



FEATURE ARTICLES

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REDISTRIBUTION AND GROWTH OF THE CASPIAN TERN POPULATION IN THE PACIFIC COAST REGION OF NORTH AMERICA, 1981–2000

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Abstract. We examined nesting distribution and demography of the Pacific Coast population of Caspian Terns (*Sterna caspia*) using breeding records and band recoveries spanning two decades since the first population assessment. Since 1980, population size has more than doubled to about 12 900 pairs, yet the proportion of the population nesting at inland (18%) versus coastal sites (82%) has remained constant. Although the breeding range of the Pacific Coast population has expanded northward into Alaska and farther south in Mexico, there was no net latitudinal shift in the distribution of breeding pairs or new colonies. The distribution of breeding birds among areas changed dramatically, however, with 69% of breeding terns now nesting in Oregon (primarily in the Columbia River estuary) versus 4% during the late 1970s. During the past 20 years, there has continued to be a greater proportion of Caspian Terns breeding at anthropogenic sites compared to natural sites. Estimated annual survival rates for hatch-year and after-third-year birds during 1981–1998 were greater than during 1955–1980, consistent with the higher rate of population increase in recent decades. Fecundity required to maintain a stable population ($\lambda = 1$) was estimated at 0.32–0.74 fledglings pair⁻¹, depending on band recovery probabilities for sub-adults. Caspian Terns readily moved among breeding sites and rapidly colonized new areas; however, a greater concentration of breeding Caspian Terns among fewer colonies in response to anthropogenic factors is an important conservation concern for this species.

Key words: anthropogenic effects, Caspian Tern, population size, range expansion, redistribution, *Sterna caspia*, survival rates.

Redistribución y Crecimiento de la Población de *Sterna caspia* en la Región de la Costa Pacífica de América del Norte entre 1981 y 2000

Resumen. Se examinó la distribución de anidamientos y la demografía de la población de *Sterna caspia* en la costa del Pacífico usando registros reproductivos y anillos recobrados de aves marcadas durante dos décadas desde la primera evaluación poblacional. Desde 1980 el tamaño poblacional se duplicó a 12 900 parejas, aunque la proporción de la población anidando en la zona interior (18%) versus la zona costera (82%) permaneció constante. A

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pesar de que el rango reproductivo de la población costera del Pacífico se expandió hacia el norte llegando a Alaska y hacia el sur hasta México, no hubo un cambio latitudinal neto en la distribución de parejas reproductivas o de nuevas colonias. Sin embargo, la distribución de aves reproductivas entre las áreas cambió dramáticamente, con un 69% de los individuos reproductivos de *Sterna caspia* anidando ahora en Oregón (principalmente en el estuario del Río Columbia) comparado con un 4% a fines de la década del 70. Durante los últimos 20 años continuó habiendo una mayor proporción de individuos de *Sterna caspia* anidando en sitios con actividad antropogénica en comparación con áreas naturales. Las tasas de supervivencia anual para aves con menos de un año y aves con más de tres años fueron mayores durante 1981–1998 que durante 1955–1980, lo que es consistente con una mayor tasa de crecimiento poblacional en décadas recientes. La fecundidad requerida para mantener estable la población ($\lambda = 1$) se estimó en 0.32–0.74 volantones producidos por pareja, dependiendo de la probabilidad de recuperación de anillos en aves subadultas. *Sterna caspia* es capaz de moverse entre sitios reproductivos y coloniza nuevas áreas rápidamente. No obstante, una mayor concentración de individuos reproductivos de *Sterna caspia* en unas pocas colonias, como respuesta a factores antropogénicos, es una importante preocupación para la conservación de esta especie.

INTRODUCTION

Many species of terns (Sterninae) nest in unstable habitats (McNicholl 1975) that are susceptible to flooding and erosion or to desiccation of nearby shallow-water foraging areas. Terns, especially Caspian Terns (*Sterna caspia*), that use such habitats tend to exhibit low philopatry relative to other seabirds (Gill and Mewaldt 1983, Cuthbert 1988, Cairns 1992, Monaghan 1996). This trait has likely facilitated the dramatic changes in distribution of the Caspian Tern population in the Pacific Coast region of North America during the twentieth century (Gill and Mewaldt 1983, Wires and Cuthbert 2000).

Prior to 1920, Caspian Terns in the western United States were known to breed only at inland lakes and marshes (Bailey 1902, Finley 1907, Wetmore 1919, Willett 1919); they were not documented to nest in coastal habitats in this region until the late 1920s and 1930s, when breeding was first recorded in San Francisco Bay, California (DeGroot 1931, Miller 1943). By the 1950s, a major northward range expansion had begun with establishment of new colonies in coastal Washington (Marshall 1951, Marshall and Giles 1953, Alcorn 1958). This expansion continued through 1980, as documented by Gill and Mewaldt's (1983) review of population status for the prior 25 years. In addition to this range expansion, the size of the Pacific Coast population of Caspian Terns increased about 70% during 1960–1980, to approximately 5700 pairs at 23 discrete colonies (Gill and Mewaldt 1983). During this period of range expansion and population increase, many breeding terns shifted from nesting in small inland colonies at natural sites to large coastal colonies at

anthropogenic sites (e.g., islands created by dredged sediment). The largest breeding concentrations of Caspian Terns in the early 1980s were in Grays Harbor, Washington (ca. 2200 pairs or 37% of the Pacific Coast population), and San Francisco Bay, California (ca. 1500 pairs or 25% of the Pacific Coast population; Gill and Mewaldt 1983).

