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California Gull (*Larus californicus*) Space Use and Timing of Movements in Relation to Landfills and Breeding Colonies

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Abstract.—Expanding gull (Laridae) populations throughout the world have been attributed to the availability of anthropogenic food subsidies. The influence of landfills on California Gull (*Larus californicus*) space use and the timing of their movements was evaluated in San Francisco Bay, California, USA. Using radio telemetry, 108 California Gulls were tracked, > 7,000 locations were recorded, and > 1 million detections were obtained at automated logger systems placed at the two main landfills and three major breeding colonies. Population home range (31-35 km^2) and core use areas (2-3 km^2) overlapped landfills and colonies, and expanded after breeding. California Gull attendance at landfills (1.6-19.0 km from colonies) increased throughout breeding and post-breeding, whereas attendance at colonies was low during pre-breeding (20%-40% per day), increased during breeding (60%-80% per day), and declined into and during post-breeding (< 20% per day). California Gull attendance at landfills was greatest when garbage was delivered from 06:00 hr in the morning until 18:00 hr at night. In contrast, California Gull attendance at colonies during breeding was greater at night from 20:00 hr to 05:00 hr (50%-70% per hr) than during the day from 06:00 hr to 18:00 hr (30%-40% per hr). Landfills played a predominant role in California Gull space use and the timing of their movements in this highly urbanized estuary. *Received 27 February 2018, accepted 5 April 2018.*

Key words.—bird movements, California Gull, colony, garbage, gull management, gull predation, landfills, *Larus californicus*, radio telemetry.

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Many populations of *Larus* gulls have increased substantially over the last century (Kadlec and Drury 1968; Conover 1983; Duhem *et al.* 2008; Giroux *et al.* 2016), with recent declines in some areas (Coulson 2015; Hario and Rintala 2016; Mittelhauser *et al.* 2016; Washburn *et al.* 2016). The increase in *Larus* gull populations is thought to be due to protection from hunting and egg harvesting; the expanded availability of anthropogenic food resources from landfills, fisheries discards, and irrigated agriculture; and the anthropogenic creation of new and protected nesting habitats, such as islands within reservoirs (Conover 1983; Horton *et al.* 1983; Duhem *et al.* 2008; Coulson 2015). In many situations, large gull populations have been problematic for humans and other wildlife (Thomas 1972; Jones and Kress 2012). In particular, gulls often reduce the productivity of other colonial waterbirds by competing for preferred nesting sites (Kress 1983; Nisbet and Spendelow 1999), causing harassment (Hatch 1970; Stienen *et al.* 2001), and depredating eggs, chicks, and adults (Spear 1993; Becker 1995; Oro *et al.* 2005; Ackerman *et al.* 2014a, 2014b). Consequently, gulls are actively managed in many places throughout the world, including extensive gull culling programs (Thomas 1972; Bosch *et al.* 2000; Jones and Kress 2012; Coulson 2015).

Use of landfills by gulls has been widely documented, and garbage often makes up a large proportion of gull diets (Smith and Carlile 1993; Brousseau *et al.* 1996; Belant *et al.* 1998; Weiser and Powell 2011). Population increases at many gull colonies often are attributed to the availability of food subsidies at landfills (Hunt 1972; Pons 1992; Duhem *et al.* 2008; Weiser and Powell 2010). However, some studies have shown that garbage in gull diets can reduce reproductive success (Pierotti and Annett 1990, 1991; Annett and Pierotti 1999). Coulson (2015) suggested that landfills likely did not play a major role in the population growth of Herring Gulls (*Larus argentatus*) in Great Britain. Typically, the effects of landfills on local gull populations appear to be related to the proximity of food resources in relation to the breeding colony (Hunt 1972; Pons 1992; Duhem *et al.* 2008; Weiser and Powell 2010).

The California Gull (*L. californicus*) breeding population in the San Francisco Bay, California, USA, has increased from 24 individuals in 1980 to over 53,000 in 2014 (Strong *et al.* 2004; Burns *et al.* 2018). The San Francisco Bay contains one of the largest California Gull breeding populations in the world (Winkler 1996; Burns *et al.* 2018). California Gulls could be limiting productivity of several other waterbird species breeding within the estuary (Herring *et al.* 2011; Ackerman *et al.* 2014a, 2014b; Takekawa *et al.* 2015). Because the San Francisco Bay is highly urbanized and California Gull colonies breed in close proximity to several large landfills, anthropogenic food resources derived from landfills may have subsidized the California Gull population's rapid growth and heavily influenced its use of the landscape (Burns *et al.* 2018).

In this study, we evaluated the influence of landfill and colony locations on California Gull space use and timing of movements throughout the pre-breeding, breeding, and post-breeding time periods. We used two distinct, but complimentary, methodological approaches to track radio-marked California Gulls in San Francisco Bay, including: 1) truck- and aerial-based telemetry to study general space use; and 2) automated logger systems placed at each of the two main landfills and three major breeding colonies to study temporal use. Our objective was to determine the relative importance of landfills in influencing California Gull space use and the timing of their movements.

METHODS

Study Area

We studied the three largest California Gull colonies in the San Francisco Bay: Alviso Pond A6 (hereafter Alviso), Mowry Ponds 1/2 and 4/5 (hereafter Mowry), and Coyote Hills Ponds N3A/4AB (hereafter Coyote Hills; Fig. 1). Together, these three colonies made up 99% and 97% of all the breeding California Gulls in San Francisco Bay during 2007 (nearly 37,000 individuals) and 2008 (nearly 47,000 individuals), respectively (Burns *et al.* 2018). During 2007 and 2008, approximately 60% of California Gulls bred at Alviso, 10% at Coyote Hills, 12% at Mowry 4/5, and 18% at Mowry 1/2 (Burns *et al.* 2018). The habitats at the breeding colonies were sparsely vegetated levees within former salt evaporation ponds (Coyote Hills and Mowry) or the dry bed of a former salt pond (Alviso). The two major landfills within the south San Francisco Bay that receive residential waste were Newby Island Landfill and Tri-Cities Landfill, and were located 1.6 km to 19.0 km from the California Gull colonies (Fig. 1). There were no active California Gull hazing programs at these landfills during the study. The largest landfill, Newby Island Landfill, received approximately 800 m^3 of garbage each year (E. Boyd, pers. commun.).

California Gull Capture and Tagging

We captured adult California Gulls in 2007 and 2008 before the breeding season, between 6 March and 26 April, at the Alviso and Coyote Hills colonies using rocket nets (Dill and Thornsberry 1950) and remotely detonated net-launchers (Coda Enterprises). We weighed birds to the nearest 5 g using a 1-kg Pesola spring scale (Pesola AG) and collected body morphometrics, including culmen length, bill depth at the gonys, head-to-bill length, and flattened wing length, to the nearest 0.01 mm using digital calipers or 1 mm using a wing rule. A drop of blood was collected from every bird for sex determination (Zoogen Services, Inc.), and, for birds without usable genetic results, a discriminant function based on California Gull morphometric measurements was used to determine sex (Herring *et al.* 2010). California Gulls were temporarily held in shaded and screen-lined poultry cages (Murray McMurray Hatchery, model 5KTC) and released within 3 hr at the capture site after instrumentation.

Radio transmitters (Advanced Telemetry Systems, Inc., model A1135) were attached to California Gulls using a backpack harness composed of 4.8-mm ribbon with cyanoacrylate glue (Loctite 422, Henkel Corporation) to secure knots. In addition, radio transmitters were affixed to leg bands on 13 additional California Gulls in 2007 (12% of all transmitters). Transmitter packages weighed approximately 18 g and represented, on average, < 3% of a California Gull's body mass.

Radio Tracking

We used radio telemetry to track California Gulls from capture until 9 September with the goal of locating

