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PATTERNS AND PROCESSES OF THE OCCURRENCE OF PELAGIC AND SUBTROPICAL WATERBIRDS AT THE SALTON SEA

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Abstract. The Salton Sea attracts a higher diversity of pelagic and subtropical waterbirds than do any other lakes, saline or fresh water, in the interior of western North America. All recorded species of Procellariiformes and subtropical species of Pelecaniformes, Ciconiiformes, Anatidae, and Laridae occur by far most frequently between late April and early October. Several factors appear to facilitate the species' dispersal to the Salton Sink, but restrict their dispersal to other inland bodies of water. Proximity to the Gulf of California, the source of most species, is clearly important. There are no prominent geographic barriers separating the Sea from the Gulf; instead, the intervening region is low-lying and easily crossed. Such barriers do exist in the form of mountain ranges to the west and to the north, and as an expanse of arid land of moderate relief to the east of the Salton Sea, presumably discouraging dispersal beyond the Sink. Seasonality of occurrence coincides with general periods of monsoonal winds, which develop annually in May through October in the Gulf of California and push northward through the Salton Sink. Winds blow predominantly in the opposite direction in winter. During summer months, the presence of thermal air currents in the warm northern gulf and the relatively uniform sea surface temperatures between it and the waters further south along the mainland coast of Mexico may aid movements northward. Such factors probably have a strong influence on dispersal of only some species (e.g., Procellariiformes, pelicans, and frigatebirds). The high diversity of subtropical waterbirds at the Salton Sea appears to result from a combination of factors, which include proximity to the Gulf of California, lack of barriers to dispersal from the Gulf due to the continuous low delta topography, and presence of mountains surrounding the Sea that may act to funnel birds toward the Sink, though the Sea's ecology and size also contribute to the observed patterns.

Key Words: dispersal; procellariiformes; Salton Sea; subtropical waterbirds; vagrants.

PATRONES Y PROCESOS DE OCURRENCIA DE AVES ACUÁTICAS PELÁGICAS Y SUBTROPICALES EN EL MAR SALTON

Resumen. El Mar Salton atrae una diversidad mayor de aves acuáticas pelágicas y subtropicales que cualquier otro lago, ya sea de agua salada o dulce, en el interior del oeste de Norteamérica. Todas las especies de Procellariiformes y especies subtropicales de Pelecaniformes, Ciconiiformes, Anatidae y Laridae registradas ocurren más frecuentemente entre finales de abril y principios de octubre. Varios factores parecen facilitar la dispersión de especies a la Cuenca del Salton, pero restringen su dispersión a otros cuerpos de agua en el interior. La proximidad al Golfo de California, la fuente de la mayoría de las especies, es claramente importante. No hay barreras geográficas prominentes que separen el Mar Salton del Golfo; por el contrario, la región intermedia es un sitio bajo y fácil de cruzar. Dichas barreras existen en forma de cadenas montañosas hacia el oeste y el norte, y como una expansión de tierras áridas de moderado relieve hacia el este del Mar Salton, presumiblemente desalentando la dispersión más allá de la Cuenca. La ocurrencia estacional coincide con períodos generales de vientos monsónicos, que se desarrollan anualmente de mayo a octubre en el Golfo de California y soplan hacia el norte a través de la Cuenca del Salton. En invierno los vientos soplan predominantemente en la dirección opuesta. Durante los meses de verano, la presencia de corrientes térmicas de aire en la cálida zona norte del Golfo y las temperaturas relativamente uniformes entre la superficie de la zona norte y las aguas hacia el sur a lo largo de la costa continental de México, podría propiciar movimientos hacia el norte. Dichos factores probablemente tienen una gran influencia en la dispersión de algunas especies (por ejemplo: Procellariiformes, pelícanos y aves fragatas). La alta diversidad de aves acuáticas subtropicales en el Mar Salton parece resultar de una combinación de factores, los cuales incluyen la proximidad al Golfo de California, la ausencia de barreras para la dispersión desde el Golfo debido a la topografía baja del delta, y la presencia de montañas rodeando el Mar Salton que podrían actuar para dirigir las aves hacia la Cuenca, aunque la ecología del lago y su tamaño también contribuyen al patrón observado.

Palabras claves: dispersión; Procellariiformes; Mar Salton; aves acuáticas subtropicales; migratorias accidentales.

