THE INFLUENCE OF NEST SUBSTRATE AND NEST SITE CHARACTERISTICS ON THE RISK OF SAN CLEMENTE SAGE SPARROW NEST FAILURE

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Abstract—Relatively small areas of critical habitat in island ecosystems can be essential to the survival and persistence of endemic threatened and endangered species. The San Clemente sage sparrow (*Amphispiza belli clementeae*) is a federally threatened, non-migratory subspecies endemic to San Clemente Island. During the breeding season, the population is limited to the lower marine terraces along the island's western shore. From 1999 through 2006, we located 870 San Clemente sage sparrow nests in 25 nest substrates; 73% of which were in boxthorn. We examined nest site characteristics that most influenced nest failure rates and compared nest survival among nest substrates and nest substrate types. The risk of nest failure varied annually and was significantly reduced when pairs nested in boxthorn and placed their nests near the center of the shrub. However, we found no significant differences in daily nest survival rates between boxthorn and non-boxthorn nest substrates and among nest substrate types. Three times as many nests were built in boxthorn as were built in all other substrates combined. These results suggest that the availability of boxthorn as nesting habitat may be an important factor driving the distribution and growth of the San Clemente sage sparrow population.

INTRODUCTION

Conservation of critical habitat for threatened and endangered bird species is essential for their long-term protection and management (Taylor et al. 2005). In some cases the habitat critical to the conservation of a species is not designated at the time of its listing because the species' habitat requirements are not adequately known. In these circumstances, it is crucial to determine those habitat features that are necessary to the long-term viability of the protected species.

The San Clemente sage sparrow (*Amphispiza belli clementeae*) is a non-migratory subspecies endemic to San Clemente Island (SCI), a U.S. military installation located off the coast of California. Once it was described as a common island resident (Grinnell 1897; Linton 1908; Howell 1917; Grinnell and Miller 1944; Miller 1968). However, following a 1976 estimate of 93 individuals (Byers 1976), concerns were raised about the long-term persistence of the San Clemente sage sparrow because of low population levels and

limited distribution, severe habitat degradation by feral goats (*Capra hircus*), predation pressure from feral cats (*Felis catus*), and habitat loss and degradation due to invasive plant growth and human disturbance (U.S. Fish and Wildlife Service 1976). In 1977, the U.S. Fish and Wildlife Service listed the San Clemente sage sparrow population as a federally threatened subspecies, but did not officially describe their critical habitat (Greenwault 1977). Before potential management actions such as habitat restoration can be considered, it is important to characterize the habitat requirements of this species.

Essential bird habitat is often assessed in terms of the "quality" of the habitat to a particular life stage and most often refers to nesting habitat (Pidgeon et al. 2006). Willey (1997) was the first to describe the nesting habitat used by San Clemente sage sparrows in 1985, and he reported that they nested exclusively in boxthorn. However, his study was restricted to a single breeding season and his sample size was limited by a small population (Willey 1997). The Institute for Wildlife Studies

(IWS) has monitored the sage sparrow population on San Clemente Island since 1999, and has documented several other substrates used for nesting (Beaudry 2004; Kaiser et al. 2007). The objective of this paper is to determine the importance of boxthorn to successful reproduction and recruitment for the resident sage sparrow population. To achieve this objective, we utilized data from 1999 through 2006 to compare nest survival among different nest substrates. We also examine the influence of other nest site characteristics on the probability of nest failure. Examining the importance of nest substrates and characteristics of nest sites to successful reproduction will improve our understanding of the relationship between habitat preferences and suitability.

METHODS

Study Species

Sage sparrows are socially monogamous (Martin and Carlson 1998), but male polygyny is not uncommon and varies annually (Kaiser et al. 2007). Adults begin reproducing in their first year (Hyde 1985) and can attempt up to five nests in a breeding season (Stahl et al. 2008). The timing of territory establishment may depend on winter rainfall patterns, with establishment in late December after high rainfall totals and later in the season with drought conditions (Beaudry et al. 2003; Stahl et al. 2008). Breeding activity and breeding season length may also depend on rainfall, with peak activity occurring during March and April (Hyde 1985). During their breeding months, sage sparrows are mostly found on the lower marine terraces along the western shore of SCI in maritime desert scrub habitat. However, sage sparrows have been observed in small numbers on the central plateaus, along the eastern slope where a narrow band of maritime sagebrush (*Artemisia californica*) is found, and in canyons in woody shrubs (Hyde 1985; Kaiser et al. 2007).