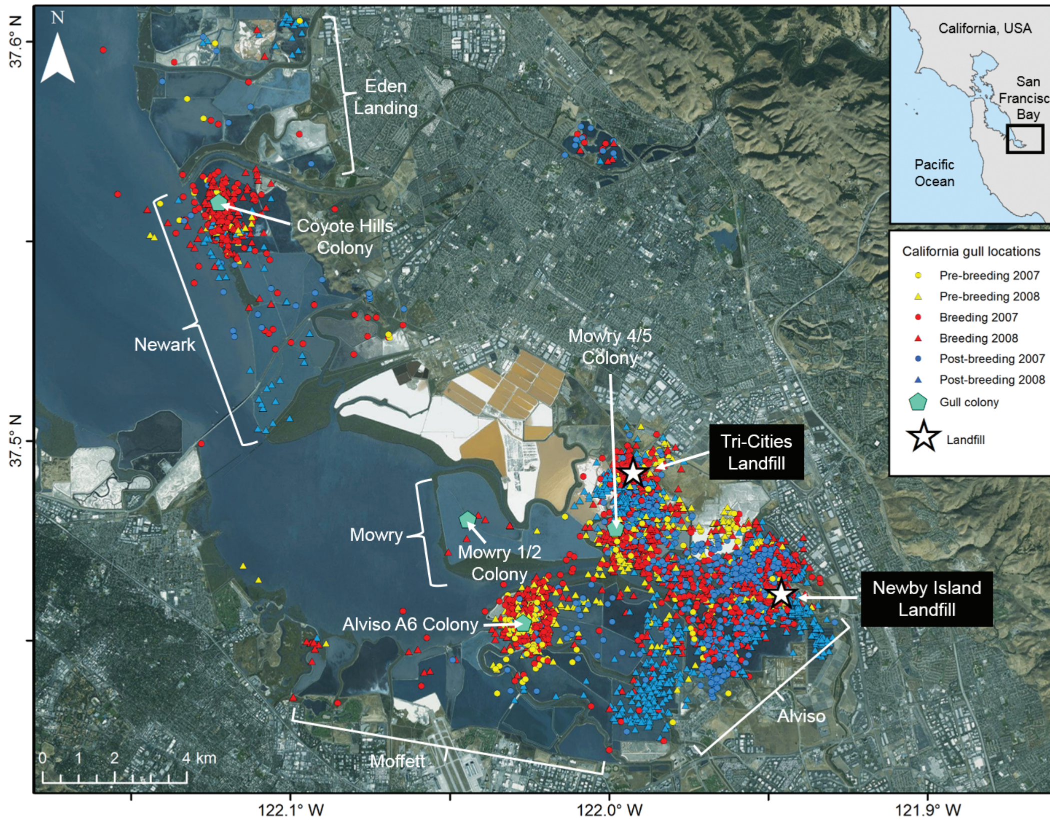

Figure 1. Locations of radio-marked California Gulls in south San Francisco Bay, California, USA, during pre-breeding (yellow), breeding (red), and post-breeding (blue) in 2007 (circles) and 2008 (triangles). The locations of major urban areas, wetland complexes, gull colonies, and landfills are shown. Newby Island Landfill was located 7.2 km from the California Gull colony at Alviso, 8.9 km from Mowry 1/2, 4.9 km from Mowry 4/5, and 19.0 km from Coyote Hills. Tri-Cities Landfill was located 5.2 km from Alviso, 4.8 km from Mowry 1/2, 1.6 km from Mowry 4/5, and 13.7 km from Coyote Hills. The World Imagery base layer was provided through Environmental Systems Research Institute (2006).

gulls daily by truck and monthly by fixed-wing aircraft. To obtain consistent coverage of the study region, fixed driving routes were maintained during the daytime that included the five main pond complexes, the edge of San Francisco Bay, and the two major landfills (Fig. 1). Both the starting location and direction that the route was driven throughout the study period were alternated to minimize potential bias associated with California Gull behavior and time of day. California Gulls were tracked using trucks equipped with dual 4-element Yagi antennas (Advanced Telemetry Systems, Inc.) and null-peak systems (AVM Instrument Company) to obtain three azimuths for each radio frequency within several minutes to minimize error associated with movement. Using similar techniques, we estimated that the mean telemetry error was 154 ± 25 (SE) m (Bluso-Demers *et al.* 2016). In 2007, California Gulls also were tracked using an airplane equipped with dual side-view 4-element Yagi antennas and a left-right control box (Advanced Telemetry Systems, Inc.) to locate California Gulls on either side of the aircraft (Gilmer *et al.* 1981). Universal Transverse Mercator coordinates were determined for every ground location using Location of a Signal (LOAS) software (Ecological Software Solutions 1999), and location estimates with an error polygon > 5 ha were removed (Ackerman *et al.* 2009).

Statistical Analysis of Tracking Data

We used locations to estimate population- and individual-level home range and core use areas from fixed kernel density estimates (Worton 1989). The population-level home range analyses were used to describe the general space use of the California Gull population, whereas the individual-level home range analyses were used to statistically examine factors influencing their space use. Kernel density estimates were calculated using the *kde* tool in the Geospatial Modelling Environment (Beyer 2014). The smoothing parameter was determined using likelihood cross-validation (CVh) for small sample sizes (Horne and Garton 2006). The 50th and the 95th percentile contours from the kernel density estimates were used to represent core use areas and home ranges, respectively (Laver and Kelly 2008). Population- and individual-level kernel density estimates were calculated for three time periods: pre-breeding (6 March to 1 May), breeding (1 May to 15 July), and post-breeding (15 July to 20 September).

Population home range. We calculated population-level kernel density estimates separately for each year, and then further calculated them for each season. We included individual California Gulls with ≥ 10 locations in a year in the annual population-level home range analysis. To estimate population-level home ranges by season, separate analyses were conducted for each year, and California Gulls were required to have ≥ 10 locations per season to be included. As individuals contributed varying numbers of locations to the population-level home range estimates, we applied a multi-step weighting process to account for differences in sample size. We did not want California Gulls with the largest sample sizes to dictate the resulting population estimates of space use and instead wanted each California Gull to contribute approximately equally to the population home range and core area estimates. First, we weighted the contribution of each California Gull equally by dividing each location by the number of California Gulls and then divided this value by the number of locations for the individual California Gull. Second, we further adjusted each location by giving more weight to locations coming from California Gulls with higher sample sizes by multiplying the weight of each individual location by the square root of the number of locations per individual. This weighting procedure adjusted each location so that individual California Gulls contributed approximately equally but with a slight adjustment to increase the weights (equal to the square root of the number of locations) for California Gulls with larger sample sizes.

Individual home range. Small sample sizes can cause over-smoothing and consequently can over-estimate home range size (Seaman *et al.* 1999; Horne and Garton 2006). To determine a threshold for the minimum number of locations for inclusion in the home range analysis, we used a subset of seven birds with > 50 locations during the breeding season to examine the influence of sample sizes on estimates of home range size. From each California Gull, we randomly selected a subset of data from 10 to 30 locations (in increments of 2 locations), in addition to a subset with 50 locations per California Gull, to use in kernel density estimates, and we calculated the 95th percentile contours on each of the 12 subsets of locations. From this analysis, 20 locations per California Gull was established as the minimum sample size necessary to estimate individual home ranges. Therefore, we restricted analysis to only those California Gulls with ≥ 20 locations per season. This sample size was similar to that selected by King *et al.* (2012), but we recognize that this analysis is still vulnerable to the influence of small sample size. Therefore, we used the estimated home range and core use area sizes to compare relative spatial use among seasons and did not focus on the absolute size of individual home ranges in our interpretation.

Movement distance. To examine the proximity of California Gulls to the colonies and landfills, we calculated straight line distances between every location and the centroid of the capture location, suspected breeding colony (as identified using autonomous data loggers as described below), and the nearest of the two landfills. To examine distance from the breeding colony, we used California Gulls that were breeding at the Alviso and Coyote Hills colonies. To examine distance from the nearest landfill, we used California Gulls that were breeding at Alviso, Coyote Hills, or Mowry colonies and included a fourth group composed of California Gulls that were either non-breeders or had an unknown breeding colony (hereafter called unknown breeders). Similar to the population home range analyses, we only included California Gulls that had ≥ 10 locations in any given season for the location analyses.

Statistics. We examined space use and movements of California Gulls in relation to their breeding colony and season (pre-breeding, breeding, or post-breeding) while accounting for the potential effects of year and sex. Specifically, linear mixed effects models were used to examine if home range size, core use area size, and distance from the colony or landfill were influenced by season, colony location, year, sex, or specific interactions between these variables (season × colony, year × colony, and season × year), with individual California Gull included as a random effect. We began analyses with a global model and removed non-significant interaction terms ($P > 0.05$). When the season × colony interaction was significant, each colony was analyzed separately. We used the capture location for comparisons of individual home ranges, and the suspected breeding colony was used when calculating the distance California Gulls were observed traveling from the colony.

For the home range and core use area analyses, the season × colony and year × colony interactions were not significant and therefore were removed. We were unable to test for an overall season × year interaction as there were no home range estimates for pre-breeding 2007; therefore, we made a five-level season × year factor (2007: breeding and post-breeding; 2008: pre-breeding, breeding, and post-breeding) and examined the pairwise interactions. We then removed this factor because there were no significant differences between years during breeding or post-breeding, and we observed the same results when breeding and post-breeding were compared for both years. Thus, the final model included season, colony, year, and sex.

For the distance California Gulls were located from colonies and landfills, there was a significant colony × season interaction. Therefore, each of the colony groups was analyzed separately. There was not a significant season × year interaction on the distance that California Gulls were located from the nearest landfill for any colony group, thus the interaction was removed. The final distance model for each colony group included season, year, and sex, although year was excluded for the Mowry colony model because there was only one radio-tracked California Gull breeding at Mowry in 2007.

Statistical tests were conducted using the statistical program R (R Development Core Team 2017). Differences among categories for significant variables in the final model were tested using Tukey's Honest Significant Difference pairwise comparisons. All response variables (home range size, core use area size, and distances to the colonies and landfills) were $\log_e$-transformed to meet the assumptions of general linear models. The Kenward-Roger approximation was used to estimate the degrees of freedom (Singmann *et al.* 2015). We report model-based, back-transformed least squares means ± SEs when natural log transformations were employed. In these cases, SEs were approximated using the delta method (Seber 1982).

