of adults, and x = number of years elapsed. The number of mature offspring produced during the period and surviving at the end of the period was determined by an iterative process. For each succeeding year (n) of the period, the number of adult females (pairs) at the colony (N_n) is equal to the number of adult females surviving from the previous year ($N_{n-1} \cdot S_{ATY}$) plus the number of female young that reached maturity that year ($N_{n-3} \cdot 0.5R_F \cdot S_{FB}$), where N_{n-3} is the number of adult females that produced young that matured in year n , R_F is the average number of young fledged per pair for the population, and S_{FB} is the proportion of fledglings that reached maturity. The process of determining the fledging rate (R_F) necessary to sustain the observed growth at the colony involved substituting trial values of R_F and tracing the growth of the colony over the given number of years.

The following collections were searched for egg sets and skins: MVZ—Museum of Vertebrate Zoology, University of California, Berkeley; CAS—California Academy of Sciences, San Francisco; San Diego Natural History Museum, San Diego, California; WFVZ—Western Foundation of Vertebrate Zoology, Los Angeles, California; San Bernardino County Museum, California; University of Puget Sound, Tacoma, Washington; and Thomas Burke Museum, University of Washington, Seattle.

RESULTS

History of nesting.—Although Caspian Terns were suspected of nesting in Pacific Coast states as early as the late 1800's (in Ridgway 1877, Grinnell 1915), it was not until the turn of the century that nesting was confirmed. In 1899 Bailey (1902) reported large numbers of Caspian Terns nesting among gulls at Tule Lake, California, and Finley (1907) found them among

gulls on adjacent Lower Klamath Lake, Oregon in 1905. Either birds from these areas then colonized other freshwater marshes or previous nesting had been overlooked, for within 15 yr they were reported nesting in the Sacramento Valley of California (55 egg sets, MVZ, CAS, WfVZ; Wetmore 1919) and in southeastern Oregon (Willett 1919; 7 egg sets, MVZ), and by 1915 they were suspected of nesting in the San Joaquin Valley and at Goose Lake, California (Linton 1908, Lamb and Howell 1913, Dawson 1916, Tyler 1916, Mailliard 1927, Van Rossem 1933). Also during this period several lakes and large tracts of marsh were reclaimed for agriculture, and birds responded by gradually shifting their nesting to new, human-created habitats. These included the levees associated with salt evaporation ponds in San Francisco Bay (DeGroot 1931), islands in the recently created Salton Sea (Grinnell 1908, Pemberton 1927), and islands in several reservoirs and lakes (Kitchen 1930; 31 egg sets, MVZ). Terns were also found nesting on sand islands in Scammon's Lagoon, Baja California during this period (Bancroft 1927). By 1930 no large colonies existed away from the Pacific Coast, but birds continued to nest in small numbers at several scattered locations in interior Washington, Oregon, and California. Between 1930 and 1940 several colonies grew in size, but the nesting distribution of the species remained relatively fixed. The colony at San Francisco Bay increased from 150 to 400 pairs between 1926 and 1943 (DeGroot 1931, Miller 1943), and two smaller colonies became established in adjacent parts of the Bay. Beginning in the early 1940's a major expansion began in the Pacific Coast population. Three new sites were colonized in western Nevada (Alcorn 1946, Marshall 1951, Marshall and Giles 1953); birds began nesting on salt pond levees in San Diego Bay (ca. 1940) and adjacent areas (Emblen 1954, Kirven 1969; 3 egg sets, WfVZ); and in 1957 they began nesting on dredge-spoil islands in coastal Washington (Alcorn 1958). Concomitantly, birds ceased to nest at Salton Sea (ca. 1960, G. McCaskie pers. comm.) and throughout the Sacramento-San Joaquin Valley (ca. mid-1950's). During the mid-1960's and continuing through the 1970's another period of colony expansion occurred. Three new colonies were formed in San Francisco Bay during this period, and overall numbers increased from around 400 pairs to over 1,500 pairs (Gill 1977, M. Rig-

ney pers. comm.). Colonies in Grays Harbor and Willapa Bay, Washington shifted sites locally several times, but the overall population increased from 50 pairs in 1957 to 3,000 pairs by 1981 (Alcorn 1958; Penland 1976, 1981; Peters et al. 1978; D. Martin and E. Cummins pers. comm.). Also during this period colonies were discovered at Humboldt Bay and Moss Landing, California (S. Harris pers. comm., Baldrige et al. 1970).

