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Research Article

Forster's Tern Chick Survival in Response to a Managed Relocation of Predatory California Gulls

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ABSTRACT Gull populations can severely limit the productivity of waterbirds. Relocating gull colonies may reduce their effects on nearby breeding waterbirds, but there are few examples of this management strategy. We examined gull predation and survival of Forster's tern (*Sterna forsteri*) chicks before (2010) and after (2011) the managed relocation of the largest California gull (*Larus californicus*) colony (24,000 adults) in San Francisco Bay, California. Overall, survival of radio-marked Forster's tern chicks from hatching to fledging was 0.22 ± 0.03 (mean $\pm$ SE), and daily survival rates increased with age. Gulls were the predominant predator of tern chicks, potentially causing 54% of chick deaths. Prior to the gull colony relocation, 56% of radio-marked and 20% of banded tern chicks from the nearest tern colony were recovered dead in the gull colony, compared to only 15% of radio-marked and 4% of banded chicks recovered dead from all other tern colonies. The managed relocation of the gull colony substantially increased tern chick survival (by 900%) in the nearby (<1 km) colony from 0.04 ± 0.02 in 2010 to 0.40 ± 0.12 in 2011 but not at the more distant (>3.8 km) reference tern colony (0.29 ± 0.10 in 2010 and 0.25 ± 0.09 in 2011). Among 19 tern nesting islands, fledging success was higher when gull abundance was lower at nearby colonies and when gull colonies were farther from the tern colony. Our results indicate that the managed relocation of gull colonies away from preferred nesting areas of sensitive waterbirds can improve local reproductive success, but this conservation strategy may shift gull predation pressure to other areas or species. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS California gull, chick survival, fledging success, Forster's tern, gull management, gull predation, *Larus*, radio telemetry, *Sterna*.

Gull populations, particularly *Larus* gulls, have increased substantially over the last century in North America and Europe (Kadlec and Drury 1968, Drury 1973, Chabrzyk and Coulson 1976, Conover 1983). This increase in gull abundance is generally attributed to their protection from hunting and egging, and the expanding availability of anthropogenic food resources from landfills, fisheries discards, and agriculture (Drury 1965, 1973; Hunt 1972; Conover 1983; Horton et al. 1983). Unfortunately, the increased abundance of gulls has been problematic for other colonial waterbirds.

Gulls can severely limit the productivity of waterbirds through predation of eggs, chicks, and adults (Thomas 1972, Spear 1993, Becker 1995, Bowman et al. 2004, Oro et al. 2005), kleptoparasitism (Hatch 1970, Stienen et al. 2001), and displacement from preferred nesting sites (Drury 1965, Kress 1983, Nisbet and Spendelow 1999). In particular, tern populations have been severely affected by gulls. For example, *Larus* gulls depredated 77% of roseate tern (*Sterna dougallii*) chicks that hatched at Country Island, Nova Scotia (Whittam and Leonard 1999), 63% of the common tern (*Sterna hirundo*) chicks that hatched on a sand spit in Québec, Canada (Guillemette and Brousseau 2001), and 62% of the common tern chicks that hatched on Mellum Island in the Wadden Sea, Germany (Becker 1995). Additionally, *Larus* gulls depredated up to 73% of all eggs produced by 3 species of terns (*Sterna*) and black skimmers (*Rynchops niger*) nesting on the Virginia barrier islands (O'Connell and Beck 2003), and 32% of arctic tern (*Sterna paradisaea*), 23% of common tern, and 6% of roseate tern nests at Eastern Egg Rock, Maine (Donehower et al. 2007). Consequently, multiple large-scale gull culling programs have been conducted in North America and Europe (Thomas 1972, Duncan 1978, Kress 1983, Harris and Wanless 1997, Anderson and Devlin 1999, Bosch

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et al. 2000), and most seabird restoration projects involve some type of gull management (Blokpoel et al. 1997, Anderson and Devlin 1999, Nisbet and Spendelow 1999, Jones and Kress 2012).

Although they have been successful, gull culling programs are expensive, require permits for the destruction of migratory birds, and often require continuous management (Thomas 1972, Kress 1983, Blokpoel et al. 1997, Guillemette and Brousseau 2001). Relocation of gull colonies by removing or altering their breeding habitat presents an alternative management action for reducing negative effects of gull populations on other breeding waterbirds (Thomas 1972). In theory, relocating a particularly problematic gull colony could improve the productivity of waterbirds nesting nearby, but there are few actual examples of this management strategy.

San Francisco Bay has experienced a dramatic increase in California gulls (*Larus californicus*) over the past 3 decades, from <100 breeding adults in 1980 to >52,000 in 2012 (Strong et al. 2004, Donehower and Tokatlian 2012). The largest California gull colony in San Francisco Bay has accounted for an annual average of 76% of the breeding gulls in the bay (Strong et al. 2004). This colony has been located in the dry bed of a 150-ha former salt evaporation pond (hereafter Pond A6), and centered within a 6-km radius of many waterbird nesting colonies (Ackerman et al. 2009*b*). As part of the South Bay Salt Pond Restoration Project, the levees of Pond A6 were breached to San Francisco Bay's tidal flow in late 2010 to allow tidal marsh habitat to develop within the site. As a result, the once dry pond bed was flooded, evicting nearly 24,000 California gulls, many of which moved to a new colony location in 2011. Herein, we examined gull predation and survival rates of Forster's tern (*Sterna forsteri*) chicks at several colony locations both before (2010) and after (2011) this managed relocation of the largest gull colony in San Francisco Bay.

STUDY AREA

We examined survival of Forster's tern chicks from hatch to fledging in South San Francisco Bay, California (37.4° N, 122.0° W) at most of the tern colonies before (2010) and after (2011) the Pond A6 flooding and subsequent California gull colony relocation. We monitored tern chicks using mark-recapture methods at all 7 of the known tern colonies that produced chicks in the south bay in 2010 (Moffett Pond Complex: Ponds A1, AB1, AB2, A2W; Alviso Pond Complex: Ponds A7, A8, A16) and at all 5 known colonies that produced tern chicks in 2011 (Moffett Pond Complex: Ponds A1, A2W; Alviso Pond Complex: Ponds A7, A8, A16; Fig. 1). We estimated tern chick survival using radio telemetry methods at 6 of the 7 colonies that produced tern chicks in 2010 (excludes Pond A1) and 4 of the 5 colonies in 2011 (excludes Pond A16). Unlike the gull colony, tern colony locations were not directly affected by the Pond A6 flooding (Fig. 1). Each tern colony nested on 1 to 5 islands within former salt evaporation ponds that had little vegetation. This habitat structure enhanced our ability to locate tern chicks.