Autonomous Data Loggers

Autonomous data logger systems were used to passively record the presence and absence of California Gulls at the three main colonies in south San Francisco Bay (Alviso, Coyote Hills, and Mowry) and the two major landfills (Newby Island Landfill and Tri-Cities Landfill). Data logger systems included a telemetry receiver (Advanced Telemetry Systems, Inc., model R4500S) paired with an omni-directional dipole or H-antenna (Advanced Telemetry Systems, Inc.) and powered by a 12-volt marine battery. All frequencies were scanned continuously in a cycle that lasted ≤ 20 min. Due to the slight variability between scanners for the duration of logger cycles, each hour was divided into three 20-min detection periods (hereafter cycles), which guaranteed that each frequency would be scanned at least once during that 20-min time period. We interpreted the lack of detection during a cycle as an absence from the site, and ≥ 1 detection during a cycle as a presence at the site. The receiver's gain was set to only detect frequencies within the specified colony site (as determined during site-specific field tests with reference transmitters), and two receivers were used at each of the Coyote Hills (North and South) and Mowry (Mowry 1/2 and Mowry 4/5) California Gull colonies because multiple systems were needed to cover the entire area of these colonies. Reference transmitters were placed within the colony sites to continually verify that the autonomous data logger systems were properly functioning. Additionally, system function was confirmed manually at least every other week. A complete day of recording for each of the loggers included 72 cycles. For the few occasions where the system failed due to a lack of battery power, we excluded time periods without a full day of recording from all of our analyses. Additionally, some California Gulls were entirely removed from a specific logger due to localized frequency interference for the specific transmitter.

Statistical Analysis of Autonomous Data Loggers

We examined attendance of each colony and landfill at both a daily and an hourly scale to examine how attendance patterns changed through the seasons as well as during the day. At the daily scale, we determined the proportion of the 72 cycles per day with detections of each California Gull, resulting in one data point per California Gull for each site per day. To evaluate hourly attendance at the colonies and landfills relative to season (pre-breeding, breeding, and post-breeding) and the time of day, we analyzed 24 1-hr time intervals per site and determined the proportion of cycles where each California Gull was detected during each season. Thus, each California Gull contributed 24 detection proportions (one for each hour of the day) for each of the three seasons. The number of detection cycles used varied individually by California Gull, and were based on the deployment date of the transmitter and the last date when the California Gull was detected by either a logger or via the truck-based radio tracking.

Because adult California Gulls were captured before the breeding season at two known colonies that were nearby a third known colony, we assigned each California Gull to an actual breeding colony using the data collected from the autonomous data loggers. If a California Gull spent > 50% of nighttime hours (20:00 hr to 05:00 hr) during the breeding season at one colony, we designated it as the suspected breeding colony. Secondarily, if a California Gull spent > 25% of nighttime hours during the breeding season at one colony and used that colony > 4 times as much as any of the other two monitored California Gull colonies then we assigned it as the suspected breeding colony. If a California Gull did not meet these criteria, than we designated it as an unknown breeder.

The data logger analyses for each breeding colony were restricted to the birds suspected to be breeding at that colony, and this same subset of California Gulls was used to examine attendance patterns at the two landfills. All three breeding colonies were analyzed separately, as well as those same three groups of California Gulls visiting each of the two landfills. Our response variable was the count of the number of successful logger detections, either daily or hourly for each season. For each California Gull, the count was out of 72 possibilities per day for the daily analysis, whereas the count for the hourly analysis was out of the number of detection opportunities during each of the 24 1-hr time-periods over the entire season.

We used an extension of a generalized linear mixed model using the *gamlss* package in the statistical program R (R Development Core Team 2017) for both hourly and daily analyses, with a negative binomial distribution and individual bird as a random effect. Diagnostic plots showed that the variance of the error residuals decreased disproportionately to the predicted mean values, so we extended our generalized linear model by including an additional term that modeled the variance using the same set of terms as the model to estimate the mean. Models were fit using a zero-inflated negative binomial distribution, which was determined by comparing the residuals from models with and without the zero-inflation term. Likelihood ratio tests were used to determine variable importance by comparing the full model to each model where one of the covariates was removed from both the mean and variance terms of the model. We report the χ^2, df, and *P*-value for the full model vs. the null model where one of the variables was removed. For the daily analysis, our fixed effects included median-centered Julian day (hereafter date), $date^2$ (quadratic), $date^3$ (cubic), year, and sex. For the hourly analysis, we first transformed hour of the day into a circular variable. To do so, we: 1) scaled the time value between 0 and 1 by dividing the hour by 24; 2) multiplied this value by 2π to obtain a value in radians; and 3) calculated the sine (sin) and cosine (cos) of this value (Zar 1999), which were both entered into our statistical models. The fixed effects in the hourly models included sin-hr, cos-hr, season, year, and sex, as well as sin-hr × season and cos-hr × season interactions. Additionally, we included an offset term in the hourly model to account for varying numbers of detection opportunities for each count value. For the hourly analyses, if the interaction was a significant variable to include, we report the results for sex and year from the global model and then conducted subsequent analyses for each season separately.

RESULTS

We captured and radio-marked 108 adult California Gulls at the two largest California Gull colonies in south San Francisco Bay (Fig. 1). We obtained 7,228 usable locations, and averaged 51 ± 19 (SD) locations per California Gull in 2007 and 66 ± 21 (SD) locations per California Gull in 2008. Additionally, over 1.1 million detections were obtained from the fixed autonomous data loggers at the three main breeding colonies and two main landfills.

California Gull Space Use Based on Tracking Data

The overall population home range size was 35.2 km^2 (2.9 km^2 core use area) in 2007 and 30.7 km^2 (2.4 km^2 core use area) in 2008. Population home ranges and core use areas were generally centered around the two major landfills, in addition to the three California Gull colonies (Fig. 2), indicating the importance of these sites for California Gull movements. There were some small differences in California Gull distributions among seasons, notably that core use areas were more likely to include the Newby Island Landfill during the post-breeding season.

Individual home range and core use areas of California Gulls were influenced by season ($F_{2,149.8} = 5.21$; $P = 0.006$ and $F_{2,145.5} = 11.94$; $P < 0.001$, respectively) and year ($F_{1,180.1} = 7.99$; $P = 0.005$ and $F_{1,179.3} = 6.46$; $P = 0.01$, respectively), but not by sex ($F_{1,64.3} = 0.34$; $P = 0.56$ and $F_{1,66.7} = 0.63$; $P = 0.43$, respectively), while accounting for capture location ($F_{1,65.6} = 3.78$; $P = 0.06$ and $F_{1,67.6} = 2.72$; $P = 0.10$, respectively). Pair-wise tests further revealed that home range and core use areas during post-breeding were 57% and 117% larger than during breeding ($P = 0.006$ and $P < 0.001$, respectively) and 64% and 105% larger than during pre-breeding ($P = 0.07$ and $P = 0.01$, respectively), whereas there was no difference in home range or core use areas between pre-breeding and breeding ($P = 0.98$ and $P = 0.97$, respectively). Home range and core use areas also were 53% larger in 2007 than in 2008.

Distance California Gulls were Located from Breeding Colonies and Landfills based on Tracking Data

Distance from breeding colonies. The maximum (mean ± SD) distance individual California Gulls were located from their suspected breeding colony was 9.6 ± 3.3 km for the Alviso colony and 19.0 ± 1.2 km for the Coyote Hills colony. There was a significant season × colony interaction ($F_{2,4682.7} = 57.02$; $P < 0.001$) for the distance California Gulls were located from their colony; therefore, we separated data by colonies for further analysis. In general, California Gulls were located substantially further away from their breeding colony during post-breeding than during pre-breeding or breeding.

For the Coyote Hills colony, the distance California Gulls were located from the breeding colony was influenced by season ($F_{2,1003.1} = 189.05$; $P < 0.0001$), but not year ($F_{1,682.5} = 0.29$; $P = 0.59$) or sex ($F_{1,11.0} = 3.04$; $P = 0.11$) after dropping the non-significant interaction term for season × year ($F_{2,1000.1} = 1.30$; $P = 0.27$). Pair-wise tests revealed that California Gulls were located 8.4 times farther from the colony during post-breeding (8.6 ± 1.5 km) and 2.8 times farther from the colony during pre-breeding (2.9 ± 0.6 km) than during breeding (1.0 ± 0.2 km; all $P < 0.0001$; Fig. 3B).