Approximately 6,000 pairs of Caspian Terns presently nest in 24 colonies at 20 sites along the Pacific Coast (Table 2). This represents almost a 74% increase over the numbers reported at these sites in the early 1960's. Birds no longer nest at 18 sites (all interior) from which breeding records exist, and only one area, Humboldt Bay, experienced a significant decrease in numbers of breeding terns during the past 20 yr, down from 150 pairs in 1964 to 27 pairs in 1969. The largest colonies now occur along the coast and are associated with human-created habitats: those in San Diego Bay, Moss Landing, and San Francisco Bay, California occur on salt pond levees, while that in Grays Harbor, Washington occupies a sand island formed by sedimentation resulting from human-caused changes in the hydrodynamics of the harbor (Peters et al. 1978). The colonies at Scammon's Lagoon and Pyramid Lake are presumed active, but their current status was not determined (Table 2). Pacific Coast Caspian Terns are evidently still expanding their range northward (Campbell 1971; Gibson 1981, 1982; Hunn and Mattocks 1981) and, given suitable habitat, could soon be found nesting along coastal British Columbia or southeast Alaska.

Survivorship and longevity.—The annual survival of SY, TY, and ATY birds was 0.79, 0.87, and 0.89, respectively (i.e. 79% of SY birds entered their TY). The survival rate for HY birds was 0.82 for the 4-month period between fledging and the end of their first calendar year, which would project to an annual survival rate of 0.55. Based on the annual ATY mortality rate ($11.0\% \pm 1.5\%$ SE), the mean breeding life expectancy in the Pacific Coast population was 8.6 yr.

Age-related movements.—Between fledging and first breeding, Pacific Coast Caspian Terns exhibit distinct age-related seasonal movements. Of the 192 HY birds recovered, 78% were recovered at or near their natal colonies (Table 3) and represent almost entirely birds

TABLE 2. Current status of Pacific Coast Caspian Tern colonies.

Location	Habitat association	Number of pairs	Source
Mexico			
Scammon's Lagoon	Salt pond levees	50-60 (1975) ^a	B. Massey (pers. comm.)
California			
Clear Lake	Islands in natural lake	200 (1979)	E. O'Neill (pers. comm.)
Harston Reservoir	Islands in reservoir	10-20 (1979)	A. Lapp (pers. comm.)
Big Sage Lake	Islands in reservoir	75 (1979)	E. O'Neill (pers. comm.)
Meiss Lake	Islands in reservoir	50 (1979)	E. O'Neill (pers. comm.)
Goose Lake	Islands in natural lake	200 (1979)	D. Winkler (pers. comm.)
Lower Klamath Lake	Islands in natural lake	20 (1979)	E. O'Neill (pers. comm.)
Mono Lake	Islands in natural lake	10 (1979)	D. Winkler (pers. comm.)
Humboldt Bay	Dredge-spoil island	20 (1979)	S. Harris (pers. comm.)
San Francisco Bay ^b	Salt pond levees	1,500 (1981)	M. Rigney (pers. comm.)
Moss Landing	Salt pond levees	160-180 (1979)	T. Harvey (pers. comm.)
San Diego Bay	Salt pond levees	409 (1981)	F. Schaffner (pers. comm.)
Nevada			
Pyramid Lake	Island in natural lake	10-125 (1951-1965)	Woodbury (1966)
Stillwater Pt. Reservoir	Island in reservoir	5 (1977)	D. Winkler (pers. comm.)
Washington			
Grays Harbor	Sand islands	2,157 (1981)	E. Cummins (pers. comm.)
Willapa Bay	Sand islands	500-800 (1981)	E. Cummins (pers. comm.)
Potholes Reservoir	Island in reservoir	100 (1981)	P. Wimberger (pers. comm.)
Oregon			
Columbia River	Natural islands	200 (1978)	Thompson and Tabor (1981)
Idaho			
Magic Reservoir	Natural islands	20 (1977-1980)	L. Peterson and C. Trost (pers. comm.)
Blackfoot Reservoir	Natural Islands	5 (1981)	C. Trost (pers. comm.)