Study Area

San Clemente Island (118° 30'W, 33° 00'N) is the southernmost of the California Channel Islands located approximately 92 km off the coast of California. The island is 14,764 ha in area extending 34 km north to south and between 2.5 and 6.5 km east to west. SCI is characterized by a series of marine terraces on the west side and a steep escarpment on the east side. The island experiences a Mediterranean dry summer subtropical climate with mild average mean summer and winter temperatures of 18°C and 13°C, respectively, with almost constant 8–24 km/h wind speeds. SCI receives an average of 13 cm of rainfall annually, mostly between December and April, and is often covered by heavy fog along the coastline.

The lower western and southern marine terraces of SCI are associated with the maritime desert scrub – boxthorn plant community. At lower elevations, maritime desert scrub habitat is dominated by boxthorn interspersed with snake cactus (*Bergerocactus emoryi*), island tarplant (*Deinandra clementina*), Australian saltbush (*Atriplex semibaccata*), California saltbush (*Atriplex californica*), coastal prickly-pear cactus (*Opuntia littoralis*), mixed grasses (*Avena* spp., *Stipa comata*, and *Hordeum jubatum*) and forbs, and lichen cover on shrubs (Kellogg and Kellogg 1994). At higher elevations, maritime desert scrub habitat is dominated by prickly pear and coastal cholla cactus (*Opuntia prolifera*).

The study region monitored by IWS extends along the western shore of the island and includes land cover that is predominantly the maritime desert scrub – boxthorn plant community (Fig. 1). In 1999, eight 12.5 ha study plots were established to monitor a portion of the sage sparrows on San Clemente Island (Munkwitz et al. 2000). Locations of the plots were based on documented habitat use by San Clemente sage sparrows (Hyde 1985; Willey 1990; KEA 1997), and plot sizes were dictated by dimensions of the marine terraces. In 2000, after sage sparrow nesting pairs were detected in areas they had not previously been known to occupy, the eight original plots were replaced with six larger plots ranging in size from 20 to 40 ha (Munkwitz et al. 2000). Three plots on the lower terraces covered the area monitored in 1999. In addition, two plots were located on mid-level terraces, and one plot was located on an upper terrace (Munkwitz et al. 2000). In 2002, the sampling design was adjusted according to improved knowledge of sage sparrow distribution and density patterns, adding one plot to the mid-level terrace and one plot to the upper terrace, and removing one plot from the lower
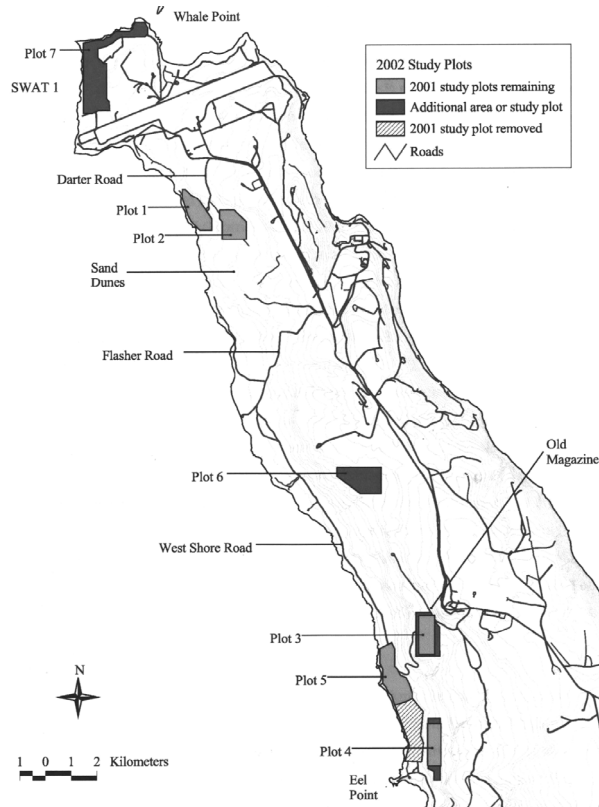
Figure 1. Location of the study plots searched for San Clemente sage sparrow nests on San Clemente Island, California. Plot boundaries from 2000–2001 (in gray) were refined in 2002 to include additional area (plots 3, 4, 6, 7, in black) and reduce area (plot 5, hatched).

terrace (Beaudry et al. 2003). The sizes of these plots ranged in size from 20 to 60 ha. The distance between two plots on the same terrace was 2–4 km, and plots on different terraces were 50 m apart. For six of the study plots we placed pin flags every 50 m in a grid system to facilitate nest searching. For the seventh plot, which was located in a military training range, we generated a map using a global positioning system receiver (GPS; Garmin eTrex Venture®, GARMIN Corporation, Olathe, KS) by marking landmarks such as boulders, posts, and fences.

