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Effects of a habitat-altering invader on nesting sparrows: An ecological trap?

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Abstract Many invading species impact native species through predation, parasitism or competition, while others affect natives indirectly by restructuring their habitat. How invasive plants affect native animals, and to what extent native animals respond to changes in their habitat and the novel selection pressures that follow, is not well known. We investigated the impacts of a habitat-altering invader, the Atlantic cordgrass *Spartina alterniflora*, on the nesting success of Alameda song sparrows (*Melospiza melodia pusillula*), a California Species of Special Concern, in tidal marshes in three sites in San Francisco Bay. Date of laying was the most influential factor in determining daily survival rate of nests, but whether the nest was placed in exotic *Spartina* was the most important ecological variable. Nests placed in exotic *Spartina* had a success rate that was 30% lower than those placed in native vegetation. Nests in exotic *Spartina* were significantly more likely to fail due to tidal flooding than were nests placed in native vegetation, because the densest stands of exotic *Spartina* occurred at significantly lower elevations relative to the tides. Our results suggest that exotic *Spartina* may be an ecological trap for song sparrows in San Francisco Bay, attracting birds to nest sites that are often destroyed by tidal flooding.

Keywords Alameda song sparrow · Behavior · Ecological trap · Exotic species invasions · Invasive cordgrass · *Melospiza melodia* · Nest success · *Spartina alterniflora* · Tidal salt marsh

Introduction

Non-native species can profoundly affect the native biota of ecosystems they invade (Mack et al. 2000), such as exotic predators that have caused extinction of endemic island species (Wiles et al. 2003). Less well understood, however, is how the invasion of exotic plant species affects the fauna of invaded ecosystems and whether, or to what extent, native species are able to respond to changes in their habitat and the novel selection pressures that follow. When ecosystems are invaded and altered by non-native plants, animals must choose whether to occupy and

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breed in the novel habitat using cues that evolved in, and were appropriate for, the native ecosystem. An ‘ecological trap’ occurs when an animal’s habitat choices become maladaptive in the face of alterations to its environment associated with exotic species invasions (Remes 2003; Schmidt and Whelan 1999), habitat fragmentation (Gates and Gysel 1978; Purcell and Verner 1998; Schlaepfer et al. 2002) or other stressors. For example, native birds that continue to occupy invaded ecosystems may use outdated cues for selecting nest sites and may experience lower reproductive success through increased rates of nest predation (Borgmann and Rodewald 2004; Remes 2003; Schmidt and Whelan 1999), delays in the onset of breeding (Ortega et al. 2006), slower growth rate of nestlings (Lloyd and Martin 2005), or increased rates of nest parasitism (Stoleson and Finch 2001).

In this study, we examine the effect of an invasive exotic cordgrass (*Spartina alterniflora*) on nesting success of Alameda song sparrows (*Melospiza melodia pusillula*) in South San Francisco Bay. The natural state of the San Francisco Bay estuary is characterized by open-canopied marshes and broad flat expanses of open intertidal mud. Marsh plants in this system occur in characteristic zones that are generated by varying tidal inundation and competitive displacement (Peinado et al. 1994). *Spartina foliosa* (Pacific cordgrass), the only native cordgrass in the region, occurs in a narrow low-marsh zone that is low in elevation and regularly flooded by tides. *S. foliosa* has narrow leaf blades, grows sparsely and reaches heights ≤1.2 m. The high-marsh zone, where native bird species maintain breed territories, is higher in elevation and thus less influenced by tides. This zone is composed mainly of low-growing (≤0.4 m in height) *Salicornia virginica* (pickleweed) with narrow areas of *Grindelia stricta* (gumplant, ≤1 m in height) lining the meandering tidal channels.

S. alterniflora, native to the Atlantic and Gulf coasts of North America, was introduced to San Francisco Bay in the early 1970s (Ayres et al. 2004). The exotic cordgrass subsequently hybridized with the native cordgrass, *S. foliosa*, and this hybrid has spread to over 720 ha of tidal flat and tidal marsh habitat (Zaremba and McGowan 2004). The tall, dense, thick growth of exotic *Spartina* (*S. alterniflora* and/or the hybrid *S. alterniflora x foliosa*) changes profoundly the composition and structure of salt marsh habitat. Exotic *Spartina* reaches heights of 2.5 m and can grow further down the tidal gradient than any native tidal marsh plant species and so is able to colonize open tidal flats. Exotic *Spartina* can also grow further up the tidal gradient than the native *S. foliosa* and can displace other native plant species in the high-marsh zone as well (Ayres et al. 1999). When invaded by exotic *Spartina*, substantial portions of these marshes can ultimately be transformed into solid alien cordgrass meadows (Daehler and Strong 1996).

