Studies in Avian Biology No. 27:24–32, 2004.

POPULATION CHANGES AND BIOGEOGRAPHIC AFFINITIES OF THE BIRDS OF THE SALTON SINK, CALIFORNIA/ BAJA CALIFORNIA

MICHAEL A. PATTEN, RICHARD A. ERICKSON, AND PHILIP UNITT

Abstract. Since the Salton Sea's formation in 1905, permanent water, introduced aquatic prey, and extensive habitat conversion have altered its birdlife greatly. A number of waterbird and landbird species colonized the Sea and the associated Salton Sink early in the twentieth century. Other landbirds suffered from the loss of desert scrub and, particularly, mesquite (*Prosopis* spp.) thickets, with the Vermilion Flycatcher (*Pyrocephalus rubinus*), Le Conte's Thrasher (*Toxostoma lecontei*), and Lucy's Warbler (*Vermivora luciae*) eventually extirpated as breeders. Although some waterbird species have declined since 1950, many have increased or held steady. Populations of 60% of breeders that colonized or increased markedly originated in the Gulf of California or adjacent western Mexico. Since 1950, the Wood Stork (*Mycteria americana*), Fulvous Whistling-Duck (*Dendrocygna bicolor*), American Wigeon (*Anas americana*), and Northern Pintail (*A. acuta*) are the only waterbirds, and the Crissal Thrasher (*Toxostoma crissale*) the only landbird, that have declined markedly. After a decline in the 1930s, the Large-billed Savannah Sparrow (*Passerculus sandwichensis rostratus*) has increased since the 1980s and began nesting in the Mexicali Valley in the late 1990s. Landbird species that colonized the Salton Sink since 1950 include the Inca Dove (*Columbina inca*), Great-tailed Grackle (*Quiscalus mexicanus*), and Bronzed Cowbird (*Molothrus aeneus*)—species that have increased dramatically throughout the American Southwest—and the White-tailed Kite (*Elanus leucurus*), Anna's Hummingbird (*Calypte anna*), and the non-native European Starling (*Sturnus vulgaris*). Landbird species colonizing the Salton Sink generally have colonized from the Colorado River Valley, whereas landbird subspecies generally have colonized from coastal California.

Key Words: avian biogeography; colonization; population changes; Salton Sea.

CAMBIOS POBLACIONALES Y AFINIDADES BIOGEOGRÁFICAS DE LAS AVES DE LA CUENCA DEL SALTON, CALIFORNIA/BAJA CALIFORNIA

Resumen. Desde la formación del Mar Salton en 1905, agua permanente, la introducción de presas acuáticas y extensiva conversión de hábitats han alterado en gran medida su avifauna. Un número de especies de aves acuáticas y terrestres colonizaron el Mar y la asociada Cuenca del Salton a principios del siglo veinte. Otras especies terrestres sufrieron de la pérdida del hábitat arbustivo de desierto y, particularmente, de densos mezquites (*Prosopis spp.*) con la consiguiente pérdida de la reproducción del Mosquero Cardenal (*Pyrocephalus rubinus*), el Cuitlacoche Pálido (*Toxostoma lecontei*) y el Chipe Rabadilla Rufa (*Vermivora luciae*). Aunque algunas especies de aves acuáticas han reducido sus poblaciones desde 1950, muchas han aumentado o se han mantenido constantes. Las poblaciones de 60% de aves reproductivas que colonizaron o se incrementaron marcadamente, fueron originadas en el Golfo de California o en tierras adyacentes del oeste de México. Desde 1950, la Cigüeña Americana (*Mycteria Americana*), el Pijije Canelo (*Dendrocygna bicolor*), el Pato Chalcuán (*Anas americana*) y el Pato Golondrino (*Anas acuta*), son las únicas aves acuáticas, y el Cuitlacoche Crisal (*Toxostoma crissale*) la única ave terrestre, que han disminuido marcadamente. Después de una reducción en los años 1930, el Gorrión Sabanero de Pico Largo (*Passerculus sandwichensis rostratus*) ha incrementado desde los años 1980 y comenzó a anidar en el Valle de Mexicali a fines de los años 1990. Las especies de aves terrestres que colonizaron la Cuenca del Salton a partir de 1950 incluyen la Tórtola Cola Lagra (*Columbina inca*), el Zanate Mexicano (*Quiscalus mexicanus*), el Tordo Ojo Rojo (*Molothrus aeneus*)—especies que han incrementado dramáticamente a lo largo del sureste de los Estados Unidos—y el Milano Cola Blanca (*Elanus leucurus*), el Colibrí Cabeza Roja (*Calypte anna*), y el introducido Estornino Pinto (*Sturnus vulgaris*). Las especies de aves terrestres que colonizan la Cuenca del Salton generalmente lo han hecho desde el Valle del Río Colorado, mientras que las subespecies de aves terrestres generalmente han colonizado desde la costa de California.