Nest Monitoring

We searched for San Clemente sage sparrow nests in each established study plot throughout the breeding season (February – July) from 1999 through 2006. We located nests by observing behavioral cues such as adults carrying nesting material, food, or removing fecal sacs from nests, and followed incubating females returning to their nests (Martin and Geupel 1993). In addition, we located nests on an *ad hoc* basis outside of the plot boundaries while walking line transects surveyed as part of our larger monitoring project. We found most nests during the building and laying stages and estimated the age of each nest when it was found. If, however, a nest was found during the incubation or nestling stages, we estimated nest age by backdating using the average length of each nest stage calculated from previous years of data. We monitored nests every three to five days to determine the status of the contents, until the nest fledged or failed. We visited the nest more frequently during the fledging window and recorded a nest as fledged if a parent was seen with at least one young near the nest or if parents were behaving as if dependents were nearby (i.e., parents seen carrying food several times to one or more locations on the ground and reappearing without food; Ralph et al. 1993). We recorded a nest as failed if the nest was abandoned with eggs or nestlings in the nest or if the nest was depredated. We recorded a nest as depredated if the predation event was observed, if there was damage to the nest structure (e.g., nest torn out of substrate) with remains of eggs (e.g., broken eggshells) or nestlings, or if no parents were observed near the nest with fledglings and the nest was empty and intact (Ralph et al. 1993). If no adult behavior was observed and there was no evidence of predation or fledging at the nest site, we assigned the nest an uncertain fate. A nesting attempt was considered successful if at least one San Clemente sage sparrow fledged. We recorded locations of nests using a GPS receiver and marked them with flagging at a 5 m distance.

Nest Site Characteristics

From 1999 through 2006, we collected data on the primary species of plant supporting each nest (nest substrate). From 2000 to 2005, we measured eight additional characteristics of each nest site (height, distance to canopy, distance to center, distance to edge, substrate height, substrate width, vertical nest concealment, and horizontal nest concealment) after nests became inactive. Nest height, distance to canopy, distance to center, and distance to edge were respectively, the distance from the rim of the nest to the ground, top of shrub, center of the shrub, and nearest edge. Substrate height and width were height and maximum width

of the supporting nest substrate. We quantified nest concealment by visually estimating the percentage of the nest hidden through vegetation by standing 1 m in front of the nest from the four cardinal directions and from 1 m directly above the nest. We report vertical concealment as the amount of concealment from above. Horizontal concealment is the mean concealment among the four cardinal directions.

Statistical Analyses

The Mayfield method (Mayfield 1961, 1975) was used to estimate mean daily nest survival rates (DSR) during the incubation and nestling stages for each nest substrate species that supported greater than 15 nests (Table 1), which is the minimum sample size recommended for accuracy using Mayfield's method (Hensler and Nichols 1981; Hines and Sauer 1989). We terminated exposure (i.e., number of days during which a nest was observed) using Mayfield's midpoint approach for nests of known fate, which assumes that nests failed between nest check intervals (Mayfield 1975; Manolis et al. 2000). We used data collected from 1999 through 2006 to calculate the average length of the incubation stage (12 days) and the nestling stage (11 days). These averages were based only on nests that we found prior to the beginning of the stage and that successfully completed that stage in the nesting cycle. Nest survival rates (NSR) for the entire nesting cycle were calculated as the product of the stage survival rates (SSR) for the incubation and nestling stages. Standard errors and confidence intervals for Mayfield estimates were calculated according to Johnson (1979).

Our primary objectives were to determine whether nest survival was lower in boxthorn nests and whether nest substrate influenced nest failure rate. We used χ^2 tests in program CONTRAST (Hines and Sauer 1989) to determine whether boxthorn DSR were significantly different from all other nest substrates combined. Comparisons were made for the incubation and nestling stages separately and for the entire nesting cycle because Mayfield's method assumes constant survival over the entire nesting cycle, which is an assumption that is often violated and can lead to biased estimates (Manolis et al. 2000). It is not possible to examine factors that affect nest survival rates using Mayfield's method except for grouping the data by the different levels of the factor, which is limited by sample size. This approach restricts the examination of multiple potential factors influencing nest survival. Thus, we compared DSR among substrate types (e.g., woody shrub/sub-shrub, cactus, grass and forbs, non-woody shrub/sub-shrub; Table 1). We grouped nest substrates by these substrate types to utilize all nest substrate data in comparisons of DSR among vegetation that had similar characteristics for nest support, protection, and concealment. We chose to use Mayfield's method because DSR are widely reported and this allows for direct comparison with DSR of nesting sage sparrow subspecies on the mainland. We also report apparent nest success, which is the ratio of successful nests to total nests found.