Gill and Mewaldt (1983) also conducted a demographic analysis of the Pacific Coast population of Caspian Terns on the basis of recoveries of banded birds. They estimated that 57% of fledglings survived to breeding age (fourth year; Ludwig 1965), with a subsequent annual adult survival rate of 89%. Given these survival rates, they estimated that an average fecundity of 0.64 fledglings pair⁻¹ year⁻¹ was required to support the observed average annual population growth rate (λ) of 1.027 during 1960–1980. Gill and Mewaldt (1983) postulated that growth in this population was likely from intrinsic production, but that the establishment and rapid growth of certain colonies, particularly at coastal sites, required extensive immigration of birds from other colonies.

Recent studies (Wires and Cuthbert 2000, Roby et al. 2002, Shuford and Craig 2002) indicate that the Pacific Coast population of Caspian Terns has continued to increase since Gill and Mewaldt's (1983) population assessment, with proportionally more breeding terns concentrated at fewer coastal colonies. This, along with increasing conflicts with fish stocks of conservation concern (i.e., juvenile salmonids [*Oncorhynchus* spp.] in the Columbia River basin; Collis et al. 2001, Roby et al. 2002), prompted our investigation into the dynamics of the Pacific

Coast population of Caspian Terns over the past two decades. Here we evaluate the recent and unprecedented build-up of nesting colonies on the northern coast of Oregon, discuss the causes for colony site abandonment and initiation, and report the results of a demographic analysis to assess recent trends in survival and population growth rates. We present general population trends for Caspian Terns within the Pacific Coast region; for more in-depth colony-by-colony descriptions, including population estimates, management activities, threats, and conservation recommendations, see Shuford and Craig (2002). Our objectives here are to evaluate the characteristics of growth in this population, assess whether current fecundity could support continued population growth, and identify gaps in current data that may limit a comprehensive demographic analysis. The latter is of particular interest given the conservation concerns regarding this tern population and its prey.

METHODS

We compiled estimates of Caspian Tern colony size (breeding pairs) in the Pacific Coast region of North America for two periods: 1979–1981 and 1997–2000. Consistent with Gill and Mewaldt (1983), we defined the Pacific Coast region as including Alaska, British Columbia, Washington, Oregon, Idaho, Nevada, California, and northwestern Mexico (Fig. 1). Although Wires and Cuthbert (2000) included Wyoming and Utah and Shuford and Craig (2002) included Montana in the range of the Pacific Coast/Western population of Caspian Terns, there were no band return data that link colonies in these three states with colonies in our study area. Even if Caspian Terns nesting in Montana, Wyoming, and Utah were included in our analyses, they would collectively total less than 3% of the Pacific Coast population.

Colony size estimates for 1979–1981 are from Gill and Mewaldt (1983), with some corrections, and estimates for 1997–2000 are from Shuford and Craig (2002). Methods used to estimate colony sizes were not consistent among years or colonies, and are described in detail by Shuford and Craig (2002) and, for the Columbia River estuary, by Collis et al. (2002). Methods used included direct counts on site or from aerial photographs of nests or breeding pairs during incubation and of chicks just prior to fledging, counts of adults on colony multiplied by 0.62 to

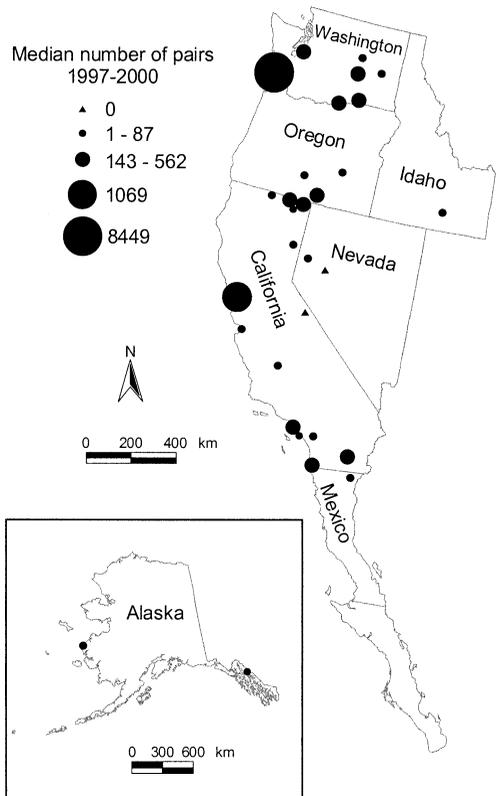


FIGURE 1. Locations and median sizes of active Caspian Tern colonies in the Pacific Coast region of North America, 1997–2000. Colonies were mapped if the site was occupied by at least one pair in one of the four years (Shuford and Craig 2002). Multiple colonies within the Columbia River estuary, San Francisco Bay, and Tulare Basin are represented by one dot.

approximate the number of breeding pairs (H. Carter, G. McChesney, D. Jacques, C. Strong, M. Parker, J. Takekawa, D. Jory, and D. Whitworth, unpubl. data), and estimates of the range of breeding pairs (in which case the midpoint was used). Because not all colonies were surveyed within a single year, we used a series of years to estimate the population size during each of the two periods noted above. For colonies with estimates available for multiple years within each period, we used the median. Survey effort varied by period; greater effort was likely expended during the second of the two periods (1997–2000). Although survey effort has apparently increased in recent years, the much higher number of terns nesting in the Columbia River estuary (which drives recent trends for the Pacific Coast population as a whole) is not a result

of changing census efforts (Shuford and Craig 2002, G. Dorsey, US Army Corps of Engineers, pers. comm.). Finally, some of the estimates of colony size are rough approximations, particularly smaller colonies that were visited infrequently. The effect of these approximations on our summary of population trend, however, is minor because those colonies represent a small fraction of the total number of terns counted in surveys for each period.