Palabras claves: biogeografía de aves; colonización; cambios poblacionales; Mar Salton.

Lake Cahuilla, the vast precursor of the Salton Sea, was ephemeral. Floodwaters from the Colorado River filled this lake periodically. But intense heat and direct sunlight removed its water at a rapid rate, producing an alkaline flat within a few decades. The ebb and flow of surface water implies an ebb and flow of habitats, with bird communities presumably changing in kind. We know little about the avifauna of Lake Cahuilla and nothing of patterns of range expansion and retraction around that lake. Yet we do know that various waterbird species that occur at the Salton Sea also occurred at Lake Cahuilla (Patten and Smith-Patten *this volume*). Logic dictates that

these species vacated the region when the lake dried, although we do not know how soon before desiccation they departed, let alone how long after flooding they colonized, although some species likely colonized rapidly (Grinnell 1908; see below).

The Salton Sea is essentially a miniature version of Lake Cahuilla, created by the same processes and harboring, so far as we know, similar species of birds (Patten and Smith-Patten *this volume*). A key difference is that the Salton Sea receives a substantial influx of irrigation runoff, effectively maintaining the Sea's surface level—an ephemeral lake has become permanent. Runoff is the result of broad-scale conversion of desert scrub to agriculture; for decades the Imperial and Coachella valleys have been among the greatest crop-producing regions in the United States (Steere 1952). The sudden emergence of a mesic environment in the heart of the western Sonoran Desert (the Sea was created in under two years), coupled with the subsequent introduction—deliberate and accidental—of various fishes and invertebrates (see Walker 1961, Jehl and McKernan 2002) led to drastic changes in the region's birdlife. Perhaps equally profound in impact was the piecemeal clearing of riparian habitats and the methodical irrigation and development of agriculture in the valleys surrounding the Salton Sea.

Patterns of avian colonization and retreat at Lake Cahuilla are likely to remain unknown. Yet ornithological exploration of the Salton Sink since its inception (Garrett et al. *this volume*) has provided some insight into how habitat alteration generally, and the existence of the Salton Sea specifically, permitted various species to colonize and forced others to evacuate. On the basis of habitat descriptions near the turn of the twentieth century, such as those of Mearns (1907) and Parish (1914), it appears that the amount of both open water and of parks, ranches, and suburbia increased greatly after 1900, whereas the amount of desert scrub and of mesquite (*Prosopis* spp.) thickets decreased greatly as land was converted to agriculture. Likewise, the amount of marshes and riparian vegetation appears to have held steady, although the character of each has changed, the former now heavily managed, the latter now dominated by non-native tamarisk (*Tamarix ramosissima*) rather than native willow (*Salix* spp.), Fremont cottonwood (*Populus fremontii*), and bordering mesquite.

In this paper we summarize often scant data on range expansions into the Salton Sink. We focus particularly on range changes in the last half of the twentieth century, during which the surface level of the Sea has been relatively stable and conversion to agriculture was largely complete. We use these data to explore colonization patterns for species of waterbirds, species of monotypic landbirds, and subspecies of polytypic landbirds. We summarize biogeographic affinities of avian taxa occupying the Salton Sink and compare these affinities with patterns of colonization.

METHODS

The Salton Sea National Wildlife Refuge and Point Reyes Bird Observatory have censused various waterbirds since the early 1980s, and volunteers have conducted Christmas Bird Counts regularly at the north and south ends of the Salton Sea since 1970, sporadically before then. Our efforts to examine trends since 1900 were thus constrained by the virtual lack of quantitative data on population sizes prior to the 1960s. Given this constraint, and because our goal was to deduce and outline general patterns, we often attempted to make only qualitative statements about range expansion and biogeographic affinities. Therefore, the information we present in the tables and figures is often qualitative, meant only to provide a heuristic guide to general patterns and to summarize the more obvious trends. Nonetheless, we did examine waterfowl and other data from the Salton Sea (south) Christmas Bird Count, conducted in the winters of 1939/1940–1941/1942, 1955/1956–1957/1958, 1965/1966, and 1968/1969–present, and we gathered and present some additional quantitative data. Numerous small fluctuations or trends in range or population size, and probably some larger ones, likely went undetected.

We gathered data from a variety of sources, detailed by Patten et al. (2003). In summary, we relied mainly on published sources (particularly regional reports in *North American Birds* and its predecessors and notes in the *Condor*), specimen data (chiefly from the San Diego Natural History Museum), and our field notes and those of Guy McCaskie. Taxonomy follows Patten et al. (2003). Tables list scientific names not in the text. We derived data for our pie charts from accounts of subspecies' occurrences in the Salton Sink (Patten et al. 2001, 2003), which we chiefly based on comparisons of specimens. We created pie charts for heuristic comparison; they do not reflect exact percentages of occurrences.