With the eight-year nest site characteristics dataset, we used survival time analysis with Cox proportional hazards regression as an alternative to Mayfield's method to examine the influence of year, elevation, and nine nest site characteristics including nest substrate on the probability of daily nest failure rates (PROC PHREG; SAS Institute 2004). Mayfield's method has limited power to detect significant differences in statistical comparisons if the sample size of nests in each group is small, which results in wide confidence intervals and less robust estimates (Manolis et al. 2000; Hazler 2004). Thus, because the majority of sage sparrow nests were supported by boxthorn, we needed a more powerful analysis to detect potential differences in nest survival between boxthorn and all other nest substrates. We evaluated nest survival time (exposure days) as risk factors and included nest fate as a censor variable, where successful and uncertain nests were censored and failed nests uncensored. In this semi-parametric regression model there is no underlying distribution assumption and the hazard of any nest is a fixed proportion of the hazard for any other nest (Allison 1997). The hazard ratios are the effects of each nest site characteristic on the risk of nest failure. The hazard function is unspecified; therefore it is difficult to obtain actual estimates of daily nest survival (Hazler 2004), which is another reason why we report Mayfield's DSR estimates. Cox regression does not assume constant mortality and the response variable is exposure days, rather than nest fate (Manolis et al. 2000). Nests that are observed only during the incubation or nestling

Table 1. Species of vegetation that supported 870 San Clemente sage sparrow nests of known and uncertain fate on San Clemente Island, California, 1999–2006. We only included species that supported >1% of the nests in our sample. Thirty-one nests were built in substrates that represented <1% of the nests in our sample.

Species	Nest substrate type	n	Percent of total
Boxthorn (*Lycium californicum*)	Woody shrub sub-shrub	636	73.1
Island tarplant (*Deinandra clementina*)	Woody shrub sub-shrub	42	4.8
Island butterweed (*Senecio lyonii*)	Woody shrub sub-shrub	41	4.7
Grass (*Avena, Bromus, Hordeum, Nassella* spp.)	Grass and forbs	41	4.7
Snake cactus (*Bergerocactus emoryi*)	Cactus	20	2.3
Island morning glory (*Calystegia macrostegia amplissima*)	Woody shrub sub-shrub	20	2.3
Prickly-pear (*Opuntia littoralisi*)	Cactus	16	1.8
California wishbone bush (*Mirabilis californica*)	Non-woody shrub sub-shrub	13	1.5
Australian saltbush (*Atriplex semibaccata*)	Woody shrub sub-shrub	10	1.1
California saltbush (*Atriplex californica*)	Non-woody shrub sub-shrub	5	0.6
Silver birds-foot trefoil (*Lotus argophyllus argenteus*)	Non-woody shrub sub-shrub	4	0.5
Lupine (*Lupinus guadalupensis*)	Grass and forbs	4	0.5
Forb (Unknown spp.)	Grass and forbs	3	0.3
Russian thistle (*Salsola tragus*)	Non-woody shrub sub-shrub	2	0.2
Clover (*Trifolium* spp.)	Grass and forbs	2	0.2
Pineapple weed (*Amblyopappus pusillus*)	Grass and forbs	1	0.1
Sagebrush (*Artemisia* spp.)	Woody shrub sub-shrub	1	0.1
San Clemente Island milk-vetch (*Astragalus nevinii*)	Woody shrub sub-shrub	1	0.1
Island sunflower (*Encelia californica*)	Woody shrub sub-shrub	1	0.1
Fern (Unknown spp.)	Grass and forbs	1	0.1
(*Gnapthalium* spp.)	Grass and forbs	1	0.1
Leafy Malacothrix (*Malacothrix foliosa*)	Grass and forbs	1	0.1
Cholla (*Opuntia prolifera*)	Cactus	1	0.1
Threadstem (*Pterostegia drymarioides*)	Grass and forbs	1	0.1
Pickleweed (*Salicornia subterminalis*)	Non-woody shrub sub-shrub	1	0.1
Wirelettuce (*Stephanomeria* spp.)	Non-woody shrub sub-shrub	1	0.1

period are not given the same weight as nests observed throughout the entire nesting period. For the nest substrate variable, nests supported primarily by boxthorn were binary coded (1) and all other nest substrates were coded (2). Year, elevation, substrate width and height, vertical and

horizontal nest concealment, nest height, and nest distance to substrate edge, center, and canopy were entered as continuous variables. We excluded 44 nests with uncertain nest fates from the analysis to improve our ability to detect differences between successful and failed nests.