Alteration of salt marsh habitat by exotic *Spartina* has serious implications for the native species that inhabit these marshes. Fundamental changes in habitat structure, shifts in primary productivity and the modification of trophic pathways (Brusati and Grosholz 2006; Levin et al. 2006) will likely have their biggest impacts on species that are largely or wholly dependent on tidal salt marsh. The Alameda song sparrow is one of three song sparrow subspecies that are endemic to the tidal marshes in San Francisco Bay. They are non-migratory and territorial, so rely solely on local resources within each marsh. The Alameda song sparrow is currently listed as a California Species of Special Concern, imperiled because over 80% of its tidal marsh habitat has been lost to human development activities over the past 200 years (Grossinger et al. 1998; Marshall 1948). Song sparrows in this system typically occupy linear nesting territories along tidal channels that are composed of areas of the taller *G. stricta* along tidal channels and the shorter *S. virginica* that make up most of the high-marsh plain (Grenier 2004; Johnston 1956). Although these birds will forage in areas of native cordgrass, they do not use it for nesting (Grenier 2004) presumably because *S. foliosa* is sparse and will not effectively support or conceal their open-cup nests. Furthermore, the low-marsh areas occupied by *S. foliosa* are inundated regularly by the tides.

Alameda song sparrows nest in a physically challenging environment and typically face no competition from other passerine species for nesting territories. Recently, however, marsh wrens (*Cistothorus palustris*) have been observed establishing breeding territories in salt marshes that have been invaded by exotic *Spartina* in Willapa Bay, WA (Williamson 1994) and San Francisco Bay (Nordby and Cohen, personal observation). Marsh wrens on the Pacific Coast characteristically nest in dense reeds in fresh- or brackish-water marsh, not in salt marshes (Verner 1965). They are perhaps now able to nest in salt marshes because exotic *Spartina* provides taller and more supratidal plant biomass than native salt marsh plants. Marsh wrens are highly territorial, and are known to defend their territories against other wrens and other species by breaking the eggs in nests that are close to their own territories (Picman 1977).

We hypothesized that the habitat changes associated with exotic *Spartina* have resulted in net detrimental effects on Alameda song sparrow populations. To test this hypothesis, we examined song sparrow nesting habitat preferences and compared the daily survival rate of nests placed in native vegetation to those placed in exotic *Spartina* at three sites that varied in the degree of invasion by exotic *Spartina*. We also examined whether the proximity of marsh wrens affected nest success and looked for evidence of the destruction of song sparrow eggs by marsh wrens.

Methods

Study sites

We chose three tidal salt marsh study sites on the eastern shore of San Francisco Bay, CA, USA that supported populations of Alameda song sparrows and differed in the degree of invasion by exotic *Spartina*. The first site was a 2.5 ha native tidal salt marsh within Audubon Marsh in the Don Edwards San Francisco Bay National Wildlife Refuge (hereafter 'Audubon'), that was composed almost entirely of native vegetation and no exotic *Spartina*. It included a broad *S. virginica* plain with *G. stricta* lining the edges of numerous meandering tidal channels, with patches of *Jaumea carnosa* (fleshy jaumea), *Frankenia salina* (alkali-heath), *Distichlis spicata* (saltgrass) and *S. foliosa*. There were also some small patches of *Salsola soda* (a Eurasian species). This site was ~950 m from the bayward edge of the marsh and was separated from adjacent, previously contiguous marshes by a railroad levee on one side and a pipeline and access road on the opposite side. The second study site was a 9 ha area at Robert's Landing in San Leandro, CA (hereafter 'San Leandro'). This site was composed of heterogeneous patches of native vegetation (including *S. virginica*, *G. stricta*, *J. carnosa*, *F. salina*) and exotic *Spartina* that covered 33% of the site, as estimated from color-infrared aerial photographs. This area was located ~110 m upstream from where the main tidal channel meets the open bay and was separated from the bay and from adjacent, previously contiguous marshes by levees, but was fully tidal and contained several tidal channels. The third site was an 8 ha area in the Elsie Roemer Bird Sanctuary in Alameda, CA (hereafter 'Alameda') that was highly invaded by exotic *Spartina*. This area was composed of a band along the shore that included a variety of native plants (*S. virginica*, *G. stricta*, *J. carnosa*, *F. salina*) and a bayward area of nearly solid exotic *Spartina* that was estimated from aerial photographs to cover 68% of the site. This site was open to the bay (no levees), and there were no adjacent marshes. Several other exotic plants in addition to exotic *Spartina* were present in these study sites, particularly in the high-elevation areas adjacent to the upland edges of the marshes (e.g., fennel, grasses and thistles). These other exotic plants were rarely used as nesting sites by song sparrows, and their percent coverage within each site was negligible compared to the coverage of native vegetation and exotic *Spartina*.

