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The Salton Sea: Critical Migratory Stopover Habitat for Caspian Terns (*Hydroprogne caspia*) in the North American Pacific Flyway

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Abstract.—For migratory waterbirds, the availability and quality of suitable stopover habitat can affect body condition and demographic parameters throughout the annual cycle. This study investigates the importance of the Salton Sea, a large saline lake located in the southwestern United States near the USA–Mexico border, for migrating Caspian Terns (*Hydroprogne caspia*) fitted with long-duration satellite telemetry tags in the northwest contiguous USA. During fall migration, 100% (n = 25) in 2014 and 98% (n = 63) in 2015 of all tagged individuals were tracked to the Salton Sea, with median durations of stay lasting 36 and 25 days, respectively. Use of the Salton Sea during subsequent spring migrations was less consistent than in fall, but still substantial, with 91% (n = 23) and 68% (n = 53) of all birds conducting brief stops there during 2015 and 2016, respectively. The future of the Salton Sea as suitable habitat for fish and piscivorous birds is uncertain due to rising salinity levels caused by reduced input flows. It is also uncertain if other wetlands in the region can serve as replacement habitat for Caspian Terns and other migratory piscivorous species should the Salton Sea cease to provide fish prey. *Received 30 April 2017, accepted 26 June 2017.*

Key words.—Caspian Tern, *Hydroprogne caspia*, migration, Salton Sea, satellite telemetry, stopover habitat.

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For migratory birds, the presence and quality of stopover habitat can impact fitness, both during migration and subsequent breeding or winter seasons (Newton 2006; Norris and Marra 2007). Stopover periods provide opportunities for migrating birds to accumulate energy reserves prior to breeding or restore reserves following breeding, as well as provide the opportunity to accomplish other annual requirements, like molt. The successful acquisition of resources during migratory stopovers can enhance subsequent reproductive potential or overwinter survival. Poor conditions at stopover locations can constrain these activities and have significant consequences for population dynamics (Drent *et al.* 2007).

In western North America, many species of waterbirds migrate through various segments of the Pacific Flyway, a region generally defined as extending from Alaska and northwest Canada south to Central America, and bounded by the nearshore Pacific Ocean on the west and the Rocky Mountain continental divide to the east. Within the Pacific Flyway, the lower Colorado River and delta region, straddling the USA–Mexico border, historically provided important stopover habitat for migrating waterbirds (Mellink *et al.* 1997). One topographic feature of this region, the Salton Trough, has periodically provided large lake habitat during recent geologic history (i.e., when the meandering route of the Colorado River has filled this area of natural subsidence; Buckles *et al.* 2002). Since the unintended establishment of the contemporary Salton Sea early in the 20th century (Cohen 2009), this large lake has been recognized as a wetland system of significant importance to a variety of waterbird species within the Pacific Flyway (e.g., Shuford *et al.* 2002). With growing economic development of water resources in the Central Valley of California (Kelly 1989) and Colorado River basin (Fradkin 1981), the Salton Sea has become more significant for waterbird species in this flyway as alternative wetland habitat has declined or disappeared altogether. In particular, the Salton Sea has substituted for wetland areas of the Colorado River delta and the Central Valley's Tulare Lake basin, formerly the largest fresh waterbody in western North America, as those systems declined due to water withdrawals for agricultural and urban uses (Pitt 2001; Adams *et al.* 2015).

A variety of piscivorous waterbirds, including pelicans, cormorants, gulls, and terns, within the Pacific Flyway use the Salton Sea as migratory habitat (Shuford *et al.* 2002). Several species, including Double-crested Cormorants (*Phalacrocorax auritus*), California Gulls (*Larus californicus*), Gull-billed Terns (*Sterna nilotica*), Caspian Terns (*Hydroprogne caspia*), and Black Skimmers (*Rynchops niger*), also nest at the Salton Sea in most years (Shuford *et al.* 2002). The extent to which non-resident individuals of these species that breed elsewhere in the Pacific Flyway use the Salton Sea, both in terms of the proportion of their populations and the duration of their use, is largely unknown.

The goal of this study was to characterize use of the Salton Sea and Colorado River delta by non-resident piscivorous waterbirds, using Caspian Terns as the focal study species. Caspian Terns are a cosmopolitan species with a globally significant population within the Pacific Flyway (Suryan *et al.* 2004), and were previously known to migrate from breeding areas throughout the Pacific Flyway to wintering areas in Mexico and Central America (Suryan *et al.* 2004). Specific objectives were to describe the importance of the Salton Sea as a migratory stopover location by: 1) quantifying the proportion of Caspian Terns that visited the Salton Sea during either the post-breeding southward ("fall") migration or the pre-breeding northward ("spring") migration; 2) mapping fall migration routes from the breeding region to the latitude of the Salton Sea; and 3) obtaining arrival dates, departure dates, and durations of stay during each migration. To examine the importance of the lower Colorado River region in a broader geographic context, we also investigated use of the Colorado River delta using similar metrics.