RESULTS

We monitored 870 sage sparrow nests on the seven study plots between 1999 and 2006. Of 307 failed nests, eight (3.7%) were abandoned after eggs failed to hatch and all of the remaining 209 (96.3%) nest failures were attributed to predation. Eighty-three nests were depredated during the incubation stage and 126 during the nestling stage. Apparent nest success was 75% over all years and the entire nesting cycle.

Between 1999 and 2006, sage sparrows were observed to nest in 25 nest substrates (Table 1). The range of the nest site characteristics measured between 1999 and 2006 was large, but the variation around the mean measurement for each variable was small (Table 2).

For each substrate with >15 observations, Table 3 presents daily survival rates for the incubation and nestling stages, as well as stage survival rates for the incubation stage, nestling stage, and nest survival rate for the entire nesting cycle. Mean daily survival rates of nests in all substrates combined were 0.982 ± 0.002 for the incubation stage and 0.981 ± 0.002 for the nestling stage. The incubation stage survival was 80%; the nestling stage was 81%; and the nest survival rate was 65% for all substrates combined (Table 3).

Results of the chi-square tests indicated that there were no significant differences in daily nest survival rates between boxthorn and non-boxthorn nest substrates for the incubation ($\chi^2_1 = 1.0$, $P = 0.32$) and nestling stages ($\chi^2_1 = 1.0$, $P = 0.33$), or for the entire nesting cycle ($\chi^2_1 = 1.8$, $P = 0.18$).

Results of the Cox regression model (Table 4) indicated that the risk of nest failure was significantly influenced by year ($\chi^2 = 11.3$, $P < 0.001$), nest substrate ($\chi^2 = 8.6$, $P < 0.01$), and the distance from the nest to the center of the nest substrate ($\chi^2 = 3.8$, $P = 0.05$). The hazards ratios (Table 4) suggest that nests built in substrates other than boxthorn were 1.14 times more likely to fail,

the risk of failure increased the further from the center of the nest substrate the nest was placed, and failure rates differed among years.

DISCUSSION AND CONCLUSIONS

The nesting area of San Clemente sage sparrows was first described by Willey (1997) based on 31 monitored nests in a single breeding season. We collected measurements on 870 nests over an eight-year period and some of Willey's (1997) initial findings were supported by our data. However, we also gained new insights into the importance of boxthorn to the successful reproduction of sage sparrows on SCI.

While the nests that Willey (1997) found were built exclusively in boxthorn, we discovered that San Clemente sage sparrows are capable of greater flexibility in their choice of nest substrates. Although species other than boxthorn accounted for

Table 2. Means and standard errors of nest site characteristics of San Clemente sage sparrow nests on San Clemente Island, California, 1999–2006.

Variable	n	Mean ± SE	Range
Elevation (m)	713	46 ± 2	0–169
Nest substrate	815	-	-
Substrate width (cm)	662	383 ± 11	20–2200
Substrate height (cm)	664	55 ± 0.6	25–167
Vertical nest concealment (%)	649	67 ± 1	0–100
Horizontal nest concealment (%)	651	91 ± 1	18–100
Nest height (cm)	642	24 ± 0.3	7–69
Nest distance to substrate edge (cm)	648	46 ± 2	0–315
Nest distance to substrate center (cm)	601	67 ± 3	0–580
Nest distance to substrate canopy (cm)	641	25 ± 0.3	0–75

Table 3. Mayfield's daily nest survival rates (DSR), associated standard errors (SE), and stage survival rates (SSR) during the incubation and nestling stages, apparent nest success and the nest survival rates (NSR) of San Clemente sage sparrow nests on San Clemente Island, California for each nest substrate and substrate type, 1999–2006.