RANGE AND POPULATION CHANGES

1900–1950

Shortly after the turn of the twentieth century, permanent surface water and extensive habitat conversion for agriculture greatly altered the avifauna of the Salton Sink. Many waterbird species colonized the Salton Sea within a few years of its formation; both the American White Pelican (*Pelecanus erythrorhynchus*) and Double-crested Cormorant (*Phalacrocorax auritus*) were breeding there by the time Grinnell (1908) conducted the first ornithological exploration of the Sea. Over the next two decades the Sea was colonized by various other waterbird species, such as the Gull-billed Tern (*Sterna nilotica*) by

TABLE 1. STATUS AND PROVENANCE OF SELECTED SPECIES OF WATERBIRDS THAT HAVE COLONIZED OR APPEAR TO BE COLONIZING THE SALTON SEA

Species[a]	Appearance	Current status	Provenance
American White Pelican	1907	common visitor; former breeder	Great Basin
Brown Pelican	1951	common post-breeder; breeds	Gulf of California
Double-crested Cormorant	1907	common breeder	?
Neotropic Cormorant	1982	rare post-breeder; increasing	west Mexico
Cattle Egret	1970[b]	common breeder	west Mexico
White-faced Ibis	1954[b]	common visitor; breeds	Great Basin
Black-bellied Whistling-Duck	1951	rare post-breeder; increasing	west Mexico
Fulvous Whistling-Duck	ca. 1906	former breeder	west Mexico
Laughing Gull	1928[b,c]	common post-breeder; breeds	Gulf of California
Heermann's Gull	1967	rare post-breeder; increasing?	Gulf of California
California Gull	1996[b]	common visitor; breeds	Great Basin
Yellow-footed Gull	1965	common post-breeder	Gulf of California
Western Gull	1969	increasing perennial visitor	Pacific coast
Gull-billed Tern	1927	fairly common breeder	Gulf of California
Caspian Tern	1927[b,c]	common breeder	?
Elegant Tern	1985	increasing post-breeder	Gulf of California
Forster's Tern	1970[b]	common visitor; breeds	?
Least Tern	1964	uncommon visitor; increasing?	Gulf of California
Black Skimmer	1968	fairly common breeder	Gulf of California

[a] Scientific names in text or Table 2, except: Neotropic Cormorant (*Phalacrocorax brasilianus*), Black-bellied Whistling-Duck (*Dendrocygna autumnalis*), and Elegant Tern (*Sterna elegans*).
[b] Date of first breeding, not of first occurrence.
[c] Extirpated as a breeder in 1950s; recolonized in 1992 (Caspian Tern) and 1994 (Laughing Gull).

1927 (Pemberton 1927) and the Laughing Gull (*Larus atricilla*) by 1928 (Miller and van Rossem 1929).

During the early decades of the twentieth century a host of landbird species also colonized the Salton Sink, presumably drawn to the greener, wetter habitats of ranch yards, towns, orchards, and agricultural fields. Notable among the early landbirds colonizing were the White-winged Dove (*Zenaida asiatica*), Gila Woodpecker (*Melanerpes uropygialis*), Northern Mockingbird (*Mimus polyglottos*), and Brown-headed Cowbird (*Molothrus ater*), each of which reached the region before the close of the 1930s (Hoffmann 1927, Arnold 1935, Rothstein 1994, Patten et al. 2003). Even the non-native House Sparrow (*Passer domesticus*), introduced on the east coast of North America, marched across the continent and reached the Salton Sink by the early 1910s (van Rossem 1911). Of these species, only the mockingbird reached the Salton Sea from the west (see below).

With the loss of desert scrub, particularly thickets of mesquite, various species of landbirds paid the price. Notable among these species were the Vermilion Flycatcher (*Pyrocephalus rubinus*), Le Conte's Thrasher (*Toxostoma lecontei*), and Lucy's Warbler (*Vermivora luciae*), each of which showed sizeable declines by the 1930s and are now extirpated from the region as breeders (Patten et al. 2001, 2003). Neither the thrasher nor the warbler occurs regularly anymore, whereas the flycatcher occurs only as a sparse winter visitor. The Vermilion Flycatcher's decline is curious in light of this species' tolerance of human-altered habitat, such as agricultural areas and golf courses, in other parts of its range (Wolf and Jones 2000). Moreover, the species occasionally summers in northeastern Baja California along the Río Colorado (where it bred in 2002; O. Hinojosa-Huerta, pers. comm.) and Río Hardy (Patten et al. 2001).