Nest monitoring

All adult song sparrows within each site were captured using mist nets and banded with a unique combination of one U.S. Geological Survey aluminum band and three plastic, colored leg bands. At each site we identified 15–18 sparrow territories and attempted to find every nest within each territory during the entire breeding season (late February–mid-July) in 2002 and 2003. Nests were located by observing female behavior and occasionally by systematic searches. Once a nest was found, we drew a map of its location based on surrounding vegetation and distant landmarks to relocate it; no flagging was used.

Each nest was monitored every 2–6 days until it was successful (fledged at least one young) or failed. Reasons for failure included (1) predation (eggs were found broken, or the nest was empty and dry; these included eggs that appeared to have been destroyed and not consumed by marsh wrens, as described under 'Results'), (2) tidal flooding (during a period of high tides, nests were found soaking wet and empty, sometimes with intact or broken eggs present in surrounding vegetation or on the ground; if broken eggs were present, we assumed this was due to breakage or predation that occurred after nest flooding), (3) abandoned (eggs were intact and the nest was dry), and (4) weather (nest collapsed due to wind or rain).

Once a nest succeeded or failed, we mapped the nest's location using a Trimble GPS Pathfinder Pro XRS, recorded the plant species supporting and concealing the nest, and estimated nest concealment as the mean of the percentage of the nest visible from each cardinal direction and from above. We also calculated the elevation of the bottom of the nest relative to the local Mean Higher High Water (MHHW) tide level, in three steps: (1) by line-of-sight leveling we measured the elevation of the ground below the nest relative to a local benchmark at each site and added the distance from the ground to the bottom of the nest; (2) we measured tide levels relative to the local benchmarks at all three sites simultaneously over 5 months with pressure sensors and data loggers deployed as water level monitors (Telog Instruments Model WLS-31); (3) we then used a modification of the Height Difference Method (Collins 2002) to calculate the local MHHW datums for the most recent tidal epoch (1983–2001), regressing the observed water levels of the five highest tides of each tide series against the verified water levels of the corresponding tides recorded at the nearest National Ocean Service permanent tide station (the control station), and used the best fit tide series ($r^2 > 0.95$ for all three sites) to calculate the local datums. Finally, using ArcView 3.3, we manually measured the distance from each nest to the upland edge of the marsh on geo-referenced aerial photographs of each site, and the distance to the center of the nearest male marsh wren territory on geo-referenced maps of male marsh wren territories created for another study.

Statistical analysis

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate competing models of the daily survival rate of nests (probability that a nest survives a given day) using the generalized linear modeling approach (Shaffer 2004). Logistic-exposure models were fit using PROC GENMOD (SAS Institute 2003), a binomial response distribution and the link function defined by Shaffer (2004). We included nine variables that could affect the daily survival rate of song sparrow nests. Three were temporal variables that have repeatedly been found to affect nest success in songbirds: (1) YEAR (2002 or 2003)—annual variation in nest success is frequently observed and has various causes including weather patterns, variation in food supply, or predator fluctuations (Morrison and Bolger 2002); (2) JULIAN—the Julian date of the first laid egg in a nest or the date of failure if the nest failed before laying occurred. Song sparrows in San Francisco Bay marshes have a five-month breeding season and, as with other species that have a long breeding season, nest success may vary due to seasonal shifts in weather, food availability, and predator populations (Siikamaki 1998), or, in San Francisco Bay, maximum tidal heights; and (3) STAGE—the stage of the nest (building/laying, incubating, or nestling) strongly affects daily survival rate in many passerine species (Martin et al. 2000). Minimal parental activity occurs during building or laying, a moderate amount of activity occurs during incubation, and a high level of activity occurs during the nestling stage when parents feed chicks. Predators may cue on these activities to find nests, so nests are potentially more vulnerable to predators during the later stages of the nesting cycle.

The remaining six variables are based on ecological factors: (4) SPARTINA—whether the nest was placed in exotic *Spartina*; (5) ELEVATION—elevation of the nest relative to MHHW; (6) CONCEAL—mean of the percent of the nest visible from each cardinal direction as well as from above; (7) EDGE—distance of nest to the upland edge of the site; (8) MAWR—distance to nearest marsh wren territory center; and (9) SITE—Audubon, San Leandro or Alameda. We made no *a priori* prediction about which, if any, site would have higher or lower daily survival rates, but we included this variable to investigate the possibility. In each of the two sites that contained exotic *Spartina*, San Leandro and Alameda, there were also substantial areas of native vegetation present, so birds had the choice of whether or not to nest in the exotic vegetation. In the third site, Audubon, no exotic *Spartina* was present. If SITE turned out to be a strong predictor of daily survival rate, it might be partly due to the presence of exotic *Spartina*; however, we examine this by considering the relative strength of each variable to predict the daily survival rate of nests.