METHODS

Mark-Recapture of Tern Chicks from Hatch to Fledging

We conducted research under the guidelines of the United States Geological Survey, Western Ecological Research Center, Animal Care, and Use Committee. We hand-captured Forster's tern chicks weekly during the nesting season (May to Aug) until the last tern chick fledged. We entered colonies each week, monitored each nest to locate newly hatched chicks, hand-captured every chick on the island nesting colony, banded newly hatched chicks, recorded band numbers from previously banded chicks, weighed each chick with an electronic balance (±0.1 g; Scout Pro SP401, Ohaus Corporation, Pine Brook, NJ), and measured short tarsus (tarso-metatarsus bone) and exposed culmen length with digital calipers (±0.01 mm; Fowler, Newton, MA) and flattened wing length with a wing ruler (±1.0 mm). We held chicks in shaded 5-gallon buckets or screen-lined poultry cages during processing (small, young chicks were separated from larger, older chicks) and returned chicks back to their nest site typically within 1 hour.

We estimated the age of each tern chick at its initial capture. If we observed the hatching date for an individual chick during our routine nest monitoring visits, we calculated the chick's age at every subsequent capture event by subtracting the date of hatching from the date of recapture. For chicks with unknown hatch dates, we estimated chick age at initial capture using an age model based on morphometric measurements (Ackerman et al. 2011). We then calculated hatch date by subtracting the chick's model-estimated age from the date on which it was captured and measured for the first time. For subsequent recaptures of the same chick, we estimated the chick's current age by subtracting the estimated hatch date from the date it was recaptured.

Radio-Marking and Tracking Tern Chicks

We radio-marked only recently hatched chicks (mean ± SD: 1.2 ± 0.6 days old, all <4 days old). We randomly selected only 1 chick per brood for survival rate estimation, but we also radio-marked 2 siblings from each of 7 broods in evaluating predator types. We used radio transmitters containing thermistor switches (model BD-2T, Holohil Systems, Ontario, Canada) that had an advertised lifespan of 21–35 days. Thermistor switches improved detection of chick mortality because an increase or decrease in a chick's body temperature resulted in a corresponding increase or decrease in the radio transmitter signal's pulse rate. Transmitter weight (0.85 g) was ≤5% of initial chick mass and <1% of chick mass at fledging (experimental transmitter weight authorized by U.S. Geological Survey Bird Banding Lab). We attached transmitters to a chick's back with sutures (Vicryl FS-2, 3-0, Ethicon, Piscataway, NJ) through front and rear channels, and tied a third suture in the middle and over the top of the transmitter. We secured each suture with 2–3 knots and cyanoacrylic glue (Loctite 422, Henkel Corp., Rocky Hill, CT).

We tracked radio-marked tern chicks daily to determine mortality and predator type. We determined locations of

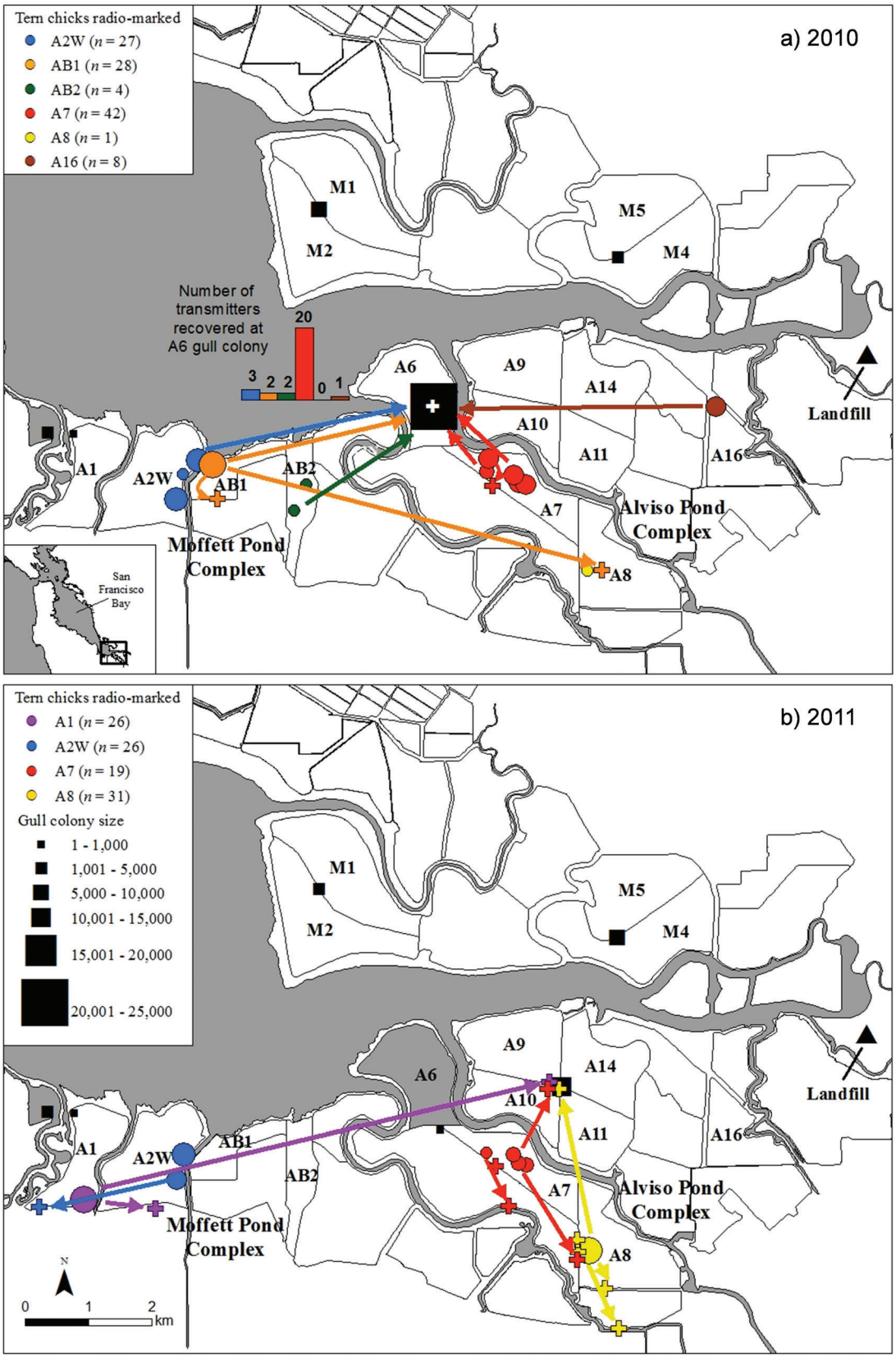

Figure 1. Forster's tern chicks were radio-marked at their site of hatching (circles) and were recovered dead (crosses) after being depredated in South San Francisco Bay, California in (a) 2010 and (b) 2011. The gray shading shows the San Francisco Bay, and the outlined areas depict the numbered wetlands along the bay's margins. Each cross represents 1 chick death, except for the white cross at Pond A6 in 2010, which represents the 28 chick deaths detailed in the histogram. The histogram indicates the number of dead chicks recovered at the Pond A6 gull colony in 2010 (histogram colors indicate site of marking). The relative size of circles indicates the number of tern chicks that were radio-marked at each nesting island. Colors of recovery sites (crosses) indicate the colony site where a chick was originally radio-marked. Black squares indicate the location and population size of each California gull nesting colony in South San Francisco Bay. The triangle depicts the location of the Newby Island Landfill, which is used extensively by California gulls.