	Incubation stage		Nestling stage		Incubation and nestling stages				
Nest substrate	DSR ± SE	SSR (%)	DSR ± SE	SSR (%)	Nests with eggs or young	Nests lost	Nests with uncertain fate	Apparent nest success	NSR (%)
Boxthorn (*Lycium californicum*)	0.983±0.002	81.7	0.982±0.002	81.9	636	148	27	76.7	66.9
Island butterweed (*Senecio lyonii*)	0.995±0.005	94.6	0.982±0.007	81.5	41	8	0	80.5	77.1
Island tarplant (*Deinandra clementina*)	0.972±0.010	71.8	0.972±0.010	73.4	42	16	4	61.9	52.7
Grass (*Avena, Bromus, Hordeum, Nassella* spp.)	0.979±0.009	77.2	0.978±0.008	77.9	41	13	5	68.3	60.1
Snake cactus (*Bergerocactus emoryi*)	0.969±0.015	68.3	1.000±0.000	100	20	4	2	80	68.3
Island morning glory (*Calystegia macrostegia amplissima*)	0.963±0.018	63.4	0.978±0.013	77.9	20	7	3	65	49.4
Prickly-pear (*Opuntia littoralis*)	1.000±0.000	100	0.976±0.014	76.7	16	3	1	81.3	76.7
Total	0.982±0.002	80.5	0.981±0.002	80.9	870	217	44	75.1	65.1
Woody shrub/ sub-shrub	0.982±0.002	80.6	0.981±0.004	80.8	752	185	35	75.4	65.1
Cactus	0.981±0.009	79.5	0.989±0.006	88.8	37	7	3	81.1	70.6
Grass and forbs	0.982±0.007	80.0	0.973±0.008	74.3	55	18	5	67.3	59.1
Non-woody shrub/sub-shrub	0.983±0.012	81.7	0.974±0.012	74.3	26	7	1	73.1	61.1

just 25% of the nests we monitored, we found nests supported by 25 different plant species. The apparent increase in the number of nest substrates used by sage sparrows since Willey's (1997) study may have resulted from vegetation recovery after feral goats were removed in 1992. Another potential explanation for the increase in substrate use is that baseline data from Willey (1997) was spatially biased because study plots were restricted to habitat containing higher densities of sage sparrows and greater cover of boxthorn on the two lower marine terraces. Boxthorn density has been shown to be significantly lower on upper terrace plots compared to lower and mid-level study plots (Kellogg and

Table 4. Cox proportional hazards regression results examining the effect of elevation and nine nest site characteristics on the probability of daily nest failure rates in San Clemente sage sparrow nests on San Clemente Island, California, 1999–2006. In the regression model, the hazard for any nest is a fixed proportion of the hazard for any other nest.

Variable	χ^2	P-value	Hazard ratio
Year	11.3	<0.001	1.211
Elevation (m)	0.2	0.64	1.001
Nest substrate	8.6	<0.01	1.140
Substrate width (cm)	0.7	0.42	0.953
Substrate height (cm)	0.02	0.89	0.883
Vertical nest concealment (%)	0.2	0.67	1.002
Horizontal nest concealment (%)	0.9	0.36	1.008
Nest height (cm)	0.1	0.74	0.995
Nest distance to substrate edge (cm)	0.6	0.45	1.002
Nest distance to substrate center (cm)	3.8	0.05	1.003
Nest distance to substrate canopy (cm)	0.5	0.48	1.009

Kellogg 1994; Munkwitz et al. 2002). Our study design incorporated existing data on spatial variability in sage sparrow and boxthorn density, allowing us to sample all available habitats on the three terrace levels when the study plots were established. The difference in the number of nest substrates observed in Willey's (1997) study compared to ours may partially be explained by these density patterns. However, our data did not support the argument that these new nest substrates were used more frequently where boxthorn cover was lower at higher elevations.

Boxthorn had only the fourth highest Mayfield's nest survival rate following island butterweed, snake cactus, and prickly pear. However, there were no significant differences in comparisons of Mayfield's nest survival among nest substrates and the sample size of nests was low in the latter three substrates with 73% of the nests

found in boxthorn. Island butterweed is a dense, leafy woody sub-shrub that is uncommon in high densities on the lower marine terraces along the western shore where sage sparrows breed (K. Klementowski, pers. comm.). Typically, island butterweed will leaf out in the spring and become dormant by mid-summer and lose its lower leaves (Hickman 1993), which would reduce its effectiveness at concealing nests later in the season. The nests we found in island butterweed became active during the first few months of the breeding season (January – April) in normal to wet years only. No nests were initiated in this substrate in the later months of the breeding season when its canopy cover would be reduced. Snake cactus and prickly pear are low, sprawling plants that grow in wide, tangled clumps. Snake cactus is protected by interlacing spines and prickly pear by very sharp narrow spines that may deter nest predators. While all three of these substrates do provide cover and protection from aerial and ground predators during nesting, they may not be as effective as boxthorn at concealing fledglings or providing immediate food resources (i.e., invertebrates, fruit) for nestlings, fledglings, and adults. However, cacti are interspersed throughout boxthorn habitat and nests built in cacti may benefit from proximity to boxthorn (Willey 1997), which is a spatial component that should be addressed in future research.