The Salton Sea is one of a number of large saline lakes in the interior of the western United States. There are also numerous large fresh-water lakes and reservoirs in the region, particularly along dammed portions of the Colorado River. Each saline lake has much in common (Hammer 1986, Jehl 1994), with Bayly (1972) noting that "despite their chemical diversity" land-

TABLE 1. THE STATUS OF SPECIES OF PELAGIC AND SUBTROPICAL WATERBIRDS AT THE SALTON SEA IN COMPARISON TO THEIR STATUS IN ARIZONA AND NEVADA

Species	Approximate number of records		
	Salton Sea	Arizona	Nevada
Laysan Albatross (*Phoebastria immutabilis*)	4	2	0
Cook's Petrel (*Pterodroma cookii*)	3	0	0
Wedge-tailed Shearwater (*Puffinus pacificus*)	1	0	0
Buller's Shearwater (*P. bulleri*)	1	0	0
Sooty Shearwater (*P. griseus*)	8	1	0
Black-vented Shearwater (*P. opisthomelas*)	0	2	0
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	2	0	0
Black Storm-Petrel (*O. melania*)	3	2	0
Least Storm-Petrel (*O. microsoma*)	3	2	1
White-tailed Tropicbird (*Phaethon lepturus*)	0	1	0
Red-billed Tropicbird (*P. aethereus*)	0	5	0
Blue-footed Booby (*Sula nebouxii*)	>100	15	2
Brown Booby (*S. leucogaster*)	27	7	2
Neotropic Cormorant (*Phalacrocorax brasilianus*)	7	>100	1
Brown Pelican (*Pelecanus occidentalis*)	1000s	>50	30
Magnificent Frigatebird (*Fregata magnificens*)	100s	>50	5
Little Blue Heron (*Egretta caerulea*)	>100	±40	5
Tricolored Heron (*E. tricolor*)	±40	±40	2
Reddish Egret (*Egretta rufescens*)	10	6	1
Yellow-crowned Night-Heron (*Nyctanassa violacea*)	1	3	0
White Ibis (*Eudocimus albus*)	1	5	0
Glossy Ibis (*Plegadis falcinellus*)	1	1	0
Roseate Spoonbill (*Ajaia ajaja*)	>100	23	1
Wood Stork (*Mycteria americana*)	1000s	17	2
Black-bellied Whistling-Duck (*Dendrocygna autumnalis*)	21	100s	4
Fulvous Whistling-Duck (*D. bicolor*)	1000s	100s	2
Laughing Gull (*Larus atricilla*)	1000s	12	3
Heermann's Gull (*L. heermanni*)	100s	±40	5
Yellow-footed Gull (*L. livens*)	1000s	2	1
Gull-billed Tern (*Sterna nilotica*)	1000s	1	0
Royal Tern (*S. maxima*)	5	0	0
Elegant Tern (*S. elegans*)	17	4	0
Least Tern (*S. antillarum*)	100s	±25	5
Black Skimmer (*Rynchops niger*)	1000s	6	1

Note: Some records involved several (e.g., Elegant Tern, Least Tern) to thousands (e.g., Least Storm-Petrel) individuals.

locked saline lakes "possess a real biological unity." Yet the Salton Sea differs drastically from all of these lakes and reservoirs in its avian diversity (Hammer 1986). Over 400 species have been recorded in the Salton Sink (Patten 1999)—about 160 of them waterbird species—and the millions of birds frequenting the area annually (Patten et al. 2003) is as great an abundance as anywhere on the continent (see Page and Gill 1994). In particular, as we show here, a greater variety and number of pelagic and subtropical waterbirds occur at the Salton Sea than at any other inland lake or waterway in western North America. This pattern is typified by several species that regularly visit the Salton Sea, such as the Brown Pelican (see Table 1 for scientific names), Wood Stork, and Yellow-footed Gull, but are virtually unknown elsewhere in the interior of western North America. In addition, many more pelagic and subtropical waterbirds have occurred as vagrants to the Salton Sea than to these other lakes.

The large size of the Salton Sea might be viewed as the chief reason for the observed diversity, but size alone is not a particularly satisfying explanation. After all, the Great Salt Lake is a vastly larger body of water, several saline lakes in the Great Basin are nearly as large as the Salton Sea (Jehl 1994), and the combined surface area of the lower Colorado River and its anthropogenic reservoirs exceeds that of the Sea (Rosenberg et al. 1991). It thus appears that one or several other factors contribute to the disproportionately high occurrence of waterbirds at the Salton Sea.

