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Comparative reproductive biology of sympatric species: nest and chick survival of American avocets and black-necked stilts

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Identifying differences in reproductive success rates of closely related and sympatrically breeding species can be useful for understanding limitations to population growth. We simultaneously examined the reproductive ecology of American avocets *Recurvirostra americana* and black-necked stilts *Himantopus mexicanus* using 1274 monitored nests and 240 radio-marked chicks in San Francisco Bay, California. Although there were 1.8 times more avocet nests than stilt nests, stilts nonetheless fledged 3.3 times more chicks. Greater production by stilts than avocets was the result of greater chick survival from hatching to fledging (avocet: 6%; stilt: 40%), and not because of differences in clutch size (avocet: 3.84; stilt: 3.77), nest survival (avocet: 44%; stilt: 35%), or egg hatching success (avocet: 90%; stilt: 92%). We reviewed the literature and confirmed that nest survival and hatching success are generally similar when avocets and stilts breed sympatrically. In addition to species, chick survival was strongly influenced by age, site, and year. In particular, daily survival rates increased rapidly with chick age, with 70% of mortalities occurring ≤ 1 week after hatch. California gulls *Larus californicus* caused 55% of avocet, but only 15% of stilt, chick deaths. Differential use of micro-habitats likely reduced stilt chick's vulnerability to gull predation, particularly during the first week after hatch, because stilts nested in vegetation 2.7 times more often than avocets and vegetation height was 65% taller at stilt nests compared with avocet nests. Our results demonstrate that two co-occurring and closely related species with similar life history strategies can differ markedly in reproductive success, and simultaneous studies of such species can identify differences that limit productivity.

Closely related bird species that have similar life history strategies and breed sympatrically might be expected to have similar demographic rates (Ricklefs 1969, Sæther 1988, Martin 1995, Grant and Shaffer 2012). Yet, ecological differentiation that allows closely related species to coexist can cause differences in key demographic parameters among species (Martin 1988, 1993). In particular, reproductive success may vary between closely related bird species if there are important differences in the use of nesting or brooding environments. In such cases, identifying differences in reproductive success rates of closely-related and sympatrically-breeding species can be useful for understanding the limitations to population growth of an individual species (Sieving 1992, Martin 1993, Koons and Rotella 2003, Traylor et al. 2012). Further, identifying the specific life stages when reproductive success rates differ between species could allow for targeted management, but few studies have examined reproductive success at multiple life stages for sympatric species. Egg and chick survival are often the life stages where population growth is most limited (Wisdom et al. 2000, Hoekman et al. 2002, Clark and Martin 2007). Differences in nest survival between sympatric species often occur when differences in nest-site characteristics are prevalent (Martin 1993, Koons and Rotella 2003, Khoury et al. 2009). Fewer studies have examined chick survival, but those that have typically report differences in survival between sympatrically breeding species (Uttley et al. 1989, Savard et al. 1991, Gendron and Clark 2002). Simultaneously comparing the reproductive success rates of two closely related and sympatric species during both the egg and chick life stages could provide a useful approach for assessing limitations to productivity.

American avocets *Recurvirostra americana* (hereafter avocets) and black-necked stilts *Himantopus mexicanus* (hereafter stilts) are the two members of the family Recurvirostridae that breed in North America. Both species specialize in using shallow wetlands in coastal and interior areas of western and mid-western areas. These species have similar life history strategies, overlap substantially in their distributions, and often breed sympatrically (Robinson et al. 1999, Ackerman et al. 2013).

Although they often use similar habitats and occur within the same wetlands, key differences in micro-habitat use have been documented. Stilts tend to use more vegetated wetlands, such as managed and diked marshes, whereas avocets often use wetlands with more open water habitat, such as salt ponds and mudflats (Hamilton 1975, Rintoul et al. 2003, Ackerman et al. 2007, Hickey et al. 2007). When

both species occur within the same wetland, avocets tend to use more open water and mudflat habitats whereas stilts use more vegetated areas (Rintoul et al. 2003). Differential use of micro-habitats is perhaps most evident in the selection of nest sites. Avocets and stilts will co-locate nests within wetlands, often in loose, mixed-species colonies. Yet, avocets are more colonial than stilts, and nest sites often contain little or no surrounding vegetation (Hamilton 1975, Sordahl 1996). Stilt nests are generally more widely spaced than avocet nests, and stilts typically nest in closer proximity to vegetation than avocets (Hamilton 1975, Sordahl 1996).

Despite these species' close association, their differential use of micro-habitats could result in substantial differences in breeding demographic rates and may reflect differential selection pressures on specific life-history traits. Preference by stilts for nesting within taller and denser vegetation could better conceal stilt nests and chicks from predators, thereby improving chick production compared to avocets, which nest predominantly on bare ground. Avocets' more colonial nature and higher nesting densities could provide eggs and chicks better protection from predators via greater communal mobbing.

In this study, we compared the reproductive biology of sympatrically breeding avocets and stilts in San Francisco Bay, California. We first compared the use of nesting micro-habitats by avocets and stilts. We then examined species differences in nest survival and chick survival to fledging and the factors influencing these survival rates. Lastly, we reviewed the literature and summarized studies which have reported either nest survival, egg hatching success, or chick survival for both avocets and stilts to determine if there was a general pattern of differential survival between species where they co-occur. Our study is one of the few bird studies that has simultaneously compared reproductive success rates in sympatrically breeding species by evaluating potential differences in both nest and chick survival.

Methods

Study site

We studied avocets and stilts in South San Francisco Bay, California (37.4°N, 122.0°W) in 2005 and 2006. Avocets and stilts are the most abundant breeding shorebirds in San Francisco Bay, totaling more than 4000 avocets and 1000 stilts, representing the largest breeding populations for these species on the Pacific Coast (Stenzel et al. 2002, Rintoul et al. 2003). Our study site was located within the Don Edwards San Francisco Bay National Wildlife Refuge and Eden Landing Ecological Reserve where most avocets and stilts nest on islands within former salt evaporation ponds and in managed pickleweed *Salicornia pacifica* marshes.

Nest monitoring

We entered avocet and stilt nesting colonies weekly throughout the nesting season from April through August. We marked each newly initiated nest with a uniquely numbered aluminum tag placed at the nest and a 40-cm colored pin flag placed 2 m north of the nest. During the initial nest visit, we measured vegetation height (cm) at the nest site and visually characterized habitat within 1 m of the nest into the percentage of bare ground and vegetation (including dead vegetation). At each weekly nest visit, we floated eggs to determine embryo age (Ackerman and Eagles-Smith 2010), recorded clutch size, and determined nest fate. We estimated nest initiation date by subtracting the initial clutch size and the average embryo age on the day the nest was discovered from the date the nest was found.

Nest survival

We used logistic exposure models to estimate daily nest survival rates based on weekly nest visits (Shaffer 2004). This method uses general linear models with a binomial probability distribution, and a custom inverse link function that incorporates the multiple days between visits that each individual nest was exposed. A nest was considered to have survived an interval if the clutch was still completely or partially intact, embryo development had progressed, and there were no signs of nest abandonment (such as cold eggs). A nest was also considered successful if ≥ 1 egg successfully hatched. A nest was considered unsuccessful if it was destroyed or abandoned. Exposure days were calculated as the number of days between nest visits, except when a final nest fate occurred between visits (hatched, depredated, or abandoned). For hatched nests, we calculated exposure days for that interval based on the expected hatch date (Ackerman and Eagles-Smith 2010). For depredated nests, we calculated exposure days for that interval as the mid-point between nest visits. For abandoned nests, we calculated exposure days for that interval as the difference between the developmental age of the eggs when the nest was abandoned (estimated via egg flotation) and the developmental age of the eggs when the nest was last visited. We censored nests that were abandoned due to investigator disturbance.

Capture and radio-marking chicks

We used radio-telemetry to determine survival rates of chicks from hatching to fledging, and detailed methods are reported in Ackerman et al. (2008) where we used similar data to examine the effects of mercury contamination on chick survival. Based on nest monitoring data, we returned to nests at their estimated hatch date (Ackerman and Eagles-Smith 2010). We only radio-marked recently hatched chicks (≤ 2 d old) that were found in or near their nest bowl. We used only one chick per brood for survival rate estimation; if more than one chick was present during a nest visit, we randomly selected one chick for radio-marking. We weighed each chick with a spring scale ($\pm$ 1.0 g).