Analysis of the factors affecting the daily survival rate of nests proceeded in two steps. We first analyzed each variable singly and compared explanatory abilities using Akaike's Information Criterion size (Akaike 1973; Burnham and Anderson 2002) corrected for small sample size (AICc). JULIAN emerged as the most important variable, with the other two temporal variables, YEAR and STAGE, also among the top four (Table 1). Because we were interested primarily in the ecological variables, we conducted a second analysis that included all three of the temporal variables (YEAR, JULIAN and STAGE) in every model as the "base temporal model". We then developed a list of 36 candidate models that included various combinations of the six ecological variables with the base temporal model (Table 2), and used AICc values and AIC weights to evaluate the strength of each model. Models that differed from the best model by ≤ 2 ΔAIC_c units were considered to have substantial support (Burnham and Anderson 2002). To determine the relative importance of each ecological variable in predicting the daily survival rate of nests, for each variable, we summed the AIC weights over each of the 13–15 models in which the variable appeared.

We estimated nest success across years, sites and vegetation categories by building a composite model using the model-averaged parameter estimates from the top 10 ecological models (those with $\Delta AIC_c \leq 2$) and setting the continuous variables (JULIAN, ELEVATION, CONCEAL and EDGE) to their mean values to generate model-averaged daily survival rates. The number of days per nesting stage was also set to the mean values observed: building and laying stage was 5 days (which includes building the nest and laying the first egg, with incubation beginning when the second egg is laid), incubation stage was 12 days and nestling stage was 11 days.

We also directly compared the fates of nests placed in exotic *Spartina* to those placed in other vegetation by examining apparent (observed) nest success and the reasons for nest failure (predation, tidal flooding, abandonment, or weather) for nests in each of these two vegetation categories. Although apparent nest success may be biased toward successful nests, we were able to locate nearly every nest for every female in each of our three sites throughout the entire breeding season, except for a few nests that may have failed very early in the nesting cycle or very early in the breeding season (particularly in 2002). We believe there was no systematic bias regarding failed nests we may have missed (e.g., by habitat or site).

Table 1 Summary of model-selection results for single-variable models of daily nest survival rates for Alameda song sparrows in San Francisco Bay, California, 2002–2003

Model	*K*	ΔAIC_c	AIC weight
JULIAN	2	0.00	0.9986
YEAR	2	15.38	0.0005
SPARTINA	2	16.23	0.0003
STAGE	3	16.80	0.0002
ELEVATION	2	18.08	0.0001
MAWR	2	18.10	0.0001
Constant	1	18.51	0.0001
SITE	3	19.16	0.0001
CONCEAL	2	20.37	0.0000
EDGE	2	20.49	0.0000

Values are based on Akaike's Information Criterion (AICc) where *K* is the number of parameters in the model, ΔAIC_c is the difference between a given model and the top model, and AIC weight reflects the relative support for each model

Results

Nests monitored

We located a total of 364 song sparrow nests. Thirteen nests were eliminated from the study because: (1) we found them after they had already failed ($n = 10$); (2) we failed to collect the elevation of the nest ($n = 1$); or (3) the nest was placed in non-marsh upland habitat so the elevations and other nest parameters were considered outliers ($n = 2$) resulting in a sample of 351 nests to estimate daily survival rates. Of these, 123 were located in Audubon, 95 were located in San Leandro, and 133 were located in Alameda.

Nesting habitat

Song sparrows viewed exotic *Spartina* as appropriate nesting habitat: 29% of San Leandro nests and 57% of Alameda nests were placed in exotic *Spartina*,

Table 2 Summary of model-selection results for multiple-variable models of daily nest survival rates for Alameda song sparrows in San Francisco Bay, California, 2002–2003