METHODS

Study Area

Adult Caspian Terns were captured in small groups using a "Net Blaster" compressed air-powered net launcher (Wildlife Control Supplies) at two colony sites in eastern Washington State, USA (Goose Island in Potholes Reservoir, 56° 59′ 08.96″ N, 119° 18′ 30.02″ W, and Crescent Island in the Columbia River, 46° 05′ 37.29″ N, 118° 55′ 47.76″ W; Fig. 1). Captures and tagging occurred during April 2014 (n = 28; all at Goose Island) and April 2015 (n = 46; 28 at Crescent Island and 18 at Goose Island), prior to any nest initiation in the region.

Individual Tracking and Analyses

Satellite telemetry tags (platform terminal transmitters model PTT-100-12, Microwave Telemetry, Inc.) were programmed to operate on a 32-hr duty cycle, with 6 hr on and 26 hr off, transmitting at a 60-sec repetition rate during the on period of each cycle. Each tag incorporated a small solar panel that recharged a battery, allowing transmission during both daylight and nighttime hours. We attached tags using either a wing harness (n = 9; Thaxter *et al.* 2014) or a leg-loop harness (n = 65; Mallory and Gilbert 2008; Thaxter *et al.* 2014).Tags weighed 12.4-12.9 g, not including harness materials, and were ≤ 2.2% of body mass for all individuals tagged (body mass of tagged terns ranged from 590 to 720 g).

During the spring and summer breeding season, the majority of tagged individuals either bred or traveled within a network of nesting colonies within the Pacific Flyway and north of 40° N (hereafter, "breeding region"). During 2014, 25 tags were functional long enough during the fall migration to document the entire migratory route. One tag ceased operation shortly after the individual tern carrying it reached the Salton

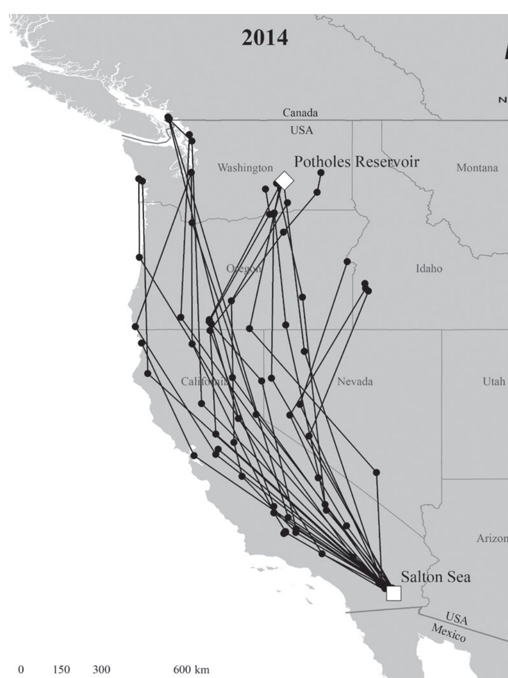

Figure 1. Post-breeding southward ("fall") migration routes of Caspian Terns following the 2014 breeding season. In 2014, all individuals were captured at a single site (Potholes Reservoir near Othello, Washington, USA).

Sea in late June 2014. Another tag ceased operation in February 2015 while that individual was residing in Mexico. A total of 23 tags were functional during the 2015 spring migration period. During fall 2015, 63 tags were functional long enough during the fall migration to document the migratory route. One tag ceased operation on 23 November 2015, 94 days after the individual carrying it arrived at the Salton Sea and before it had migrated southward; nine more ceased operation during the winter period prior to the following spring migration. A total of 53 tags was functional during the 2016 spring migration period.

Location data were collected via the Argos satellite network (Argos 2011) and conveyed to the Movebank data management system (Max Planck Institute for Ornithology, Radolfzell, Germany) via CLS America, Inc. (Largo, Maryland). We used the Douglas Argos-Filter Algorithm (Douglas *et al.* 2012), with a maximum movement rate of 80 kmph and a minimum angle of 15°, to remove unlikely raw locations. We used best-of-day locations to document Salton Sea arrival and departure dates, calculate duration of stay during both fall and spring migration, and describe space use within the Sea. Individuals were considered to be at the Salton Sea if locations fell within a 20-km buffer surrounding the Sea, as defined by the Watershed Boundary Dataset (U.S. Geological Survey 2014). All spatial analyses were conducted using standard Geographical Information Software (Environmental Systems Research Institute 2011).

To investigate tern use of areas within the Salton Sea, we also generated a kernel density-based utilization distribution map within the Salton Sea using best-of-day locations from both periods of use, June 2014-May 2015 and June 2015-May 2016. The utilization distribution included all best-of-day locations for all individuals during fall and spring migration periods, as well as during the overwinter period, for each of the non-breeding periods when location fixes were acquired. As a result, this procedure more heavily weights the area preferences of individual terns that were present at the Salton Sea for longer periods of time.