radio-marked chicks using trucks equipped with dual 4-element Yagi antenna systems (AVM Instrument Co., Colfax, CA) with null-peak systems to determine bearings via triangulation. We used an electronic compass (model Revolution, True North Technologies, Maynard, MA) and triangulation software (Location of a Signal, version 3.0.1, Ecological Software Solutions, Schwägalpstrasse 2, 9107 Urnäsch, Switzerland) to calculate Universal Transverse Mercator coordinates for each location. Periodically, when we could not locate a chick on its natal island, we also tracked radio transmitters by fixed-wing aircraft with 2 side-view directional yagi antennas and a left-right control box used to circle and pinpoint signals on either side of the plane. Within 24 hours of when we believed a chick had died, we used a hand-held Yagi antenna and receiver to find the transmitter and chick. We continued to search daily for chicks whose radio signals were not detected until we found them or until the expected lifespan of the transmitter was exceeded. We periodically entered the largest nearby California gull colonies (Ponds A6, A9/10/11/14 [hereafter A14], and Mowry 4/5; Fig. 1) on foot with hand-held Yagi antennas and receivers to search for missing transmitters that may have been brought there by gulls. Other California gull nesting colonies were smaller and closer to roads so we monitored them via our normal truck-mounted telemetry system.

Fate of Radio-Marked Tern Chicks

We considered a chick's fate to be either fledged, presumed fledged, depredated by a predator, died from an unknown cause, or unknown fate (due to radio transmitter failure). We considered chicks to have fledged if they were known to be alive $\geq$26 days after hatching. We presumed chicks to have fledged if they were known to be alive $\geq$22 days after hatching using radio telemetry data, and we did not conduct a weekly chick capture event between age 22 and 26 days to determine whether the radio transmitter had failed after 22 days of age but before fledging. We considered chicks to have been depredated if we recovered the radio transmitter and chick remains away from the nesting island. We identified predators to predator class (California gull, wading birds [herons and egrets], or mammals) by using signs of predation near the recovered transmitter (such as tooth marks, scat, or a regurgitated pellet) and location of the recovered transmitter (such as within a California gull colony, or wading bird roost). In particular, we often found regurgitated gull pellets that contained radio transmitters, bird bands, and other indigestible food items within gull colonies. We considered chicks to have been depredated by an unknown predator if the chick went missing from the nesting island when it was too young to have fledged (<22 days of age). Because tern chicks typically remain on the island where they hatched until fledging, chicks that went missing from nesting islands were most likely depredated by avian predators and removed from the island. We classified chicks as dying from an unknown cause when they were recovered dead on the island where they hatched, or in the water nearby, and we did not observe signs of trauma on the corpse. These chicks may have died from starvation, disease, contaminants, exposure, or other causes. We confirmed radio transmitter failures during weekly chick capture events.

Survival Analyses of Radio-Marked Tern Chicks

We estimated daily survival rates of radio-marked chicks using known fate survival models within the R programming language (version 2.15.2) using RMark (version 2.1.4; Laake 2013), a front-end to Program Mark (White and Burnham 1999). We built capture histories based on daily detections using radio telemetry. We included age 0 to age 26 in the capture history, because Forster's tern chicks begin to fledge at approximately 26 days of age (Ackerman et al. 2009*a*). We considered a chick to be alive if its radio transmitter provided a normal signal from the nesting-island, and dead if the chick was found dead during telemetry surveys. In addition, because chicks were located on islands where dispersal was unlikely before fledging age (Ackerman et al. 2009*a*), we assumed that a chick had been depredated by an unknown predator and considered it dead on the first day it went missing if 1) the chick was not of fledging age (i.e., <22 days of age), 2) was no longer detected during daily telemetry surveys, and 3) was no longer captured during weekly chick capture events. For radio transmitter failures, we right-censored chicks starting on the first day the chick was not detected during telemetry surveys, but was later confirmed to still be alive during weekly chick capture events. We also right-censored chicks that went missing on the first day the chick was not detected if they were $\geq$22 days of age because they were near fledging age and we presumed they had fledged and the transmitter had failed. We defined tern chick fledging success as the probability of a chick surviving to 26 days of age, and estimated success for each tern colony in a pond in each year as the cumulative 26-day product of daily survival rates. We used the delta method (Seber 1982) to estimate standard errors for colony-specific fledging success.

Effect of Relocating the Gull Colony on Tern Chick Survival Rates

We assessed the effect of the managed relocation of the largest California gull nesting colony on Forster's tern chick survival by examining the change in survival for each tern colony before (2010) and after (2011) relocation. Specifically, nearly 24,000 adult California gulls nested at Pond A6 in 2010 (Tokatlian et al. 2010) but were evicted after this pond's levees were breached to tidal flow and the pond was flooded. This led to the establishment of a gull nesting colony at Pond A14, which was the largest California gull colony in 2011 (11,956 adults; Robinson-Nilsen et al. 2011), and only 156 California gulls remained and nested on an island immediately adjacent to Pond A6 (Robinson-Nilsen et al. 2011). The tern colony at Pond A7 was directly adjacent to the gull colony at Pond A6 in 2010, whereas other tern colonies were 2.7–5.8 km away (Fig. 1). In particular, the tern colony at Pond A2W was 3.8 km away from the gull colony at Pond A6 (Fig. 1), and was our main reference site because it was 1 of only 2 sites (the other was Pond A7) where large numbers of terns nested in both 2010 and 2011,

thereby providing us opportunities to radio-mark tern chicks at the same site in each year. Therefore, the tern colony site × year interaction term represented the main test for an effect of the gull colony relocation on tern chick survival.

We built a set of candidate models based on potential predictor variables including tern colony site, tern colony complex (Alviso or Moffett), year, chick age, chick mass at marking, relative hatch date (hatch date was standardized each year using the median hatch date), and the interactions tern colony site × year and tern colony complex × year. Our a priori candidate model set included all additive combinations of variables, and a null (intercept only) model (a total of 104 models).