Here we detail the pattern of occurrences and the relative abundances of pelagic and subtropical waterbird species recorded in the Salton Sink, grouped by avian order or family. We present data on both the higher overall diversity of

these species, in comparison with the whole states of Arizona and Nevada (chiefly to demonstrate the much higher diversity at the Sea relative to other parts of inland western North America), and on the seasonality of occurrence of these species. We then explore a number of geographic, topographic, and climatic factors, most of which are not mutually exclusive, that appear to explain the Salton Sea's extraordinary diversity of pelagic and subtropical waterbirds, along with their temporal pattern of occurrence. We take a broad-brush approach, so that we might elucidate what geographic and climatic factors affect the occurrence of all subtropical waterbirds in the Salton Sink. The potential effects we posit probably drive the occurrence of some species more than others, but a broad view adds an important perspective to region-wide patterns of occurrence, and emphasizes the place held by the Salton Sea in the greater lower Colorado River region (Fig. 1). In many ways the Salton Sea is less like an isolated lake in the interior of western North America and more like an extension of the Gulf of California and Colorado River delta.

METHODS

We concentrated on five orders or families of waterbirds: Procellariiformes (albatrosses, shearwaters, and storm-petrels), Pelecaniformes (boobies, pelicans, cormorants, and frigatebirds), Ciconiiformes (herons, ibises, and storks), Anatidae (ducks and geese), and Laridae (gulls and terns). We restricted our analyses to bird species that are truly pelagic, or that are coastal but with breeding ranges and niches that are essentially subtropical.

We gathered data through an exhaustive review of regional reports published in *American Birds* and its successors (*Field Notes* and *North American Birds*), of reports of the California Bird Records Committee, of specimens in all major museum collections in the United States, and of our own field notes. Upon compilation of the data (details of which can be found in Patten et al. 2003), we plotted seasonality of occurrence and relative abundance. We also scanned *American Birds* and other published sources (McCaskie 1970a, Lawson 1977, Monson and Phillips 1981, Alcorn 1988, Rosenberg et al. 1991, Rosenberg and Witzeman 1998) to compile the approximate number of records of species of subtropical waterbirds for Arizona and Nevada. We examined topographic maps and the literature (especially Anderson et al. 1977 and Patten and Minnich 1997) to determine which processes might generate the observed patterns of occurrence of waterbirds at the Salton Sea.

We performed non-parametric statistical analyses for comparing diversity among Arizona, Nevada, and the Salton Sea. Our null hypothesis is biased in favor of finding larger numbers of waterbirds in Arizona and Nevada, both vastly larger than the Sea. Naturally, waterbirds concentrate at isolated wetlands in arid western North America, so such locales tend to receive a disproportionate amount of observer coverage in each region, but particularly in southeastern California, western and southern Nevada, and southern Arizona. We performed a Kruskal-Wallis test on ranked abundances for all species, corrected for ties. We examined seasonality by performing goodness of fit tests on sums of records in each taxonomic group for each season, with winter defined as December–February, spring as March–May, summer as June–August, and fall as September–November.

RESULTS

In general there have been more species and more individuals of pelagic and subtropical waterbirds recorded at the Salton Sea than elsewhere inland in the southwestern United States (Table 1). Arizona and Nevada, although substantially larger in area than the Salton Sea, have significantly lower diversity of these species (Kruskal-Wallis $H_{adj} = 15{,}256.0$, $df = 2$, $P < 0.001$), although a few pelagic and subtropical species, such as the Black-vented Shearwater and the tropicbirds, have been recorded in those states but not at the Sea.

Seasonal patterns of occurrence at the Salton Sea are remarkably similar across taxonomic groups (Fig. 2). Whether the species is recorded frequently or rarely, and regardless of its order or family, each of the pelagic and subtropical birds we reviewed occurs almost exclusively between late spring (May) and early fall (September). There are exceptions, with one to a few winter records of some species (see below), but the preponderance of records are for the summer months ($G = 84.6$, $df = 12$, $P < 0.001$).

Procellariiformes

The occurrence at the Salton Sea of species of Procellariiformes has been previously summarized and analyzed (Patten and Minnich 1997). Not surprisingly, all species are vagrants at the Salton Sea, occurring well outside the species' established ranges. Eight species have been recorded (Table 2), with all birds first detected between late April and late September. Some birds remained for lengthy periods, but none stayed later than 9 November (Patten et al. 2003). Two occurrences of storm-petrels, involving dozens (*Nora* in 1998) to thousands (*Kathleen* in 1977) of birds, were associated with tropical storms that moved north into southeastern California from the Gulf of California (Patten 1998). The only storm-petrels to reach Arizona were associated with these two storms (Jones 1999).