We radio-marked chicks with transmitters that had a lifespan range of 21–50 d, depending on the transmitter model. Transmitters weighed 1.1 g for avocets and 0.8 g for stilts, and were ≤ 19 mm long $\times \leq 8$ mm wide. In 2005, most chicks were radio-marked with transmitters that contained thermistor switches (model BD-2T, Holohil Systems, Carp, ON, Canada [50 avocets and 29 stilts]), but we also deployed transmitters without thermistor switches (Model A2410 modified, Advanced Telemetry Systems, Isanti, MN, USA [24 avocets and four stilts]). Radio transmitters

containing thermistor switches improved detection of chick mortality and therefore were used on all chicks in 2006 (model BD-2T; 87 avocets and 46 stilts). We attached a radio transmitter to each chick's back (skin) with sutures (Ethicon Vicryl FS-2, 3-0, Ethico, Piscataway, NJ, USA) threaded through front and rear channels on the transmitter, and knots were secured with cyanoacrylic glue (Loctite 422, Henkel, Rocky Hill, CT, USA). After radio-marking, we returned chicks to their nest within 23 ± 12 min of capture (mean $\pm$ standard deviation). Radio-marked chicks were never recaptured.

Chick radio-telemetry

We tracked radio-marked chicks daily to determine mortality and predator type. We determined locations of radio-marked chicks using trucks equipped with dual 4-element Yagi antenna systems (AVM Instrument, Colfax, CA, USA) with null-peak systems to determine bearings via triangulation. We used triangulation software (Location of a Signal, ver. 3.0.1, Ecological Software Solutions, Switzerland) to estimate coordinates for each location. Radio-marked chicks that went missing were searched for daily until they were found or until the transmitter lifespan had been exceeded. We used a hand-held Yagi antenna and receiver to locate the transmitter and chick within 24 h of suspected chick mortality. Because of the likelihood of chick predation by California gulls *Larus californicus*, we periodically entered the largest California gull colonies in South San Francisco Bay on foot, with hand-held Yagi antennas and receivers, to search for missing transmitters that were potentially brought there by gulls.

Space use of radio-marked chicks

We evaluated avocet and stilt chick movements and habitat utilization with radio-telemetry. We estimated home range size (95% kernel density estimates) and core use area (50% kernel density estimates) for each radio-marked avocet and stilt chick that survived ≥ 21 d after radio-marking using the Geospatial Modelling Environment ver. 0.7.2.0 (Beyer 2012) with a least squares cross validation smoothing parameter, and ArcMap ver. 10.0 (Environmental Research Systems Inst., Redlands, CA, USA). We further evaluated chick space use by comparing chicks that were radio-marked in Pond A16 and in New Chicago Marsh. These sites represented two distinct habitats (a former salt pond that was largely devoid of vegetation and a managed vegetated marsh) that were adjacent to each other. In particular, we determined the movement azimuth for each chick from its hatch site to the last location during the first week after hatch where it was known to be alive. We used Rayleigh's test (Zar 1999) to assess whether chick movements were randomly distributed around 360° for each nesting habitat site. When chick movements were found to be non-random, we used a one-sample *Z*-test with 95% confidence limits to test the hypothesis that chicks radio-marked in Pond A16 moved south (180°) towards the more vegetated New Chicago Marsh habitat. We also examined whether chicks tagged in New Chicago Marsh moved to the north (0°) toward Pond A16. Lastly, for each chick that survived until fledging, we calculated the proportion of their core use area that fell within New Chicago Marsh.

Survival analyses and fate of radio-marked chicks

We estimated daily survival rates of radio-marked chicks with known fate survival models and the RMark (ver. 2.1.4; Laake 2013) front-end to program Mark (White and Burnham 1999) within the R programming language (R Core Team; ver. 2.15.2). For each chick, we built a capture history based on daily radio-telemetry detections until their fledging age of 27 d. At each encounter, we considered a chick to be alive if its radio transmitter provided a normal signal and dead if the chick was found dead during telemetry surveys. We censored the few days when chicks were not tracked (7% of days due to heavy rains and holidays) or on days when we searched for individual chicks but did not find them (9% of total chick tracking days). We also right-censored chicks if the radio transmitter fell off (3% of chicks) or when chicks went missing after the first week. We assumed that a chick that went missing within the first week after hatch was depredated by an unknown predator and considered it dead on the first day it went missing. This assumption was based on the literature indicating that most waterbird chick mortality occurs within the first week after hatch (Langham 1972, Colwell et al. 2007). Also, this assumption was supported by our observations that many chicks that went missing during the first week after hatch were later found depredated and carried up to 11 km away, often to gull colonies, by aerial predators. In fact, 70% of the 53 radio-marked chicks that went missing disappeared within the first week after hatch. In a traditional known-fate survival analysis approach, all chicks that go missing are right-censored. However, because most chicks that went missing in the first week after hatch likely died, using a more traditional known-fate survival analysis would have biased chick survival estimates substantially high. For comparison, we also present fledging success estimates based on the more traditional approach of right-censoring all chicks that went missing to provide an upper limit for survival estimates.

We considered a chick's fate to be either fledged, presumed fledged, depredated by a predator, died from exposure, or unknown (chick went missing). We considered chicks to have fledged if they were alive 25 d after radio-marking, because we radio-marked chicks between 0 and two days of age and avocet and stilt chicks fledge at approximately 27 d of age (Robinson et al. 1999, Ackerman et al. 2013). We presumed that chicks had fledged ('presumed fledged') if they were alive ≥ 21 d after radio-marking, because 21 d was the minimum lifespan of the radio transmitters and some transmitters may have failed after 21, but before 25, days of age. We considered chicks to have been depredated if we recovered the radio transmitter and chick remains, and predators were grouped into categories (California gulls, wading birds [herons and egrets], raptors, mammals, snakes, or unknown predators) by using signs of predation near the recovered transmitter (such as tooth marks, scat, or regurgitated pellets), location of the recovered transmitter (such as within a California gull colony, wading bird roost, or animal burrow), and direct observation. We classified chicks as dying from exposure when they were recovered dead but had no visible

signs of trauma. These chicks may have died from starvation, disease, contaminants, weather, or other causes. For those chicks that went missing before they could have fledged, we considered chicks depredated by an unknown predator if the chick went missing within the first week after hatch, and we considered chicks to have an unknown fate (censored) if they went missing after the first week.

Statistical analyses

We examined factors influencing vegetation height and vegetation presence at the nest site (yes or no) by building a set of candidate models that included species, year, site, and nest initiation date. We used standard linear models (ANCOVA) for examining vegetation height and general linear models with a binomial distribution for assessing vegetation presence or absence at the nest site. We standardized nest initiation date by subtracting the individual nest's initiation date from the median initiation date for each year (species were grouped). For each candidate model set (a total of 16 models each), we examined all additive combinations of these variables and a null (intercept only) model.

Next, we examined factors influencing nest survival rates by building a set of candidate models which included species, year, site, nest initiation date, nest age, and the interactions of site × nest initiation date and species × nest initiation date. Nest initiation date was standardized as described above. We included all additive combinations of these variables, and a null (intercept only) model in our candidate model set (a total of 52 models).

To examine factors influencing chick survival rates, we built a set of candidate models which included species, year, site, hatch date, chick age, chick age^2, chick mass at the time of radio-marking, and the interactions species × date, species × age, and species × age^2. Chick mass was standardized by subtracting the individual chick's mass from the mean mass and dividing that quantity by the standard deviation for that species (years were grouped). Hatch date was standardized by subtracting an individual chick's hatch date from the median hatch date for each year (species were grouped). We examined all additive combinations of these variables with up to two interactions, and a null (intercept only) model in our candidate model set (a total of 208 models).

We evaluated model sets using Akaike information criterion (AIC*c*; Burnham and Anderson 2002). We considered the model with the smallest AIC*c* to be the most parsimonious and ranked models using AIC*c* differences between the best model and the other candidate models ($\Delta AICc_i$). We used Akaike weights (w_i) to assess the weight of evidence that the selected model was the best model within the candidate model set, and we assessed the relative importance of each particular variable by summing w_i across models that incorporated that particular variable. We used evidence ratios to compare the relative weight of support between models. All results represent model-averaged predictions from the full candidate model set, but we restricted the presentation of model selection results to the set of top models that contributed 90% of all model weight.

We estimated model-averaged daily nest and chick survival rates for each species, site, and year. For nest survival rates, we used the mean nest initiation date for each species, year, and site because date had an important effect on nest survival. Nest success was defined as the probability of a nest surviving to 27 d (laying and incubation periods) and estimated as the cumulative 27-d product of daily survival rates. Similarly, chick fledging success was defined as the probability of a chick surviving to 27 d of age after hatch and estimated as the cumulative 27-d product of daily survival rates. Overall nest and chick survival estimates (by species and by year) were estimated by weighting the site-specific nest survival rates by the number of nests at each site and the site-specific chick survival rates by the number of radio-marked chicks at each site. We used the delta method (Seber 1982) to estimate standard errors and 95% confidence limits for species, site, and year specific estimates of nest and fledging success.