Among the substrate types, cacti had the highest Mayfield's nest survival rate followed by woody shrubs/sub-shrubs, non-woody shrubs/sub-shrubs, and grass/forbs. These results were consistent with the high nest survival rates observed in two cacti species and the woody shrub/sub-shrub results were likely driven by nests built in boxthorn, which made up the majority of the sample. Despite that nest survival rate was highest in cacti, this was not significant and sage sparrows nested predominantly in boxthorn. As mentioned previously, cacti may offer greater structural protection against predators compared to other substrate types (Hernandez et al. 2003).

In addition, we found that nest failure differed among years. However, it is difficult to interpret the hazard for each year separately because the Cox regression treats year as a continuous variable. Thus, it is not possible to compare estimates of nest failure rates among years. The timing of nest

initiation varies considerably among years, which is influenced by rainfall (Kaiser et al., in prep). Weather conditions likely influenced the availability of nest substrates and their effectiveness at concealment from predators and protection from inclement weather.

Our results comparing nest survival between boxthorn and non-boxthorn substrates differed between the Cox proportional hazard regression and Mayfield analyses. The chi-square analysis in CONTRAST indicated no significant difference in daily nest survival rates between boxthorn and non-boxthorn nest substrates for the entire nesting cycle, and no significant difference in daily nest survival rates among nest substrate types. However, the Cox regression analysis determined that the risk of nest failure was significantly greater for nests built in substrates other than boxthorn. There are three potential explanations for this finding. First, the sample sizes used in the Mayfield analysis included 44 nests that were not included in the Cox proportional hazard regression, which consisted of 16 nests in non-boxthorn substrates. These nests could have influenced the probability of nest failure in non-boxthorn substrates considering the low sample of nests found in non-boxthorn substrates.

We excluded nests with uncertain nest fates in the regression analysis to improve detection of biologically meaningful differences between successful and failed nests where nests with uncertain outcomes were censored from analysis (Hazler 2004). We did not exclude nests with uncertain nest fates in estimates of nest survival by Mayfield's method because the exclusion of nests with uncertain nest fates can lead to more biased estimates and influence statistical comparisons (Manolis et al. 2000). Second, Cox proportional hazard regression may be more sensitive to differences in nest survival and hence more powerful than comparisons of DSR because the assumption of constant mortality is relaxed. This is especially important considering that there may be seasonal influences on the selection of available nest substrate and differences in concealment in those substrates across the nesting cycle and season (e.g., island butterweed). Thirdly, differences in DSR among substrates may reflect low power of the Mayfield method rather than a true or biologically meaningful equivalence among substrates because of the wide confidence intervals for nest substrate

types with only the minimum recommended sample size for analysis.

Several factors can potentially explain sage sparrow preferences in their selection of nesting habitat. The first is reduced predation risk. The nest survival rate of San Clemente sage sparrows, calculated at 65% for the years between 1999 and 2006, was much higher than that reported for similar subspecies on the mainland. Sage sparrows in central Oregon experienced nest survival rates as low as 17% (Rotenberry and Wiens 1989). The apparent nest success of San Clemente sage sparrows, calculated to be 75%, was also high compared to the 26% reported for mainland sage sparrows nesting in southern California (Misenhelter and Rotenberry 2000). San Clemente sage sparrows may have higher nest survival relative to the mainland subspecies because of a less diverse suite of potential nest predators. In central Oregon and southern California, snakes were the primary nest predator of mainland sage sparrows (Rotenberry and Wiens 1989; Misenhelter and Rotenberry 2000), but snakes were absent on SCI. Other predators not found on SCI that were implicated in nest failures on the mainland included long-tailed weasels (*Mustela frenata*) and chipmunks (*Eutamias spp.*) (Rotenberry and Wiens 1989). Moreover, San Clemente sage sparrows do not encounter brown-headed cowbirds (*Molothrus ater*) on the island, which were observed to be a major source of nest failure of sage sparrows nesting in southeastern Idaho and Washington (Reynolds 1981; Vander Haegen 2007). However, the island subspecies is vulnerable to predation by avian predators including the common raven (*Corvus corax*), American kestrel (*Falco sparverius*), San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*), barn owl (*Tyto alba*), and migratory raptors and owls. Potential mammalian predators include the feral cat, island fox (*Urocyon littoralis clementae*), black rats, and mice (*Peromyscus maniculatus* and *Mus musculus*) (Hyde 1985; USN 2002). Boxthorn habitat was thick, thorny, and likely more difficult to maneuver in, and the placement of nests within boxthorn shrubs where the vegetation was most dense may have provided maximal concealment and protection from predators.