To estimate population vital rates (i.e., age-specific survival and population growth), we analyzed band recoveries from dead Caspian Terns (originally banded as chicks) that were reported to the U.S. Bird Banding Laboratory (U.S. Geological Survey) between 1955 and 1998. To compare patterns reported by Gill and Mewaldt (1983) to those in recent years, we divided the recoveries into two periods: 1955–1980 and 1981–1998. Band recoveries from these two respective periods included 248 recoveries from 15 026 banded individuals and 96 recoveries from 5056 banded individuals. Our sample sizes for banded birds and recoveries for 1955–1980 are less than those reported by Gill and Mewaldt (1983); thus, although this portion of our analysis spans the same period as theirs, the data set we used was not exactly the same because certain data could not be verified. Caspian Tern chicks were banded prior to fledging in California, Idaho, Nevada, Oregon, and Washington. Recoveries of banded birds were from these states plus Alaska and Mexico. Tern age at the time of band recovery was categorized into one of four possible age classes: hatch-year (HY), second-year (SY), third-year (TY), and after-third-year (ATY). All band recoveries used in analyses were from birds that had fledged and, for HY birds only, were recovered outside the 10' latitude and longitude block of the colony where they were banded.

We also used band recoveries to quantify the proportion of adults breeding at locations other than their natal colonies. A recovered banded bird was assumed to be breeding at the time of death if the bird was recovered during the breeding season (May–July), was of breeding age (ATY), and was recovered either (1) within 25 km of an active breeding colony, (2) within an enclosed water body where terns were nesting, or (3) in a river or estuary downstream of an active colony. Although these data provided insight into some intercolony movements, band re-

covery effort was not systematic, equal among colonies, or inclusive of all colonies. Therefore, we did not use multistate mark-recapture models to quantify transition probabilities among colonies. Also, these results were not used to infer the degree of natal philopatry among individuals because it is not known where banded birds may have nested prior to recovery at a particular colony (use of multiple sites among years has been noted for other tern species; Lebreton et al. 2003).

SURVIVAL RATE AND POPULATION GROWTH

We estimated annual survival rates using Seber's (1970) parameterization of the recovery model in program MARK (White and Burnham 1999). We classified survival and recovery parameters for two groups representing the periods 1955–1980 and 1981–1998. We constructed models where survival rate varied by age (S_a), age and group (S_{a*g}), and age with group as an additive effect (S_{a+g}). Our most complex model included survival rate varying by time with an additive effect of age (S_{a+t}) and with recovery rate varying by group (R_g).

We were not able to estimate age-specific recovery probabilities because all banded individuals were HY birds (Francis 1995, Danchin et al. 1995). Given the postbreeding dispersal patterns of Caspian Terns, differential recovery rates among age classes would be expected. In particular, subadult birds generally remain on the wintering grounds in Mexico and Central America, where band recovery and reporting rates are almost certainly lower than for adult birds that return north to the breeding colonies (Gill and Mewaldt 1983). Because estimates of HY and SY band-recovery rates were not available for this population, we simulated the effect of various recovery rates as a fraction (p) of recovery rate for TY and ATY birds, $R_{HY,SY} = p * R_{TY,ATY}$, where $p \in (0.25, 0.50, 0.75, 1.0)$. Therefore, we provide a range of survival rates for HY and SY birds, depending on differences in recovery probabilities between age classes.

Goodness of fit for the model $S_{a*g} R_g$ was tested using Pearson chi-square implemented in program SURVIV (White 1983). Cells with expected values less than five were pooled within ages and across years. In older age classes (>14 years) additional pooling was necessary across ages. We calculated the degree of overdispersion (\hat{c}) with total chi-square divided by degrees of

freedom. We used Akaike’s Information Criterion corrected for small samples (AIC_c) to compare models in terms of parsimony (Burnham and Anderson 1998).

We did not consider the effect of band loss on estimates of survival rate within any of these models. We refrained from band loss corrections because we did not have an estimate of band loss for this population, and when Gill and Mewaldt (1983) applied a correction for band loss from a Great Lakes population of Caspian Terns (Ludwig 1981), their survival estimates remained unchanged.

For population growth analysis, we used a Leslie matrix (based on a postbreeding census; Caswell 1989) to determine the average number of fledglings raised per breeding pair in order to achieve the population growth rate observed from 1980 to 1998. We used a deterministic four-by-four matrix (M) of survival and recruitment rates to calculate the asymptotic annual population growth rate λ (the dominant eigenvalue),

$$M = \begin{bmatrix} 0 & 0 & 0 & F_{ATY} \\ S_{HY} & 0 & 0 & 0 \\ 0 & S_{SY} & 0 & 0 \\ 0 & 0 & S_{TY} & S_{ATY} \end{bmatrix}$$

In this model we assumed birds began breeding at age 4 (ATY), after which age-specific fecundity and survival were constant (admittedly both are questionable assumptions, but insufficient data exist for more complex modeling of population vital rates in this population). Survival rates were those produced using select models from the band recovery analysis (models $S_{a+g} R_g$, and $S_{a+g} R_{a(p)+g}$, where $p \in [0.25, 0.5, 0.75, 1.0]$). For a range of fecundities (F_{ATY}), we determined the dominant eigenvalue of M representing the population growth rate $\lambda_{F(ATY)}$.