Model	K	ΔAIC_c	AIC weight
Base + SPARTINA	6	0	0.097
Base + SPARTINA + SITE	8	0.57	0.073
Base + ELEVATION	6	0.83	0.064
Base + SITE + ELEVATION	8	0.86	0.063
Base + SPARTINA + ELEVATION	7	1.15	0.055
Base	5	1.19	0.053
Base + SPARTINA + CONCEAL	7	1.48	0.046
Base + SPARTINA + JULIAN*SPARTINA	7	1.53	0.045
Base + SITE	7	1.64	0.043
Base + SPARTINA + EDGE	7	1.97	0.036
Base + SPARTINA + MAWR	7	2.01	0.036
Base + SPARTINA + SITE + ELEVATION	9	2.05	0.035
Base + MAWR	6	2.40	0.029
Base + SITE + ELEVATION + CONCEAL	9	2.41	0.029
Base + SPARTINA + ELEVATION + EDGE	8	2.51	0.028
Base + ELEVATION + CONCEAL	7	2.67	0.026
Base + ELEVATION + JULIAN*ELEVATION	7	2.77	0.024
Base + SPARTINA + ELEVATION + CONCEAL	8	2.77	0.024
Base + EDGE	6	2.80	0.024
Base + CONCEAL	6	2.93	0.022
Base + SPARTINA + ELEVATION + MAWR	8	3.04	0.021
Base + SITE + CONCEAL	8	3.17	0.020
Base + SITE + MAWR	8	3.62	0.016
Base + SITE + EDGE	8	3.65	0.016
Base + SPARTINA + ELEVATION + CONCEAL + EDGE	9	3.98	0.013
Base + EDGE + MAWR	7	4.41	0.011
Base + ELEVATION + CONCEAL + EDGE + MAWR	9	4.52	0.010
Base + SITE + CONCEAL + MAWR	9	5.17	0.007
Base + SPARTINA + CONCEAL + EDGE + MAWR	9	5.38	0.007
Base + SITE + EDGE + MAWR	9	5.63	0.006
Base + CONCEAL + EDGE + MAWR	8	5.80	0.005
Base + SITE + ELEVATION + CONCEAL + EDGE + MAWR	11	5.86	0.005
Base + SPARTINA + ELEVATION + CONCEAL + EDGE + MAWR	10	5.99	0.005
Base + SPARTINA + SITE + ELEVATION + CONCEAL + EDGE + MAWR	12	6.79	0.003
Base + SITE + CONCEAL + EDGE + MAWR	10	7.18	0.003
Constant	1	22.46	0

Values are based on Akaike's Information Criterion (AICc) where K is the number of parameters in the model, ΔAIC_c is the difference between a given model and the top model, and AIC weight reflects the relative support for each model. "Base" represents the three temporal variables (YEAR, JULIAN and STAGE) that were included in each model

resulting in a total of 104 nests (29% of all nests) in exotic *Spartina*. Of the 247 nests that were not placed in exotic *Spartina*, 140 (57%) were placed in native *G. stricta*, 62 (25%) were placed in native *S. virginica*, 24 (10%) were placed in other types of native vegetation (e.g., *F. salina*), and 21 (8%) were placed in other types of non-native vegetation (e.g., fennel or thistle). Because we were investigating the effect of exotic *Spartina* on nesting success, for the rest of our analyses, we lumped the 21 nests that were placed in non-native vegetation (other than exotic *Spartina*) together with the nests that were placed in native vegetation.

Daily survival rates of nests and nest success

JULIAN was by far the single most important predictor of daily survival rate (AIC weight = 0.9986; Table 1). All other variables had minimal support compared to JULIAN alone. The other two temporal variables, YEAR and STAGE represented the second and fourth most important predictors of nesting success.

Exotic *Spartina* had an important effect on nesting success (Table 2). When we added ecological variables to our temporal base model (YEAR, JULIAN and STAGE), the best model included SPARTINA as the only ecological variable (AIC weight = 0.097), but nine other models differed from this model by ≤ 2 $\Delta\mathrm{AIC_c}$ units. Exotic *Spartina* occurred in 6 of the top 10 models. The overall importance of each of the six ecological variables in predicting daily nest survival was further portrayed by summing the AIC weights over all 36 models in which the variable appears (Burnham and Anderson 2002). The variable SPARTINA had the highest sum (ΣAIC weight = 0.524, 15 models), followed by ELEVATION (ΣAIC weight = 0.405, 15 models), SITE (ΣAIC weight = 0.319, 13 models), CONCEAL (ΣAIC weight = 0.225, 15 models), EDGE (ΣAIC weight = 0.172, 14 models) and MAWR (ΣAIC weight = 0.164, 14 models).