Nesting in the center of the shrub may have offered protection from the wind, provided shading,

and reduced heat loss (Rich 1980). Willey (1997) demonstrated that sage sparrows on SCI placed their nests most often on the leeward side of boxthorn shrubs and suggested that their non-random nest placement would provide protection from the intense, prevailing winds that the west shore marine terraces regularly endure. Sage sparrows nesting in the Great Basin were sagebrush obligates and showed similar preferences in nest orientation (Peterson and Best 1985). Additionally, boxthorn acts as a substrate for insects, caterpillars, and spiders and produces seeds and berries throughout the breeding season (Hyde 1985). Thus, nesting in boxthorn may have provided a direct benefit by supporting a greater variety of food resources that could be acquired under concealment, necessary for the production of young (i.e., invertebrates and seeds), feeding of young and dependents (invertebrates) (Willey 1988; Martin and Carlson 1998), and surviving the molting period (i.e., fruit, invertebrates, and seeds) (Hyde 1985). Further, boxthorn offers numerous perches for singing males and enables females to enter their nests from any direction.

The condition and trend of SCI's plant communities between 1994 and 2003 were compared to baseline surveys conducted between 1992 and 1993 (USN 2004). Areas of SCI that were previously mapped as grassland or maritime desert scrub – grassland prior to goat eradication showed an increase in shrub cover after 1993 and was comprised of as much as 35% boxthorn (USN 2004). Maritime desert scrub – boxthorn habitat showed a maximum increase in boxthorn frequency of 35% (USN 2004). The increase in shrub cover appeared mostly at higher elevations in the southern part of the island (USN 2004) where goats were historically more abundant (USN 2002). Hence, although we do not know the pre-disturbed composition of vegetation prior to goats, the vegetation trends post eradication suggest that sage sparrow habitat has the potential to recover now that feral animals have been extirpated from the island. The change in ground and shrub cover in their nesting habitat could influence their preference for nest substrates. In addition, the availability of substrates may vary annually because of differences in yearly rainfall. Boxthorn, snake cactus, prickly pear, and island morning-glory were available as substrates in both wet and dry years, whereas, herbaceous plants such as island tarplant, island butterweed, and grasses did not grow or did not survive long in years with lower rainfall (Kaiser et al. 2007).

In conclusion, San Clemente sage sparrows overwhelmingly built their nests in boxthorn and 25 new substrates were documented for nesting since Willey's (1997) earlier study. Although nest predation was considerably low for this population compared to mainland subspecies, the risk of nest failure was significantly reduced when pairs nested in boxthorn and placed their nests near the center of the shrub. These results suggest that the availability of boxthorn as nesting habitat may be an important factor driving the distribution of the population across the island. Hence, the expansion of the population during the breeding season to habitat on the island not containing boxthorn is uncertain. However, we have observed seemingly suitable habitat that has remained largely unoccupied on the island across years when density and population levels have fluctuated (Kaiser et al. 2007). But given the importance of boxthorn to successful breeding, maritime desert scrub – boxthorn habitat should be evaluated further and protected as essential to the long-term persistence of this species.

We recommend exploring the factors affecting habitat use and dispersal to better understand the differences in foraging benefits and predation risk between boxthorn habitat and other available habitat dominated by cactus and grasses. This information will be especially important if habitat restoration becomes a necessary management consideration to offset increasing military use of maritime desert scrub – boxthorn habitat. Given the effect of year on nest failure rate, the influence of annual rainfall and temperature on the availability of nest substrates and nest failure among nest substrates should be investigated. Finally, we recognize that a species may require several habitat types for different stages of their life cycle and that breeding habitat requirements cannot fully be determined from nest site characteristics alone (Anders et al. 1998; Cohen and Lindell 2004). We advise investigating how habitat associations may differ during the fall and winter and examining mortality risks during these stages of their life cycle.

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