We evaluated models using second-order Akaike's Information Criterion (AIC_c) and considered the model with the smallest AIC_c to be the most parsimonious (Burnham and Anderson 2002). We used AIC_c differences between the best model and each of the other candidate models (ΔAIC_{ci}; where i is the candidate model number) to determine the relative ranking of each model. We used Akaike weights (w_i) to examine the weight of evidence that the selected model was actually the best model within the set of candidate models. We also assessed the relative importance of each variable by summing Akaike weights across models that incorporated the same variable. We used evidence ratios to compare the relative weight of support between models. We used model-averaged predictions from all candidate models, but for brevity we present only the set of top models that contributed 90% of all model weight.

Gull Predation Pressure and Tern Fledging Success

In the next stage of our analysis, we examined how the size and proximity of California gull colonies to tern nesting islands influenced tern fledging success. We calculated tern fledging success for each tern nesting island in each year where the number of radio-marked chicks was >1, and then developed annual, tern nesting island-specific estimates of gull predation pressure. For each Forster's tern colony, we calculated 7 variables of annual gull predation pressure and tested their effects on tern chick fledging success: 1) distance to the nearest gull colony, 2) distance to the largest gull colony, 3) number of gulls at the nearest gull colony, 4) angle from the tern colony to the nearest gull colony's flight path to the nearby landfill, 5) angle from the tern colony to the largest gull colony's flight path to the nearby landfill, 6) gull predation pressure index 1 (GPP_1 defined below), and 7) gull predation pressure index 2 (GPP_2 defined below). We calculated angles to the nearest and largest gull colonies (variables 4 and 5) as the deviation (in degrees) a gull travelling from their nesting colony to the local landfill (Newby Island Landfill; Fig. 1) would need to undertake to arrive at a given tern colony. For these variables of gull predation pressure, we used our prior knowledge that the majority of California gull movements from colonies are largely dictated by the location of a major landfill (Ackerman et al. 2009*b*), and hypothesized that tern colonies that were located farther from a gull's flight path to the landfill might experience lower gull predation rates.

Our gull predation pressure indices (variables 6 and 7) assumed gull predation pressure experienced by a specific tern nesting island would be a cumulative function of all California gull colonies in the South San Francisco Bay (7 in 2010 and 8 in 2011), and that gull predation pressure of any single gull colony would decrease with increasing distance from the tern nesting island and increase with the abundance of gulls. GPP_1 and GPP_2 varied only in their functional form, which described how gull abundance at a given colony affected gull predation pressure. GPP_1 assumed that gull predation pressure was linearly related to each gull colony's abundance, and inversely related to the gull colony's distance from the tern nesting island. GPP_2 assumed that the per-capita impact of a gull colony based on its size would diminish as the number of gulls in the colony increased, because additional gulls to an already large gull population might have little additional effect on tern chick predation rates. Gull predation pressure at each of the tern colonies was therefore modeled as either

$$a)\ GPP_1 = \sum_j \frac{N_j}{D_j} \text{ or } b)\ GPP_2 = \sum_j \frac{logN_j}{D_j}$$

where j = index to specific California gull colony, N_j = number of California gulls at gull colony j, $\log N_j$ = natural log (number of California gulls at gull colony j), and D_j = distance of California gull colony j from tern colony. We obtained California gull abundance data from Tokatlian et al. (2010) and Robinson-Nilsen et al. (2011), which are part of a >30-year dataset on California gull population growth in San Francisco Bay (Strong et al. 2004).

Using these 7 variables of gull predation pressure, we built a candidate model set based on all possible additive combinations of gull predation pressure variables and year without any interactions. This model set was reduced by not allowing GPP_1 and GPP_2 to be in the same model, and combinations of distance, abundance, and angle variables were required to match the specific gull colony in question (e.g., if the distance metric was based on the nearest gull colony, then the gull abundance and angle of the deviation from the gull colony's flight path must also be for the nearest gull colony). Our a priori candidate model set included a null model and totaled 34 models. We evaluated models using AIC_c and present the set of top models that contributed 90% of all model weight. All results represent model-averaged predictions and standard errors from the full candidate model set.

RESULTS

Predators of Tern Chicks

We radio-marked and tracked 212 Forster's tern chicks at 6 colonies in 2010 (n = 110) and 4 colonies in 2011 (n = 102; Table 1). In addition, we banded 891 tern chicks at 7 colonies in 2010 and 358 tern chicks at 5 colonies in 2011. A total of 35 radio transmitters failed prematurely (15 in 2010, 20 in 2011; Table 1), precluding the determination of fates for 35 chicks. Thus, we derived final chick fate statistics from the 177 chicks for which fate was determined.

Table 1. Fate of Forster's tern chicks radio-marked at hatch in wetlands within the South San Francisco Bay, California, during 2010 and 2011.

Year and tern colony location	Chicks radio-marked	Radio failed, fate unknown	Chicks radio-marked, excluding radio failures	Chicks fledged[a]	Chicks presumed fledged[b]	Depredated by				Unknown cause of death[g]	Transmitters recovered in A6 gull colony
						California gull[c]	Heron/ Egret[d]	Mammal[e]	Unknown predator[f]		
2010											
A2W	27	7	20	2	2	3	0	0	4	9	3
AB1	28	2	26	7	6	3	0	0	3	7	2
AB2	4	0	4	0	0	2	0	0	2	0	2
A7	42	6	36	1	1	20	1	0	6	7	20
A8	1	0	1	1	0	0	0	0	0	0	0
A16	8	0	8	2	4	1	0	0	0	1	1
2010 total	110	15	95	13	13	29	1	0	15	24	28
2011											
A1	26	6	20	1	1	1	0	1	11	5	0
A2W	26	6	20	1	2	0	0	0	12	5	0
A7	19	4	15	3	1	1	3	0	3	4	0
A8	31	4	27	0	1	1	3	0	15	7	0
2011 total	102	20	82	5	5	3	6	1	41	21	0
2010–2011 total	212	35	177	18	18	32	7	1	56	45	28

[a] We considered chicks to have fledged if they were known to be alive at least 26 days after hatching.
[b] We presumed chicks to have fledged if they were known to be alive at least 22 days after hatching and we did not observe final fate.
[c] We identified California gulls as the predator when we recovered transmitters in a gull colony (31) or near regurgitated pellets in an area used by gulls (1).
[d] We identified herons or egrets as the predator when we found transmitters in association with heron and egret feathers and regurgitations, and in areas frequently used by herons and egrets.
[e] We identified mammals as the predator when we recovered transmitters that were attached to tern chicks in mammal scat.
[f] We considered chicks that went missing from the nesting island when they were too young to have fledged to have been killed by a predator of unknown type. These chicks were most likely depredated by avian predators and removed from the island.
[g] We classified chicks as dying from an unknown cause of death when we recovered them dead on the island where they hatched or in the water nearby and no visible signs of trauma were evident on the corpse.