^a Date of census.

^b Composed of five colonies.

TABLE 3. Location of recoveries of Caspian Terns of different age classes during the breeding season (April–August) and nonbreeding season (September–March) in relation to the natal colony.

Age ^b	Within 100-km radius of natal colony ^a			Farther than 100 km from natal colony ^a						Total
	At natal colony	At a different colony		At a colony			Not at a colony			
		N	S	N	S	E	N	S	E	
Hatching year										
Breeding	127 (3) ^c	0	1	0	1	2	8	2	0	141
Nonbreeding	22	0	0	0	2 (1)	0	2	25 (1)	0	51
Second year										
Breeding	1	0	0	0	0	0	0	15	0	16
Nonbreeding	1	0	0	0	0	0	0	39 (2)	1	41
Third year										
Breeding	2	0	1	1	0	1	3	2	0	10
Nonbreeding	1	0	0	0	0	0	1	12	0	14
After third year										
Breeding	33 (5)	0	2	41 (2)	3	0	6	6	3 (1)	94
Nonbreeding	5	0	0	4	0	0	3	33	0	45
Total	192	0	4	46	6	3	23	134	4	412

^a Direction of recovery from natal colony: N = north, S = south, E = east. See text for definition of sectors.

^b Age based on calendar year following banding. All birds banded prior to fledging.

^c Numbers in parentheses refer to numbers of birds of each group that were captured alive and subsequently released. The three Hatching Year birds captured during the breeding season were captured at the colony; we do not know if they fledged. All others are assumed to have returned to the population following release.

that had not fledged. Included among these are five birds recovered the second year in the same 10-min latitude/longitude block in which they were banded. These probably represent HY birds that died before fledging but were not found or reported until spring or summer of the second year when investigators returned to the colony (our experience in San Francisco Bay colonies). Only 21 (14%) of the HY birds recovered at or near the natal colony had actually fledged, as evidenced by their recovery outside of the 10-min latitude/longitude block of banding. These included 6 birds recovered during the nonbreeding season and 15 during the breeding season. Following fledging, HY birds disperse, with some wandering north in late summer before migrating south. Indeed, two HY birds were recovered during the nonbreeding season 800 and 1,500 km north of their natal colonies 2 months following banding. An analysis of recoveries from the San Diego colony, for which the most complete data exist, is indicative of these and other age-related movements between wintering and breeding grounds (Fig. 1).

All recoveries of SY birds away from colonies

during the breeding and nonbreeding seasons came from Mexico except one, which was recovered at the Salton Sea in February, 160 km east of its natal colony (Table 3). Two SY birds were recovered near their natal San Diego colony (Table 3); we do not know if they wintered there (see beyond) or had died previously and were not found until the second year.

By their third summer most birds return north (Fig. 1), and a few may attempt to breed (see also Ludwig 1965). Five of 10 recoveries of TY birds during the breeding season came from colonies (Table 3). Only one TY bird was recovered in Mexico during the summer, and the remaining four were in California and Washington but apparently were not associated with any colonies. During the third winter, most birds return south to wintering grounds (Fig. 1). One was recovered south in Los Angeles, California, a known wintering area (in Gill and Mewaldt 1979, Garrett and Dunn 1981), and 11 were recovered in Mexico. Only two birds were recovered at or north of their natal colonies during this period (Table 3), both during September when birds could have been wandering before migration.