RESULTS

NUMBER AND DISTRIBUTION OF BREEDING BIRDS

The Pacific Coast population of Caspian Terns has increased markedly during the past 20 years. Population size more than doubled, reaching an estimated 12 922 breeding pairs during 1997–2000 (Table 1). Because of unequal survey effort and incomplete coverage of all areas, it was difficult to assess the change in the number of colonies between 1979–1981 and 1997–2000.

The large increase in breeding pairs, however, was not simply an artifact of unequal survey effort; the increase also was evident at those colonies surveyed during both periods (5739 breeding pairs during 1979–1981 versus 12 572 breeding pairs during 1997–2000; Table 1). Only 33% of the sites that were surveyed during 1979–1981 and 1997–2000 were occupied by breeding terns during both periods, indicating the ephemeral use of many of these colony sites.

During 1997–2000, fewer colonies were located on the coast (18, or 42%) than inland (25, or 58%), but coastal colonies averaged much larger (mean of median counts [range of median counts] = 589 [1–7740]) than inland colonies (mean of median counts [range of median counts] = 93 [0–562]), and included 82% of individuals from the population (Table 1). These patterns were similar to those during 1979–1981, when only 43% of colonies but 84% of the population were coastal (Table 1). Also, the largest colonies occurred on artificial substrates both during 1979–1981 (Gill and Mewaldt 1983) and during 1997–2000.

Although Caspian Terns continued to expand their breeding range northward since 1980 and have recently been recorded nesting in Alaska (McCaffery et al. 1997), there was no consistent northward or southward trend in the distribution of the breeding population during the past 20 years. Instead, numbers of breeding birds shifted both northward from California and southward from Washington to Oregon (Fig. 1). Oregon was the area with the greatest increase in number of breeding birds between 1979–1981 and 1997–2000 (4151% increase), whereas there was a net decrease in breeding pairs for all other areas combined. During 1979–1981, most of the Pacific Coast population was divided between Washington (51%) and California (45%). The large influx of birds into the Columbia River estuary over the past 20 years, however, has resulted in 69% of the Pacific Coast population residing in Oregon, compared to 4% before 1980.

The greatest recorded changes in numbers of breeding birds occurred in Washington and Oregon. In Washington, large coastal colonies on islands in Grays Harbor (estimated 3590 pairs in 1987) and Willapa Bay (approximately 1500 pairs in 1982; Speich and Wahl 1989), were abandoned by 1989 and remained inactive throughout the 1990s (Penland 1982; M. Zahn,

TABLE 1. Estimated median numbers (range in parentheses, when available) of breeding pairs of Caspian Terns at colonies in the Pacific Coast region of North America (Alaska, Washington, Oregon, Idaho, Nevada, California, Mexico; Fig. 1) during 1979–1981 and 1997–2000. British Columbia, Canada, was excluded because the colony location of breeding activity by Caspian Terns remains unconfirmed. Blank entries indicate that no survey was conducted or no data are available, and zeros indicate that a survey was conducted but no evidence of nesting was observed. For areas where individual colony locations are not listed, the number of colonies is noted in parentheses, and the median presented as the sum of colony medians. Totals are likely underestimates because of incomplete surveys at some sites in some years, and in some geographic regions in all years (e.g., Mexico). For a comprehensive list of colonies during these periods see Shuford and Craig (2002).

	1979–1981 ^a	1997–2000 ^b
Alaska (all colonies coastal)		
Neragon Island, Yukon-Kuskokwim Delta		3 ^c
Twin Glacier Lake, Taku Inlet, southeast Alaska		4 ^d
Washington		
Coastal		
Commencement Bay, Pierce Co.	0	522 (423–620)
Grays Harbor, Grays Harbor Co.	2157	0 (0)
Willapa Bay, Pacific Co.	650	0 (0)
Inland		
Crescent Island, Walla Walla Co.	0	562 (357–614)
Banks Lake, Grant Co.		10
Potholes Reservoir, Grant Co.	100	205 (150–259)
Sprague Lake, Adams Co.		35 (20–50)
Oregon		
Coastal		
Columbia River Estuary, Clatsop Co. (3 colonies)	0	8449 (7151–9728)
Inland		
Threemile Canyon Island, Morrow Co.	210	249 (210–354)
Malheur Lake, Harney Co.		48 (25–192)
Crump Lake, Warner Valley, Lake Co.		155
Summer Lake, Lake Co.		27 (16–38)
California		
Coastal		
Humboldt Bay	20	
San Francisco Bay (12 colonies)	~1500	1069 (150–1320)
Moss Landing, Monterey Co. (2 colonies)	105	15 (0–80)
Bolsa Chica, Orange Co. ^e	0	55 (40–175)
Pier 400, Los Angeles Harbor, Los Angeles Co.	0	198 (25–336)
South San Diego Bay, San Diego Co.	409	291 (198–380)
Inland		
Meiss Lake, Siskiyou Co.	50	22 (16–27)
Lower Klamath National Wildlife Refuge, Siskiyou Co.	20	0 (0)
Clear Lake National Wildlife Refuge, Modoc Co.	200	149 (68–242)
Goose Lake, Modoc Co.	200	143 (4–310)
Big Sage Reservoir, Modoc Co.	75	48 (0–62)
Honey Lake, Lassen Co.	15	87 (82–152)
Mono Lake, Mono Co.	12	0 (0–8)
Tulare Basin, Kings Co. (6 colonies)		24 (0–153)
Lake Elsinore, Riverside Co.		14
Salton Sea, Imperial Co.	0	506 (207–1200)
Idaho		
Magic Reservoir, Camas and Blaine Counties	20	
Blackfoot Reservoir, Caribou Co.	5	
Minidoka National Wildlife Refuge, Cassia Co.		
Nevada		
Carson Sink, Churchill Co.		0 (0–685)
Anaho Island National Wildlife Refuge, Washoe Co.	6	1 (0–5)
Stillwater Point Reservoir, Churchill Co.	5	0 (0)

TABLE 1. Continued.