Overall, 80% of radio-marked tern chicks died ($n = 141$) and only 20% fledged or were presumed to have fledged ($n = 36$; Table 1). Of the 141 radio-marked tern chicks known to have died, 23% ($n = 32$) were depredated by California gulls, 5% ($n = 7$) were depredated by wading birds (herons and egrets), 1% ($n = 1$) were depredated by mammals, 40% ($n = 56$) went missing from their nesting island before they were of appropriate age to fledge and were presumed to have been depredated (by an unidentified predator), and 32% ($n = 45$) died from unknown causes.

Of the 85 (54 in 2010 and 31 in 2011) radio-marked Forster's tern chicks with a known mortality cause (excludes chicks that went missing), 54% (29 of 54) were depredated by California gulls in 2010, but only 10% (3 of 31) were depredated by California gulls in 2011 (Table 1). However, many of the radio-marked tern chicks simply went missing from their nesting colony before they were old enough to have fledged ($n = 56$; unknown predator in Table 1), and this likely indicated predation by aerial predators such as California gulls. In 2010, we also recovered 59 bands (7% of all banded tern chicks) at the Pond A6 California gull colony from tern chicks that were banded at their nesting colonies, but which were never fitted with transmitters (see Table S1, available online at www.onlinelibrary.wiley.com). California gulls accounted for 80% of the 40 cases where we were able to confirm the identity of the predator. If we assume a similar proportion (i.e., 80%) of the tern chicks that went missing (i.e., 15 in 2010 and 41 in 2011) were actually depredated by California gulls (i.e., 12 [2010] and 33 [2011] missing chicks assumed dead via gulls), then 59% (41 of 69) of tern chick deaths may have been caused by California gulls in 2010 and 50% (36 of 72) may have been caused by California gulls in 2011.

In 2010, we recovered 56% (20 of 36) of radio transmitters from the Pond A7 tern colony in the adjacent Pond A6 California gull colony, compared to only 14% (8 of 59) from all the other tern colonies (Table 1). Similarly, in 2010, 20% (33 of 165) of bands from non-radio-marked tern chicks in Pond A7 were recovered in the Pond A6 California gull colony compared to only 4% (26 of 726) of bands from non-radio-marked chicks at all other tern colonies (see Table S1, available online at www.onlinelibrary.wiley.com). In 2011, after the Pond A6 California gull colony had been relocated, we recovered 7% (1 of 15) of radio-marked tern chicks from the Pond A7 tern colony in the newly established Pond A14 California gull colony compared to 3% (2 of 67) from all other tern colonies (Table 1), and we did not recover any bands from the 358 non-radio-marked chicks at any gull colony. We found all but 1 of the 29 mortalities caused by gulls in 2010 at the Pond A6 California gull colony, and found all 3 mortalities caused by gulls in 2011 at the newly established California gull colony at Pond A14 (Table 1; Fig. 1).

Survival Rate of Tern Chicks

Survival of Forster's tern chicks ($n = 205$) from hatching to fledging at 26 days of age was 0.22 ± 0.03 (mean $\pm$ SE) overall, 0.25 ± 0.04 in 2010, and 0.19 ± 0.04 in 2011 (Table 2). Fledging success ranged from 4% to 69% among

Table 2. Forster tern colony locations, number of nests initiated, number of chicks banded, number of chicks radio-marked, and chick survival rates (±SE) in South San Francisco Bay, California, during 2010 and 2011. The number of chicks radio-marked for survival analyses ($n = 205$) does not include 5 radio-marked siblings in 2010 and 2 radio-marked siblings in 2011 that we also used to determine predator types.

Complex and tern colony location	Number of tern nests		Number of tern chicks banded		Number of tern chicks radio-marked		Tern chick survival	
	2010	2011	2010	2011	2010	2011	2010	2011
Alviso complex								
Pond A7	209	139	207	116	42	18	0.04 (0.02)	0.40 (0.12)
Pond A8	114	108	47	133	1	31	0.99 (na)	0.07 (0.04)
Pond A16	59	27	58	9	8	0	0.69 (0.18)	
Moffett complex								
Pond A1	76	103	94	77	0	25		0.11 (0.06)
Pond A2W	231	282	214	125	25	26	0.29 (0.10)	0.25 (0.09)
Pond AB1	252	8	354	0	25	0	0.43 (0.11)	
Pond AB2	28	5	27	0	4	0	0.11 (na)	
Total	969	672	1001	460	105	100	0.25 (0.04)	0.19 (0.04)

tern colonies. The most parsimonious model describing tern chick survival rates included tern colony site, year, age, and the site × year interaction, and had an Akaike weight of 0.50 (Table 3). Furthermore, all models containing colony site, year, age, and the year × site interaction had a cumulative Akaike weight of 0.99. Two other models containing these variables plus either hatch date or mass at marking, were within a $\Delta AIC_c \leq 2.0$, but their addition did not improve model fit as indicated by no improvement in model log-likelihoods (Table 3).

We estimated the relative importance of individual variables and found that the data strongly supported effects of tern colony site (relative variable importance = 1.00), year (1.00), age (1.00), and the year × site interaction (0.99). In contrast, other variables we investigated had little influence on chick survival rates, including hatch date (0.31), mass at marking (0.27), and colony complex (0.01). To further determine the importance of variables in the best model, we compared the best model (reference) to the same model structure but omitting 1 of the variables of interest. Using an evidence ratio, we estimated that the model including chick age was 1.70×10^8 times more likely than the same model without chick age. Depending on site and year, Forster's tern chick daily survival rate increased 4–39% during the fledging period from 0.701–0.958 at 1 day of age to 0.976–0.994 at 26 days of age. The average age of tern chicks when they were confirmed depredated by California gulls was 4.7 days old, and ranged from 1 to 13 days old.

The best model contained the year × site interaction term, and was 145 times more likely than the same model but without this interaction term (Table 3). The overriding importance of the year × site interaction indicated that changes in tern chick survival rates between years were not consistent among tern colony sites. Specifically, Forster's tern chick survival rates at 2 of the largest tern colonies, that were consistently used for nesting in both 2010 and 2011 (Pond A2W and Pond A7; Table 2), differed markedly before (2010) and after (2011) the relocation of the Pond A6 California gull colony. Tern chick fledging success at reference Pond A2W was similar between years (0.29 in 2010 and 0.25 in 2011; −14% change), whereas tern chick fledging success at Pond A7 increased dramatically from 0.04 in 2010 to 0.40 in 2011 (+900% change) after the relocation of the nearby Pond A6 gull colony (Fig. 2). Compared to the reference tern colony at Pond A2W, daily survival rates of tern chicks at Pond A7 increased between years more among younger tern chicks (<15 days old) than for older tern chicks (Fig. 3).