Subtropical Pelecaniformes

Totipalmate birds are common at the Salton Sea, with the two temperate species, the American White Pelican (*Pelecanus erythrorhynchos*)

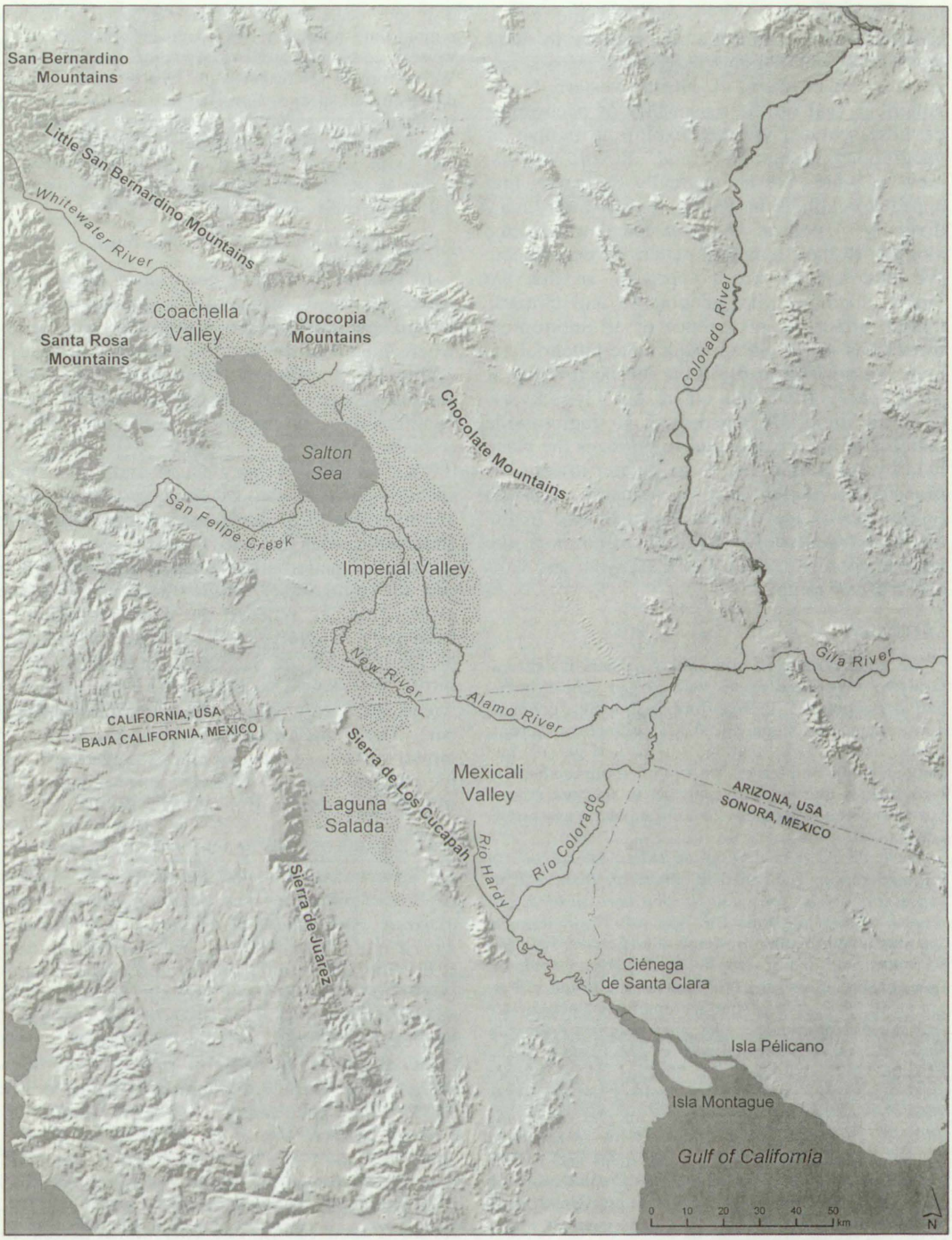

FIGURE 1. Topographic relief of the Salton Sink and Colorado River Delta. Stippling signifies the area below sea level. Prepared by L. Lewis, Redlands Institute.