RANGE AND POPULATION CHANGES 1950–2000

WATERBIRDS

In the past half century numerous species of breeding and non-breeding waterbirds have either colonized the Salton Sea or increased there markedly (Tables 1, 2). By contrast, two species, the Wood Stork and Fulvous Whistling-Duck, have decreased so much that each may soon be extirpated in California. The stork occurs principally as a post-breeding visitor to the Salton Sink, with the largest numbers in late summer and early fall (August and September). It used to occur in the thousands, but the 1990s brought ≤75 individuals every year, with as few as 12 in the most austere (Fig. 1). In 2002 the species again was scarce (G. McCaskie, pers. comm.), although a remarkable 36 storks were in the southern Mexicali Valley in July (E. Mellink, pers. comm.). Similarly, the multitude of whis-

TABLE 2. SELECTED WATERBIRD SPECIES THAT HAVE SHOWN MARKED DECREASES, OR INCREASES AS NONBREEDERS, AT THE SALTON SEA SINCE 1950

Species	Change[a]	Season	Since
Brown Pelican (*Pelecanus occidentalis*)	↑↑↑	summer/fall	1951
Cattle Egret (*Bubulcus ibis*)	↑↑↑	year round	1963
White-faced Ibis (*Plegadis chihi*)	↑↑	winter	1970s
Wood Stork (*Mycteria americana*)	↓↓↓	summer/fall	mid-1960s
Fulvous Whistling-Duck (*Dendrocygna bicolor*)	↓↓↓	summer/breeder	1980s
Ross's Goose (*Chen rossii*)	↑↑↑	winter	mid-1960s
Canada Goose (*Branta canadensis*)	↓↓↓	winter	1980s
Brant (*Branta bernicla*)	↑↑	spring	1962
Gadwall (*Anas strepera*)	↑	winter	1970s
American Wigeon (*Anas americana*)	↓↓↓	winter	1960s
Northern Shoveler (*Anas clypeata*)	↑↑	winter	1950s
Northern Pintail (*Anas acuta*)	↓↓↓	winter	1950s
Canvasback (*Aythya valisineria*)	↓↓	winter	1970s
Ruddy Duck (*Oxyura jamaicensis*)	↑	winter	1970s
Western Gull (*Larus occidentalis*)	↑	year round	1969
Yellow-footed Gull (*Larus livens*)	↑↑	summer/fall	1965

[a] Each arrow is a rough guide to the magnitude, such that a single arrow signifies a relatively small change, two a relatively moderate change, and three a relatively substantial change.

tling-ducks is gone; the species used to occur in the hundreds as a post-breeding visitor in the 1950s, and at least 20 pairs bred there in the 1960s (Patten et al. 2003). Although breeding numbers declined markedly, dozens of post-breeding birds continued to visit into the early 1990s (Patten et al. 2003). Only one pair was known to have bred in the Salton Sink in 2000; none were known to breed there in 2001 or 2002 (G. McCaskie, pers. comm.). Non-breeders and post-breeding visitors have declined as well; only four were located in 2000 and only one was noted in 2001 (Patten et al. 2003).

Four other species of waterfowl, the Canada Goose, American Wigeon, Northern Pintail, and Canvasback, have also declined (Patten et al. 2003; cf. Barnum and Johnson *this volume*), the goose and the Canvasback steadily (Figs. 2, 3), the wigeon and pintail abruptly after the 1950s (Table 3). The bulk of the populations of the goose and the Canvasback may now winter farther north, such that a few hundred rather than a few thousand now winter in the Salton Sink. This hypothesis requires the gathering and testing of long-term population data throughout California. These two species have declined or were

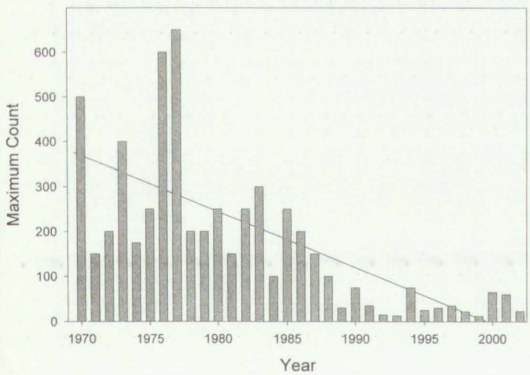

FIGURE 1. Decline of the Wood Stork (*Mycteria americana*) at the Salton Sea since 1970 (Spearman rank correlation: $r_s = -0.82$, $P < 0.001$); thousands of storks used to occur in the 1960s (Garrett and Dunn 1981). The trend line is from a linear regression ($y = -12.48x + 24{,}958.55$, $r^2 = 0.52$). Count data courtesy of G. McCaskie.

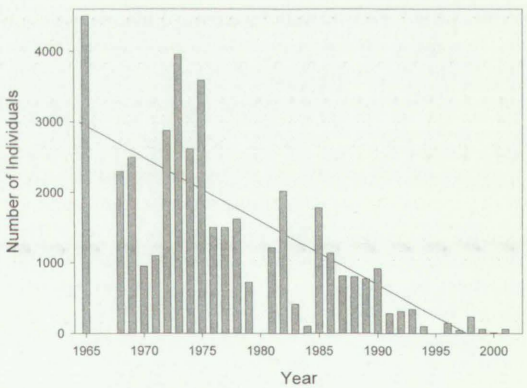

FIGURE 2. Decline of the Canada Goose (*Branta canadensis*) at the Salton Sea since 1965 (Spearman rank correlation: $r_s = -0.87$, $P < 0.001$). The trend line is from a linear regression ($y = -90.42x + 180{,}614.46$, $r^2 = 0.65$). Data are from the Salton Sea (south) Christmas Bird Count.