For the purpose of assessing use of the Colorado River delta by tagged Caspian Terns, we defined the delta region as a 20-km buffer around the boundaries of the Alto Golfo de California UNESCO Biosphere Reserve (United Nations Environment Programme 2016). To compare use of this region to that of the Salton Sea, we: 1) quantified the proportion of Caspian Terns with active tags that were tracked to the delta; 2) determined the durations of stay during each migration period; and 3) generated a utilization distribution map to describe use within the delta region.

RESULTS

Following the 2014 breeding season, all tagged Caspian Terns (n = 25) that were tracked through the southward (fall) migration period visited the Salton Sea. Numerous routes were taken southward from the breeding region, with some birds migrating along the Pacific Coast initially and others migrating 500 km or more inland (Fig. 1). Following the 2015 breeding season, 98% of Caspian Terns tracked through the fall migration (n = 63) visited the Salton Sea. Fall migratory routes were similar in 2015 to those in 2014 (Fig. 2).

During the 2014 fall migration, tagged Caspian Terns migrated southward over an extended period, arriving at the Salton Sea between early June and early September, with a median arrival date of 11 August (Table 1; Fig. 3). Departure dates ranged from 12 June to 6 November 2014. The median duration of stay at the Salton Sea during fall migration was 36 days (Range = 1-152 days). There was the suggestion of a negative correlation between arrival date and duration of stay (P = 0.07, r^2 = 0.15). Peak stopover use occurred during

Figure 2. Post-breeding southward ("fall") migration routes of Caspian Terns following the 2015 breeding season. In 2015, individuals were captured at two sites (Potholes Reservoir near Othello, Washington, and Crescent Island near Pasco, Washington, USA).

Table 1. Arrival and departure dates and duration of stay periods for tagged Caspian Terns visiting the Salton Sea during 2014 post-breeding southward ("fall"; June-December) and 2015 pre-breeding northward ("spring"; January-May) migrations. All Caspian Terns with active tags through the fall migration period (*n* = 25) visited the Salton Sea. During the spring migration period, 91% of Caspian Terns with active tags (*n* = 22) were tracked there.

	Fall			Spring		
Measure	Arrival	Departure	Duration of Stay (Days)	Arrival	Departure	Duration of Stay (Days)
Median	11 Aug	10 Sep	36	10 Apr	12 Apr	5
Earliest/Min	3 Jun	12 Jun	1	31 Mar	5 Apr	2
Latest/Max	3 Sep	6 Nov	152	6 May	9 May	11
n	25	23	23	19	20	19

the weeks of 17 and 24 August, when over 60% of tagged individuals were present at the Salton Sea (Fig. 4A). One tagged individual remained at the Salton Sea throughout the winter.

Fall migration patterns were similar between 2014 and 2015. In 2015, Caspian Terns again arrived at the Salton Sea between June and early September, with the median arrival date = 1 August (Table 2; Fig. 3). The median duration of stay was 25 days (Range = 3-139 days). Later arrival dates correlated to shorter duration stays at the Salton Sea (P = 0.003, r^2 = 0.15). Peak use again occurred during the latter half of August (Fig. 4B), with departure dates ranging from 22 June to 15 November. Four individuals resided at the Salton Sea throughout the entire winter period until they migrated north in the spring.