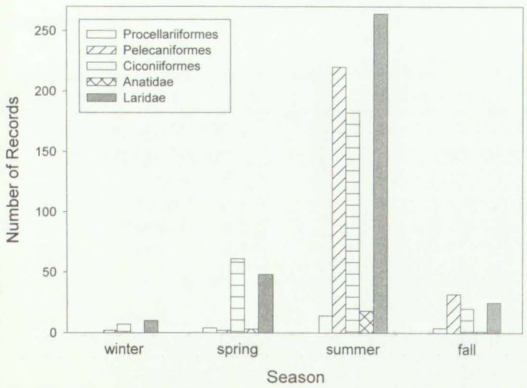

FIGURE 2. Seasonality of occurrence of pelagic and subtropical waterbirds at the Salton Sea (data are for species in Tables 2 and 3). For all five groups peak occurrence is from late spring through early fall. Breeders and regular visitors (e.g., Brown Pelican, Gull-billed Tern, Black Skimmer) show the same seasonal pattern of occurrence.

TABLE 2. A SUMMARY OF DATES FOR PROCELLARIIFORMES RECORDS AT THE SALTON SEA

Species	First detection date
Laysan Albatross	02–21 May
Cook's Petrel	10–24 July
Wedge-tailed Shearwater	31 July
Buller's Shearwater	06 August
Sooty Shearwater	28 April–24 August
Leach's Storm-Petrel	30 June–15 September
Black Storm-Petrel	14 August–28 September
Least Storm-Petrel	10 July–27 September

Notes: "First detection" refers to the date a bird was first detected at the Salton Sea (for a given record); the span is of dates of first detection for multiple records. Note the strong seasonal aspect of occurrence (records are exclusively from late spring through early fall).

and Double-crested Cormorant (*Phalacrocorax auritus*), occurring regularly. Five subtropical pelecaniforms have been recorded at the Salton Sea: the Blue-footed and Brown boobies, Brown Pelican, Neotropic Cormorant, and Magnificent Frigatebird. The two boobies and the cormorant are vagrants to the Salton Sea (Table 3), having occurred well outside the species' established ranges. All boobies have arrived at the Sea between mid-July and mid-September, with a few remaining into winter. The cormorant has been recorded only seven times, all but once between 24 April and 1 September. The exception was an adult occasionally present as early as 27 February and as late as 10 September during its six summers at the Sea, which included a breeding attempt (Patten et al. 2003).

The Brown Pelican is common in summer and fall, mainly from early May through mid-November, and has recently attempted nesting, once successfully. Year-round numbers have increased substantially since the 1970s (Patten et al. *this volume*), but the species nonetheless continues to have a tenfold to hundredfold higher abundance in summer. The Magnificent Frigatebird occurs nearly annually in small numbers, with all records between early June and mid-September, save for one in February (the species level identification of which is tentative; Patten et al. 2003). Numbers present in any given summer vary from none to 25 or more.

SUBTROPICAL CICONIIFORMES

The Wood Stork is the only subtropical ciconiiform that occurs regularly at the Salton Sea, and it has declined markedly over the past 50 years (Patten et al. *this volume*). Nevertheless, despite its sharp decrease in numbers, its seasonality of occurrence has changed little, with almost all birds found 2 May–29 October and a decided peak in July and August (Patten et al. 2003).

Four southerly herons have occurred at the Salton Sea. The Little Blue and Tricolored herons are both casual spring and summer visitors to the Salton Sea that have nested, the former twice, the latter probably once (Patten et al. 2003). Apart from one in winter, all records of Little Blue Herons fall between early May and mid-September, and most Tricolored Heron records fall between mid-April and late September. The Reddish Egret has reached the Salton Sea ten times, nine between mid-July and early September, and once in winter. The only Yellow-crowned Night-Heron was present 27 April–18 June 1996.

Three other subtropical ciconiiforms have been recorded at the Salton Sea. The Roseate Spoonbill is a highly irregular and a declining summer and fall vagrant to the Salton Sea, with virtually all records between early May and the end of October (most mid-May to late September); only three birds have been recorded in the past 20 years (Patten et al. 2003). The only White Ibis recorded was one present 10 July–5 August 1976 that returned 25 June–14 July 1977. The first record of Glossy Ibis at the Salton Sea occurred from 27 May–8 August 2000 (Patten et al. 2003). The last species has expanded its range into North America during the twentieth century, first colonizing Florida, spreading west to Texas and reaching west Mexico in the 1990s and Arizona in 2001 (Patten and Lasley 2000, Rosenberg and Jones 2001). It is possible that birds wandering to the Salton Sea and southern Arizona originate from western Mexico, although it is perhaps equally likely