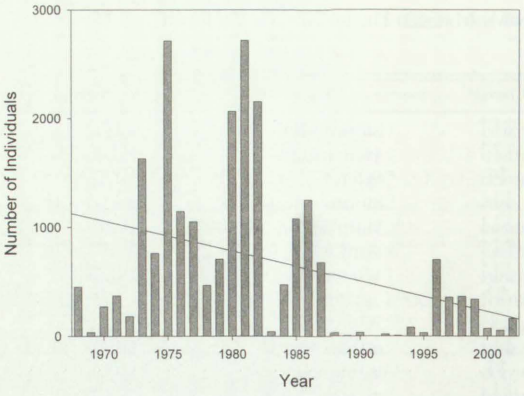

FIGURE 3. Decline of the Canvasback (*Aythya valisineria*) at the Salton Sea since 1968 (Spearman rank correlation: $r_s = -0.42$, $P < 0.01$). The trend line is from a linear regression ($y = -27.77x + 55{,}765.29$, $r^2 = 0.14$). Data are from the Salton Sea (south) Christmas Bird Count.

always scarce in northern Baja California and Sonora (Russell and Monson 1998, Patten et al. 2001). The downward trend of the pintail has been noted across North America (Banks and Springer 1994). Only three species of waterfowl, the Ross's Goose, Northern Shoveler, and Ruddy Duck, have increased markedly since 1970 (Fig. 4, Table 3; Patten et al. 2003, Barnum and Johnson *this volume*). Breeding populations of the goose have burgeoned across the Canadian arctic (Ryder and Alisauskas 1995). Similar broad-scale population increases for the Brown Pelican (Anderson and Gress 1983), Cattle Egret (Larson 1982), White-faced Ibis (Shuford et al. 1996), and Black Skimmer (Collins and Garrett 1996) have been mirrored at the Salton Sea.

The status of larids in the Salton Sink has also changed considerably since 1970, with five species colonizing or recolonizing as breeders (Tables 1, 2). Both the Laughing Gull and Caspian Tern colonized the Sea in the late 1920s, disappeared within in a few decades, and recolonized in the 1990s, the latter species' increase in concert with growing populations across the West (Wires and Cuthbert 2000). Similarly, numbers of the Double-crested Cormorant plummeted in the 1970s and 1980s, until it may have been extirpated (census data are lacking) as a local breeder (K. C. Molina, pers. comm.; W. D. Shuford, pers. comm.). By the mid-1990s, concomitant with increases across the continent (Carter et al. 1995), the species was again breeding in large numbers at the Salton Sea (Shuford et al. 2002b). Even so, breeding populations of both the tern and the cormorant have varied con-

TABLE 3. MEAN (± SE) NUMBERS, BY DECADE, OF DABBLING DUCKS (*Anas* SPP.) REGULARLY WINTERING AT THE SALTON SEA

Species[a]	1939–1941	1955–1957	1965, 1968–1969	1970–1979	1980–1989	1990–1999	2000–2002
Gadwall	2	25	15	33	100	144	67
	(0.5)	(14.5)	(10.9)	(12.8)	(18.6)	(36.1)	(25.1)
American Wigeon	113,667	33,847	405	389	149	926	849
	(14,983.9)	(5,749.8)	(198.1)	(114.7)	(37.7)	(226.8)	(25.6)
Mallard	20	116	18	36	48	51	46
	(13.1)	(62.9)	(9.6)	(23.0)	(8.0)	(9.1)	(8.3)
Cinnamon Teal	89	134	16	24	50	26	44
	(65.9)	(44.8)	(9.7)	(10.0)	(30.4)	(5.2)	(19.9)
Northern Shoveler	164	6,367	1,417	4,073	6,442	8,743	5,914
	(101.1)	(562.4)	(688.1)	(834.6)	(2,025.4)	(975.9)	(1,635.3)
Northern Pintail	123,000	9,693	5,357	4,278	1,537	4,365	1,062
	(18,779.4)	(5,459.8)	(2,159.6)	(759.7)	(404.7)	(1,396.7)	(202.1)
Green-winged Teal	566	11,043	1,283	1,388	1,731	1,836	2,486
	(296.1)	(3,447.2)	(555.2)	(181.3)	(495.9)	(340.1)	(658.0)

Note: Data are from all available Salton Sea (south) Christmas Bird Counts ($N = 42$).
[a] Scientific names in text and Table 2.