	1979–1981 ^a	1997–2000 ^b
Mexico ^f		
Cerro Prieto geothermal ponds, Mexicali Valley (inland)		30 (0–34)
Pacific region totals		
Breeding pairs	5759	12 922
Number of known colonies	23	43

^a From Gill and Mewaldt (1983) with some modifications (see Shuford and Craig 2002).

^b All data from Shuford and Craig (2002).

^c McCaffery et al. (1977).

^d J. Johnson, U.S. Fish and Wildlife Service, pers. comm.

^e Counts are of total nest attempts, which likely overestimates nesting pairs because of reneating by failed breeders.

^f Cerro Prieto was the only site documented during 1997–2000. Between 1988 and 1997 Caspian Tern breeding was suspected at Montague Island (northern Gulf of California; Shuford and Craig 2002) and confirmed at Laguna Figueroa, Laguna Oja de Liebre, and Laguna San Ignacio (estuaries along the Baja California coast; Massey and Palacios 1994, Danemann and Carmona 2000, Shuford and Craig 2002).

unpubl. data; C. Sundround, J. Smith, and E. Cummins, unpubl. data). In Oregon, two new coastal colonies became established in the Columbia River estuary since 1980 and collectively grew to over 9000 pairs by 2000. All Caspian Terns breeding in the Columbia River estuary relocated to one site, East Sand Island, by 2001 (Roby et al. 2002).

IMMIGRATION AND EMIGRATION

Movements by individual Caspian Terns among colonies in the Pacific Coast region were frequent between 1980 and 2000, as was the case previously (Gill and Mewaldt 1983). Of the 35 on-colony recoveries of adults banded as chicks, 77% were not at their natal colony. Most of the non-natal colony returns (11 of 27, or 41%) were from adults recovered at the Rice Island colony in the Columbia River estuary during 1997–2000. These adults had been banded as chicks at the Sand Island colony in Grays Harbor, Washington, during the late 1970s or early 1980s, consistent with the shift in distribution of breeding birds to the Columbia River estuary. These band recovery data are biased, however, because a greater effort to recover bands was made at colonies in the Columbia River estuary than elsewhere. Nonetheless, six additional banded terns from Grays Harbor were recovered during the breeding season on or near four other colony sites in eastern Oregon, central California, and southern California, plus one in Alaska. Additional exchanges of individuals among colonies included four chicks banded at southern

California colonies that were recovered at colonies in central California, northern Oregon, and northern Washington. The remaining six individuals were banded and recovered at southern California colonies. Overall, there was no consistent latitudinal trend in the occurrence of breeding birds at non-natal colonies.

DEMOGRAPHIC ANALYSIS

Survival rates. Annual survival rates of Caspian Terns were estimated using the recovery model $S_{a+g} R_g$, which accounted for the effects of age (HY, SY, TY, ATY) and year grouping (1955–1980 and 1981–1998). This model was selected on the basis of a Pearson chi-square test pooled to examine age and year effects ($\chi^2_{97} = 35.9$, $P > 0.99$, $\hat{c} < 1.0$) and selected according to rank of AIC_c values uncorrected for lack of fit (Table 2). Our estimates of HY survival during the period 1955–1980 averaged 76% (95% CI = 71–81%), which was 21% higher than that reported by Gill and Mewaldt (1983; Table 3) for the same period. Our estimate of HY survival during 1981–1998 averaged 86% (95% CI = 76–93%; Table 3). Furthermore, survival estimates of ATY birds also increased between 1955–1980 and 1981–1998 (Table 3). Greater HY and ATY survival rates during 1981–1998 compared to 1955–1980 is concordant with the highest ranking model, $S_{a+g} R_g$, which allowed survival rate to vary by period. Survival rates of TY and ATY terns were consistently greater than those for HY and SY terns (Table 3).

TABLE 2. List of band-recovery models used ($\hat{c} = 1.0$) to estimate survival rates of Caspian Terns in the Pacific Coast population of North America. The various models included the effects of age (a), year (t), and recovery period (g ; 1955–1980 or 1981–1998) and their additive (+) or interactive (*) effects. Models were ranked according to Akaike’s Information Criterion adjusted for small samples (AIC_c). ΔAIC_c is the difference in AIC_c between a given model and the best-approximating model. AIC_c weights indicate the relative likelihood of a given model and sum to 1.

Model	Deviance	No. of Parameters	ΔAIC_c^a	AIC_c weight
$S_{a+g} R_g$	501.63	7	0	0.70
$S_{a*g} R_g$	498.65	10	3.0	0.15
$S_a R_g$	506.78	6	3.1	0.15
$S_{a+t} R_g$	439.92	48	20.5	0.00

^a The lowest AIC_c value in the analysis was 5234.1

The estimated average breeding lifespan of Caspian Terns in this population, given an annual survival of 0.91 for ATY birds, was 11 years (based on the formula $[2-M]/2M$, which assumes age-constant mortality $[M]$; Gill 1990). The maximum age of a Caspian Tern recovered during this study was 25 years.