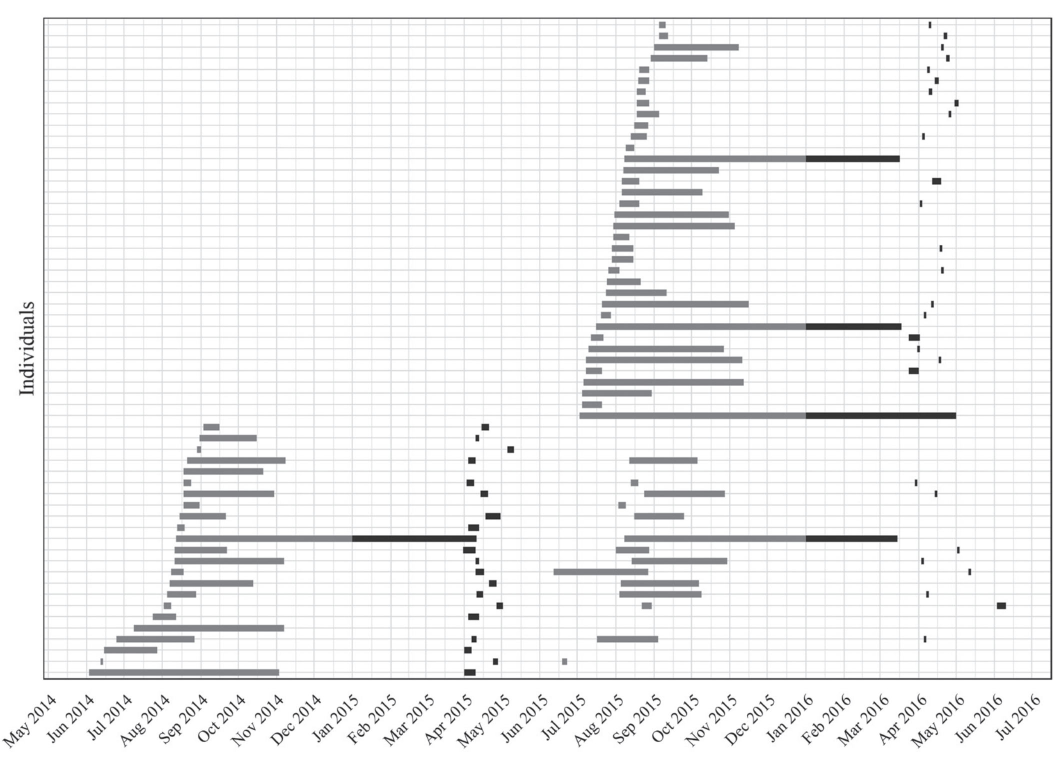

Figure 3. Periods of use of the Salton Sea by individual tagged Caspian Terns from May 2014 to July 2016. Residence periods during fall migration (June-December of each year) are shown in gray shading and periods during spring migration (January-May of each year) are shown in black shading. Individuals are sorted by date of first arrival to the Salton Sea.

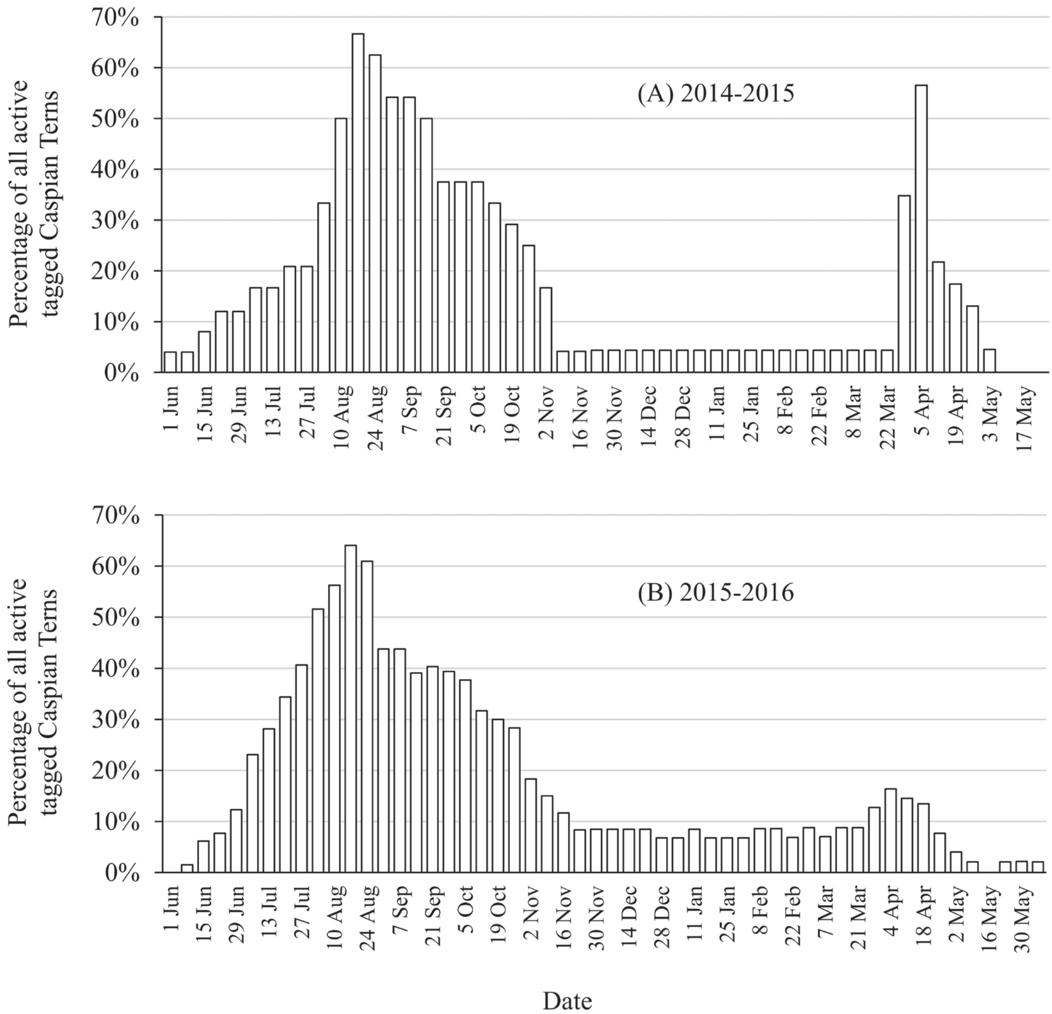

Figure 4. Cumulative use of the Salton Sea by tagged Caspian Terns during (A) the fall 2014 and spring 2015 migrations and (B) the fall 2015 and spring 2016 migrations, as well as during the intervening overwinter period. The percentage present of all individuals with active tags during each week is shown.