TABLE 3. A TEMPORAL SUMMARY OF OCCURRENCES OF VAGRANT SUBTROPICAL PELECANIFORMS, CICONIIFORMS, ANATIDS, AND LARIDS AT THE SALTON SEA

Species	First detection date	Peak
Blue-footed Booby	12 July–18 October*	August/September
Brown Booby	12 July–06 September	August/September
Neotropic Cormorant	27 February–10 September	May–July
Magnificent Frigatebird	04 June–23 September	July/August
Little Blue Heron	07 May–15 September*	June–August
Tricolored Heron	17 April–01 October*	May–August
Reddish Egret	11 July–04 September*	August
Yellow-crowned Night-Heron	27 April	—
White Ibis	25 June–10 July	—
Glossy Ibis	27 May	—
Roseate Spoonbill	5 May–28 October*	July–September
Black-bellied Whistling-Duck	20 April–15 October	June–August
Heermann's Gull	02 March–04 November*	July/August
Royal Tern	12 June–20 July	July
Elegant Tern	24 April–24 August	May–July
Least Tern	15 April–17 August	May/June

Notes: "First detection" refers to the date a bird was first detected at the sea (for a given record); the span is of dates of first detection for multiple records. "Peak" refers to the period when most records have accumulated. An asterisk signifies that the species has wintered at the Salton Sea once or twice (see Patten et al. 2003). Note the strong tendency for birds to appear between late spring and early fall.

they originated from southeastern North America.

SUBTROPICAL ANATIDAE

Both subtropical whistling-ducks found in continental North America occur at the Salton Sea. The Fulvous Whistling-Duck was formerly a fairly common resident, most abundant in summer and fall. It is now rare and declining as a breeder (Patten et al. *this volume*), occurring between early April and early November, with a minor influx of birds from the south in June through August. The Black-bellied Whistling-Duck, which has been increasing in numbers in northwestern Mexico (Russell and Monson 1998) and Arizona (Rosenberg and Witzeman 1998), is a casual summer and fall visitor to the Salton Sea, primarily between late May and late August, with two records for mid-April and another 15 October–4 November.

Various essentially seagoing waterfowl occur regularly at the Salton Sea (Patten et al. 2003), particularly the Brant (*Branta bernicla*), scoters (*Melanitta* spp.), and Red-breasted Merganser (*Mergus serrator*), but these north-temperate breeders do not have the same pattern of occurrence as their subtropical relatives. Most occur principally as uncommon or rare spring migrants, moving through the Salton Sink concomitant with the passage of spring shorebirds (Patten et al. 2003).

SUBTROPICAL LARIDAE

An impressive number and variety of gulls and terns nesting north of the Salton Sea pass through the area as migrants, or spend the winter on the Sea. The same variety can be expected to occur at any saline lake in the West. It is the more southerly gulls and terns and the Black Skimmer that we consider subtropical.

Both the Gull-billed Tern and Black Skimmer nest fairly commonly at the Salton Sea, the former since 1927 (Pemberton 1927; Molina *this volume*), the latter since 1972 (McCaskie et al. 1974; Molina *this volume*). Gull-billed Terns arrive in mid-March (earliest 5 March 1995), and most have departed by September. Skimmers arrive in early April (earliest 1 April 1978), and most have departed by mid-October. The Laughing Gull formerly nested (until 1957) at the Salton Sea, and has attempted to do so recently (since 1994; Molina 2000a, *this volume*), but it is now primarily a fairly common post-breeding visitor from nesting colonies in the Gulf of California. Most occur between mid-June and late-September, with counts as high as 800+ in late July 1979. The Yellow-footed Gull is a common post-breeding visitor from the Gulf of California. Most are present between late May and the end of August, with hundreds or even thousands present in July (Patten 1996).

Heermann's Gull and the Least Tern are both rare visitors to the Salton Sea. The gull generally occurs between early April and early October, with most records from July and August. All records of the Least Tern fall between mid-April and mid-August, with most from June. The Elegant Tern is a casual visitor, with most occurring between mid-May and mid-June, but with single records for late April and mid-August. The Royal Tern is even rarer, with four or five records between mid-June and mid-July.