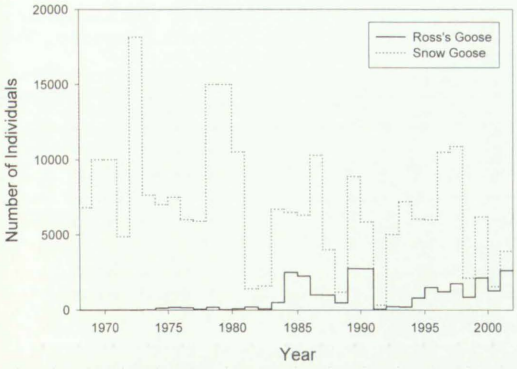

FIGURE 4. Population trends of the Snow Goose (*Chen caerulescens*) and Ross's Goose (*C. rossii*) in the Imperial Valley since 1968. The wintering population of the Snow Goose has been fairly constant since the 1950s (Patten et al. 2003), but wintering population of Ross's Goose has increased since the late 1970s. Data are from the Salton Sea (south) Christmas Bird Count.

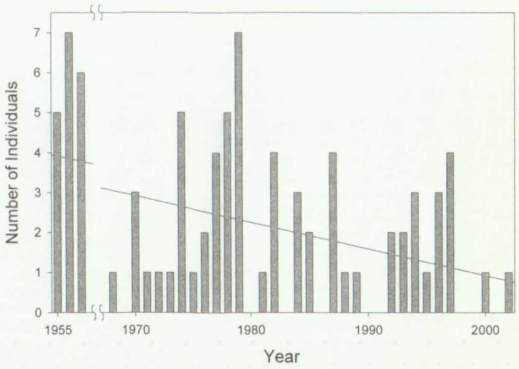

FIGURE 5. Decline of the Crissal Thrasher (*Toxostoma crissale*) at the Salton Sea since 1955 (Spearman rank correlation: $r_s = -0.33$, $P < 0.05$). The trend line is from a linear regression ($y = -0.07x + 134.12$, $r^2 = 0.17$). Data are from the Salton Sea (south) Christmas Bird Count.

siderably from year to year (Molina *this volume*, Molina and Sturm *this volume*).

In addition to the breeders, two species, the Western and Yellow-footed gulls, first appeared at the Salton Sea in the 1960s but are regular now, the former a rare but increasing perennial visitor (Patten et al. 2003), the latter occurring in the thousands as a post-breeding visitor (Patten 1996). Two others, Heermann's Gull (*L. heermanni*) and the Least Tern (*Sterna antillarum*), appear to be increasing although each remains rare enough that changes in status are difficult to judge. Even so, we predict that these two species and the Yellow-footed Gull are the most likely additions to the breeding avifauna of the Salton Sea. Since 1990, pairs of Heermann's Gulls have summered and pairs of Yellow-footed Gulls have been observed performing mating displays (Patten et al. 2003). In July 2002, two adult Least Terns accompanied by a juvenile were at the same location where a pair of adults had been observed in May (Patten et al. 2003).

Populations of most (63%) species that colonized or appear to be colonizing the Salton Sea and adjacent irrigated valleys have their origins in the Gulf of California or adjacent western Mexico (Table 1; see Patten and McCaskie *this volume*). Nine of these 12 southerly species have colonized since 1950 (Table 1), with all but the Cattle Egret and Black Skimmer still on the increase at the Salton Sea (Patten et al. 2003). Of the southerly species, only the Wood Stork and Fulvous Whistling-Duck have undergone steep declines at the Salton Sea, mirroring their declines in Sonora and elsewhere in western Mexico (Russell and Monson 1998, Hohman and Lee 2001).

Landbirds

Population changes

Since the middle of the twentieth century, the Crissal Thrasher (*Toxostoma crissale*) is the only species of landbird that has declined markedly in the Salton Sink, most noticeably after the mid-1980s (Fig. 5). Extensive removal of thickets of honey mesquite (*Prosopis glandulosa*) and screwbean (*P. pubescens*) presumably precipitated this mesquite-dependent thrasher's decline. Nonetheless, populations of the thrasher have persisted longer than those of other mesquite-dwelling species, such as the Vermilion Flycatcher and Lucy's Warbler (see above). The Phainopepla (*Phainopepla nitens*) has had an intermediate response, declining as a breeder but persisting commonly in some small areas, especially during winter (Patten et al. 2003). The Summer Tanager (*Piranga rubra*) no longer breeds in the Salton Sink (Table 4), though its population in the region was likely always small (Patten et al. 2001, 2003).