Spring stopover arrival dates were more condensed and stopover durations were shorter in spring 2015 than in the preceding fall. Spring arrivals at the Salton Sea occurred between 31 March and 6 May with the median arrival date of 10 April (Table 1; Fig. 3). Only 9% (n = 23) of individuals tracked during this period migrated northward without any reported locations at the Salton Sea, although their migration routes may have briefly passed over or nearby. One individual (4% of the total tracked in spring) that wintered in Mexico did not migrate northward in spring 2015 and never approached 33° N latitude during the 2015 breeding season. Durations of stay at the Salton Sea were much shorter during spring (median = 5 days, Range = 2-11 days; Fig. 3) than in fall (median difference in duration [fall minus spring] = 25 days, Range = -3 to 144 days; paired two-sided t-test, $P < 0.001$) and there was no correlation between an individual's duration of stay during fall 2014 and the subsequent spring ($P = 0.79$). There was also no apparent relationship between spring arrival date and duration of stay ($P = 0.21$). Peak use occurred during the first half of April, when more than 50% of all terns with active tags were present (Fig. 4A).

Table 2. Arrival and departure dates and duration of stay periods for tagged Caspian Terns visiting the Salton Sea during 2015 post-breeding southward ("fall"; June-December) and 2016 pre-breeding northward ("spring"; January-May) migrations. During the fall migration period, 98% of Caspian Terns with active tags (*n* = 63) visited the Salton Sea. During the spring migration period, 68% of Caspian Terns with active tags that migrated northward (*n* = 50) were tracked there (three tagged terns remained in Mexico during the 2016 breeding season).

	Fall			Spring		
Measure	Arrival	Departure	Duration of Stay (Days)	Arrival	Departure	Duration of Stay (Days)
Median	1 Aug	27 Sep	25	10 Apr	11 Apr	1
Earliest/Min	12 Jun	22 Jun	3	19 Mar	13 Mar[1]	1
Latest/Max	5 Sep	15 Nov	139	3 Jun	8 Jun	8
n	62	57	57	30	32	28

[1]For the spring migration, one tagged individual that resided at the Salton Sea throughout the overwintering period departed northward on 13 March, before the first individual that wintered in Mexico arrived at the Salton Sea while migrating northward (19 March).

During the 2016 spring migration, tagged individuals moved northward over a more protracted period of time than in spring 2015, and a similar proportion (6%; *n* = 53) did not migrate northward out of Mexico. The first tern moving north from Mexico arrived at the Salton Sea on 19 March and the last on 3 June, a 76-day span compared to a 36-day span in 2015 (Table 2; Fig. 3); the median arrival date of 10 April was the same as during the 2015 spring migration, however. Peak use again occurred during the week of 4 April; however, only a maximum of 16% of tagged terns were tracked to the Salton Sea during a given week, indicating much less synchrony in migration timing compared to 2015 (Fig. 4). A smaller proportion (68%; *n* = 50) of the tagged terns that migrated north reported locations at the Salton Sea in 2016 than did in 2015 (91%). The median duration of stay during the 2016 spring migration period was only 1 day (Range = 1-8 days; Table 2; Fig. 3), much shorter than during the previous fall (median difference in duration = 33 days, Range = 1-124 days; paired two-sided t-test, $P < 0.001$) and shorter than in the spring of 2015. Unlike the previous year, there was the suggestion of a negative relationship between an individual's duration of stay during fall 2015 and the subsequent spring ($P = 0.09$, $r^2 = 0.11$). There was no relationship between spring arrival date and duration of stay ($P = 0.97$).

While using the Salton Sea, Caspian Terns were most often located along the periphery, with the highest utilization along the northern and southern shores, and particularly at areas of agricultural drainage water input (Fig. 5). Caspian Terns also used portions of the Salton Sea near historical or recently active Caspian Tern colonies within the Sonny Bono Salton Sea National Wildlife Refuge (Suryan *et al.* 2004).

A substantial proportion of tagged Caspian Terns also used the nearby Colorado River delta region in the 2014-2015 nonbreeding period, both during both fall (46%; *n* = 24) and spring (41%; *n* = 22) migrations. The median durations of stay in the delta were short (1 day in both fall and spring), with the exception of one individual during fall migration (52 days) and a different individual during the spring migration (10 days). During the 2015-2016 non-breeding period, a lower proportion of tagged terns were tracked to the delta during fall 2015 (31%; *n* = 61; median duration of stay = 1 day) than during fall 2014. During spring 2016, a higher proportion of tagged terns were tracked to the delta (58%; *n* = 53) than in spring 2015, and longer durations of stay were observed (median = 4 days, maximum = 77 days). These longer spring stopovers in the delta were associated with delayed northward migration for some individuals. During each migration period, paired Wilcoxon signed-rank tests indicated that the duration of stays in the Salton Sea and Colorado River delta were negatively correlated. In fall 2014, the median stay at the Salton Sea was 41 days