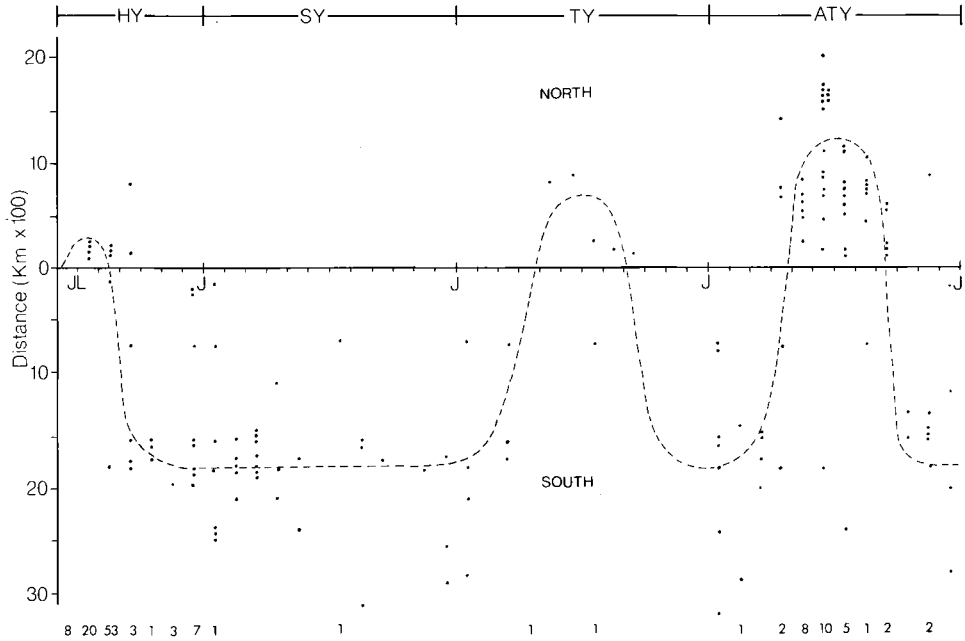


Fig. 1. Age-related seasonal movements of Caspian Terns banded at San Diego Bay, California. Months, beginning with July (JL), appear along the abscissa (J = January). Numbers at the bottom of the figure represent birds recovered at the natal colony each month. The dotted line is fitted by eye and is a schematic representation of the annual cycle of age-related movements between fledging and adulthood. HY = Hatching Year, SY = Second Year, TY = Third Year, and ATY = After Third Year.

During their fourth and subsequent summers the majority of birds return to the breeding grounds; 79 (84%) of 94 ATY birds recovered during the breeding season were associated with active colonies (Table 3). Of the 15 ATY birds recovered farther than 100 km from a colony during the breeding season, several might also have bred, as suggested by circumstances related to the time and location of the recoveries. For instance, of the 6 birds recovered north, 3 were recovered only 127-178 km from an active colony, and 2 were recovered in April and late August and were possibly in migration. The six recoveries farther than 100 km south of a colony during the breeding season (Table 3) were all from mainland Mexico. Two of these were recovered in early April and had probably not yet moved north to the breeding grounds, and two were reported found as skeletons and had probably died during the previous winter. The remaining two were 38 and 48 months old when recovered, and we have no explanation for their being on the wintering grounds during June

and July. The three birds recovered well east of active colonies were all recovered at the Salton Sea, 8-14 yr after terns had ceased to nest there. The Salton Sea may be part of a regular migration route between wintering areas in the Gulf of California and breeding areas near San Diego. It is possible, however, that two of the birds (12 and 15 yr old) had once bred at the Salton Sea colony and still had a predilection to return there during the breeding season.

The distribution of recoveries of ATY birds during the nonbreeding season closely parallels the winter distribution reported by other authors for this species along the Pacific Coast (Kirven 1969, Small 1974, Garrett and Dunn 1981). Of the 45 recoveries during the nonbreeding season, 39 were south of Santa Monica, California; the great majority (31) occurred in Mexico and Guatemala. Of the 6 birds recovered north of Santa Monica, 4 were found in September, and they may have been migrating south from more northerly colonies (2), or still tending volant young near colonies (2).

Plotting recoveries both of birds south of their

TABLE 4. Location of birds of all age classes recovered south of the natal colony and not associated with another colony.