Gull Predation Pressure and Tern Chick Fledging Success

The most parsimonious model describing fledging success among Forster's tern colonies included only the California gull abundance at the nearest gull colony, and had an Akaike weight of 0.28 (Table 3). The second ranked model supported by the data ($\Delta AIC_c = 2.00$) included only gull predation pressure index 1 (GPP_1), and had an Akaike weight of 0.10. Using evidence ratios, the best model that included only the California gull abundance at the nearest gull colony was 4.4 times more likely than the null model, and the second ranked model that included only GPP_1 was 1.6 times more likely than the null model. The relative importance of individual variables was 0.50 for the size of the nearest gull colony, 0.19 for GPP_1, 0.18 for year, 0.16 for the angle of the tern colony to the nearest gull colony's flight path to the landfill, 0.15 for distance to the nearest gull colony, 0.08 for the angle of the tern colony to the largest gull colony's flight path to the landfill, and 0.09 for gull predation pressure index 2 (GPP_2). Model-averaged coefficients and standard errors for the size of the nearest gull colony ($5.4 \pm 3.5\%$ decline in tern fledging success per 10,000 gulls added at the nearest gull colony) and GPP_1 (-0.00207 ± 0.00199) further indicated that although better than the null model, the influence of gull predation pressure variables on tern chick fledging success were weak. Nonetheless, tern fledging success tended to decrease as the size of the nearest gull colony increased (Fig. 4a). Similarly, tern fledging success tended to be higher when the gull predation pressure index was lower (Fig. 4b).

DISCUSSION

Forster's tern chick survival from hatching to fledging at 26 days of age was 0.22, which is considered low for chicks raised on islands. In comparison, survival of least terns

Table 3. Ranking of candidate model set describing radio-marked Forster's tern chick daily survival ($n = 205$ chicks) from hatch to fledging and fledging success at nesting islands ($n = 19$ tern nesting islands) in South San Francisco Bay, California during 2010 and 2011. We present only the top models that represented 90% of total model weight, along with the null model. For candidate models of tern fledging success, we modeled gull predation pressure index 1 (GPP_1) and 2 (GPP_2) at each of the tern colonies as $GPP_1 = \sum_j \frac{N_j}{D_j}$ or $GPP_2 = \sum_j \frac{\log N_j}{D_j}$ where j = index to specific California gull colony, N_j = number of California gulls at gull colony j, $\log N_j$ = natural log (number of California gulls at gull colony j), and D_j = distance of California gull colony j from tern colony.

Model set	Model structure[a]	K[b]	−2logL	AIC_c[c]	ΔAIC_c[d]	Akaike weight (w_i)[e]	Evidence ratio[f]	Cumulative weight
Tern chick daily survival rate	Site + year + age + site × year	11	820.69	842.86	0.00	0.50	1.00	0.50
	Site + year + age + date + site × year	12	820.25	844.45	1.59	0.22	2.22	0.72
	Site + year + age + mass + site × year	12	820.64	844.84	1.99	0.18	2.70	0.91
	Intercept only (null)	1	926.99	928.99	86.13	0.00	5.05×10^{18}	1.00
Tern chick fledging success among nesting islands	Gull abundance at nearest colony	3	−12.16	−4.56	0.00	0.28	1.00	0.28
	GPP_1	3	−10.16	−2.56	2.00	0.10	2.72	0.38
	Distance to nearest gull colony + gull abundance at nearest colony	4	−12.59	−1.73	2.84	0.07	4.13	0.44
	Gull abundance at nearest colony + angle from nearest gull colony's flightpath	4	−12.53	−1.67	2.89	0.07	4.24	0.51
	Intercept only (null)	2	−6.34	−1.59	2.98	0.06	4.43	0.57
	Year + gull abundance at nearest colony	4	−12.20	−1.34	3.22	0.06	5.01	0.63
	GPP_2	3	−8.86	−1.26	3.30	0.05	5.21	0.68
	Distance to nearest gull colony	3	−8.30	−0.70	3.86	0.04	6.90	0.72
	Angle from largest gull colony's flightpath + GPP_1	4	−11.34	−0.48	4.08	0.04	7.71	0.76
	Angle from nearest gull colony's flightpath + GPP_1	4	−10.42	0.43	5.00	0.02	12.17	0.78
	Distance to largest gull colony	3	−7.08	0.52	5.08	0.02	12.71	0.80
	Year	3	−6.94	0.66	5.22	0.02	13.62	0.82
	Year + GPP_1	4	−10.18	0.68	5.24	0.02	13.75	0.84
	Angle from largest gull colony's flightpath	3	−6.48	1.12	5.68	0.02	17.14	0.86
	Angle from nearest gull colony's flightpath	3	−6.47	1.13	5.69	0.02	17.21	0.87
	Year + distance to nearest gull colony	4	−9.41	1.45	6.01	0.01	20.23	0.89
	Year + gull abundance at nearest colony + angle from nearest gull colony's flightpath	5	−13.00	1.61	6.18	0.01	21.93	0.90

[a] The + denotes an additive effect and the × denotes an interaction.
[b] The number of parameters in the model, including the intercept.
[c] Second-order Akaike's Information Criterion (AIC_c).
[d] The difference in the value between AIC_c of the current model and the value for the most parsimonious model.
[e] The likelihood of the model given the data, relative to other models in the candidate set (model weights sum to 1.0).
[f] The weight of evidence that the top model is better than the selected model, given the candidate model set.

(*Sternula antillarum*) from hatching to fledging was 0.45 on barrier islands in South Carolina (Brooks et al. 2013), 0.30 in the United States Virgin Islands (Lombard et al. 2010), 0.14–0.74 on beaches in Maine (Bailey and Servello 2008), and 0.43–0.62 on islands within the Mississippi River (Dugger et al. 2000). Additionally, survival was 0.23–0.27 for black-fronted tern (*Chlidonias albostriatus*) chicks on exposed gravel beds of the Tasman River in New Zealand (Cruz et al. 2013). Although Forster's tern chick survival to fledging was higher than that of American avocet chicks (*Recurvirostra americana*; 0.06), it was much lower than those of black-necked stilt chicks (*Himantopus mexicanus*; 0.40) studied at similar sites in San Francisco Bay in 2005 and 2006 (Ackerman et al. 2014). Once fledged, Forster's tern cumulative survival rate during the subsequent 35-day postfledging time period was 0.81 in San Francisco Bay (Ackerman et al. 2008). Combining these data for postfledging survival (Ackerman et al. 2008) with our current study's estimate for overall tern chick survival from hatch to fledging (0.22), provides an estimated Forster's tern chick survival from hatch to 35-days postfledging of 0.18 (61 total days after hatching).