DISCUSSION

The five orders and families we considered are taxonomically unrelated, yet species in each group show the same general pattern of seasonal occurrence in the Salton Sink. Namely, most records are between late April and early October, with peak numbers from June through early September (Fig. 1). Several species have never reached other areas in inland western North America (Table 1), and there are many fewer records for some that have (e.g., Brown Pelican, Magnificent Frigatebird, Heermann's Gull, Least Tern), with southern Arizona generally having more records than southern Nevada (see McCaskie 1970a, Monson and Phillips 1981, Alcorn 1988, Rosenberg et al. 1991). Only two species occurring in substantial numbers show a contrary pattern; the Neotropic Cormorant and Black-bellied Whistling-Duck have expanded into southeastern Arizona from Sonora (Rosenberg and Witzeman 1998) but remain rare farther west and north. Patterns in our data lead us to two questions: (1) why are pelagic and subtropical waterbirds encountered so much more frequently at the Salton Sea than at the other inland lakes in the West (saline or not)? and (2) why do pelagic and subtropical waterbirds occur in the Salton Sink almost exclusively between late spring and early fall?

Occurrence

Although the Salton Sea provides a relatively large target for passing waterbirds, we suggest that the geography and climate of the region also figure prominently in understanding the disparity observed in subtropical waterbird diversity between the Salton Sea and other inland locations in western North America. The topography of the Salton Sink and its proximity to the Gulf of California (Fig. 1), and weather patterns in the region as a whole combine to affect bird movement and occurrence.

The Salton Sea is farther south than the other saline lakes in the West, and considerably closer to the Gulf of California, where seabirds and subtropical waterbirds regularly occur. The Gulf supports nesting colonies of four of the five subtropical Pelecaniformes, and the Neotropic Cormorant nests commonly in those parts of Mexico adjacent to the eastern shore of the Gulf (Palacios and Mellink 1992, 1993; Mellink and Palacios 1993, Patten et al. 2001). Wood Storks and Roseate Spoonbills nest, formerly commonly, in the western parts of Mexico adjacent to the Gulf of California (Russell and Monson 1998). All four of the subtropical herons nest in southern Baja California as well as in mainland west Mexico (Russell and Monson 1998, Howell et al. 2001), and all seven of the subtropical Laridae found at the Salton Sea nest in the northern Gulf of California (Palacios and Mellink 1992, 1993; Patten et al. 2001). Of the eight Procellariiformes recorded on the Salton Sea, only the Black and Least storm-petrels are known to nest in the Gulf of California, the other six originating from farther south.

Brown Pelicans regularly disperse northward along the Pacific coast after nesting, evidenced from records from as far north as British Columbia (Campbell et al. 1990). Large numbers of Brown Pelicans also move northward in the Gulf of California at this same time (Anderson et al. 1977), and small numbers of boobies and Magnificent Frigatebirds sporadically do so as well. Subtropical Ciconiiformes in the eastern United States and Canada show a similar northward pattern of dispersal after nesting (Palmer 1962). Breeding populations of Elegant Terns and Laughing and Yellow-footed gulls in the Gulf commonly disperse northward after nesting (Garrett and Dunn 1981, McCaskie 1983, Burness et al. 1999). Each of these species is coastal and seldom occurs even a short distance away from the ocean, except for at the Salton Sea.

However, mere proximity to the Gulf of California may not fully explain these patterns (Fig. 1). After all, southwestern Arizona, including many large reservoirs on the Colorado River, is equally close to the Gulf, but has had a small fraction of the number of records and the number of individuals that occur regularly. If subtropical species simply tended to wander northward after breeding, one might expect them to occur on a broader front throughout southern Nevada and Arizona, rather than concentrated in a single locale. Topography at the head of the Gulf of California and surrounding the Salton Sink is probably an important factor in explaining the observed patterns of occurrence. Land is low-lying and flat between the head of the Gulf of California and the Salton Sink (the elevation not exceeding 50 m), and there are mountains on the other three sides: the Peninsular Ranges to the west, the Transverse Ranges to the north, and the Orocopia and Chocolate mountains to the east. If a major mountain range separated the Gulf from the Sea, dispersal between them would likely be much lower. Instead, the low-lying area, much of it below sea level, does not function as a barrier to dispersal. In addition to the vast expanse of aquatic habitat at the Salton Sea and its environs, northbound birds leaving the shores of the Gulf of California immediately encounter numerous wetlands in northeastern Baja California and northwestern Sonora that offer suitable habitat for seabirds and other species associated with freshwater. Some of these im-

portant wetlands include the Ciénega de Santa Clara, Laguna Salada, oxbow lakes on the Río Hardy (Fig. 1; Hinojosa-Huerta et al. *this volume*), and the extensive pond system at Campo Geotérmico Cerro Prieto (Molina and Garrett 2001; Patten et al. 2001, 2003), which likely facilitate movement between the Gulf of California and Salton Sink. Similar linkages of aquatic habitat extend from the Gulf up the lower Colorado River to Arizona and Nevada, but many fewer subtropical waterbirds follow this route northward (Rosenberg et al. 1991, Patten et al. 2003). This eastern portion of the lower Colorado River drainage and the surrounding Sonoran Desert has relatively greater topographic relief compared to the Sink, likely limiting dispersal in that direction. Once pelagic and subtropical waterbirds move north into the Salton Sea, they find an environment in which they can survive, but may be inhibited from moving farther north, west, or east by mountains. Although some birds certainly do move over these mountains, or through passes between them, these mountain ranges and the arid lands lying beyond probably discourage movement by some species.