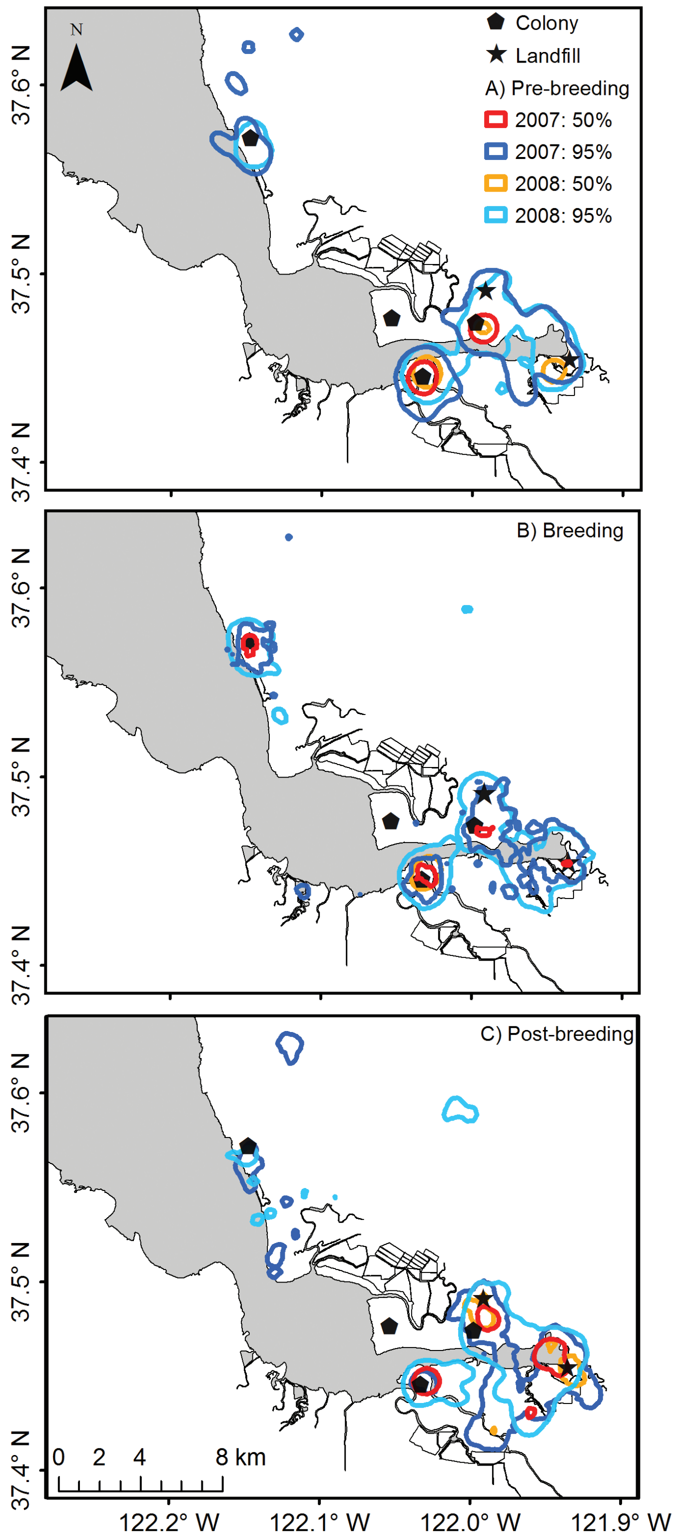

Figure 2. Population home range and core use areas (95th and 50th percentile contours from kernel density estimates, respectively) of California Gulls in San Francisco Bay, California, USA, during (A) pre-breeding, (B) breeding, and (C) post-breeding in 2007 and 2008. Individual telemetry locations are shown in Fig. 1.

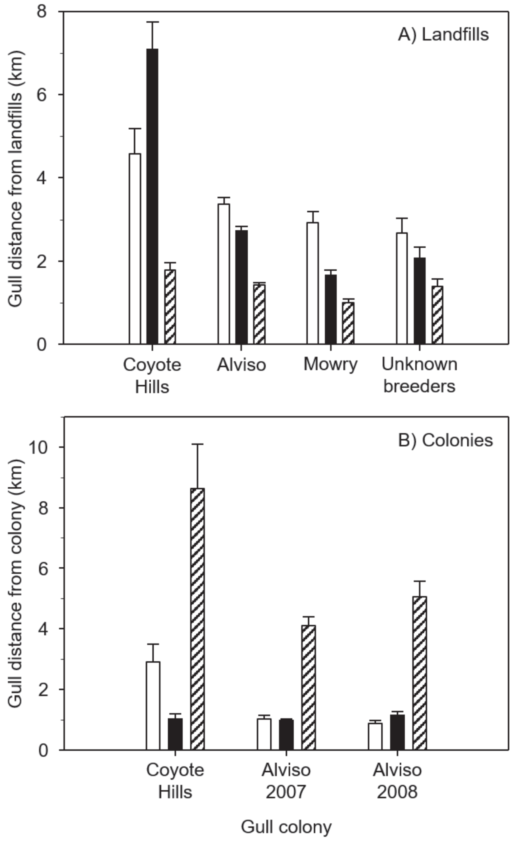

Figure 3. Distance California Gulls were located from (A) the nearest landfill (white stars in Fig. 1) and (B) their suspected breeding colony (black pentagons in Fig. 1) during pre-breeding (open), breeding (filled black), and post-breeding (shaded) in south San Francisco Bay, California, USA. Unknown breeders could not be assigned to a breeding colony with confidence, and may have been non-breeders. Values are least squares means ± SE.

For the Alviso colony, we observed a significant season × year interaction ($F_{2,3671.6}$ = 4.71; $P = 0.01$); therefore, we separated data by year for further analysis. During 2007, the distance California Gulls were located from the Alviso colony was influenced by season ($F_{2,1425.4}$ = 244.33; $P < 0.0001$) and sex ($F_{1,31.8}$ = 5.18; $P = 0.03$). Pair-wise tests revealed that California Gulls were located > 4 times farther from the breeding colony during post-breeding (4.1 ± 0.3 km) than during pre-breeding (1.0 ± 0.1 km) or breeding (1.0 ± 0.1 km; both: $P < 0.0001$), but distance from the breeding colony was not different between pre-breeding and breeding ($P = 0.88$). Females (1.8 ± 0.1 km) tended to be located further from the colony than males (1.4 ± 0.1 km). During 2008, the distance California Gulls were located from the Alviso colony was influenced by season ($F_{2,2031.7}$ = 465.79; $P < 0.0001$), but not sex ($F_{1,27.0}$ = 0.99; $P = 0.33$). Pair-wise tests showed that California Gulls were located 5.7 and 1.3 times farther from the breeding colony during post-breeding (5.1 ± 0.5 km) and breeding (1.2 ± 0.1 km), respectively, than during pre-breeding (0.9 ± 0.1 km; all $P < 0.0001$; Fig. 3B).

Distance from landfills. Based on tracking data, we located 83% of all radio-marked California Gulls within 0.5 km from the center of either landfill at least once during the study period. Overall, 78%-94% of California Gulls were located within 6 km of the nearest landfill (75th percentile of all locations per individual) during each of the three seasons and two years (Fig. 4). Post-breeding California Gulls were located significantly closer to landfills than pre-breeding or breeding California Gulls. For example, 66%-67% of post-breeding California Gulls, compared to 7%-9% of pre-breeding and 8%-27% of breeding California Gulls, were located within 3 km of landfills (Fig. 4).

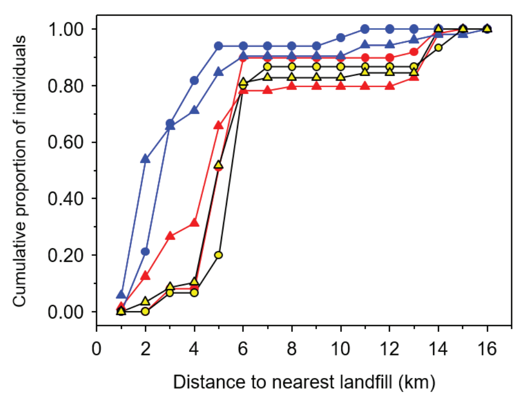

Figure 4. The cumulative proportion of individual California Gulls within a specified distance to the nearest landfill (km) in south San Francisco Bay, California, USA, during pre-breeding (yellow), breeding (red), and post-breeding (blue) in 2007 (circles) and 2008 (triangles). Distances were calculated between each radio-marked California Gull's location and the nearest landfill (Newby Island Landfill or Tri-Cities Landfill). The cumulative proportion of individuals within a specified distance to the nearest landfill was represented by each individual's 75th percentile.

There was a significant breeding colony × season interaction ($F_{6,6800.3} = 26.28$; $P < 0.0001$) for the distance California Gulls were located from the closest landfill; therefore, we separately analyzed the four groups (three colonies and unknown breeders). The distance California Gulls were located from the nearest landfill was strongly influenced by season for each colony group (Alviso: $F_{2,3671.2} = 239.70$; $P < 0.0001$; Coyote Hills: $F_{2,998.2} = 116.72$; $P < 0.0001$; Mowry: $F_{2,795.0} = 75.80$; $P < 0.0001$; unknown breeders: $F_{2,1286.5} = 29.16$; $P < 0.0001$), but not by year (Alviso: $F_{1,342.6} = 3.00$; $P = 0.08$; Coyote Hills: $F_{1,286.9} = 0.06$; $P = 0.81$; Mowry: only one year; unknown breeders: $F_{1,170.9} = 0.27$; $P = 0.61$) or sex (Alviso: $F_{1,51.9} = 2.97$; $P = 0.09$; Coyote Hills: $F_{1,10.8} = 1.26$; $P = 0.29$; Mowry: $F_{1,11.2} = 0.17$; $P = 0.68$; unknown breeders: $F_{1,19.5} = 1.52$; $P = 0.23$) after dropping the non-significant interaction terms for season × year (Alviso: $F_{2,3611.0} = 0.16$; $P = 0.85$; Coyote Hills: $F_{2,998.5} = 1.34$; $P = 0.26$; Mowry: only one year; unknown breeders: $F_{2,1283.6} = 0.25$; $P = 0.78$).

In contrast to the distance from breeding colonies, pair-wise tests for each colony group (all $P < 0.01$) revealed that California Gulls were located closer to landfills during post-breeding (Alviso: 1.4 ± 0.1 km; Coyote Hills: 1.8 ± 0.2 km; Mowry: 1.0 ± 0.1 km; unknown breeders: 1.4 ± 0.2 km) than during breeding (Alviso: 2.7 ± 0.1 km; Coyote Hills: 7.1 ± 0.7 km; Mowry: 1.7 ± 0.1 km; unknown breeders: 2.1 ± 0.3 km) or pre-breeding (Alviso: 3.4 ± 0.2 km; Coyote Hills: 4.6 ± 0.6 km; Mowry: 2.9 ± 0.3 km; unknown breeders: 2.7 ± 0.4 km; Fig. 3A).