We estimated the number of avocet and stilt eggs hatched each year as the product of the annual number of nests, mean clutch size, mean nest survival, and mean hatching success. This value was then multiplied by mean chick survival to estimate the total number of chicks fledged. Nest survival and chick survival were estimated as described above. For clutch size estimation, we used only those nests found during egg laying that survived until egg laying was complete; nests found after egg laying was completed were excluded to reduce the potential that partial clutch depredation influenced apparent clutch sizes (Ackerman et al. 2003). Hatching success was defined as the proportion of eggs that hatched within a nest that was successful (where ≥ 1 egg hatched). We included only those successful nests with known clutch sizes and final fates for each individual egg in estimates of egg hatching success.

Results

Nesting biology

We monitored 1274 nests, including 816 avocet nests (2005: n = 337; 2006: n = 479) and 458 stilt nests (2005: n = 123; 2006: n = 335). The nesting period (defined as the central span of days when 80 percent of nests were initiated) was longer for avocets (59 d: 18 April–16 June) than for stilts (48 d: 20 April–6 June), even though the range was similar (avocets: 87 d: 9 April–4 July; stilts: 93 d: 7 April–8 July). Mean nest initiation date (± standard deviation) was slightly earlier for stilts (9 May ± 18 d; n = 458) than avocets (18 May ± 21 d; n = 816). Mean clutch size (± standard deviation) was 3.84 ± 0.47 eggs for avocets (n = 173) and 3.77 ± 0.53 eggs for stilts (n = 62). Four-egg clutches were the most common (avocets: 83%, stilts: 82%), followed by three-egg (avocets: 13%, stilts: 13%), two-egg (avocets: 1%, stilts: 5%), five-egg (avocets: 2%, stilts: 0%), and one-egg (avocets: < 1%, stilts: 0%) clutches. Egg hatching success (mean ± standard deviation) in successful nests was 0.90 ± 0.17 for avocets (n = 246) and 0.92 ± 0.17 for stilts (n = 156). Total chick production was 1248 avocet and 561 stilt chicks, or 1.53 avocet and 1.22 stilt chicks per nesting attempt. Total number of fledged chicks was 72 avocets and 239 stilts, or 0.09 avocet and 0.52 stilt chicks fledged per nesting attempt. Therefore, even though there were 1.8 times more avocet nests than stilt nests, stilts still fledged 3.3 times more chicks.

Nest site vegetation

Model selection confirmed that species differed in their selection for the presence and height of vegetation at their nest sites. The best model describing the presence or absence of vegetation within 1 m of the nest site included species, year, nest initiation date, and site, and had an Akaike weight of 1.00 (Table 1a). The best model which included species was 614 times more likely than the same model but without the species effect. For vegetation height, the best model included species, nest initiation date, and site, and had an Akaike weight of 0.64 (Table 1b). Models containing the species variable had a cumulative Akaike weight of 1.00. The best model which included species was 3.18×10^{23} times more likely than the same model but without the species effect. Stilts nested within vegetation 2.7 (95% CI: 1.7–4.5)

Table 1. Ranking of candidate model sets describing (a) presence or absence of vegetation within 1 m of the nest site, (b) vegetation height at nest sites, (c) nest survival, and (d) chick survival for American avocets (n = 816 nests and 161 chicks) and black-necked stilts (n = 458 nests and 79 chicks) in San Francisco Bay, California during 2005 and 2006. Only the top models that represented 0.90 of total model weight are presented, along with the null model.

Model[a]	k[b]	–2logL	AICc[c]	ΔAICc[d]	Akaike weight (w_i)[e]	Evidence ratio[f]	Cumulative weight
(a) Nest site vegetation presence or absence							
Year + Species + Date + Site	11	652.25	674.49	0.00	1.00	1.00	1.00
Intercept Only (null)	2	1568.80	1572.81	898.33	0.00	1.17×10^{195}	1.00
(b) Nest site vegetation height							
Species + Date + Site	10	7935.21	7955.40	0.00	0.64	1.00	0.64
Year + Species + Date + Site	11	7934.29	7956.52	1.12	0.36	1.75	1.00
Intercept Only (null)	2	8689.36	8693.37	737.96	0.00	1.77×10^{160}	1.00
(c) Nest survival							
Year + Site + Species + Date + Age + Site × Date	18	3077.62	3113.67	0.00	0.28	1.00	0.28
Year + Site + Date + Age + Site × Date	17	3079.89	3113.93	0.26	0.25	1.14	0.53
Year + Site + Species + Date + Site × Date	17	3080.69	3114.74	1.07	0.17	1.71	0.70
Year + Site + Date + Site × Date	16	3083.22	3115.26	1.59	0.13	2.22	0.82
Year + Site + Species + Date + Age + Species× Date + Site × Date	19	3077.61	3115.67	2.00	0.10	2.72	0.93
Intercept Only (null)	2	3321.62	3325.62	211.96	0.00	1.06×10^{46}	1.00
(d) Chick survival							
Year + Site + Species + Mass + Age	10	852.84	872.98	0.00	0.17	1.00	0.17
Year + Site + Species + Mass + Age + Age²	11	851.24	873.41	0.43	0.14	1.24	0.31
Year + Site + Date + Species + Mass + Age	11	852.45	874.63	1.64	0.08	2.27	0.39
Year + Site + Species + Mass + Age + Species × Age	11	852.81	874.99	2.01	0.06	2.73	0.45
Year + Site + Date + Species + Mass + Age + Age²	12	850.88	875.08	2.10	0.06	2.86	0.51
Year + Site + Species + Mass + Age + Age² + Species × Age²	12	851.02	875.23	2.25	0.06	3.08	0.57
Year + Site + Species + Mass + Age + Age² + Species × Age	12	851.23	875.43	2.45	0.05	3.41	0.62
Year + Site + Date + Species + Mass + Age + Species × Date	12	852.05	876.26	3.27	0.03	5.13	0.66
Year + Site + Species + Age	9	858.16	876.28	3.30	0.03	5.20	0.69
Year + Site + Species + Age + Age²	10	856.41	876.56	3.58	0.03	5.98	0.72
Year + Site + Species + Mass + Age + Age² + Species × Age² + Species × Age	13	850.38	876.62	3.64	0.03	6.16	0.75
Year + Site + Date + Species + Mass + Age + Species × Age	12	852.44	876.65	3.66	0.03	6.24	0.77
Year + Site + Date + Species + Mass + Age + Age² + Species × Date	13	850.48	876.73	3.74	0.03	6.50	0.80
Year + Site + Date + Species + Mass + Age + Age² + Species × Age²	13	850.69	876.93	3.95	0.02	7.21	0.82
Year + Site + Date + Species + Mass + Age + Age² + Species × Age	13	850.87	877.11	4.13	0.02	7.89	0.85
Year + Site + Date + Species + Age	10	857.75	877.90	4.91	0.01	11.67	0.86
Year + Site + Date + Species + Age + Age²	11	856.03	878.20	5.22	0.01	13.61	0.87
Year + Site + Species + Age + Species × Age	10	858.13	878.27	5.29	0.01	14.09	0.89
Year + Site + Date + Species + Mass + Age + Species × Date + Species × Age	13	852.05	878.29	5.31	0.01	14.19	0.90
Intercept Only (null)	1	1107.06	1109.06	236.08	0.00	1.84×10^{51}	1.00

[a]The + denotes an additive effect and the × denotes an interaction.
[b]The number of parameters in the model, including the intercept.
[c]Akaike's information criterion (AICc).
[d]The difference in the value between AICc 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.

times more often than avocets, with 90% (n = 403) of stilt nests having vegetation within 1 m of their nest compared with only 35% (n = 735) of avocet nests. When vegetation was present at a nest, vegetation height (mean ± standard deviation) was 18.2 ± 8.4 cm (n = 334) for stilts and 11.0 ± 8.9 cm (n = 231) for avocets.

Nest survival

The most parsimonious model describing nest survival rates included species, site, year, nest initiation date, nest age, and site × nest initiation date, and had an Akaike weight of 0.28 (Table 1c). Four other models were within $\Delta AIC_c \leq 2.0$, and all included the variables site, year, nest initiation date, and site × nest initiation date. In fact, all the models containing these variables had a cumulative Akaike weight of 0.99. Importantly, the second best model, which was similar to the top model except it excluded the species effect, had a Akaike weight (0.25) similar to the top model which included species. We estimated the relative importance of individual variables and found that the data strongly supported the effects of site (relative variable importance = 1.00), nest initiation date (1.00), and year (0.99), with some support for nest age (0.64) and species (0.62). To further determine the importance of variables in the best model, we compared the best model to the same model structure but omitted one of the variables. Using this evidence ratio approach, we estimated that the best model which included site was 4.52×10^{29} times more likely than the same model without site effects. Similarly, the best model was 1.21×10^{28} times more likely than the same model without nest initiation date effects, 63 times more likely than the same model without year, 1.7 times more likely than the same model without nest age, and only 1.1 times more likely than the same model without species. Therefore, species appeared to play a relatively small role in influencing nest survival rates compared to the other variables. The null model was not supported ($\Delta AIC_c = 211.96$; $w_i = 0.00$).