California gulls were the predominant predator of Forster's tern chicks, as they were in a related study on American avocet chicks at these same sites (Ackerman et al. 2014). Overall, predation by California gulls accounted for 23% of tern chick deaths, yet another 40% ($n = 56$) of chick deaths were those that went missing from their nesting island before they were old enough to have fledged. Because tern chicks typically remain on their natal island until fledging, these chicks that went missing likely were also depredated by aerial predators and carried from the island. For example, we found 90 different tern chicks (by recovering their transmitters or bands) within California gull colonies that were carried there by gulls and often regurgitated within pellets. California gulls accounted for 80% of the identified predation events of radio-marked chicks. If we assume a similar proportion of the tern chicks that went missing were depredated by California

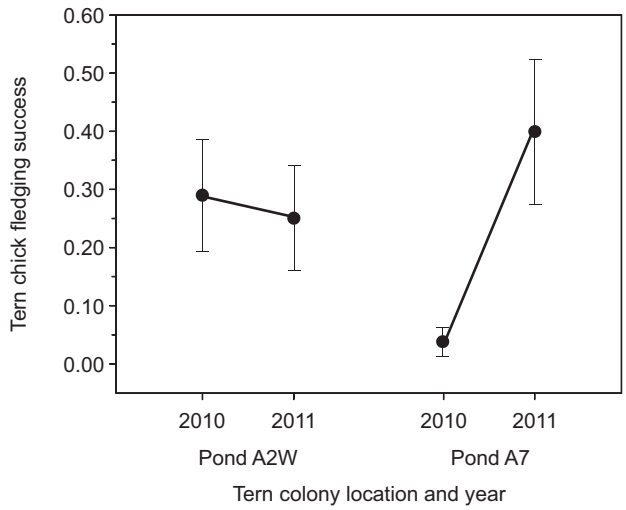

Figure 2. Survival to fledging (±SE) of Forster's tern chicks radio-marked at hatching in South San Francisco Bay, California increased by 900% between years at Pond A7 after the relocation of the nearby Pond A6 gull colony but was similar (14% decrease) between years at the Pond A2W reference site. The Pond A7 Forster's tern colony was located directly adjacent to the largest California gull colony in 2010 at Pond A6 (24,000 adults), but Pond A6 was flooded in 2011, which forced the relocation of the Pond A6 California gull colony. The Pond A2W Forster's tern colony acted as a reference site because it was always >3.8 km away from the largest California gull colony in each year.

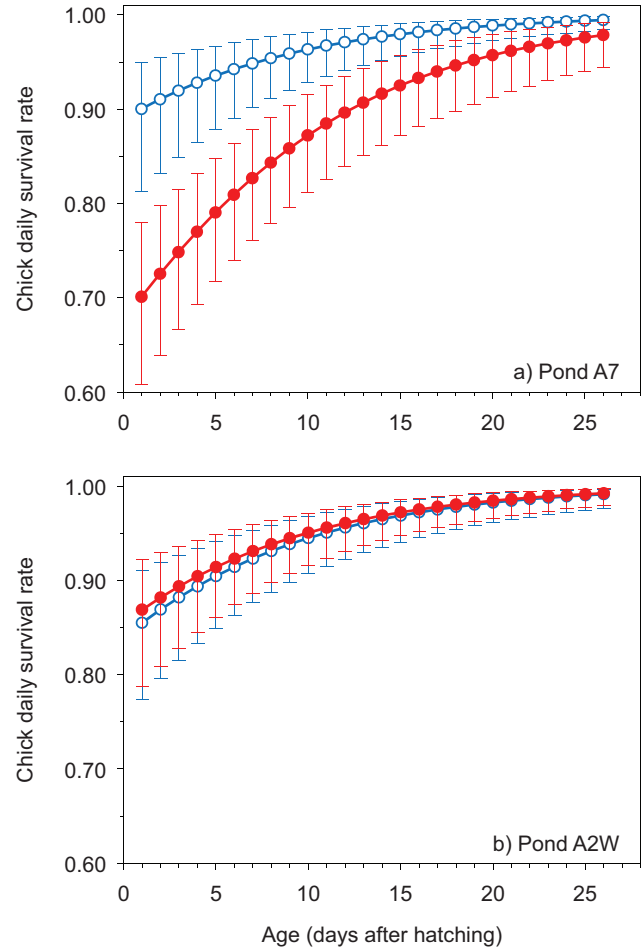

Figure 3. Daily survival rate of radio-marked Forster's tern chicks from hatch (age = 0 days) to fledging (age = 26 days) in 2010 (red, solid) and 2011 (blue, open) in South San Francisco Bay, California. (a) The Pond A7 Forster's tern colony was located directly adjacent to the largest California gull colony in 2010 at Pond A6, but Pond A6 was flooded in 2011, which forced the relocation of the Pond A6 California gull colony. (b) The Pond A2W Forster's tern colony acted as a reference site because it was always >3.8 km away from the largest California gull colony in each year. Error bars represent lower and upper 95% confidence limits.

gulls, then 54% of tern chick deaths may have been caused by gulls. This estimate might be closer to the true impact of California gulls on Forster's tern chick survival, especially considering the difficulty of identifying predation events where tern chicks were carried by gulls up to 7.8 km away from their nesting island.

The managed relocation of the largest gull colony in San Francisco Bay greatly altered chick survival of Forster's terns nesting in an adjacent pond. Specifically, tern chick fledging success at the adjacent Pond A7 increased 900% from 0.04 in 2010 to 0.40 in 2011 after the relocation of the Pond A6 gull colony. Conversely, Forster's tern chick fledging success at the reference pond that was 3.8 km away was similar between years (Pond A2W: 0.29 in 2010 and 0.25 in 2011), indicating little effect of the relocation of the Pond A6 gull colony on tern chick survival. Band and transmitter recoveries further demonstrated that Forster's tern chicks at the Pond A7 tern colony were more susceptible to predation by California gulls from the A6 gull colony than were chicks at other, more distant tern colonies. Our results also showed that young tern chicks at Pond A7 benefitted most from the gull colony relocation. Daily survival rates of tern chicks at Pond A7 increased in 2011 much more so for younger tern chicks than for older tern chicks, and California gulls depredated most tern chicks at a mean age of 5 days. Thus, the relocation of the gull colony was successful at reducing predation on the adjacent tern colony during the most vulnerable period for tern chicks.