Daily California Gull Attendance at Colonies and Landfills using Autonomous Data Loggers

Daily California Gull attendance at colonies. California Gull attendance at each of the three breeding colonies was strongly influenced by date^3 (Alviso: $\chi^2 = 350.63$; df = 2.4; $P < 0.001$; Coyote Hills: $\chi^2 = 456.30$; df = 2.2; $P < 0.001$; Mowry: $\chi^2 = 171.78$; df = 1.9; $P < 0.001$). As expected, the general attendance of California Gulls at colonies was lower during pre-breeding, increased substantially during breeding, and then declined into and during the post-breeding time period (Fig. 5). In addition to date^3, sex also was a significant factor influencing California Gull attendance at the Alviso and Coyote Hills colonies (Alviso: $\chi^2 = 127.43$; df = 1.5; $P < 0.001$; Coyote Hills: $\chi^2 = 80.73$; df = 1.4; $P < 0.001$), with males having slightly higher attendance at the colony than females, but not at the Mowry colony ($\chi^2 = 0.30$; df = 2.0; $P = 0.86$). California Gull attendance at colonies was higher in 2008 than 2007 at the Coyote Hills colony ($\chi^2 = 84.22$; df = 1.4; $P < 0.001$), but not at the Alviso colony ($\chi^2 = 4.41$; df = 2.0; $P = 0.11$; Fig. 5).

Daily California Gull attendance at landfills. Based on the continuous logger data, all but one California Gull was located at a landfill at least once during the study. California Gull attendance was strongly influenced by date^3 at the Newby Island Landfill (Alviso: $\chi^2 = 49.61$; df = 2.0; $P < 0.001$; Coyote Hills: $\chi^2 = 28.74$; df = 2.0; $P < 0.001$; Mowry: $\chi^2 = 26.60$; df = 2.0; $P < 0.001$) and Tri-Cities Landfill (Alviso: $\chi^2 = 33.98$; df = 2.2; $P < 0.001$; Coyote Hills: $\chi^2 = 14.69$; df = 2.0; $P < 0.001$; Mowry: $\chi^2 = 15.44$; df = 2.0; $P < 0.001$). Attendance generally increased at the Newby Island Landfill throughout the breeding and post-breeding time periods (Fig. 5). For the Newby Island Landfill, sex influenced attendance patterns for California Gulls from the Alviso colony ($\chi^2 = 63.66$; df = 2.0; $P < 0.001$), but not for California Gulls from the Coyote Hills colony ($\chi^2 = 1.73$; df = 2.0; $P = 0.42$). For the Tri-Cities Landfill, sex influenced attendance patterns for California Gulls from the Coyote Hills colony ($\chi^2 = 10.78$; df = 1.9; $P = 0.004$), but not strongly for California Gulls from the Alviso colony ($\chi^2 = 6.69$; df = 3.0; $P = 0.08$). In both cases where sex was statistically significant, males had slightly higher attendance at the landfills than females. Sex of California Gulls from the Mowry colony was not an important factor explaining attendance at either the Newby Island Landfill ($\chi^2 = 2.89$; df = 1.9; $P = 0.21$) or Tri-Cities Landfill ($\chi^2 = 3.21$; df = 2.0; $P = 0.19$). Year was an important factor explaining attendance at the Newby Island Landfill for California Gulls from both Alviso (χ^2 =

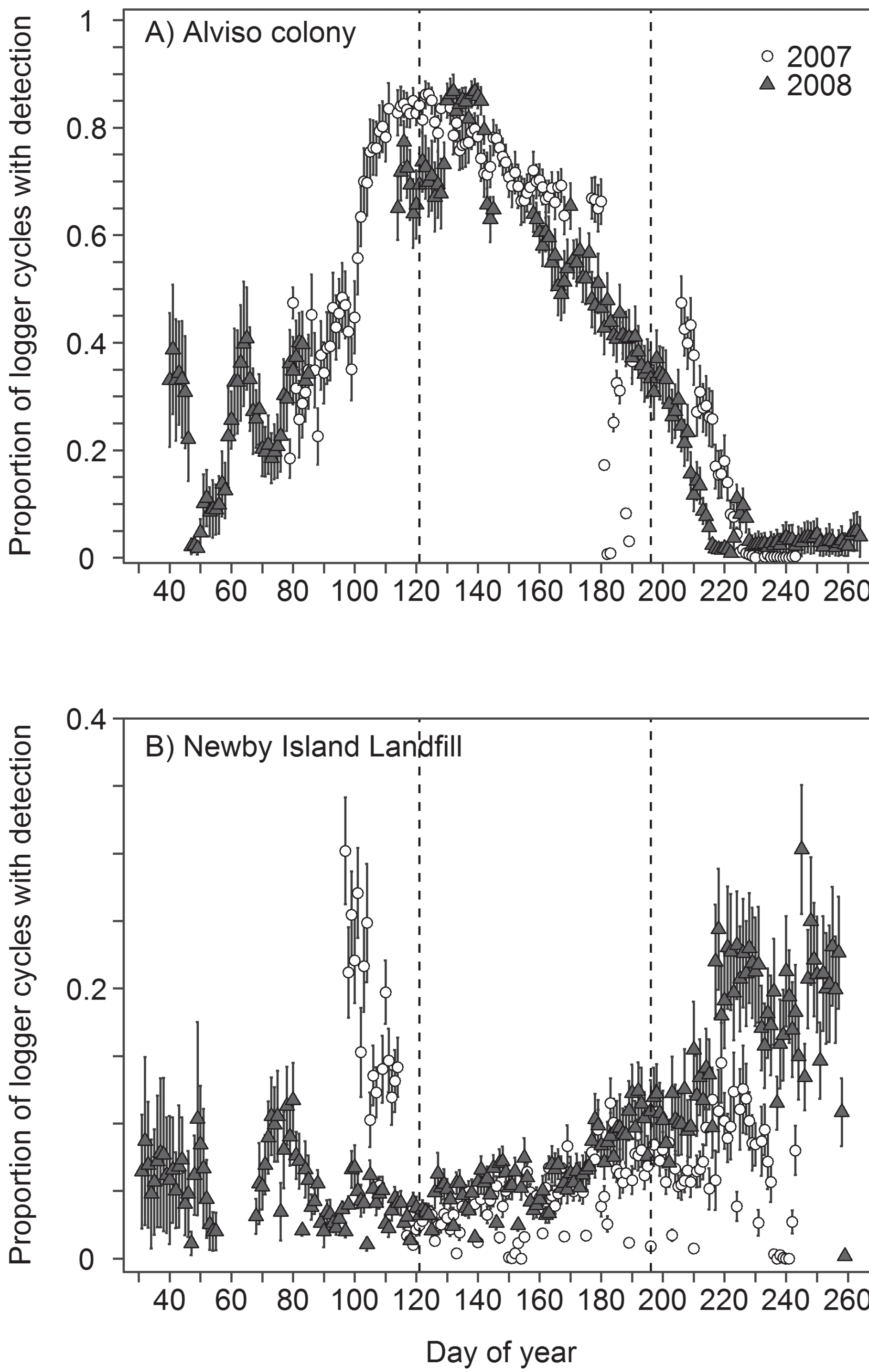

Figure 5. The proportion of each day (mean ± SD) radio-marked California Gulls spent at the (A) Alviso colony or (B) Newby Island Landfill in south San Francisco Bay, California, USA, during 2007 (circles) and 2008 (triangles). Data include only those California Gulls that were suspected of breeding at the Alviso colony. Stippled lines indicate the transitional dates used to separate pre-breeding (< May 1), breeding (1 May to 15 July), and post-breeding (> July 15). Note that the y-axis scales differ between colony and landfill.

79.39; df = 2.0; $P < 0.001$) and Coyote Hills ($\chi^2 = 11.17$; df = 2.0; $P = 0.004$); California Gulls from Alviso had greater attendance at the landfill in 2008 than in 2007, but the opposite trend was observed for California Gulls from Coyote Hills. Similarly, year was an important factor explaining attendance at the Tri-Cities Landfill for California Gulls from both Alviso ($\chi^2 = 81.76$; df = 2.3; $P < 0.001$) and Coyote Hills ($\chi^2 = 77.91$; df = 1.9; $P < 0.001$); California Gull attendance was higher in 2007 than 2008 for both colonies.

Hourly California Gull Attendance at Colonies and Landfills using Autonomous Data Loggers

Overall, the season × time of day (sin-hr × season and cos-hr × season) interaction was important in explaining California Gull attendance patterns throughout the day at the Newby Island Landfill (Alviso: $\chi^2 = 420.03$; df = 8.1; $P < 0.001$; Coyote Hills: $\chi^2 = 101.94$ df = 8.0; $P < 0.001$; Mowry: $\chi^2 = 128.07$; df = 8.2; $P < 0.001$), Tri-Cities Landfill (Alviso: $\chi^2 = 108.03$; df = 8.1; $P < 0.001$; Coyote Hills: $\chi^2 = 5.00$; df = 8.0; $P = 0.76$; Mowry: $\chi^2 = 26.79$; df = 7.9; $P < 0.001$), and all three breeding colonies (Alviso: $\chi^2 = 138.26$; df = 8.0; $P < 0.001$; Coyote Hills: $\chi^2 = 70.30$; df = 8.1; $P < 0.001$; Mowry: $\chi^2 = 78.01$; df = 8.1; $P < 0.001$).