As mentioned above, band recovery rates for HY and SY birds were likely less than for TY and ATY birds. Simulations in which band recovery rate was varied for HY and SY birds as a proportion of recovery rate of TY and ATY birds ($R_{HY,SY} = p * R_{TY,ATY}$) resulted in considerable variation in estimates of HY and SY survival. For this analysis we used the model $S_{a+g} R_{a+g}$, where survival and recovery rates were allowed to vary with age and time period. With this model, HY and SY survival-rate estimates varied by up to 50% (Fig. 2) and introduced similar variation in estimates of average fecundity required to maintain the observed average annual population growth rate (Fig. 3).

Population trends and breeding success. Between 1980 and 2000, the Pacific Coast popu-

lation of Caspian Terns grew at an average rate of about 4.3% year⁻¹. The precision of and variation about this average are unknown because of uncertainty in some estimates of colony size, but are expected to be small, as noted in the Methods. Given the above population vital rates, the Leslie matrix recovery simulations indicated that a fecundity of 0.50 to 1.15 young fledged per nesting pair was required to support the observed λ of 1.043. To maintain a stable population ($\lambda = 1$), breeding terns would have to produce 0.32 to 0.74 young per pair (Fig. 3). Our estimates of breeding success required to support a given λ encompass such a large range because of the uncertainty in recovery rates of HY and SY birds, the effect of this uncertainty on estimates of HY and SY survival rates (Fig. 2), and, therefore, on the overall population growth rate (Fig. 3).

DISCUSSION

Population size, the number of breeding colonies, and the geographic range of the Pacific Coast population of Caspian Terns all increased

TABLE 3. Survival rates of Pacific Coast Caspian Terns determined from band recoveries. We estimated survival rates for 1955–1980 to compare with results of Gill and Mewaldt (1983) and for 1981–1998. For both periods, we used the model $S_{a*g} R_g$. Discrepancies between our estimates and those of Gill and Mewaldt (1983) result from our use of an improved recovery model (particularly for estimates of hatch-year survival), and possibly because the band recovery datasets used in the two studies were not identical.

Age class	1955–1980			1981–1998	
	Gill and Mewaldt	This study		This study	
		Estimate	95% CI	Estimate	95% CI
Hatch year	0.55 ^a	0.76	0.71–0.81	0.86	0.75–0.93
Second year	0.79	0.81	0.76–0.86	0.81	0.68–0.89
Third year	0.87	0.89	0.84–0.93	0.93	0.84–0.98
After third year	0.89	0.84	0.81–0.86	0.91	0.84–0.95

^a Estimated as 0.82 for 4-month period, then projected out to a full year.

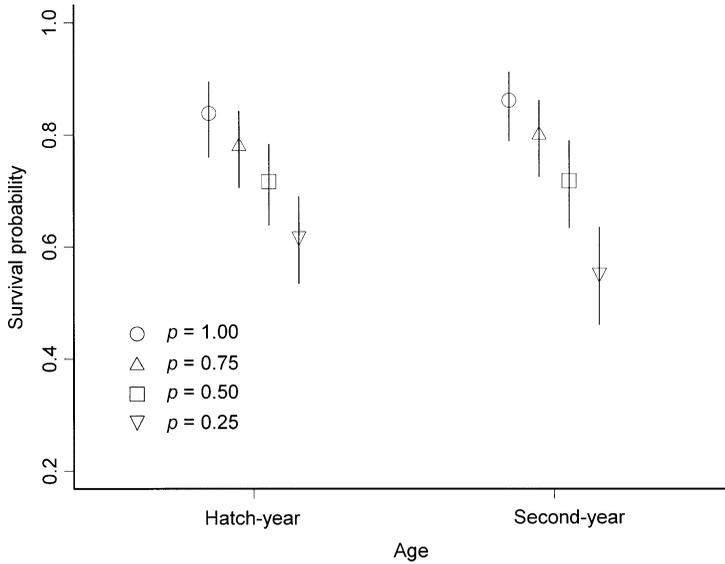


FIGURE 2. Annual hatch-year and second-year survival probability (mean \pm 95% CI) from band recoveries of Caspian Terns during 1981–1998 in the Pacific Coast population of North America (using the model $S_{a+g} R_{a+g}$; Table 2). Survival estimates were calculated for varying recovery probabilities (p) relative to those of third-year and after-third-year birds ($R_{HY,SY} = p * R_{TY,ATY}$).

substantially during 1981–2000, as they did prior to 1981 (Gill and Mewaldt 1983). The average annual rate of population increase during the last two decades, however, was greater than during 1960–1980 (4.3% yr^{-1} and 2.7% yr^{-1} , re-

spectively; Gill and Mewaldt 1983). The northward extension of breeding range documented by Gill and Mewaldt (1983) continued into Alaska (McCaffery et al. 1997) during the last decade. In British Columbia, Canada, nesting