Nest survival (mean ± standard error) was slightly higher for avocets (0.44 ± 0.20; n = 816) than stilts (0.35 ± 0.10; n = 458; Table 2). Nest survival was highly variable among sites and years. For each species, nest survival was higher in 2005 (avocet: 0.59 ± 0.19, stilt: 0.45 ± 0.06) than in 2006 (avocet: 0.34 ± 0.16, stilt: 0.32 ± 0.10). Nest survival ranged from 11–75% among avocet and 7–67% among stilt nesting sites. Daily nest survival rates increased by < 1% over the life of a nest, from 0.961 (95% confidence limits: 0.944–0.978) when the first egg was laid to 0.968 (0.954–0.982) at the end of the incubation period (i.e. nest age of 27 d; Fig. 1a). In contrast, daily nest survival decreased with nest initiation date at all sites. Cumulative nest survival rates (mean ± standard error) ranged from 0.37 ± 0.27 for the earliest (9 April) to 0.02 ± 0.17 for the latest nesting avocet (4 July) and from 0.57 ± 0.18 for the earliest (7 April) to 0.01 ± 0.10 for the latest nesting stilt (8 July). The decline in nest survival with nest initiation date is displayed for New Chicago Marsh (Fig. 2), where we had the largest sample sizes of nests for both species.

Predators of chicks

We radio-marked and tracked 240 chicks, including 161 avocets (74 in 2005 and 87 in 2006) and 79 stilts (33 in 2005 and 46 in 2006; Table 3). A total of six radio transmitters dropped off chicks, and 16 chicks went missing between

Table 2. American avocet and black-necked stilt nesting locations, nests initiated, chicks radio-marked, nest survival rates (± standard error), and chick survival rates (± standard error) in San Francisco Bay, California, during 2005 and 2006. The asterisks indicate the minimum number of nests known to be at a site. Some sub-sites where chicks were radio-marked were not also monitored for nests.

	Number of nests		Number of chicks radio-marked		Nest survival		Chick survival	
Site	Avocet	Stilt	Avocet	Stilt	Avocet	Stilt	Avocet	Stilt
New Chicago Marsh								
2005	24	89	4	30	0.37 (0.06)	0.43 (0.05)	0.02 (0.02)	0.20 (0.07)
2006	80	275	23	45	0.23 (0.05)	0.30 (0.04)	0.19 (0.07)	0.54 (0.07)
Pond A16								
2005	142	3	51	1	0.75 (0.05)	0.67 (0.06)	0.05 (0.03)	0.31 (na)
2006	16	6	1	0	0.41 (0.09)	0.44 (0.11)	0.30 (na)	na
Pond A8								
2005	147	0	17	0	0.49 (0.05)	na	0.00 (0.00)	na
2006	166	1	36	1	0.30 (0.04)	0.07 (na)	0.03 (0.02)	0.25 (na)
Coyote Creek Marsh								
2005	–	–	1	2	–	–	0.20 (na)	0.55 (0.25)
2006	32	5	2	0	0.11 (0.05)	0.15 (0.07)	0.54 (0.25)	na
Moffett Ponds								
2005	4*	0	1	0	0.42 (0.21)	na	0.00 (na)	na
2006	43	0	4	0	0.28 (0.08)	na	0.01 (0.03)	na
Newark Ponds								
2005	–	–	0	0	na	na	na	na
2006	78*	31*	21	0	0.63 (0.07)	0.46 (0.08)	0.02 (0.02)	na
Eden Landing Ponds								
2005	20	31	0	0	0.40 (0.08)	0.48 (0.07)	na	na
2006	64	17	0	0	0.33 (0.06)	0.36 (0.07)	na	na
Total	816	458	161	79	0.44 (0.20)	0.35 (0.10)	0.06 (0.09)	0.40 (0.22)
2005 total	337	123	74	33	0.59 (0.19)	0.45 (0.06)	0.04 (0.04)	0.22 (0.21)
2006 total	479	335	87	46	0.34 (0.16)	0.32 (0.10)	0.08 (0.12)	0.53 (0.20)

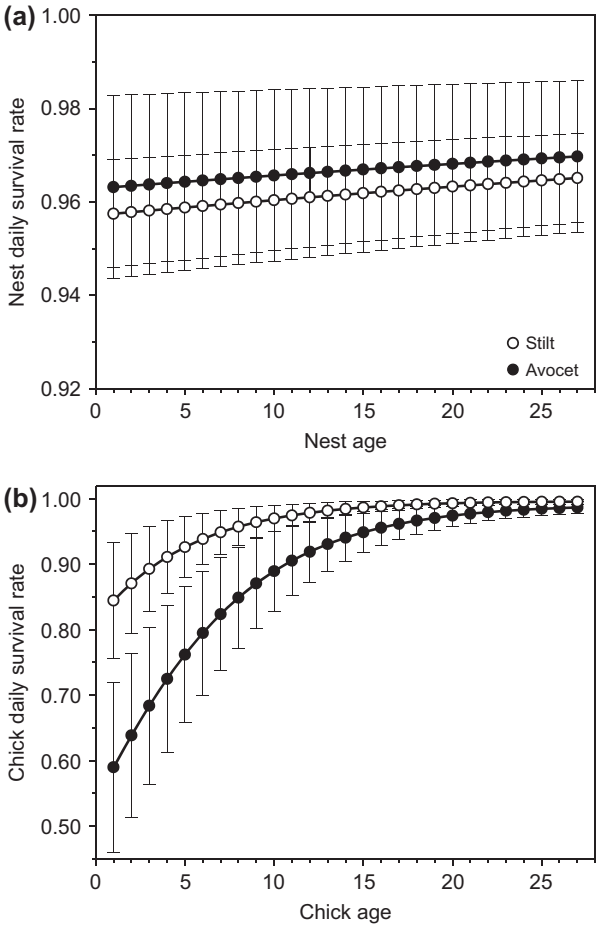

Figure 1. Daily survival rate of (a) nests from egg laying (nest age = 0 d) to hatching (nest age = 27 d) and (b) chicks from hatching (chick age = 0 d) to fledging (chick age = 27 d) for American avocets (n = 816 nests and 161 chicks; solid symbols) and black-necked stilts (n = 458 nests and 79 chicks; open symbols) in San Francisco Bay, California during 2005 and 2006. Error bars represent lower and upper 95% confidence limits.

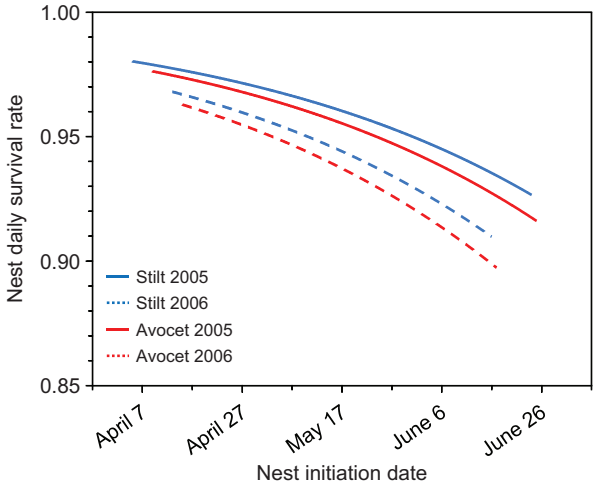

Figure 2. Daily survival rate of American avocet (red) and black-necked stilt (blue) nests declined with nest initiation date in New Chicago Marsh, San Francisco Bay, California during 2005 (solid line) and 2006 (stippled line). The lines extend to the specific range of nest initiation dates for each species and year at this site.

eight and 18 d of age which precluded the determination of fate. Thus, fate was determined for 218 chicks (Table 3), but all 240 chicks were used in survival analyses.

Overall, 93% of radio-marked avocet chicks died (n = 142) and only 7% fledged or were presumed to have fledged (n = 11; Table 3). In contrast, 60% of radio-marked stilt chicks died (n = 39) and 40% fledged or were presumed to have fledged (n = 26; Table 3). Of the 142 and 39 radio-marked avocet and stilt chicks known to have died, 41% and 8% were depredated by California gulls, 4% and 3% were depredated by wading birds (herons and egrets), 5% and 3% were depredated by raptors, 6% and 5% were depredated by unknown avian predators, 8% and 10% were depredated by mammals, 1% and 0% were depredated by snakes, 22% and 26% were depredated by unidentified predators, 8% and 33% died from exposure, and the cause of death could not be determined for 6% and 13%, respectively.