Hourly California Gull attendance at colonies. Males had higher attendance than females at the Alviso and Coyote Hills colonies (Alviso: $\chi^2 = 45.50$; df = 1.8; $P < 0.001$; Coyote Hills: $\chi^2 = 107.46$; df = 1.9; $P < 0.001$), but sex was not an important factor explaining attendance patterns at the Mowry colony ($\chi^2 = 3.55$; df = 2.0; $P = 0.16$). California Gull attendance was higher during 2008 than 2007 at Alviso ($\chi^2 = 467.45$; df = 1.8; $P < 0.001$) and Coyote Hills ($\chi^2 = 55.68$; df = 1.9; $P < 0.001$).

California Gull attendance at colonies was typically highest during nighttime hours and lower during daylight hours, especially during the breeding season (Fig. 6). When seasons were analyzed separately, California Gull attendance differed markedly by the time of day at each of the breeding colonies during pre-breeding (Alviso: $\chi^2 = 49.64$; df = 4.0; $P < 0.001$; Coyote Hills: $\chi^2 = 18.26$; df = 4.0; $P = 0.001$), breeding (Alviso: $\chi^2 = 520.90$; df = 4.5; $P < 0.001$; Coyote Hills: $\chi^2 = 204.28$; df = 4.3; $P < 0.001$; Mowry: $\chi^2 = 250.29$; df = 4.6; $P < 0.001$), and post-breeding (Alviso: $\chi^2 = 371.59$; df = 4.5; $P < 0.001$; Coyote Hills: $\chi^2 = 25.16$; df = 4.0; $P < 0.001$; Mowry: $\chi^2 = 287.73$; df = 4.5; $P < 0.001$), with the exception of pre-breeding California Gulls at the Mowry colony ($\chi^2 = 0.48$; df = 4.0; $P = 0.98$).

Hourly California Gull attendance at landfills. In contrast to California Gull attendance at the colonies, sex was not an important factor influencing attendance at the Newby Island Landfill for California Gulls from Alviso ($\chi^2 = 0.09$; df = 2.0; $P = 0.95$) or Coyote Hills ($\chi^2 = 5.53$; df = 2.0; $P = 0.06$), but males from Mowry had higher attendance than females ($\chi^2 = 81.47$; df = 1.9; $P < 0.001$). Attendance at the Tri-Cities Landfill was inconsistent among breeding colonies; females from Alviso had higher attendance than males ($\chi^2 = 38.31$; df = 2.0; $P < 0.001$), males from Coyote Hills had higher attendance than females ($\chi^2 = 65.24$; df = 2.0; $P < 0.001$), and there was no sex difference for California Gulls from Mowry ($\chi^2 = 2.57$; df = 1.8; $P = 0.24$).

Year also was an important factor in explaining California Gull attendance at landfills. For the Newby Island Landfill, attendance was higher during 2008 than 2007 for California Gulls from Alviso ($\chi^2 = 33.73$; df = 2.0; $P < 0.001$), whereas attendance was higher during 2007 than 2008 for California Gulls from Coyote Hills ($\chi^2 = 8.78$; df = 2.0; $P = 0.01$). For the Tri-Cities Landfill, attendance was higher during 2007 than 2008 for California Gulls from both Alviso ($\chi^2 = 28.44$; df = 2.0; $P < 0.001$) and Coyote Hills ($\chi^2 = 78.93$; df = 1.9; $P < 0.001$).

California Gull attendance at landfills was higher during daylight hours and lower during nighttime hours (Fig. 6), in direct contrast to the attendance patterns observed at the breeding colonies. When seasons were analyzed separately, California Gull attendance differed substantially by the time of day at landfills, especially at the Newby Island Landfill during pre-breeding (Alviso: $\chi^2 = 545.44$; df = 4.3; $P < 0.001$; Coyote Hills: $\chi^2 = 34.56$; df = 4.3; $P < 0.001$; Mowry: $\chi^2 = 159.30$; df = 4.2;

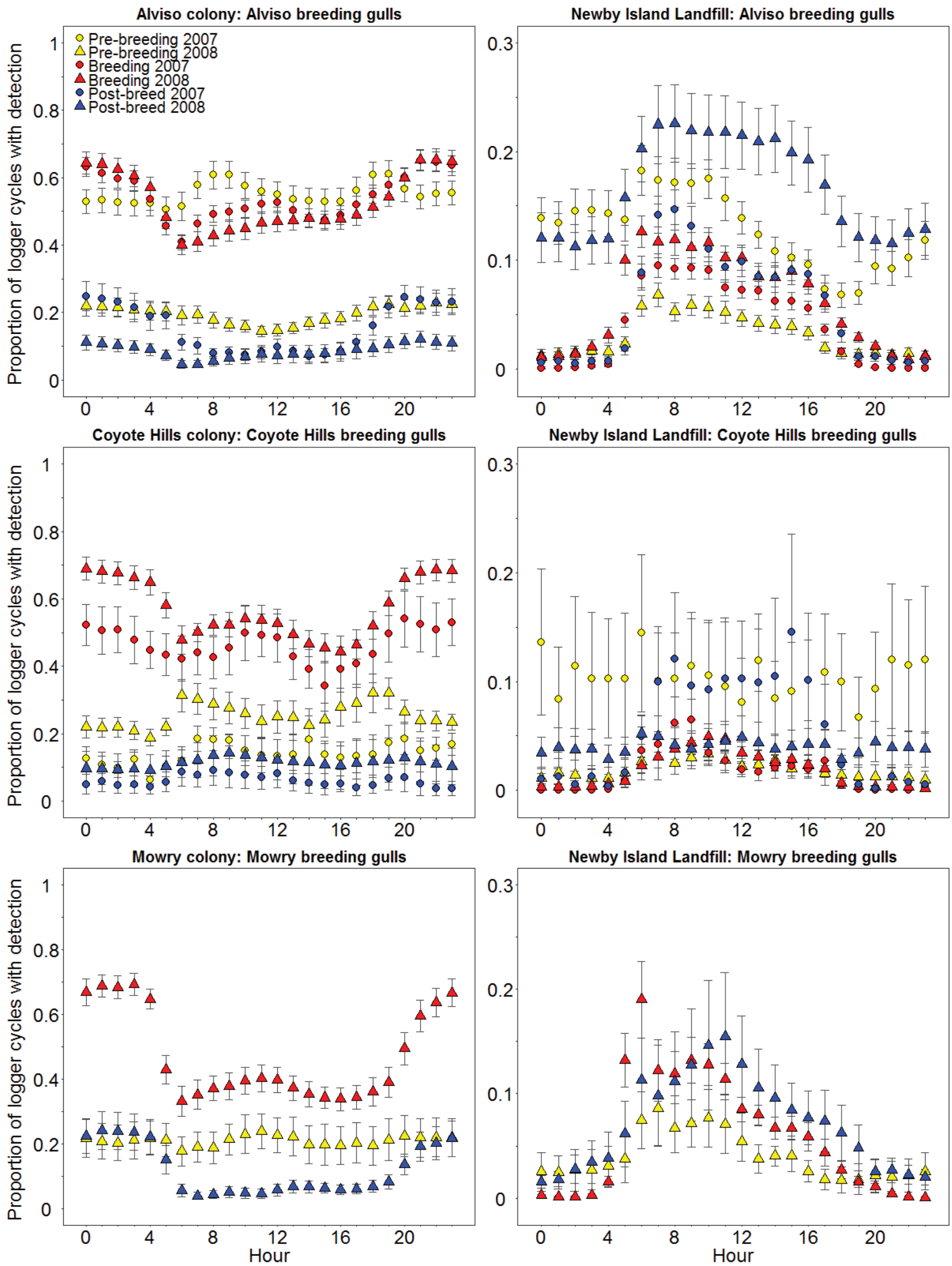

Figure 6. The proportion of each hour period (mean ± SD) over the course of the pre-breeding (yellow), breeding (red), and post-breeding (blue) seasons that radio-marked California Gulls spent at the Alviso, Coyote Hills, and Mowry colonies where they were suspected of breeding (left column) and the proportion of each hour period those same California Gulls were detected at the two largest landfills (Newby Island Landfill: right column) in the south San Francisco Bay, California, USA, during 2007 (circles) and 2008 (triangles). Note that the y-axis scales differ between colonies and landfills.

$P < 0.001$), breeding (Alviso: $\chi^2 = 1{,}969.00$; df = 4.6; $P < 0.001$; Coyote Hills: $\chi^2 = 302.88$; df = 4.1; $P < 0.001$; Mowry: $\chi^2 = 481.33$; df = 5.8; $P < 0.001$), and post-breeding (Alviso: $\chi^2 = 670.22$; df = 4.3; $P < 0.001$; Coyote Hills: $\chi^2 = 44.75$; df = 4.0; $P < 0.001$; Mowry: $\chi^2 = 193.15$; df = 4.0; $P < 0.001$; Fig. 6).