We further examined the influence of California gull colonies on survival of Forster's tern chicks by examining whether tern fledging success on a given island was related to the distance, direction, and abundance of nearby gull colonies. Forster's tern fledging success tended to decrease as the size of the nearest California gull colony increased and fledging success was higher when the gull predation pressure index (GPP_1) was lower. Although these relationships were weak, they indicated that having fewer gulls at nearby gull colonies and having gulls farther away from the tern nesting island slightly improved tern fledging success. Management actions aimed at minimizing gull numbers at gull colonies near tern colonies, and maximizing gull colony distance from tern colonies might enhance tern productivity. Similarly, enhancing or restoring potential tern nesting islands away from established gull colonies might improve the success of restoration projects.

Individual California gulls appeared to specialize on depredating Forster's tern chicks. Several times when we

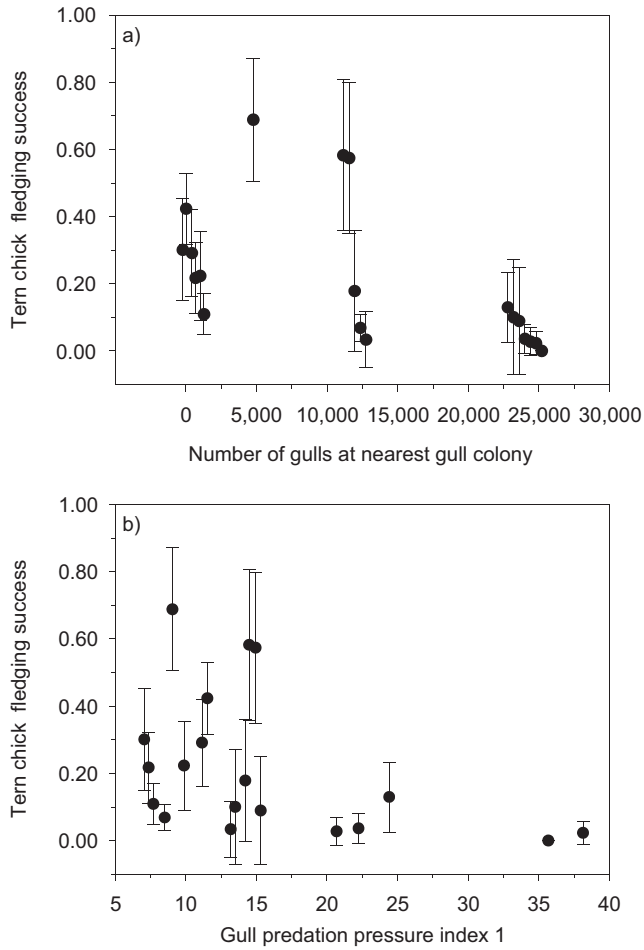

Figure 4. Fledging success (±SE) of Forster's tern chicks tended to decline with (a) the number of gulls at the nearest California gull colony and (b) California gull predation pressure index 1. Forster's tern chicks were radio-marked at 19 tern nesting islands in South San Francisco Bay, California in 2010–2011. California gull predation pressure index 1 (GPP_1) was modeled as $GPP_1 = \sum_j \frac{N_j}{D_j}$ where j = index to specific California gull colony, N_j = number of California gulls at gull colony j, and D_j = distance of California gull colony j from tern colony.

recovered a radio transmitter from a depredated tern chick within the Pond A6 California gull colony, we also found additional tern chick bands. These multiple band recoveries of depredated tern chicks at the same precise location within gull colonies, and often near a California gull nest, suggested that the same individual California gull had depredated multiple tern chicks. For example, of the 32 radio-marked Forster's tern chicks that were known to be depredated by California gulls, 13 (41%) of these instances had multiple bands and/or transmitters recovered at the same location. This included times where we recovered the remains of 2 (4 times), 3 (5 times), 6, 7, 8, and 11 Forster's tern chicks at the same location within the Pond A6 gull colony; we presumed the chicks were depredated by the same individual California gull in each instance.

Several other studies also have found that gull predation on seabird chicks was often the consequence of just a few specialist gulls. For example, Guillemette and Brousseau (2001) found that only 5 individual gulls, or 0.8% of the breeding population of herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*), were responsible for depredating an average of 63% of the common tern chicks that had hatched. Similarly, only 2% of a population of herring gulls were responsible for depredating approximately 10% of ring-billed gull chicks (*Larus delawarensis*; Southern and Southern 1984), 2–4% of a population of herring gulls were responsible for depredating approximately 21% of lesser black-backed gull chicks (*Larus fucus*; Hario 1994), and 2% of a population of western gulls (*Larus occidentalis*) were responsible for depredating 65–77% of common murre (*Uria aalge*) eggs and chicks (Spear 1993). Pierotti and Annett (1991) found that >75% of herring gulls had specialized diets and 12% of gulls specialized on depredating adult Leach's storm-petrels (*Oceanodroma leucorhoa*). Oro et al. (2005) also found that individual yellow-legged gulls (*Larus michahellis*) specialized on storm-petrels (*Hydrobates pelagicus*), and gulls accounted for up to 33% of storm-petrel mortality. Accordingly, seabird productivity tends to increase in studies that lethally remove the gulls that specialize on depredating eggs and chicks (Hario 1994, Guillemette and Brousseau 2001, Riensche et al. 2012; but see Donehower et al. 2007). Culling large populations of gulls had more variable success for improving waterbird populations and requires continual gull control measures (Thomas 1972, Harris and Wanless 1997, Anderson and Devlin 1999). Together, these data suggest that gulls that depredate seabird chicks tend to specialize, and that typically only a very small proportion of a local gull population is responsible for the majority of chick mortality by gulls.

MANAGEMENT IMPLICATIONS

Managing tern populations often includes gull control via lethal removal and egg destruction (Kress 1983, Blokpoel et al. 1997, Anderson and Devlin 1999, Nisbet and Spendelow 1999, Jones and Kress 2012). Relocation of gull colonies by habitat manipulation has been less studied but could contribute to management options for increasing waterbird productivity. The South Bay Salt Pond Restoration Project relocated the largest gull colony in San Francisco Bay by flooding a historical gull nesting area. Forster's tern colonies that had been located adjacent to this large gull colony experienced a substantial improvement in chick survival rates, although overall survival rates for tern chicks in San Francisco Bay were not higher in the year after the relocation. Further, tern fledging success tended to be higher when fewer gulls were at nearby gull colonies or when the gull colony was farther from the tern colony. These results suggest that relocating gull colonies away from preferred nesting areas of more sensitive waterbird species can improve local success, but would likely shift predation pressure to other areas or species.

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