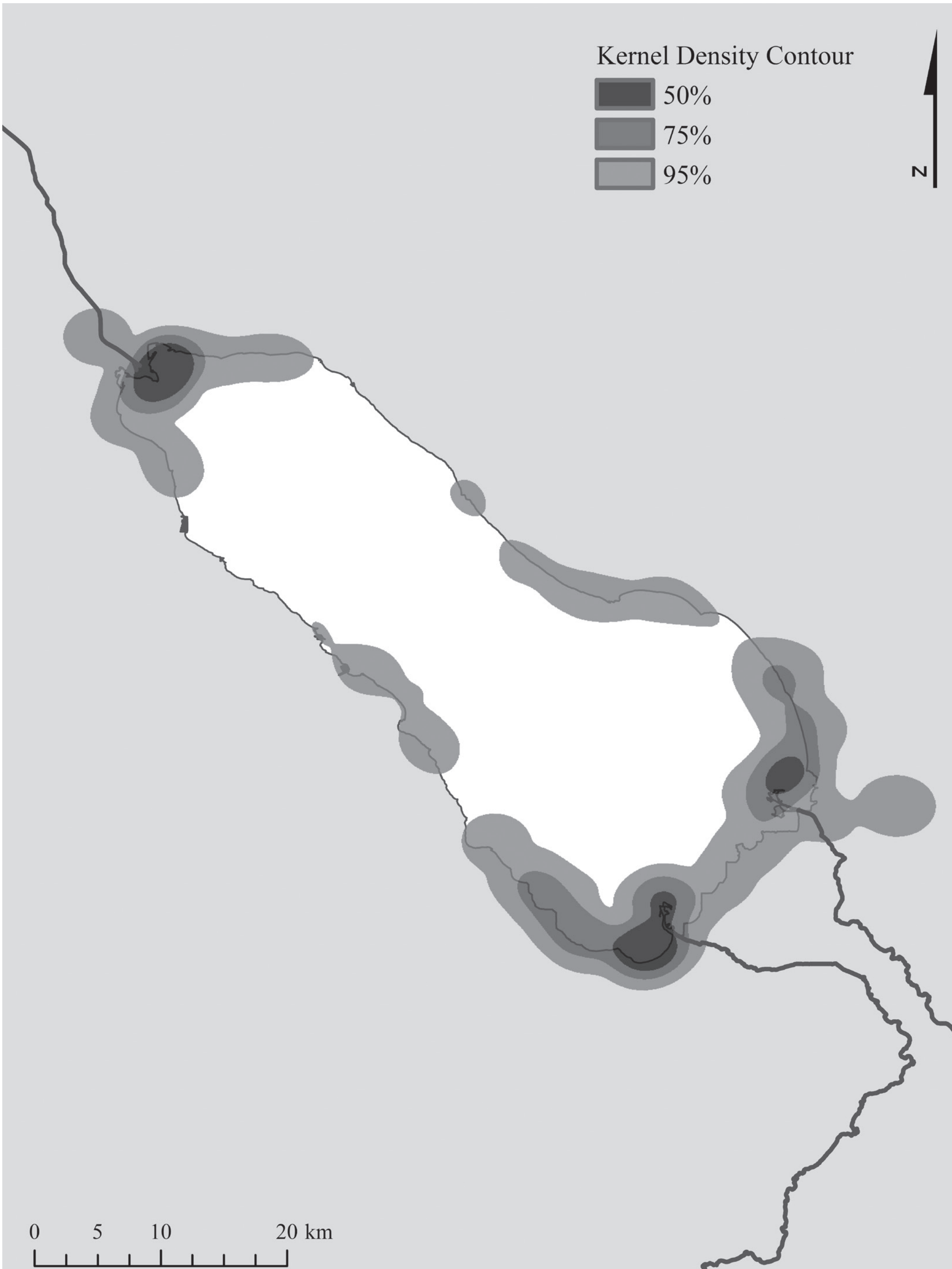

Figure 5. Utilization distribution of tagged Caspian Terns at the Salton Sea, USA. All best-of-day locations for every individual tracked to the Salton Sea were used to generate kernel density contours for the period 1 July 2014 through 30 June 2016.

and 0 days at the Colorado River delta (z = -3.65, P < 0.001). In spring 2015, the median stays were 5 and 0 days, respectively (z = -2.94, P = 0.003), and in fall 2015, 16 and 0 days, respectively (z = -5.28, P < 0.001). During the spring of 2016, longer visits occurred in the Colorado River delta, with visits lasting up to 77 days there, compared to a maximum of 8 days at the Salton Sea (z = 2.00, P = 0.05). Median stays were equal at 1 day in both locations, however. In general, individuals that displayed longer stopovers at the Salton Sea had shorter stopovers in the delta, and *vice versa.* A utilization map of the Colorado River delta region indicated that the majority of use fell along the Gulf of California coastline, rather than along the riverbed of the Colorado River or other interior wetlands (Fig. 6).