Model averaging was used to develop estimates for nesting success in the absence of a single best model. The logistic equation for the composite model generated from the top 10 models is:

$$\begin{aligned}\mathrm{Logit}\left(\widehat{S}_i\right) = {} & 3.15 - 0.252(\mathrm{YEAR} = 2002) - 0.0073(\mathrm{JULIAN}) + 0.462(\mathrm{STAGE} = \mathrm{building/laying}) \\ & + 0.112(\mathrm{STAGE} = \mathrm{incubating}) + 0.123(\mathrm{SPARTINA} = \mathrm{other\ vegetation}) \\ & + 0.082(\mathrm{SITE} = \mathrm{Audubon}) + 0.077(\mathrm{SITE} = \mathrm{San\ Leandro}) + 0.0007(\mathrm{ELEVATION}) \\ & - 0.0001(\mathrm{CONCEAL}) + 0.0001(\mathrm{EDGE}) + 0.0002(\mathrm{JULIAN} * \mathrm{SPARTINA} = \mathrm{other\ vegetation}).\end{aligned}$$

Model-averaged daily survival rates for song sparrow nests were primarily a function of year, Julian date when the nest was initiated, the stage of the nest, and whether the nest was placed in exotic *Spartina* (Fig. 1). In general, daily nest survival was lower in 2002 than in 2003, lower later in the season than earlier, lower for later nest stages, and lower if nests were placed in exotic *Spartina*. Nests had slightly higher probability of daily survival in Audubon than in Alameda, and slightly higher survival in Alameda than in San Leandro. The effects of the remaining variables were small. Daily survival was weakly but positively related to elevation, how well the nest was concealed, and distance to the edge of the marsh. Finally, the interaction of JULIAN * SPARTINA indicated a slightly higher survival for nests started earlier in the season and not placed in *Spartina*.

We determined the overall effect of placing nests in *Spartina* by calculating the average nesting success for nests by site and year. Averaging across SITE and SPARTINA (but not including any value for *Spartina* nests in Audubon as there were no such nests), nest success was estimated to be 46% lower in 2002 (5.6%) than in 2003 (10.3%). Averaging across YEAR and SPARTINA, nest success was 14% higher in Audubon (9.6%) than in Alameda (8.2%) and 17% higher in Alameda than in San Leandro (6.8%). When these effects were accounted for by averaging across YEAR and SITE, nest success was 30.4% lower in *Spartina* (6.3%) than in other vegetation (9.1%).

Apparent nest success and causes of failure

Given the impact of exotic *Spartina* on daily nest survival rates and nest success, we examined the fate of all nests relative to whether they were placed in exotic *Spartina* or other vegetation. Apparent nest success (whether a nest successfully fledged at least one young) across all sites was low (15.1%). It was particularly low for nests placed in *Spartina* (10.6%) versus other vegetation (17.0 %), although the difference was not significant ($\chi^2 = 2.498$, $P = 0.11$ NS, $n = 351$; Fig. 2). These values for apparent nest success are consistent with the

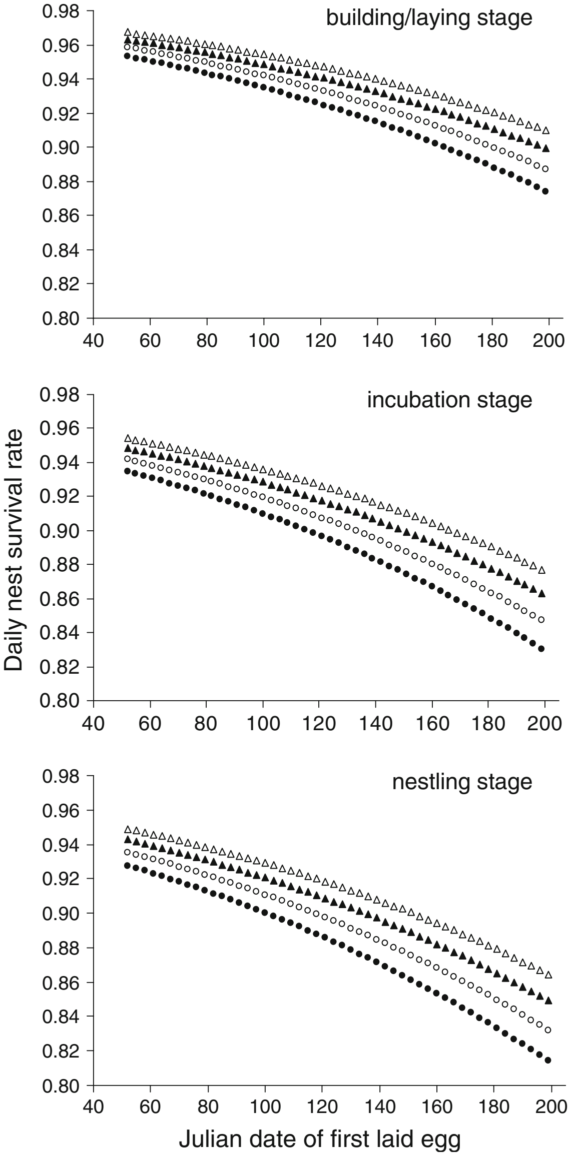

Fig. 1 Estimated Alameda song sparrow daily nest survival rate in relation to Julian date of the first laid egg in the nest (or the date of failure if the nest failed before laying), during the building/laying, incubation or nestling stage, in exotic *Spartina* (*filled symbols*) or other vegetation (*open symbols*), in 2002 (*circle symbols*) and 2003 (*triangle symbols*)

estimated nest success from the composite model above, although the values generated by the model were even lower.