Finally the Salton Sea's ecology probably also contributes to its distinction as an area of high diversity and abundance. Bayly (1972) noted that many species of fish do not tolerate high levels of salinity. The Sea is highly saline (about 40–44 ppt), although its level of salinity is not nearly as great as that of some other inland lakes in western North America such as Mono (89 ppt), Salada (100 ppt), and Great Salt (280 ppt), none of which supports fish (Hammer 1986). Other saline lakes in this region, such as Pyramid (6 ppt), Little Quill (20 ppt), and Walker (11 ppt), do support fish or even sport fisheries (Hammer 1986), but lag well behind the Salton Sea in avian diversity. Still, it is evident that the salinity of the Salton Sea, about 25% above that of the ocean, allows fish to survive and therefore obviously provides habitat for piscivorous birds.

None of the hypothesized factors that we have discussed are mutually exclusive, and each probably plays a role in producing the high waterbird diversity at the Salton Sea relative to surrounding areas.

Seasonality

The predominant flow of air into the Salton Sink in fall and winter is from the north and west. However, monsoonal flows from the south occur annually in the late spring and summer, with a strong flow of air pushing northward from the Gulf of California into the Salton Sink at this time (Patten and Minnich 1997). Monsoonal flows no doubt aid the passage of pelagic and subtropical birds from the Gulf of California to the Salton Sea (Anderson et al. 1977, Patten and Minnich 1997), as most migrating or dispersing birds are known to follow favorable tailwinds (see Gauthreaux and Able 1970). If wind flow were persistently from the north throughout the year, dispersal to the Salton Sea from the Gulf would doubtless be hampered. Additionally, high summer temperatures in the Gulf create strong thermals (Anderson et al. 1977), on which at least large soaring birds (e.g., Brown Pelicans, Magnificent Frigatebirds) can ride with ease. Such thermals, in concert with the predominant northward wind flow, probably aid summer dispersal to the Sea by these species that normally do not stray away from the immediate coast.

One other factor, seasonal changes in ocean temperature, is likely to play a role for at least some species, principally the highly oceanic procellariiforms. Sea surface temperatures in the northern Gulf of California remain constantly high, while those off west Mexico are normally low (Soto-Mardones et al. 1999). During monsoonal flows, sea surface temperatures off the central coast of west Mexico increase to create an expanse of pelagic habitat that is thermally uniform with warm waters of the northern Gulf, thus enabling Procellariiformes and other birds moving northward off western México to more easily enter the Gulf of California and stray north to the Salton Sea (Patten and Minnich 1997).

CONCLUSION

Because of its geographic setting, ecology, and climate, the Salton Sea is a unique component of the desert Southwest. Waterbirds, many of which occur sparingly or not at all elsewhere inland in arid western North America, are abundant at the Sea. There is probably no single hypothesis that best explains the Sea's remarkably high diversity of waterbirds relative to other inland areas, although its proximity to the Gulf of California and the low-lying terrain between it and the Gulf are excellent candidates. Even so, the Sea's large size and persistent populations of fish, as well as its location—bordered by mountains in nearly all directions except to the south, toward the Gulf—and the region's seasonal wind patterns, likely contribute to the patterns we described.

The patterns of occurrence of the various birds we have considered, in concert with processes of dispersal we have hypothesized, solidify the physical and biological connections between the Salton Sink and the Gulf of California recognized by previous workers (Sykes 1937, Anderson et al. 2003). Most of the Procellariiformes and some of the subtropical waterbirds we discuss do not regularly oc-

cur in the northern Gulf, and many that do occur there are found in the Salton Sink only as vagrants. However, for a few species, most notably the Brown Pelican, Wood Stork, Fulvous Whistling-Duck, and several breeding larids, we should take the broader geographic view; plans for their management and conservation at the Salton Sea must also consider their well-being in the adjacent Gulf of California.

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