Discussion

Our results suggest that a large majority of Pacific Flyway Caspian Terns use the Salton Sea as a stopover site for extended periods during the fall post-breeding southward migration. A majority of Pacific Flyway terns also stopover for a short period during the spring pre-breeding northward migration, while a small minority overwinter there. Other piscivorous waterbirds, including Double-crested Cormorants (Courtot *et al.* 2012) and American White Pelicans

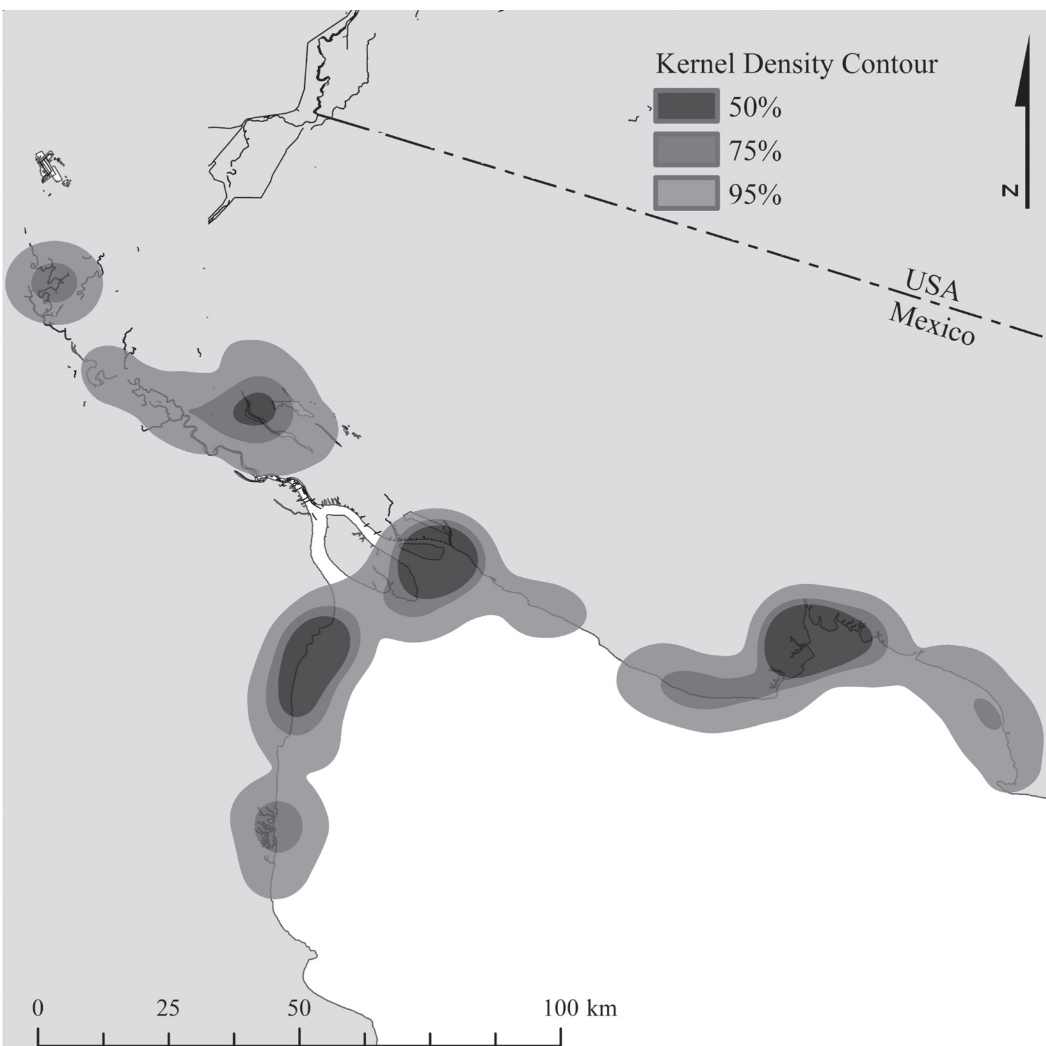

Figure 6. Utilization distribution of tagged Caspian Terns within the Alto Golfo de California UNESCO Biosphere Reserve, Mexico. All best-of-day locations for every individual tracked to this region were used to generate kernel density contours for the period 1 July 2014 through 30 June 2016.

(*Pelecanus erythrorhynchos*), migrating from distant breeding locations have also been documented to use the Salton Sea as a migratory stopover or overwintering location. Fall, winter, and spring surveys have documented flyway-significant aggregations of these species during the non-breeding portion of the annual cycle, as well as other migratory piscivorous species, including Ring-billed Gulls (*Larus delawarensis*), California Gulls, Herring Gulls (*L. argentatus*), Black Terns (*Childonias niger*), Forster's Terns (*Sterna forsteri*), and Black Skimmers (Shuford *et al.* 2002). The ubiquitous use of the Salton Sea by Caspian Terns from two colonies (> 95% of all tracked individuals) documented in this study is remarkable for a population migrating moderate or long distances (e.g., ≥ 1,500 km) within the Pacific Flyway (Courtot *et al.* 2012).