Considering only those depredated chicks where predator type could be identified (n = 83 avocet, n = 9 stilt), 70% of avocet and 33% of stilt chicks were depredated by California gulls (Table 3). In particular, we found 56 avocet (two of the 58 avocet chicks that were depredated by gulls were not found at a gull colony) and three stilt transmitters within California gull colonies (Fig. 3). All 10 of the depredated chicks found at the California gull colony in Newark (Coyote Hills) had been radio-marked at nesting sites 0.7–4.0 km away within the Newark Pond Complex. The 49 depredated chicks found at the California gull colony in Alviso (Pond A6) had been radio-marked at nesting sites 2.1–10.8 km away in both the Alviso Pond Complex (n = 48) and Newark Pond Complex (n = 1). California gulls appeared to depredate avocet chicks in proportion to the number marked within salt pond (38%, n = 125) and marsh (36%, n = 28) habitats.

Chick survival

Unlike nest survival, chick survival was strongly influenced by species. The most parsimonious model describing chick survival rates included species, site, year, initial mass, and age, and had an Akaike weight of 0.17 (Table 1). All models containing these variables had a cumulative Akaike weight of 0.83. Three other models containing these same variables plus either age^2, hatch date, or species × age were within $\Delta AIC_c \leq 2.0$. Using evidence ratios, the best model was 1.2 times more likely than the next model which included age^2, 2.3 times more likely than the third model which included hatch date, and 2.7 times more likely than the fourth model which included species × age. The addition of hatch date and species × age to the best model did not improve model fit as indicated by little improvement in the model's log-likelihoods. The null model had no support ($\Delta AIC_c = 236.08$; $w_i = 0.00$).

We estimated the relative importance of individual variables and found that the data strongly supported the effects of species (relative variable importance = 1.00), chick age (1.00), site (0.99), year (0.99), and initial mass (0.83), moderately supported age^2 (0.54), and did not support the effects of hatch date (0.38) or species × age (0.27). To further determine the importance of variables in

Table 3. Fate of American avocet and black-necked stilt chicks radio-marked at hatch in San Francisco Bay, California, during 2005 and 2006.

Year/species/pond	Chicks radio-marked	Censored, radio dropped	Censored, missing	Chicks radio-marked, excluding dropped radios and missing chicks	Chicks fledged[a]	Chicks presumed fledged[b]	Depredated by							Died from exposure[i]	Cause of death unknown[j]
							California gull[c]	Heron/ egret[d]	Raptor[e]	Unknown bird	Mammal[f]	Snake[g]	Unknown predator[h]		
2005															
American avocet	74	4	3	67	5	0	14	4	3	5	7	2	18	6	3
Pond A16	51	1	0	50	5	0	10	4	1	4	7	2	12	3	2
Pond A8	17	3	2	12	0	0	4	0	1	0	0	0	4	3	0
Coyote Creek Lagoon	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Moffett Ponds	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0
New Chicago Marsh	4	0	0	4	0	0	0	0	1	1	0	0	1	0	1
Black-necked stilt	33	2	9	22	2	1	0	1	1	1	4	0	4	5	3
Pond A16	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Coyote Creek Lagoon	2	0	1	1	0	0	0	0	0	0	0	0	0	0	1
New Chicago Marsh	30	2	8	20	1	1	0	1	1	1	4	0	4	5	2
2005 total	107	6	12	89	7	1	14	5	4	6	11	2	22	11	6
2006															
American avocet	87	0	1	86	6	0	44	1	4	3	4	0	13	5	6
Pond A16	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Pond A8	36	0	0	36	0	0	22	0	4	3	0	0	4	1	2
Coyote Creek Lagoon	2	0	0	2	1	0	1	0	0	0	0	0	0	0	0
Moffett Ponds	4	0	0	4	0	0	0	1	0	0	0	0	3	0	0
New Chicago Marsh	23	0	1	22	4	0	9	0	0	0	2	0	4	0	3
Newark Ponds	21	0	0	21	1	0	11	0	0	0	2	0	2	4	1
Black-necked stilt	46	0	3	43	12	11	3	0	0	1	0	0	6	8	2
Pond A8	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
New Chicago Marsh	45	0	3	42	11	11	3	0	0	1	0	0	6	8	2
2006 total	133	0	4	129	18	11	47	1	4	4	4	0	19	13	8
American avocet total	161	4	4	153	11	0	58	5	7	8	11	2	31	11	9
Black-necked stilt total	79	2	12	65	14	12	3	1	1	2	4	0	10	13	5
Overall total	240	6	16	218	25	12	61	6	8	10	15	2	41	24	14

[a]Chicks were considered to have fledged if they were known to be alive at least 25 d after hatching.
[b]Chicks were presumed to have fledged if they were known to be alive at least 21 d after hatching and final fate was not observed.
[c]California gulls were identified as the predator when transmitters were recovered in a gull colony or were recovered near regurgitated pellets in an area used by gulls.
[d]Herons or egrets were identified as the predator when transmitters were found in association with heron and egret feathers and regurgitations, and in areas frequently used by herons and egrets.
[e]Raptors were identified as the predator when transmitters that were attached to chicks were recovered within or below raptor roosts, nests or burrows.
[f]Mammals were identified as the predator when transmitters that were attached to chicks were recovered in mammal scat, had tooth marks, or were inside small mammal burrows.
[g]Snakes were identified as the predator when radio signals of transmitters that were attached to chicks emitted from a visible snake or snake burrow.
[h]Chicks that went missing at age ≤ 7 d were considered to have been killed by an unknown predator as were some chicks where the radio was recovered but predator could not be determined.
[i]Chicks were classified as dead from exposure when they were recovered dead and no visible signs of trauma were evident on the recovered corpse. These chicks may have died from starvation, disease, contaminants, weather, or other causes.
[j]Cause of death unknown was assigned to a chick when it could not be determined if it died from predation or another cause.

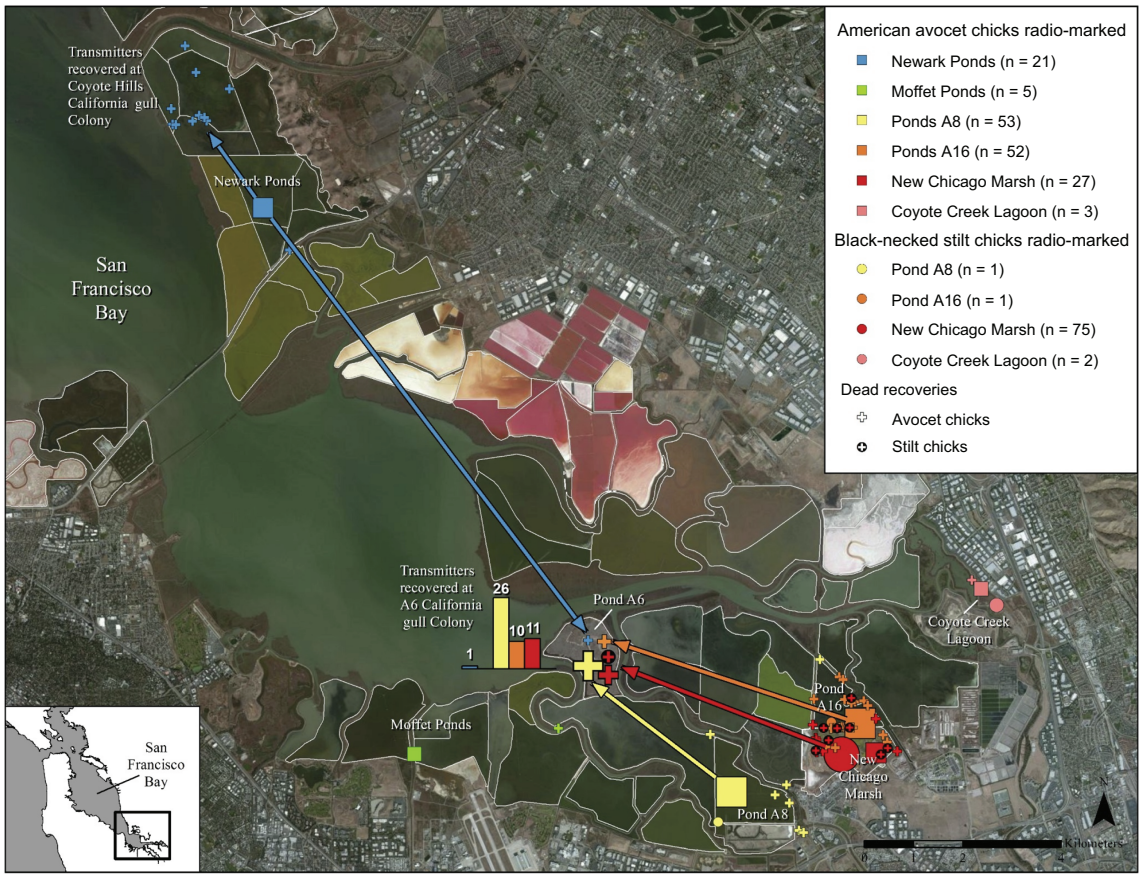

Figure 3. American avocet and black-necked stilt chicks were radio-marked at their nest site (avocets: squares, stilts: circles) and depredated chicks were recovered (avocets: crosses, stilts: crosses within black circles) in South San Francisco Bay, California in 2005 and 2006. Each cross represents one chick, except crosses in the A6 California gull colony indicate the number of chicks recovered by their relative sample size and are displayed in the histogram (histogram colors indicate nest site where they were radio-marked). Colors of the crosses reflect the location where recovered chicks were initially radio-marked. The relative size of circles and squares indicate the number of avocet and stilt chicks radio-marked at each site.

the best model, we compared it to the same model structure but omitted one of the variables. Using this evidence ratio approach, we estimated that the best model which included chick age was 2.49×10^{21} times more likely than the same model without chick age. Similarly, the best model was 1146 times more likely than the same model without site, 531 times more likely than the same model without year, 427 times more likely than the same model without species, and five times more likely than the same model without initial mass.