Nests failed due to predation, tidal flooding, abandonment, and weather. Most (84%) of the 298 nests that failed were apparently lost to predators ($n = 148$) or tidal flooding ($n = 104$). Of the nests that failed

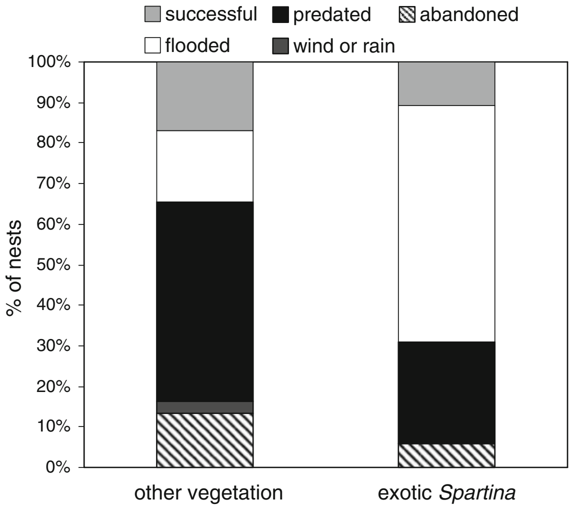

Fig. 2 Percentage of Alameda song sparrow nests that were apparently successful (*gray*), lost to tidal flooding (*white*), lost to predation (*black*), lost to weather (*dark gray*), or abandoned (*striped*) in exotic *Spartina* ($n = 104$) or other vegetation ($n = 247$)

from one of these two causes, nests placed in exotic *Spartina* were significantly more likely to fail due to tidal flooding, and nests placed in other vegetation were significantly more likely to fail due to predation ($\chi^2 = 45.613$, $P < 0.0001$, $n = 252$; Fig. 2). We hypothesized that nests placed in *Spartina* were significantly lower in elevation relative to the tides than nests placed in other vegetation (and hence were more often destroyed by flooding), and this proved to be the case ($t = 9.11$, $P < 0.0001$, $n = 351$; Fig. 3).

Proximity to marsh wren territories (MAWR) had little effect on the daily survival rate of song sparrow nests (Tables 1 and 2). We did, however, find strong circumstantial evidence that eggs had been destroyed by marsh wrens in 19 (5.4%) of the song sparrow nests that we monitored. Eggs in these nests had been punctured (holes were 0.5–2.5 mm in diameter) but the contents of the egg were intact, a type of attack that is highly consistent with the egg-destruction behavior of marsh wrens (Bent 1948; Bump 1986; Picman 1977; Picman and Isabelle 1995). Brown headed cowbirds (*Molothrus ater*), which were sometimes present in the study areas, are known to remove eggs from the nests of other species and often eat them, but there are no records of cowbirds puncturing and leaving eggs in nests (Scott et al. 1992). All egg destruction events occurred in song sparrow territories that were adjacent to a marsh wren territory.

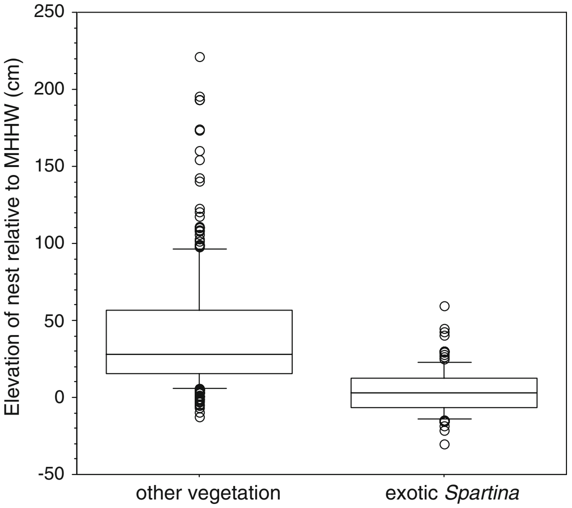

Fig. 3 Elevation of Alameda song sparrow nests relative to Mean Higher High Water tide level in exotic *Spartina* (n = 104) or other vegetation (n = 247) (box represents the 25, 50 and 75th percentiles and short lines represent the 10 and 90th percentiles)

Discussion

Our study suggests that the changes in Pacific salt marsh habitat associated with the invasion of exotic *Spartina* negatively impact Alameda song sparrows. Although song sparrows do not nest in native *S. foliosa*, they will nest in exotic *Spartina* which provides vegetation that is dense enough to support and conceal their nests. However, the daily survival rate and hence the success of nests placed in exotic *Spartina* was lower than nests placed in other types of vegetation. This was largely due to the fact that nests placed in exotic *Spartina* were generally at lower elevations and were more frequently lost to tidal flooding.