Natal colony	Where recovered															Total		
	Wash- ington formia	Mexico ^a													Guate- mala			
	BAJ	SON	SIN	NAY	JAL	COL	COL	MIC	GUE	CHI	DUR	GUA	GUA	Total				
San Diego, California	9	11	21	11	17	3	4	7	4	1							2	90
San Francisco, California	2	6	2	1	2	2	1	1										18
Humboldt Bay, California	1	1	1	1													1	5
Clear Lake, California	1												1					2
Honey Lake, California		1																1
Washington	1	3	2	5	3	1				1								16
Nevada																	1	1
Idaho																		1
Total	1	6	9	21	30	16	20	5	5	8	7	1	2	3				134

^a States of Mexico arranged by latitude from north to south; the exceptions being Durango (DUR) and Guanajuato (GUA), which are interior states. All others are coastal: Baja California (BA), Sonora (SON), Sinaloa (SIN), Nayarit (NAY), Jalisco (JAL), Colima (COL), Michoacan (MIC), Guerrero (GUE), and Chiapas (CHI).

natal colonies during the nonbreeding season and of those young birds remaining south during the breeding season illustrates the relative importance of various geographic areas to Caspian Terns when not breeding (Table 4). A full 93% of these recoveries were in Mexico, with most reported from the states of Sinaloa, Sonora, Jalisco, and Nayarit. When distances that birds were recovered south of the three major colonies are analyzed, it is clear that those born at the most northerly colony, Grays Harbor, Washington, travel the greatest distance, an average of 2,550 km (SE = 630). Those from San Francisco Bay, California, travel intermediate distances (1,930 km ± 420 SE), and those from San Diego Bay, California, do not travel far to wintering grounds (1,640 km ± 140 SE). The differences among these groups are highly significant (Kruskal-Wallis test for ranked data, $P < 0.005$; Sokal and Rohlf 1969). When the geographic location of the mean distance traveled south from each natal colony and their 95% confidence intervals are mapped, however, there is some overlap, although the Grays Harbor mean lies farthest north and the San Diego mean lies farthest south. This suggests that there may be some segregation on the wintering grounds dependent on natal origin, but the sample sizes for the Grays Harbor and San Francisco colonies are too small to quantify how much mixing occurs on the wintering grounds. We found no indication that birds segregate on the wintering grounds by age class.

Colony fidelity and origin of birds at colonies.—Adult Caspian Terns do not apparently have a strong predilection to breed at their natal colony. Of 79 ATY birds recovered at colonies during the breeding season, 46 (58%) were found at non-natal colonies, while 33 (42%) were associated with the natal colony (Table 3). An additional 3 of 6 birds recovered farther than 100 km north of their natal colony during the breeding season were probably breeding at a non-natal colony, based on the time and place of their recovery.

Among ATY birds that were recovered during the breeding season at colonies other than the natal colony (Table 3), 41 (89%) of 46 were recovered at colonies north of their natal colony (Fig. 2). Of the 5 birds that had moved to colonies south of their natal colony, 1 had moved from Grays Harbor to Humboldt Bay, 2 had traveled from San Francisco Bay to Moss Land-

ing, 1 moved from Pyramid Lake, Nevada to San Francisco Bay, and 1 moved from San Francisco Bay to San Diego Bay.

It would appear that the San Diego Bay colony has been the source of the majority of birds moving north to other colonies (Fig. 2); until comparable numbers of birds have been banded at the other major colonies (Table 1), however, such an assessment of intercolony movements is probably premature. It is apparent, however, that birds from the three coastal California colonies (San Diego, San Francisco, and Humboldt) responded to, or were the major source of, the newly formed colonies at Grays Harbor and Willapa Bay, Washington and that birds from San Diego moved to Humboldt Bay shortly after that colony began. Evidence suggests that at least some birds moved to new colonies after having bred for several years at another colony, natal or otherwise. For instance, the four birds recovered at the Humboldt Bay colony were 13, 10, 8, and 17 yr old when recovered in 1966, 1968, 1969, and 1972, respectively; three were well into adulthood and the fourth had reached potential breeding age when the colony was first reported in 1964. Similarly, birds from San Diego Bay (7) and Humboldt Bay (2) that moved to the Grays Harbor complex of colonies during its expansion (ca. 1970–1976) averaged $8.7 \text{ yr} \pm 3.4 \text{ SD}$ (range = 3–13 yr) when recovered between 1967 and 1974. The two birds that moved to Grays Harbor from San Francisco Bay were 6 and 8 yr old when recovered in 1977 and 1979, respectively. Their first probable breeding year (1975) coincided with the abandonment and relocation of a colony of 600 pairs of terns in Grays Harbor, but we do not know whether these birds were recruited to this colony their first breeding year or during a subsequent year.