Survival (mean ± standard error) from hatch to fledging at 27 d of age was much lower for avocet (0.06 ± 0.09; n = 161) than for stilt chicks (0.40 ± 0.22; n = 79) (Table 2). For comparison, we conducted the survival analysis after right-censoring all chicks that went missing to provide the potential upper limit for survival rates, and estimated chick survival to fledging to be 0.09 ± 0.09 for avocets and 0.49 ± 0.18 for stilts. For each species, fledging success was higher in 2006 (avocet: 0.08 ± 0.12, stilt: 0.53 ± 0.20) than in 2005 (avocet: 0.04 ± 0.04, stilt: 0.22 ± 0.21). Among nesting sites, fledging success ranged from 0–54% for avocets and 20–55% for stilts. Avocet chick daily survival rate increased by 67% during the fledgling period from 0.589 (95% confidence limits: 0.459–0.720) at one day of age to 0.986 (0.977–0.995) at 27 d of age (Fig. 1b). Stilt chick daily survival rate increased by 18% during the fledgling period from 0.844 (0.755–0.933) at one day of age to 0.995 (0.991–0.998) at 27 d of age (Fig. 1b). The mean (± standard error) age of chicks when they were depredated was 2.9 ± 0.4 d for avocets (n = 94) and 5.7 ± 1.7 d for stilts (n = 12). The mean age of chicks depredated by California gulls was 2.1 ± 0.3 d for avocets (n = 58; range 1–14 d) and 6.5 ± 3.5 d for stilts (n = 3; range 3–14 d). Fledging success (mean ± standard error) increased with initial chick mass from 0.06 ± 0.03 for the smallest to 0.26 ± 0.22 for the largest avocet chicks and from 0.14 ± 0.08 for the smallest to 0.51 ± 0.27 for the largest stilt chicks.

Space use and home range size of chicks

Overall, 11 avocet and 26 stilt chicks survived from hatch to ≥ 21 d of age where we could assess space use during the full pre-fledging period. Chick home range size was greater for avocet chicks (mean ± standard error: 73.1 ± 13.4 ha) than for stilt chicks (47.5 ± 5.0 ha). Chick core use areas were also greater for avocet chicks (17.0 ± 3.8 ha) than for stilt

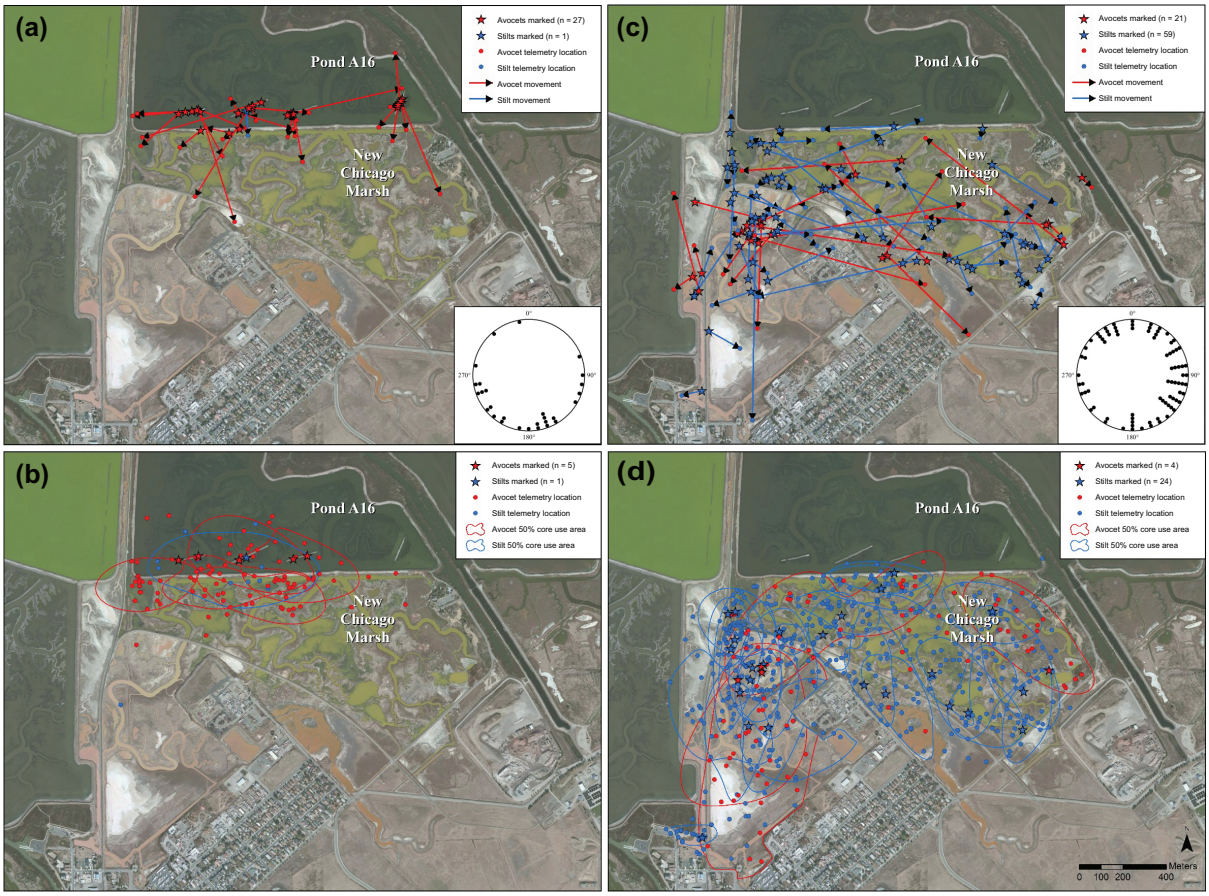

Figure 4. American avocet (red) and black-necked stilt (blue) chicks radio-marked at nesting sites (stars) in former salt Pond A16 moved south into the more vegetated New Chicago Marsh during the first week after hatch (a), and spent the majority of their time in New Chicago Marsh until they fledged (b). The majority of chicks radio-marked in New Chicago Marsh remained in the marsh during the first week after hatch (c), and spent the majority of their time in the same marsh until they fledged (d). Red polygons denote avocet chick core use areas (50% utilization distributions) and blue polygons denote stilt chick core use areas. Circles denote all telemetry locations of avocet chicks (red) and stilt chicks (blue) in (b) and (d), and the last known telemetry location of a live chick within the first week after hatching in (a) and (c). Movement directions (azimuth) from hatching to the last known telemetry location of a live chick within the first week after hatching are displayed in the bottom right hand corner of (a) and (c); each dot represents an individual chick.

chicks (10.4 ± 1.2 ha). Of the 37 chicks that fledged or were presumed to have fledged, 34 (9 avocet, 25 stilt) were radio-marked in Pond A16 and New Chicago Marsh and these were the only sites where individuals of both species survived to near fledging. Thus, we focused our evaluation of chick movements and space use to these sites (Fig. 4).

Most avocet chicks that hatched in Pond A16 moved to adjacent habitat in New Chicago Marsh within a few days of hatch (Fig. 4a). Of 52 avocet chicks radio-marked in Pond A16, 46% died and one chick's transmitter fell off before the first recorded movement. For the remaining 27 avocet chicks, azimuths during the first week after hatch were non-randomly ($Z = 5.9$, $n = 27$, $p < 0.001$) distributed in a southward direction towards New Chicago Marsh (mean ± 95% CI: 197° ± 48°). Overall, 59% of these 27 avocet chicks radio-marked in Pond A16 moved into New Chicago Marsh by the end of their first week. The stilt chick also moved south (177°) into New Chicago Marsh during the first week after hatch. Chicks radio-marked in Pond A16 that survived to fledging (five avocet, one stilt) used the New Chicago Marsh habitat (mean ± standard error: 56 ± 12%, 36% of the core use area) more so than, or nearly as often as, the Pond A16 habitat where they had hatched (Fig. 4b).