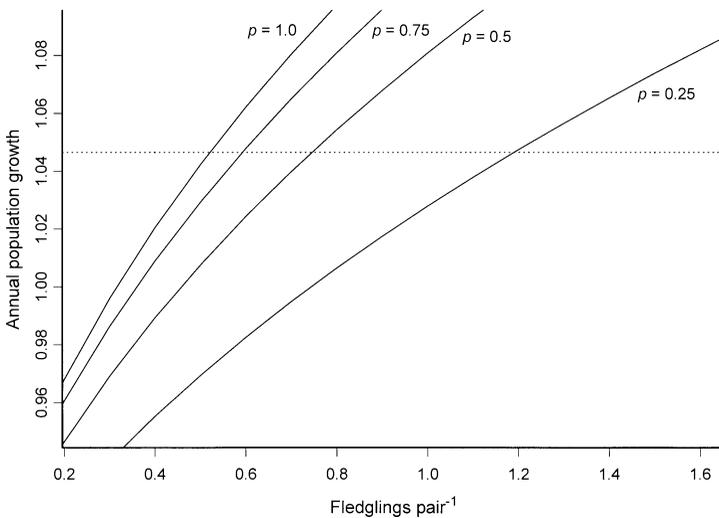


FIGURE 3. Annual population growth rate (λ) for Caspian Terns along the Pacific coast of North America as a function of breeding success (no. of fledglings produced per pair). Estimates of λ include a range of annual survival-rate estimates that depend on recovery probabilities (p) for hatch-year and second-year birds (ranging from 0.25 to 1.0 of third-year and after-third-year survival). The horizontal dashed line at 1.043 marks the observed average annual population growth rate between 1980 and 2000.

has been documented via an observation of flightless young at Roberts Bank in June 1984; however, no nests or colony sites were located (Campbell et al. 1990). Southward expansion of the Pacific Coast population also occurred, with several additional colonies documented in northwestern Mexico after 1980 (Massey and Palacios 1994, Danemann and Carmona 2000, Molina and Garrett 2001, Shuford and Craig 2002). Although new breeding sites were colonized in recent decades, many sites also were abandoned since 1980.

Temporary or complete abandonment of colony sites was most often the result of unmanaged and unpredictable conditions common in natural systems, including drought, erosion, flooding, and vegetation encroachment. Additional known or potential causes of colony site abandonment included reduced prey abundance (Molina 2004, Molina and Sturm 2004), increased predation (Penland 1976, Ryan 2000, Columbia Bird Research 2003), contaminants (Parkin 1998), and disturbance, both anthropogenic (Väisänen 1973, Shugart et al. 1978, Roby et al. 2002) and natural (Nisbet and Welton 1984, Shealer and Kress 1991). Factors that eliminate tern nesting habitat in some areas, however, can also create habitat elsewhere. For example, although winter storms can erode coastal nesting sites, unusually high rainfall inland raised water levels and covered land bridges to colony sites, providing nesting habitat that was secure from mammalian predators (Shuford and Craig 2002).

In recent decades, anthropogenic causes of habitat modification appear to have been most influential in the distribution of breeding Caspian Terns (Shuford and Craig 2002). Colony sites that attracted the majority of breeding birds included nesting habitats that were artificially improved or maintained. Such activity appeared to be important catalysts to the increase in numbers of Caspian Terns in the Pacific Coast population (Shuford and Craig 2002). For example, several nesting islands located on the Columbia River in Oregon and Washington were created by dumping dredged sediment during regular maintenance of shipping channels. Water levels at these sites have been stabilized during flood and drought years by flow control at dams. Also, annual releases of up to 200 million juvenile salmonids from Columbia Basin fish hatcheries provide a predictable food supply for terns nest-

ing on the Columbia River (Collis et al. 2001, Collis et al. 2002). The combination of these three processes provided stable nesting habitat enabling long-term growth in tern colonies on the Columbia River, in contrast to historic habitat elsewhere that was unstable and ephemeral (Wires and Cuthbert 2000, Shuford and Craig 2002). As a result, the middle and lower Columbia River, and in particular the Columbia River estuary, now support the largest known concentration of nesting Caspian Terns (Wires and Cuthbert 2000, Roby et al. 2002).

MOVEMENTS OF BIRDS AMONG COLONIES AND FOUNDING GROUPS

Movements of banded birds among colonies support Gill and Mewaldt's (1983) conclusion that Caspian Terns in this region are essentially one panmictic population. Previous studies indicated that Caspian Terns nesting in San Diego, San Francisco, and Humboldt Bays, California, were source colonies for terns forming coastal colonies in Grays Harbor and Willapa Bay, Washington (Gill and Mewaldt 1983). Subsequently, our band-return data suggested that colonies along the Washington coast were an important source of tern colonies established in the Columbia River estuary. Movement of terns among colonies is common and generally associated with recruitment of first-time breeders or dispersal of established breeders following loss of habitat, disturbance, or poor reproductive success (Penland 1981, Cuthbert 1988, Lebreton et al. 2003).

Breeding site fidelity for Caspian Terns, however, can be variable, depending on breeding conditions. Cuthbert (1988) noted strong fidelity of Caspian Terns at undisturbed sites in the Great Lakes region. Variable colony site fidelity associated with breeding success suggests a performance-based mechanism in the movements of terns among colonies. This is supported in a variety of bird species for which the abandonment of a nesting site in subsequent years is more likely to occur following reproductive failure of an individual or its neighbors (Bollinger and Gavin 1989, Danchin et al. 1998) and late-breeding-season prospecting for colonies having relatively high nesting success (i.e., performance-based conspecific attraction hypothesis; Boulinier and Danchin 1997, Danchin et al. 1998). Indeed, Cuthbert (1988) noted that Caspian Terns tended to return to the same colony

if they were successful in producing young, but moved to a new location if they failed.