DISCUSSION

During the past 20 yr, the Pacific Coast population of Caspian Terns has increased over 70%, and the breeding distribution has changed markedly. We address three questions here. (1) How has the population increase been accommodated within the reproductive constraints of the species? (2) By what means have individual colonies grown and the range of the population extended? (3) How do the dynamics of this population compare with those of other

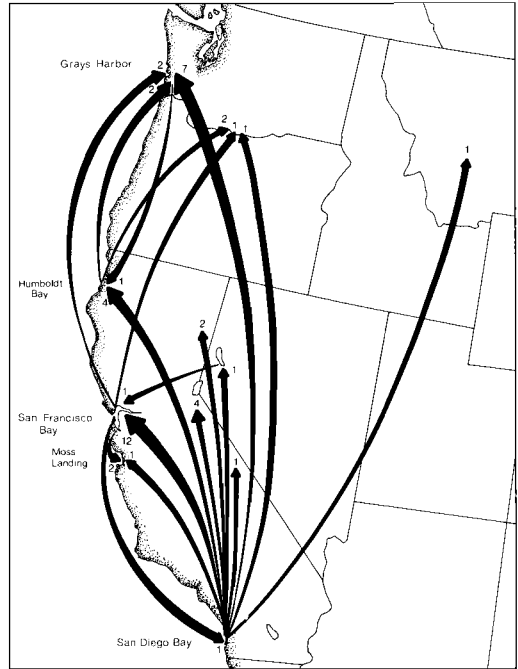


Fig. 2. Location of recoveries of After Third Year Caspian Terns at non-natal colonies during the breeding season ($n = 46$).

geographically distinct populations of Caspian Terns?

To date, all evidence has suggested non-overlapping breeding and wintering areas among the main North American populations (Ludwig 1965, 1968; Shugart et al. 1978). The distribution of recoveries of Pacific Coast terns, including that of a San Diego-born bird in Montana (Fig. 2, Table 4), confirms that all birds nesting west of the continental divide are part of a separate population. Thus, the near doubling of the Pacific Coast population was not from immigration of birds from other populations but resulted instead from intrinsic growth. During the period 1960–1980, when the Pacific population increased from about 3,500 to 6,000 breeding pairs, the annual growth averaged 2.7%. This translates to a fledging rate of 0.64 young per breeding pair necessary for the needed recruitment and is within the range of fledging rates (0.61–1.61) reported for this species from other studies (Ludwig 1965, Kirven 1969, Soikkeli 1973a, Shugart et al. 1978). Indeed, Ludwig (1965) determined that during the period 1960–1964, when the Great Lakes

population was increasing, a fledging rate of 0.79 was sufficient to produce the necessary recruitment to account for the 3.7% average annual increase.

The large increase in the Pacific Coast population has also occurred in conjunction with a notable change in breeding distribution and an expansion of breeding range. Although the numbers of birds breeding in the major colonies at San Francisco and San Diego bays have not decreased during this period, the establishment of larger colonies in Grays Harbor and Willapa Bay has shifted the major breeding concentration northward from California to Washington. The increase in the number of birds at these northern colonies from 50 pairs in 1957 to 3,000 pairs by 1981 could only have resulted from substantial immigration from the southern colonies. For this growth, averaging 18.6% annually, to have been intrinsic, an average 1.9 young per breeding pair would have had to fledge to provide the required recruitment. This is an unlikely occurrence given reproductive constraints of an average clutch size of 2.0–2.5 and a hatching success of 1.53–1.86 young per pair, as reported in several studies (Bergman 1953, Ludwig 1965, Kirven 1969, Soikkeli 1973a, Penland 1976, Gill 1977, Shugart et al. 1978).