Similarly, California Gull attendance differed by the time of day at the Tri-Cities Landfill during pre-breeding (Alviso: $\chi^2 = 236.55$; df = 4.9; $P < 0.001$; Mowry: $\chi^2 = 92.99$; df = 5.1; $P < 0.001$), breeding (Alviso: $\chi^2 = 968.15$; df = 5.7; $P < 0.001$; Mowry: $\chi^2 = 135.01$; df = 4.6; $P < 0.001$), and post-breeding (Alviso: $\chi^2 = 451.41$; df = 4.8; $P < 0.001$; Mowry: $\chi^2 = 25.05$; df = 4.1; $P < 0.001$; Fig. 6). Time of day was also an important factor influencing attendance at the Tri-Cities Landfill for California Gulls from Coyote Hills ($\chi^2 = 636.51$; df = 4.3; $P < 0.001$), but attendance was not analyzed separately by season because there was no season × time of day interaction.

DISCUSSION

California Gull movements and space use were largely dictated by the location of the two major landfills in proximity to the three main breeding colonies. California Gull population home ranges encompassed the landfills and several wetlands adjacent to the landfills where California Gulls likely roosted between foraging bouts at the landfills, as well as the colonies. Core use areas were centered on the colonies during the breeding season, as expected, and additionally included the landfills during pre-breeding and post-breeding time periods when California Gulls were less attached to their breeding sites. Space use expanded considerably after the breeding season, and California Gulls were located substantially further away from the colony, and closer to landfills, during post-breeding. Other tracking studies also have documented high use of landfills by breeding gulls (Belant *et al.* 1993, 1998; Patenaude-Monette *et al.* 2014; Frechette *et al.* 2015), even though those gull colonies were located further away from landfills and required longer foraging flights (25-50 km) than those in our study (< 19 km).

California Gull attendance at landfills depended strongly on date, with landfill use generally increasing from the breeding to post-breeding time periods. Similarly, several other tracking studies showed that gulls increased their use of landfills throughout the breeding season and had the highest use during post-breeding, after chicks had fledged (Belant *et al.* 1993, 1998; Frechette *et al.* 2015). Although the amount of time spent at the landfills might seem low, gulls will often gorge themselves at landfills in a short amount of time. For example, Smith and Carlile (1993) showed that most Silver Gulls (*L. novaehollandiae*) visited landfills only once per day and the average visit duration was only one hour despite garbage making up the vast majority of their diet. The proportion of time California Gulls spent on colony during the pre-breeding season was variable (20%-40% of the day) and generally increased over time up to the start of the breeding season when it reached a maximum (60%-80% of the day). Over the course of the breeding season, the proportion of the day spent at the colony declined substantially toward the post-breeding time period (< 20% of the day).

Hourly patterns of California Gull attendance at landfills were strongly cyclical. California Gull attendance at landfills was highest from approximately 06:00 hr in the morning until 18:00 hr at night when landfills were closed, garbage deliveries had ended, and the exposed refuse was covered. Herring Gulls in Great Britain showed a similar pattern of landfill use from 08:30 hr to 16:30 hr (Sibly and McCleery 1983) and 09:00 hr to 16:00 hr (Coulson 2015) when garbage was being delivered. This pattern of landfill attendance during the daytime is in direct contrast to colony attendance patterns; California Gulls were generally present at colonies more often at night than during the day. During the breeding season, California Gulls tended to be present at their colonies at night from 20:00 hr to 05:00 hr about 50%-70% of the time, whereas they were only present at their colonies 30%-40% of their time during the day from 06:00 hr to 18:00 hr.

Although California Gull movements and space use appeared to be strongly dictated by the location and operation of regional landfills, these results do not necessarily mean that California Gulls obtained a significant proportion of their diet from landfills. For example, Belant *et al.* (1993) showed that although Herring Gulls used landfills, they were not actively foraging during the majority of the time spent at landfills and that garbage made up a small proportion of Herring Gull diets when alternate, higher-quality food (fish) was available. Yet, in most other gull studies, garbage made up a substantial proportion of gull diets (Smith and Carlile 1993; Brousseau *et al.* 1996; Weiser and Powell 2011; Osterback *et al.* 2015). Within San Francisco Bay, the proportion of garbage in California Gull chick diets was estimated to be 40% in 1987-1988 at the same Alviso colony (Dierks 1990). Similarly, the diet of Western Gulls (*L. occidentalis*) breeding on Alcatraz Island in San Francisco Bay during 1983-1985 switched from almost entirely garbage early in the breeding season to mostly fish once chicks hatched (Annett and Pierotti 1989). More contemporary estimates of the proportion of garbage in the diets of California Gulls breeding in San Francisco Bay ranged from 19% to 81% and depended on the foraging strategy of individual California Gulls (Peterson *et al.* 2017). California Gulls with isotopic values and mercury contamination indicative of foraging in more estuarine environments were estimated to still have 33% of their diets derived from garbage, whereas California Gulls with chemical signatures that indicated they foraged primarily at landfills were estimated to have 72% of their diets derived from garbage (Peterson *et al.* 2017). Nonetheless, individual gulls can specialize on more natural prey, and California Gulls in San Francisco Bay were responsible for 55% of American Avocet (*Recurvirostra americana*; Ackerman *et al.* 2014b) and 54% of Forster's Tern (*Sterna forsteri*; Ackerman *et al.* 2014a) chick deaths and 13% of American Avocet (Herring *et al.* 2011) and 38% of Western Snowy Plover (*Charadrius alexandrinus nivosus*) egg depredations (Demers and Robinson-Nilsen 2012). Together, these results indicate that the California Gull population in San Francisco Bay derives a substantial proportion of its food resources from regional landfills.

In some studies, access to garbage has increased gull breeding production. For example, the percent occurrence of garbage in the diet was positively correlated with fledging rate among colonies of Glaucous Gulls (*L. hyperboreus*; Weiser and Powell 2010). Hunt (1972) concluded that the lower survival of Herring Gull chicks on islands that were more distant from sources of edible refuse was caused by a reduction in parental care due to adults having to spend more time traveling to find food. Further, the removal of anthropogenic food resources due to the closure of a nearby landfill resulted in a reduction in body mass, clutch size, and egg volume of Yellow-legged Gulls (*L. michahellis*; Steigerwald *et al.* 2015). Similarly, an 80% reduction in garbage dumped at a landfill resulted in a 61% decrease in the breeding success of Herring Gulls at a nearby colony, including a decrease in clutch size, egg volume, hatching success, fledging success, and the number of breeding pairs (Pons 1992). Reducing access to landfills through gull deterrence programs also has slowed gull population growth and reduced gull population size (Giroux *et al.* 2016). Population modeling of Yellow-legged Gulls over nearly a century indicated that the growth of Yellow-legged Gull colonies was closely linked to increases in anthropogenic food resources at the nearest landfills (Duhem *et al.* 2008). In contrast, there also is some evidence that the nutritional quality of garbage can be lower than more natural prey items (Pierotti and Annett 1990) and that landfill use by gulls can lead to population declines due to the spreading of diseases (Coulson 2015). Altogether, these studies indicate that landfills can play a central role in many gull populations and the rapid growth of some, but not all, gull populations can be linked to anthropogenic food subsidies.

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LITERATURE CITED

Ackerman, J. T., J. D. Bluso-Demers and J. Y. Takekawa. 2009. Postfledging Forster's Tern movements, habitat selection, and colony attendance in San Francisco Bay. Condor 111: 100-110.

Ackerman, J. T., M. P. Herzog, C. A. Hartman and G. Herring. 2014a. Forster's Tern chick survival in response to a managed relocation of predatory California Gulls. Journal of Wildlife Management 78: 818-829.

Ackerman, J. T., M. P. Herzog, C. A. Hartman and J. Y. Takekawa. 2014b. Comparative reproductive biology of sympatric species: nest and chick survival of American avocets and black-necked stilts. Journal of Avian Biology 45: 609-623.

Annett, C. and R. Pierotti. 1989. Chick hatching as a trigger for dietary switching in the Western Gull. Colonial Waterbirds 12: 4-11.

Annett, C. A. and R. Pierotti. 1999. Long-term reproductive output in Western gulls: consequences of alternate tactics in diet choice. Ecology 80: 288-297.

Becker, P. H. 1995. Effects of coloniality on gull predation on Common Tern (*Sterna hirundo*) chicks. Colonial Waterbirds 18: 11-22.

Belant, J. L., S. K. Ickes and T. W. Seamans. 1998. Importance of landfills to urban-nesting herring and ring-billed gulls. Landscape and Urban Planning 43: 11-19.

Belant, J. L., T. W. Seamans, S. W. Gabrey and S. K. Ickes. 1993. Importance of landfills to nesting Herring Gulls. Condor 95: 817-830.

Beyer, H. L. 2014. Geospatial modelling environment software v. 0.7.4.0. Spatial Ecology LLC, Brisbane, Queensland, Australia.

Bluso-Demers, J. D., J. T. Ackerman, J. Y. Takekawa and S. H. Peterson. 2016. Habitat selection by Forster's Terns (*Sterna forsteri*) at multiple spatial scales in an urbanized estuary: the importance of salt ponds. Waterbirds 39: 375-387.