The multitude of specimens from the 1910s through the 1930s indicates that the Large-billed Savannah Sparrow (*Passerculus sandwichensis rostratus*), a Gulf of California endemic, was formerly a common post-breeding visitor to the Salton Sea. For reasons unknown, potentially related to damming of the Colorado River (*fide* K. L. Garrett), by the 1960s and 1970s this sparrow was "virtually accidental" everywhere in California (McCaskie 1988). Again for reasons un-

TABLE 4. STATUS AND PROVENANCE OF SPECIES OF LANDBIRDS KNOWN TO HAVE COLONIZED THE SALTON SINK SINCE FORMATION OF THE SALTON SEA AND DEVELOPMENT OF AGRICULTURE IN THE COACHELLA, IMPERIAL, AND MEXICALI VALLEYS

Species[a]	Appearance[b]	Breeding status	Provenance
White-winged Dove	1920	common	Colorado River
Inca Dove	1984	rare	Colorado River
Anna's Hummingbird	1980s	uncommon, local	Pacific coast
Gila Woodpecker	1927	uncommon	Colorado River
Black Phoebe	1949	fairly common	?
Brown-crested Flycatcher	1978	rare, irregular	Colorado River
Cliff Swallow	1977	common	Colorado River?
Barn Swallow	1973	extirpated	?
American Robin	1992	rare, irregular	Pacific coast?
Northern Mockingbird	1911	common	Pacific coast
Summer Tanager	1928	extirpated	Colorado River
Lark Sparrow	1970s	fairly common	Pacific coast
Savannah Sparrow (*rostratus*)	1997	rare, local	Gulf of California
Yellow-headed Blackbird	1952	fairly common	Colorado River
Brewer's Blackbird	1988	fairly common, local	Pacific coast
Great-tailed Grackle	1973	common	Colorado River
Bronzed Cowbird	1989	rare, local	Colorado River
Brown-headed Cowbird	1900s	common	Colorado River

[a] Scientific names in text, except: Black Phoebe (*Sayornis nigricans*), Brown-crested Flycatcher (*Myiarchus tyrannulus*), Cliff Swallow (*Petrochelidon pyrrhonota*), Barn Swallow (*Hirundo rustica*), American Robin (*Turdus migratorius*), and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*).
[b] Date of first breeding, not of first occurrence.

known, this sparrow staged an impressive comeback beginning in the late 1980s. It is again fairly common at the Salton Sea, mainly as a postbreeding visitor (July through February). Moreover, in the late 1990s it bred at Campo Geotérmico Cerro Prieto (Molina and Garrett 2001), a locale in the southern Mexicali Valley roughly midway between the Sea and the Gulf, and singing males (harbingers of breeding at the Sea?) were at the south end of the Salton Sea in early June 1998 and in late December 1999 (Patten et al. 2003).

Other landbirds that have recently colonized or increased markedly in the Salton Sea region (Table 4; Patten et al. 2003) include species emblematic of rapid expansion in the southwestern United States (see Phillips 1968): the Inca Dove (*Columbina inca*), Great-tailed Grackle (*Quiscalus mexicanus*), and Bronzed Cowbird (*Molothrus aeneus*). The dove was first recorded in the region in 1984; it is now an uncommon breeding resident in the Imperial Valley. Records of the cowbird date back to 1956 (Cardiff 1961), but only since the mid-1980s has the species increased sufficiently to establish itself. Most dramatic has been the spread of the grackle. It was first recorded in California and the Salton Sink in 1964 (McCaskie and DeBenedictis 1966), was breeding around the Salton Sea by 1970, and is now a common to abundant resident. The Anna's Hummingbird (*Calypte anna*), Lark Sparrow (*Chondestes grammacus*), and Brewer's Blackbird (*Euphagus cyanocephalus*) also colonized in the 1980s, and the non-native European Starling (*Sturnus vulgaris*) colonized in the 1950s (Rainey et al. 1959, Zimmerman 1973). The White-tailed Kite (*Elanus leucurus*) expanded its range into the Salton Sink in the past three decades, following a trend throughout western North America (see Eisenmann 1971). The species colonized the Imperial Valley in the 1990s, as it did the Mexicali Valley sometime during the 1980s (Patten et al. 1993). Its breeding in the Imperial Valley has been documented on several occasions (Patten et al. 2003), whereas its breeding in the Mexicali Valley is strongly suspected (Patten et al. 2001).

Biogeographic affinities

Whether recent arrivals or not, affinities of landbirds breeding in the Salton Sink are typically with the Sonoran Desert avifauna (Fig. 6). Over 60% of the species known to have colonized the Salton Sink in the twentieth century are from the Sonoran Desert or Colorado River; the remainder is from the Pacific Coast and none is from the Great Basin (Table 4). The key novel habitat appears to be the lawns and planted broadleaf trees (and palms) associated with parks, ranches, and suburbia, for many colonists are human commensals (e.g., the Inca Dove, Anna's Hummingbird, and Great-tailed Grackle). Colonization presumably followed the now permanent rivers and continuous agricultural belt sprawling from the Colorado River through the Mexicali Valley to the Imperial Valley.