How then has this mass immigration been accomplished? One method by which Caspian Terns form new colonies is through "deserting flights." Väisänen (1973) attributed the formation of a group of new colonies in the Gulf of Bothnia, Finland to one such 800-km-long "deserting flight" in which an entire colony moved from the northern Baltic or Gulf of Finland after being disturbed by human activities during World War II. Staav (1979) and Bergman (1980) also recorded the establishment of new colonies by such deserting flights in the Baltic population; here, disturbance from heavy gull predation and from human activities were cited as the most probable factors influencing the moves. Because the dramatic growth of the Washington colonies has not been accompanied by any corresponding decrease in any other major colony, it does not appear that the increase in the northern colonies can be attributed to massive, long-distance deserting flights.

Nevertheless, considerable numbers of birds moved from natal colonies to other breeding areas when the population was rapidly in-

creasing and extending its breeding range (Fig. 2; Table 3). Indeed, only 42% of adults recovered at breeding areas during the summer were found at their natal colony (Table 3). This was comparable to the fidelity found by Staav (1979) in the growing population of Caspian Terns in the Baltic Sea, in which 44% of the adults bred at their natal colony. Cuthbert's (1981) study of the Great Lakes population showed that the rate of dispersal was higher among first-time breeders than among established breeders: only 10% of first-time breeders nested at their natal colony, but 58% of 75 birds banded as adults were found breeding at the colony where they had bred before. Staav (1979) also found in the Baltic population that undisturbed adults showed strong fidelity to the colony where they had bred the previous year; only when a colony had been heavily disturbed was there evidence that established breeders had moved to a new location. Greenwood (1980), in his review of mating systems, dispersal, and philopatry, stated that the individuals that are forced to disperse are often those that are younger, weaker, and socially subordinate. In other colonial Larids, newly established colonies that are increasing rapidly have a greater proportion of young birds than do long-established colonies (Coulson and White 1960), and young birds joining colonies are more attracted to dense concentrations of established breeders than to the less densely populated colonies, although they can more easily establish territories in the latter areas (Chabrzyk and Coulson 1976). All these findings suggest that the recruits to the new, growing colonies of Caspian Terns along the Pacific Coast were primarily first-time breeders, birds that may have had difficulty establishing territories in the more populated colonies at San Diego and San Francisco bays.

It is not clear what factors instigated the terns' establishment of new colonies along the Pacific Coast and the marked shift in distribution. Habitat instability, human disturbance, and low reproductive success are three factors that previously have been reported to contribute to low colony-site fidelity and extensive intercolony movement in Caspian Terns (Väisänen 1973; Penland 1976, 1981; Shugart et al. 1978; Staav 1979; Bergman 1980; Cuthbert 1981; and others). None of these, however, appears to have played a major role in the range expan-

sion of the Pacific Coast population. During the period when the population was rapidly expanding (1960–1980), there was no overall loss of nesting habitat and, in fact, three new colonies were formed in San Francisco Bay (Gill 1977, Gill and Mewaldt 1979). Disturbance has caused local shifts in colonies in Washington (Penland 1976, 1981; Peters et al. 1978) and San Francisco Bay (our observations), but there is no evidence that it has caused large numbers of birds to move *en masse* to more distant colonies. Similarly, widespread low reproductive success has not been witnessed at any of the major colonies during this period; instead, reproduction has been sufficient almost to double the size of the population during the period of range extension.

We believe a key to discovering the impetus for the northward shift and growth in the Pacific Coast population lies in understanding the dynamics of the San Diego Bay colony. During the period when the population was expanding, when colonies at both San Francisco Bay and Washington were growing, the size of the colony at San Diego Bay remained stable (about 400 pairs) despite reproductive success ample to support growth of the colony (Kirven 1969, Evans 1973, Schaffner 1982, H. Ohlendorf in litt.). What factors allowed the Pacific Coast population to increase yet promoted the dispersal of birds from the San Diego Bay colony still need to be determined. Of equal importance is gaining insight into the methods by which first-time and experienced breeders select these new and distant colonies.

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