Bosch, M., D. Oro, F. J. Cantos and M. Zabala. 2000. Short-term effects of culling on the ecology and population dynamics of the yellow-legged gull. Journal of Applied Ecology 37: 369-385.

Brousseau, P., J. Lefebvre and J. F. Giroux. 1996. Diet of Ring-billed Gull chicks in urban and non-urban colonies in Quebec. Colonial Waterbirds 19: 22-30.

Burns, C. E., J. T. Ackerman, N. B. Washburn, J. Bluso-Demers, C. Robinson-Nilsen, and C. Strong. 2018. California Gull population growth and ecological impacts in the San Francisco Bay estuary, 1980–2016. Pages 180–189 *in* Trends and Traditions: Avifaunal Change in Western North America (W. D. Shuford, R. E. Gill Jr. and C. M. Handel, Eds.), Studies of Western Birds 3, Western Field Ornithologists, Camarillo, California.

Conover, M. R. 1983. Recent changes in Ring-billed and California Gull populations in the western United States. Wilson Bulletin 95: 362-383.

Coulson, J. C. 2015. Re-evaluation of the role of landfills and culling in the historic changes in the Herring Gull (*Larus argentatus*) population in Great Britain. Waterbirds 38: 339-354.

Demers, S. A. and C. W. Robinson-Nilsen. 2012. Monitoring Western snowy plover nests with remote surveillance systems in San Francisco Bay, California. Journal of Fish and Wildlife Management 3: 123-132.

Dierks, A. J. 1990. Parental care and diet of California Gull (*Larus californicus*) chicks at Alviso, California. M.S. Thesis, San Jose State University, San Jose, California.

Dill, H. H. and W. H. Thornsberry. 1950. A cannon-projected net trap for capturing waterfowl. Journal of Wildlife Management 14: 132-137.

Duhem, C., P. Roche, E. Vidal and T. Tatoni. 2008. Effects of anthropogenic food resources on Yellow-legged Gull colony size on Mediterranean islands. Population Ecology 50: 91-100.

Ecological Software Solutions (ESS). 1999. Location of a signal (LOAS) software v. 3.0.1. ESS, Urnäsch, Switzerland.

Environmental Systems Research Institute (ESRI). 2006. ArcView v. 9.2. ESRI, Redlands, California.

Frechette, D., A.-M. K. Osterback, S. A. Hayes, J. W. Moore, S. A. Shaffer, M. Pavelka, C. Winchell and J. T. Harvey. 2015. Assessing the relationship between gulls *Larus* spp. and Pacific salmon in Central California using radiotelemetry. North American Journal of Fisheries Management 35: 775-788.

Gilmer, D. S., L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaiffer and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. Resource Publication 140, U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.

Giroux, J.-F., M. Patenaude-Monette, F. Lagarde, E. Thiériot, P. Brousseau and P. Molina. 2016. The rise and fall of Ring-billed Gulls (*Larus delawarensis*) in eastern North America. Waterbirds 39 (Special Publication 1): 87-98.

Hario, M. and J. Rintala. 2016. Population trends in Herring Gulls (*Larus argentatus*), Great Black-backed Gulls (*Larus marinus*) and Lesser Black-backed Gulls (*Larus fuscus fuscus*) in Finland. Waterbirds 39 (Special Publication 1): 10-14.

Hatch, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. Auk 87: 244-254.

Herring, G., J. T. Ackerman, C. A. Eagles-Smith and J. Y. Takekawa. 2010. Sexing California Gulls using morphometrics and discriminant function analysis. Waterbirds 33: 79-85.

Herring, G., J. T. Ackerman, J. Y. Takekawa, C. A. Eagles-Smith and J. M. Eadie. 2011. Identifying nest predators of American avocets (*Recurvirostra americana*) and black-necked stilts (*Himantopus mexicanus*) in San Francisco Bay, California. Southwestern Naturalist 56: 35-43.

Horne, J. S. and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70: 641-648.

Horton, N., T. Brough and J. B. A. Rochard. 1983. The importance of refuse tips to gulls wintering in an inland area of south-east England. Journal of Applied Ecology 20: 751-765.

Hunt, G., Jr. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53: 1051-1061.

Jones, H. P. and S. W. Kress. 2012. A review of the world's active seabird restoration projects. Journal of Wildlife Management 76: 2-9.

Kadlec, J. A. and W. H. Drury. 1968. Structure of the New England herring gull population. Ecology 49: 644-676.

King, D. T., B. K. Strickland and A. A. Radomski. 2012. Winter and summer home ranges and core use areas of Double-crested Cormorants captured near aquaculture facilities in the southeastern United States. Waterbirds 35: 124-131.

Kress, S. W. 1983. The use of decoys, sound recordings, and gull control for re-establishing a tern colony in Maine. Colonial Waterbirds 6: 185-196.

Laver, P. N. and M. J. Kelly. 2008. A critical review of home range studies. Journal of Wildlife Management 72: 290-298.

Mittelhauser, G. H., R. B. Allen, J. Chalfant, R. P. Schauffler and L. J. Welch. 2016. Trends in the nesting populations of Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) in Maine, USA, 1977-2013. Waterbirds 39 (Special Publication 1): 57-67.

Nisbet, I. C. T. and J. A. Spendelow. 1999. Contribution of research to management and recovery of the Roseate Tern: review of a twelve-year project. Waterbirds 22: 239-252.

Oro, D., A. de León, E. Minguez and R. W. Furness. 2005. Estimating predation on breeding European storm-petrels (*Hydrobates pelagicus*) by yellow-legged gulls (*Larus michahellis*). Journal of Zoology 265: 421-429.

Osterback, A.-M. K., D. M. Frechette, S. A. Hayes, S. A. Shaffer and J. W. Moore. 2015. Long-term shifts in anthropogenic subsidies to gulls and implications for an imperiled fish. Biological Conservation 191: 606-613.

Patenaude-Monette, M., M. Belisle and J.-F. Giroux. 2014. Balancing energy budget in a central-place forager: which habitat to select in a heterogeneous environment? PLOS ONE 9: e102162.

Peterson, S. H., J. T. Ackerman and C. A. Eagles-Smith. 2017. Mercury contamination and stable isotopes reveal variability in foraging ecology of generalist California Gulls. Ecological Indicators 74: 205-215.

Pierotti, R. and C. A. Annett. 1990. Diet and reproductive output in seabirds. BioScience 40: 568-574.

Pierotti, R. and C. A. Annett. 1991. Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. Ecology 72: 319-328.

Pons, J. 1992. Effects of changes in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. Ardea 80: 143-150.

R Development Core Team. 2015. R: a language and environment for statistical computing v. 3.2.2. Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/, accessed 1 September 2015.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739-747.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd ed. Macmillan, New York, New York.

Sibly, R. M. and R. H. McCleery. 1983. The distribution between feeding sites of Herring Gulls breeding at Walney Island, U.K. Journal of Animal Ecology 52: 51-68.

Singmann, H., B. Bolker and J. Westfall. 2015. afex: analysis of factorial experiments. R package v. 0.14-2. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=afex, accessed 28 July 2015.

Smith, G. C. and N. Carlile. 1993. Food and feeding ecology of breeding Silver Gulls (*Larus novaehollandiae*) in urban Australia. Colonial Waterbirds 16: 9-16.

Spear, L. B. 1993. Dynamics and effect of western gulls feeding in a colony of guillemots and Brandt's cormorants. Journal of Animal Ecology 62: 399-414.

Steigerwald, E. C., J.-M. Igual, A. Payo-Payo and G. Tavecchia. 2015. Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. Ibis 157: 439-448.

Stienen, E. W. M., A. Brenninkmeijer and C. E. Geschiere. 2001. Living with gulls: the consequences for Sandwich Terns of breeding in association with Black-headed Gulls. Waterbirds 24: 68-82.

Strong, C. M., L. B. Spear, T. P. Ryan and R. E. Dakin. 2004. Forster's Tern, Caspian Tern, and California Gull colonies in San Francisco Bay: habitat use, numbers, and trends, 1982-2003. Waterbirds 27: 411-423.

Takekawa, J. Y., J. T. Ackerman, L. A. Brand, T. R. Graham, C. A. Eagles-Smith, M. P. Herzog, B. R. Topping, G. G. Shellenbarger, J. S. Kuwabara, E. Mruz and others. 2015. Unintended consequences of management actions in salt pond restoration: cascading effects in trophic interactions. PLOS ONE 10: e0119345.

Thomas, G. J. 1972. A review of gull damage and management methods at nature reserves. Biological Conservation 4: 117-127.

Washburn, B. E., S. B. Elbin and C. Davis. 2016. Historical and current population trends of Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) in the New York Bight, USA. Waterbirds 39 (Special Publication 1): 74-86.

Weiser, E. L. and A. N. Powell. 2010. Does garbage in the diet improve reproductive output of Glaucous Gulls? Condor 112: 530-538.

Weiser, E. L. and A. N. Powell. 2011. Reduction of garbage in the diet of nonbreeding glaucous gulls corresponding to a change in waste management. Arctic 64: 220-226.

Winkler, D. W. 1996. California Gull (*Larus californicus*). No. 259 *in* The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. https://doi.org/10.2173/bna.259, accessed 28 June 2016.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Zar, J. 1999. Biostatistical analysis, 4th ed. Prentice-Hall, Upper Saddle River, New Jersey.