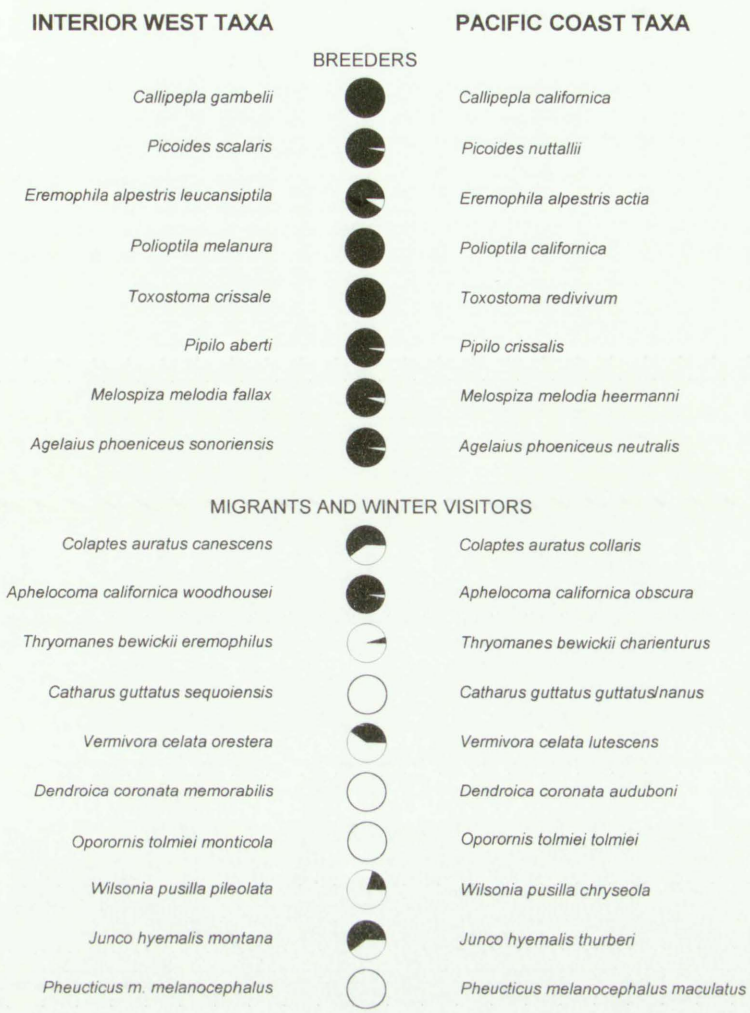

FIGURE 6. Qualitative comparison of biogeographic affinities of landbirds in the Salton Sink. A wholly black pie signifies complete affinity with the interior west avifauna, whereas a wholly white pie signifies complete affinity with the Pacific Coast avifauna. The heading "interior west" refers to the Sonoran Desert for breeders, the Great Basin for migrants and winter visitors.

Subspecies show a different pattern (Fig. 6). As with species, the common breeding subspecies is typically of Sonoran Desert affinity; examples include the Song Sparrow (*Melospiza melodia fallax*) and Red-winged Blackbird (*Agelaius phoeniceus sonoriensis*; see Patten 2001, Patten et al. 2003). The common migrating or wintering subspecies, however, is typically of Pacific Coast affinity (Fig. 6), with few from the Great Basin. In some cases, the Great Basin subspecies provides most records (e.g., 30 records of *Aphelocoma californica woodhousei* to only one of *A. c. obscura*), but in most cases these subspecies provide only a small percentage (e.g., 23 specimens of *Thryomanes bewickii charienturus* to only two of *T. b. eremophilus*) or none (e.g., *Agelaius phoeniceus nevadensis*; N > 300 specimens). Subspecies that appear to have colonized since 1950, such as *Lanius ludovicianus gambelii* and *Eremophila alpestris actia,* are from coastal California and generally have reached only the Coachella Valley (Patten et al. 2003), mirroring the pattern of *Melospiza melodia heermanni* (Patten 2001). These more "mesic-adapted" forms apparently moved southeast through the San Gorgonio Pass, where extensive irrigation of the Salton Sink provided novel habitat that could sustain their popula-

tions. Thus, the preponderance of evidence is that colonizing landbird subspecies are chiefly representatives of the cismontane California fauna.

Landbirds colonizing or occurring regularly in the Salton Sink show a different pattern than waterbirds, with breeding species and subspecies typically associated with the Colorado River Valley and migrants and winter visitors typically associated with coastal California. These different patterns underscore the complexity of biogeographic analyses. Had we analyzed all birds as a single group or had we ignored subspecific variation, we likely would have missed the patterns that we uncovered.

ACKNOWLEDGMENTS

We thank K. L. Garrett, O. Hinojosa-Huerta, G. McCaskie, E. Mellink, K. C. Molina, and W. D. Shuford for valuable information and discussion, and Garrett, Molina, Shuford, S. N. G. Howell, and J. T. Rotenberry for comments on various drafts of the manuscript.