In contrast, avocet and stilt chicks radio-marked in New Chicago Marsh largely remained there throughout the pre-fledging period (Fig. 4c, d). Of 102 chicks (27 avocet, 75 stilt) radio-marked there, 22% died before the first recorded movement. For the remaining 80 chicks (21 avocet, 59 stilt), movement azimuths were distributed randomly for avocets ($Z = 0.2$, $n = 21$, $p = 0.58$) and non-randomly for stilts ($Z = 4.9$, $n = 59$, $p < 0.001$). However, stilts did not move northward toward Pond A16 but rather eastward (mean ± 95% CI: 88° ± 59°). Their eastward movement likely was due to the fact that many stilts were radio-marked near the western boundary of the marsh. Of 80 chicks radio-marked in New Chicago Marsh, 95% remained in the marsh and only 5% moved into adjacent salt pond habitats within the first week after hatch (two chicks moved into Pond A16 and two chicks moved into Pond A12; Fig. 4c). Of those that survived to fledging (four avocet, 24 stilt), New Chicago Marsh accounted for 97 ± 2% (mean ± standard error; avocets) and 95 ± 3% (stilts) of the core use area (Fig. 4d).

Literature review

To compare our results indicating no species differences in nest survival or egg hatching success rates where avocets and stilts breed sympatrically, we examined peer-reviewed journal articles, dissertations, and unpublished reports (Table 4). We found six studies which had simultaneously investigated nest survival in avocets and stilts at the same breeding site; however, we found no publications which simultaneously investigated chick survival in both species. In total, there were 22 270 avocet and 15 926 stilt nests monitored in these studies. Mean (± standard deviation) nest survival among site and years was similar for avocets (0.48 ± 0.29) and stilts (0.47 ± 0.26). Likewise, egg hatching success among site and years was similar for avocets (0.93 ± 0.06) and stilts (0.94 ± 0.05). Individual site and year comparisons showed some variation between species, but only 27% ($n = 51$) of these site-year combinations differed by $> 15\%$ for nest survival and 24% ($n = 34$) differed by $> 5\%$ for egg hatching success. In these cases, eight site-year combinations yielded higher nest survival rates for avocets, and the other six site-year combinations yielded higher nest survival rates for stilts. For egg hatching success, four site-year combinations yielded higher success for each of avocets and stilts. Therefore, we found little evidence for a general pattern of species differences in nest survival or egg hatching success for sympatrically breeding avocets and stilts.

Discussion

Although there were nearly twice as many avocet nests as stilt nests in South San Francisco Bay, stilts nonetheless fledged more than three times more chicks. This outcome was caused by the large difference in chick survival between species (avocet: 6%; stilt: 40%), because clutch size (avocet: 3.84; stilt: 3.77), nest survival (avocet: 44%; stilt: 35%), and egg hatching success (avocet: 90%; stilt: 92%) were similar. Although no other studies have simultaneously investigated avocet and stilt chick survival, our literature review confirmed that nest survival and egg hatching success are generally similar when avocets and stilts breed sympatrically. Therefore, chick survival may be a critical period where population trajectories of these two closely-related species diverge.

Chick survival from hatch to fledging was strongly influenced by age, site, and year, in addition to the species effect. In particular, daily survival rates of chicks increased rapidly with chick age, with 70% of all identified chick mortalities occurring within the first week after hatch. Chick daily survival rates increased with age by 67% and 18% over the fledgling period for avocets and stilts, respectively. This result is consistent with survival studies of juvenile precocial birds which generally find that most chick mortality occurs within the first week after hatch (Langham 1972, Loegering and Fraser 1995, Colwell et al. 2007). Daily survival rates also increased with initial chick mass, as is often found in juvenile birds (Pelayo et al. 2003, Flint et al. 2006, Krist 2011), although this variable was less important in predicting chick survival rates than species, site, year, and age.

Some variables influencing nest survival were similar to those that influenced chick survival, particularly site and year. Yet, higher nest survival was not an indication of relatively higher chick survival at the same site. For example, avocets nesting in Pond A16 in 2005 ($n = 142$ nests) had extremely high nest survival (75%), but avocet chick survival at this same site and year was only 5% ($n = 51$ radio-marked chicks). These results indicate that sites, and perhaps management strategies, that provide good nesting habitat for shorebirds don't necessarily provide good chick rearing habitat, and vice versa. Whereas chick age strongly influenced chick survival rates, nest age had little influence on nest survival rates. Instead, nest initiation date was an important predictor of nest survival rates, and nest survival declined with nest initiation date at all sites for both avocets and stilts as is generally found for birds (Flint and Grand 1996, Sandercock 1998, Hartman and Oring 2009).

California gulls were the predominant predator of avocet chicks, but not of stilt chicks. Overall, 41% of avocet and 8% of stilt chicks were depredated by California gulls. Additionally, another 20% of avocet and 23% of stilt chicks went missing during the first week after hatching and may have been depredated by aerial predators, such as California gulls, that often removed the chick and associated transmitter from the nesting colony making them difficult to find. For example, we found 56 avocet and three stilt radio-transmitters within California gull colonies up to 11 km away that were carried there by gulls and regurgitated within pellets. Using only those depredated chicks where the predator was identified, 70% of avocet and 33% of stilt chicks were depredated by California gulls. If we assume that a similar proportion of the avocet and stilt chicks that went missing in the first week after hatch were depredated by California gulls, then 55% of avocet and 15% of stilt chick deaths were caused by gulls. These estimates are likely a more accurate assessment of the impact of California gulls on avocet and stilt chicks.

Differences in vulnerability to predators, and ultimately chick survival rates, between avocets and stilts were likely an outcome of their differential use of habitats, particularly during the first week after hatch. Avocet chicks had extremely low daily survival rates compared to stilt chicks during the first week after hatch (e.g. 43% lower survival at one day of age), but their daily survival rates were similar after two weeks of age (e.g. only 1% lower survival at fledging age). Stilts nested within vegetation nearly three times more often than avocets, and vegetation height was 65% taller at stilt nests than at avocet nests when vegetation was present. During the first 24 h after hatch, shorebird chicks remained in or near the nest site and were highly vulnerable to predators. As such, greater vegetation cover at stilt nest sites may have helped to conceal newly hatched chicks from potential predators, especially aerial predators. Conversely, avocet chicks, which hatched predominantly in sparse vegetation, were more susceptible to aerial predators, particularly California gulls. Movements of recently hatched avocet chicks were largely non-random, with avocet chicks that had hatched on islands within former salt ponds moving towards adjacent marsh habitats that were vegetated. In contrast, chicks that hatched within vegetated marshes remained in these marshes. These results indicate that within the first week after hatch, the few avocet chicks that survived quickly moved into adjacent habitat with ample vegetation cover which provided protection from aerial predators, such

Table 4. Synthesis of studies which have estimated nest survival or egg hatching success simultaneously for sympatrically breeding American avocets and black-necked stilts. DESFBNWR: Don Edwards San Francisco Bay National Wildlife Refuge.