The performance-based conspecific attraction hypothesis cannot, however, explain the sometimes rapid founding of a new colony site in a single year, as witnessed at Carson Sink, Nevada (Shuford and Craig 2002). For example, such "deserting flights" have been described for Caspian Terns where colony sites are abandoned and reestablished in new areas (up to 800 km away) in subsequent years (Väisänen 1973, Staav 1979, Bergman 1980). Early-breeding-season prospecting may also be a beneficial strategy if stochastic events (e.g., storm erosion or flooding) degrade, eliminate, enhance, or create breeding habitat during winter, and, therefore, render breeding decisions based on the previous years' chick production unreliable or irrelevant. Early season prospecting, implied by the visiting of multiple colony sites prior to breeding in a given year, has been noted for Roseate Terns (*Sterna dougallii*; Spendelov et al. 1995). Given the often stochastic nature of breeding conditions for Caspian Terns, they likely employ both strategies. It is, however, unclear which strategy is used more frequently or whether individuals may shift between the two strategies as conditions vary over the course of their reproductive lifetimes.

SURVIVAL RATES, PRODUCTIVITY, AND POPULATION CHANGE

Our band recovery model produced similar results to those of Gill and Mewaldt (1983) for the period 1955–1980 in all age classes, except for HY birds. Our estimate for survival of HY birds during 1955–1980 was notably higher than that of Gill and Mewaldt (1983). Although we cannot validate our results, we believe our recovery model provides a more accurate estimate of HY survival because we estimated the parameter for a full year, rather than estimating survival for the first four-month period, when most mortality of HY terns likely occurs, and then extrapolating this value out to a year, the method used by Gill and Mewaldt (1983). Annualized estimates of survival probabilities for prebreeding birds is also the approach recommended by Spendelov et al. (2002). The greater survival estimates for HY and ATY birds during the last two decades compared to pre-1980 suggest that environmental conditions for the Pacific Coast population

have improved, consistent with the increase in population size.

On the basis of available data on reproductive success for the Pacific Coast population, the average fecundity appeared to be sufficient to maintain a population increase. Despite occasional reproductive failures, mean fecundity for Pacific Coast colonies ranged from roughly 0.4 to 1.1 fledglings pair⁻¹ (Kirven 1969, Ohlendorf et al. 1985, Shugart and Tirhi 2001, Roby et al. 2002), seemingly well within or above our estimated bounds (0.32–0.74) and those of Gill and Mewaldt (1983) for maintaining a stable population. Indeed, throughout North America it appears that the number of Caspian Terns is not currently being limited by any single factor or combination of factors (Shuford and Craig 2002). Given, however, that approximately 69% of Caspian Terns in the Pacific Coast population nest in the Columbia River estuary (ca. 25% of the North American metapopulation, and ca. 10% of the world population; Wires and Cuthbert 2000), chronically low productivity (<0.32 fledglings pair⁻¹ year⁻¹) or some stochastic event (e.g., natural or introduced predators, oil spill, disease) at this one site could have a major effect on the Pacific Coast population. Hence, this unprecedented concentration of breeding pairs is a conservation concern for the species (Wires and Cuthbert 2000, Roby et al. 2002).

The considerable variation in our estimates of age-specific survival was in part due to the limited number of band recoveries, but also because the estimates spanned such large spatial and temporal scales. Survival estimates of Caspian Terns banded throughout the range of the Pacific Coast population over a 20-year period include many potential sources of variation known for other tern species, such as colony location (e.g., Roseate Terns; Spendelov et al. 1995) and environmental forces (e.g., effects of El Niño–Southern Oscillation on survival of Least Terns [*Sterna antillarum*], Massey et al. 1992; and hurricanes on Roseate Terns, Spendelov et al. 2002). Variation of up to 55% in annual adult survival rates has been documented over periods of 3–20 years for other waterbirds, including Roseate Terns (0.74–0.90; Spendelov et al. 1995), Great Cormorants (*Phalacrocorax carbo*, 0.74–0.95; Frederiksen and Bregnballe 2000), and Black-legged Kittiwakes (*Rissa tridactyla*, 0.62–0.97; Coulson and Wooler 1976). Such large variation in survival rates can have a pro-

found effect on population projection of long-lived birds and, consequently, estimates of fecundity required to maintain a stable population. Furthermore, although λ is most sensitive to changes in adult survival for long-lived species (Eberhardt and Siniff 1977, Kosinski and Podolski 1979), uncertainty in HY and SY band recovery rates for Caspian Terns and its effect on respective estimates of survival caused estimates of fecundity at $\lambda = 1$ to vary twofold.

Our results demonstrate the importance of increasing the precision of age-specific survival estimates, particularly for HY and SY age classes. This could best be accomplished through live resighting (recapture) of individually banded (color or field-readable bands; Spendelov et al. 2002) birds of known age groups at multiple colonies throughout this population's range (and potentially incorporating live-recapture models with the current dead-recovery model). This is of particular importance because management objectives for some populations may best be achieved and monitored by identifying target population vital rates (including immigration and emigration). Additionally, to effectively model the demographics of this population it is imperative to increase the regularity and precision of estimates of colony sizes throughout the population range. Furthermore, the fact that previous authors have differed in their inclusion of certain states or territories within the Pacific Coast vs. the Western North America populations indicates that boundaries for this population are unclear and warrant further study. Finally, for long-lived species like the Caspian Tern, it is critical that research and monitoring programs are of sufficient duration to capture natural variation in population vital rates at decadal or multigenerational timescales.

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