The future of the Salton Sea as suitable habitat for fish is uncertain. Since the modern establishment in 1905, agricultural drainage water input has been inadequate to maintain stable salinity levels. Salinity has risen from about 3.6 g/L in 1905 (Hely *et al.* 1966) to values exceeding 50 g/L in recent years (Lorenzi and Schlenk 2014; Barnum *et al.* 2017). As salinity levels have risen, there have been dramatic changes in fish community composition (Hurlbert *et al.* 2007). In the last two decades, three of the four abundant fish species present during 1999-2000 (bairdiella (*Bairdiella icistia*), orangemouth corvine (*Cynoscion xanthulus*), and sargo (*Anisotremus davidsoni*)) have declined precipitously as salinity exceeded 40 g/L, leaving a feral hybrid tilapia strain (*Oreochromis mossambicus* × *O. urolepis hornorum*) as the only abundant fish type present (Riedel 2016). Osmoregulatory stress tests on individual tilapia from the Salton Sea indicate that survival rates for this population will decline as salinities approach 60 g/L, particularly at winter and summer temperature extremes (Lorenzi and Schlenk 2014); tilapia reproduction rates likely decline at even lower salinity levels (Rodriguez-Montes de Oca *et al.* 2015). However, salinity levels may increase even more rapidly than current trends predict beginning in 2018, when the level of agricultural return flowing into the Salton Sea is scheduled to drop from the 1.2-1.3 million acre-feet per year recorded in recent decades to 0.7-0.8 million acre-feet per year, due to increased agricultural-to-urban water transfers and the termination of mitigation water negotiated in 2003 (California Resources Agency 2007).

Critical stopover habitat has been identified for many species of migratory waterbirds (Clark *et al.* 1993; Oppel *et al.* 2009; Bamford and Moro 2011; Moores *et al.* 2016). This is particularly the case for species that rely upon rare habitats subject to widespread human modification, such as shorebirds that rely upon estuarine tidal mud flats. In some of these cases (e.g., in Korea and China bordering the Yellow Sea), the loss or degradation of critical stopovers has led to significant shorebird population declines (e.g., Baker *et al.* 2004; Moores *et al.* 2016). To our knowledge, the degree of consistent use of a single stopover location indicated in this study has not been previously documented in a migratory piscivorous waterbird population, suggesting a serious risk for the dependent population if the Salton Sea and the resources it supports are lost.

Pacific Flyway Caspian Terns experienced strong population growth during much of the 20th century (Gill and Mewaldt 1983; Suryan *et al.* 2004). Previously, this growth has been primarily attributed to the exploitation of novel stable and secure nesting habitat, such as dredge disposal sites, in large productive coastal estuaries (e.g., San Francisco Bay, various sites in coastal Washington, and the Columbia River estuary). Our results suggest an additional hypothesis: that the presence of the Salton Sea as migratory stopover habitat has offered more advantageous foraging opportunities than were previously available in this region, to the benefit of Caspian terns nesting throughout the Pacific Flyway. Profitable foraging at the Salton Sea may have allowed individuals to recover to a robust nutritional state more quickly following the breeding season, allowed efficient foraging during molt, and had positive carry-over effects during the overwinter period. These benefits could have fueled higher survival during the migration and overwinter periods, and contributed to robust population growth. If this were the case, then elimination of the Salton Sea as fish habitat and a migratory stopover could be associated with declines in the Pacific Flyway population of Caspian Terns, as well as other migratory piscivorous species.

It is unclear how important the Colorado River delta was as a stopover for migratory species of piscivorous birds prior to establishment of the Salton Sea. Given the successful exploitation of large estuaries in the breeding region by Caspian Terns and other species, it seems likely that the delta was favorable stopover habitat of significant importance. Wetland areas associated with the San Joaquin River of California's Central Valley were also likely of greater importance prior to their extensive modification for irrigated agriculture. Today, both of these alternative systems support much less fish habitat and use by migrating Caspian Terns than does the Salton Sea. Their suitability as alternative stopover habitat is likely further reduced during periods of drought, which was the case during our study period (Diaz and Wahl 2015). If the Salton Sea is lost as suitable fish habitat, it is not clear that either of these areas can consistently offer sufficient alternative foraging and loafing opportunities given the current and planned water withdrawals for agricultural and domestic use and more extreme drought cycles projected under future climate change (Williams *et al.* 2015). In our study, we documented greater use of Gulf of California coastal areas associated with the delta by individuals that used the Salton Sea less, but a majority of terns used the delta only in one season, spring 2016. In some flood years, waters fill a playa lakebed to the west of the Colorado River channel and south of the Salton Sea in Mexico (the Laguna Salada). The lake that develops can cover up to 9,300 ha and at times supports salt-water fisheries (Cohen and Henges-Jeck 2001). When water is occasionally present, the Laguna Salada could serve as alternative stopover habitat for piscivorous birds; the lakebed was dry during 2014-2016, however.

Given the uncertainty regarding the future of the Salton Sea as fish habitat, and the apparent lack of equivalent alternative stopover habitat in the region, we suggest continued monitoring of migratory piscivorous waterbird populations in the Pacific Flyway, particularly during and after the period when tilapia die-offs are expected at the Salton Sea. In addition, studies of both migratory behavior and demography would contribute to understanding the trajectory of these populations following either the loss of this important habitat or the possible reconfiguration to provide some amount of fish habitat into the future. Such studies would inform our understanding of the resilience of piscivorous waterbird populations in this flyway, and of similar species in other areas.

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