		Avocet		Stilt		Avocet		Stilt		
Site	Year	Nest survival	n	Nest survival	n	Egg hatching success	n	Egg hatching success	n	Citation
California, San Francisco Bay, DESFBNWR, New Chicago Marsh	2005	0.37	24	0.43	89	0.72	6	0.91	40	Ackerman et al. (this study)
California, San Francisco Bay, DESFBNWR, New Chicago Marsh	2006	0.23	80	0.30	275	0.88	22	0.92	85	Ackerman et al. (this study)
California, San Francisco Bay, DESFBNWR, Pond A16	2005	0.75	142	0.67	3	0.93	65	1.00	3	Ackerman et al. (this study)
California, San Francisco Bay, DESFBNWR, Pond A16	2006	0.41	16	0.44	6	1.00	3	na	0	Ackerman et al. (this study)
California, San Francisco Bay, DESFBNWR, Pond A8	2006	0.30	166	0.07	1	0.89	36	na	0	Ackerman et al. (this study)
California, San Francisco Bay, DESFBNWR, Coyote Creek Marsh	2006	0.11	32	0.15	5	1.00	1	na	0	Ackerman et al. (this study)
California, San Francisco Bay, DESFBNWR, Newark Ponds	2006	0.63	78	0.46	31	0.90	34	0.90	10	Ackerman et al. (this study)
California, San Francisco Bay, Eden Landing Ecological Reserve	2005	0.40	20	0.48	31	0.75	3	0.98	11	Ackerman et al. (this study)
California, San Francisco Bay, Eden Landing Ecological Reserve	2006	0.33	64	0.36	17	0.91	12	0.92	7	Ackerman et al. (this study)
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	1995	0.65	754	0.63	1303	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	1996	0.75	829	0.72	747	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	1997	0.84	1631	0.75	1539	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	1998	0.86	2052	0.84	1782	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	1999	0.93	1362	0.82	1272	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	2000	0.90	1374	0.79	996	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	2001	0.78	2442	0.76	1348	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	2002	0.87	1631	0.72	1262	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	2003	0.76	1362	0.70	1665	na	na	na	na	Davis et al. 2008
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District	2004	0.86	2387	0.81	1220	na	na	na	na	Davis et al. 2008
Utah, Great Salt Lake, Bear River Migratory Bird Refuge	2005	0.44	311	0.45	29	0.96	143	0.98	10	Cavitt 2006
Utah, Great Salt Lake, Bear River Migratory Bird Refuge	2006	0.56	302	0.76	23	0.94	151	0.91	18	Cavitt 2006
Utah, Great Salt Lake, Farmington Bay Waterfowl Management Area	2005	0.55	481	0.56	411	0.96	247	0.97	201	Cavitt 2006
Utah, Great Salt Lake, Farmington Bay Waterfowl Management Area	2006	0.56	641	0.76	313	0.93	369	0.96	221	Cavitt 2006
Utah, Great Salt Lake, Great Salt Lake Shorelands Preserve	2006	0.03	106	0.56	7	0.89	14	0.94	4	Cavitt 2006
Utah, Great Salt Lake, Inland Sea Shorebird Reserve	2006	0.06	158	0.01	8	0.98	29	na	0	Cavitt 2006
Texas, Playa Lakes Region, many sites combined	1998	0.12	38	0.21	26	na	na	na	na	Conway et al. 2005
Texas, Playa Lakes Region, many sites combined	1999	0.39	73			na	na	na	na	Conway et al. 2005

(Continued)

Table 4. Continued.

Site	Year	Avocet Nest survival	n	Stilt Nest survival	n	Avocet Egg hatching success	n	Stilt Egg hatching success	n	Citation
California, San Joaquin Valley, Tulare Basin, Corcoran	1991	0.70	26	0.47	51	0.97	20	0.96	23	Marn 2003
California, San Joaquin Valley, Tulare Basin, Liberty	1991	0.38	205	0.33	25	0.93	147	0.95	12	Marn 2003
California, San Joaquin Valley, Tulare Basin, Pryse	1991	0.86	98	0.58	21	0.93	89	0.93	15	Marn 2003
California, San Joaquin Valley, Tulare Basin, Pryse	1992	0.72	96	0.77	24	0.93	78	0.93	19	Marn 2003
California, San Joaquin Valley, Tulare Basin, Pryse	1993	0.94	115	0.74	17	0.94	109	0.94	14	Marn 2003
California, San Joaquin Valley, Tulare Basin, Lost Hills Water District	1991	0.97	100	0.10	77	1.00	2	0.93	14	Marn 2003
California, San Joaquin Valley, Tulare Basin, Lost Hills Water District	1992	0.16	56	0.27	61	1.00	12	0.94	26	Marn 2003
California, San Joaquin Valley, Tulare Basin, Lost Hills Water District	1993	0.54	100	0.58	42	0.90	61	0.70	33	Marn 2003
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District: South	1992	0.42	870	0.56	164	0.94	418	0.95	87	Marn 2003
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District: South	1993	0.54	642	0.80	94	0.94	393	0.97	79	Marn 2003
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District: Hacienda	1992	0.28	418	0.28	208	0.94	151	0.98	81	Marn 2003
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District: Hacienda	1993	0.09	285	0.09	71	0.93	51	1.00	15	Marn 2003
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District: North	1992	0.04	55	0.05	96	0.95	5	0.95	12	Marn 2003
California, San Joaquin Valley, Tulare Basin, Tulare Lake Drainage District: North	1993	0.02	23	0.12	13	1.00	3	1.00	4	Marn 2003
California, San Joaquin Valley, Tulare Basin, Westlake-South	1992	0.25	17	0.81	13	na	na	0.93	11	Marn 2003
California, San Joaquin Valley, Tulare Basin, Westlake-South	1993	0.19	340	0.14	28	0.96	92	0.93	8	Marn 2003
Utah, Cache County, Barrens Company Hunting Club	1977	0.21	22	0.20	6	0.84	8	0.92	3	Sordahl 1996
Utah, Cache County, Barrens Company Hunting Club	1978	0.17	46	0.44	6	0.87	16	1.00	3	Sordahl 1996
California, San Joaquin Valley, Kesterson National Wildlife Refuge, Kesterson Reservoir	1983	0.87	17	0.72	125	0.98	16	0.91	92	Ohlendorf et al. 1989
California, San Joaquin Valley, Kesterson National Wildlife Refuge, Kesterson Reservoir	1984	0.15	51	0.06	189	1.00	17	0.96	48	Ohlendorf et al. 1989
California, San Joaquin Valley, Kesterson National Wildlife Refuge, Kesterson Reservoir	1985	0.30	35	0.32	96	0.91	19	0.88	47	Ohlendorf et al. 1989
California, San Joaquin Valley, Volta Wildlife Area	1983	0.67	10	0.44	11	1.00	8	1.00	7	Ohlendorf et al. 1989
California, San Joaquin Valley, Volta Wildlife Area	1984	0.18	62	0.10	31	0.96	24	1.00	5	Ohlendorf et al. 1989
California, San Joaquin Valley, Volta Wildlife Area	1985	0.21	25	0.10	48	1.00	9	1.00	10	Ohlendorf et al. 1989
Total		0.48	22270	0.47	15926	0.93	2701	0.94	1278	

as California gulls. These movement patterns are common among shorebirds where parents often move their chicks to more vegetated brood-rearing areas which can provide greater concealment from potential predators as well as greater availability of food resources (Schekkerman and Beintema 2007, Hartman and Oring 2009). Stilts likely experienced higher chick survival rates because they nested in vegetated habitats more than avocets, which provided greater protection from aerial predators during the critical first week after hatching. Yet, even where avocets and stilts nested together at high densities, stilt chick survival was always higher than avocet chick survival, suggesting that micro-habitat use, and

possibly factors beyond chick-rearing habitat, contributed to the large difference in chick survival between species.

Our finding of very low survival for avocet chicks is similar to our results from a similar study on Forster's tern *Sterna forsteri* chick survival in San Francisco Bay (Ackerman et al. 2014). In that study, 54% of tern chick deaths were caused by California gulls, and 31 radio-marked and 59 leg-banded Forster's tern chicks were found depredated within the same California gull colony. Forster's tern chick survival to fledging was 22%, which is higher than what we found for avocets (6%) but much lower than that for stilts (40%). Although these studies were not conducted concurrently (Forster's terns: 2010 and 2011, avocets and stilts: 2005 and 2006), they indicated relative levels of predation experienced by each species. In San Francisco Bay, Forster's terns and avocets often nest together on islands within large ponds (formerly salt evaporation ponds) that are mostly devoid of vegetation that could conceal chicks from aerial predators. In contrast, most stilt nests are located within marshes and their nests are associated with vegetation structure which likely conceals stilt chicks from aerial predation. The high nesting densities and similar use of island nesting habitats by avocets and Forster's terns likely contributes to increased chick vulnerability to aerial predators, especially California gulls, compared to stilt chicks which often nest at lower densities and use more vegetated marshes. The breeding population of California gulls in South San Francisco Bay, California has increased rapidly from $<$ 100 breeding adults in 1980 to an average of 31 400 during the two years of this study and $>$ 52 000 by 2012 (Strong et al. 2004, San Francisco Bay Bird Observatory unpubl.). The increasing dominance of California gulls within the San Francisco Bay predator community may further exacerbate predation levels on waterbird chicks, especially those chicks that are raised in unvegetated habitats where they are more susceptible to visual-oriented aerial predators.

In summary, by simultaneously studying the reproductive success of two closely related species that breed sympatrically, we found that nest survival and egg hatching success was comparable between species but avocet chick survival was much lower than would be expected when compared with stilt chick survival. This difference in chick survival was likely driven by different habitat use, which in turn resulted in different vulnerability to predators. In particular, avocet chicks were much more susceptible to gull predation compared to stilts due to avocets' tendency to nest at unvegetated sites. Additionally, we found that sites with high nest survival rates did not necessarily have correspondingly high chick survival rates – in fact, the opposite pattern often occurred. These results suggest that wetland managers may be able to improve productivity of shorebirds by placing nesting habitat, such as the unvegetated islands often preferred by avocets, in close proximity to vegetated marshes which provide chicks protection from aerial predators.

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