While the type of vegetation the nest was placed in (*Spartina* vs. other vegetation) was the most important ecological variable associated with the daily survival rate of nests, nest initiation date was by far the most important temporal variable. Nests that were started earlier in the season had a higher daily survival rate than those started later. There are at least two possible explanations for this finding. First, the maximum tide range in San Francisco Bay generally increases over the season, so the highest tides become higher and the lowest tides become lower (e.g., in 2003 the monthly highest tide increased from 1.89 m in March to 2.13 m in July). Therefore, the risk of a nest flooding increases as the season progresses. Second, the risk of predation often increases later in the season because predators may become more abundant or more active (Morrison and Bolger 2002), although we do not have data on predator populations in this system.

Our finding that nests in exotic *Spartina* were more likely to be lost due to flooding than to predation could suggest that exotic *Spartina* affords more protection from predators than does native vegetation. However, flooding and predation are mutually exclusive events, so we do not know whether nests that were flooded would have been predated later had they survived.

There were small differences in daily nest survival rates and nest success among the three sites with slightly higher survival in Audubon (uninvaded) than in Alameda (~68% invaded) and slightly higher survival in Alameda than in San Leandro (~33% invaded). Because we do not have true replicate sites at each level of invasion, these differences may be confounded with the presence of exotic *Spartina*. Nevertheless, site effects were small in comparison to the effects of *Spartina* (Table 2). Therefore, we conclude that any differences at the site level—including the level of *Spartina* invasion or any other variable such as predator abundance—were less important in determining sparrow nest success.

Although proximity to marsh wrens was not a strong predictor of daily nest survival, we did find punctured but unpredated eggs in over 5% of the nests, apparently due to attack by marsh wrens. In our study, the incidence of punctured eggs may be an underestimate of the impact from marsh wrens because these birds will typically pierce the eggs and then toss them out of a nest, and sometimes attack nestlings (Picman 1977; Scott et al. 1992). Given the low nest success rate for song sparrows in this system, additional losses to interspecific aggression by marsh wrens could be detrimental to the long-term survival of these populations.

Flooding and predation are two main selection pressures for nesting success for birds that nest in tidal marshes (Greenberg et al. 2006). The rate of nest failure for Alameda song sparrows apparently due to flooding (30%) was much higher than for other song sparrow subspecies in San Francisco Bay (9–11% for *M. m. samuelis* and 2% for *M. m. maxillaris*) and other tidal marsh bird species on the Atlantic coast

(Greenberg et al. 2006). Our data suggest that the rate of nest failure due to flooding is high for Alameda song sparrows because, in marshes that have been invaded by exotic *Spartina*, the birds are being drawn to nesting sites that are too low in elevation relative to the tides. While exotic *Spartina* does grow at elevations similar to that of native vegetation used for nesting, most of it, including the densest growth, is found at lower elevations in the *S. foliosa* band and below, where song sparrows would not otherwise nest.

We do not yet know whether exotic *Spartina* is an ecological trap that greatly reduces the overall reproductive success of the Alameda song sparrow. The cues that the birds use to select nesting sites (e.g., density of vegetation) appear to be maladaptive in exotic *Spartina* habitat because these areas are lower in elevation and thus are more susceptible to flooding. Similar miscuing could be occurring with other nesting bird species in this habitat, such as the federally endangered California clapper rail (*Rallus longirostrus obsoletus*). It is also possible that additional nest failures from marsh wren aggression further exacerbates the negative impact of exotic *Spartina*. For exotic *Spartina* to be a true ecological trap, song sparrows would have to prefer to nest in the exotic habitat over other available habitat (native or non-native) that was more appropriate and where they would experience higher nest success (Robertson and Hutto 2006). We are currently investigating this possibility.

Exotic species can devastate native populations and their overall impact is second only to habitat loss or destruction (Wilcove et al. 1998). Because invasions can occur at such rapid rates (Ricciardi and Cohen 2007), assessing the behavior of native species and how they respond to novel environmental conditions is a crucial component of understanding the impacts of invasive species (Schlaepfer et al. 2002). This approach is important for understanding the effects of other types of rapid ecosystem perturbations as well (e.g., habitat fragmentation or degradation). Whether individual behavioral plasticity coupled with natural selection can act fast enough to modify maladaptive responses to cues and counteract the effects of ecological traps may mean the difference between the survival and extinction of a species.

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