AVIAN RESPONSES TO RESTORATION: NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS IN SONG SPARROWS

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Abstract.—Riparian habitats typically support high diversity and density of both plants and animals. With the dramatic loss of riparian habitats, restoring them has become a priority among conservation practitioners. Diversity and density of avian species tend to increase following riparian restoration, but little is known about how restored habitats function to meet particular species' needs. Habitat structure is an important factor affecting species diversity and density and can influence nest-site selection and reproductive success. To evaluate habitat restoration, we examined interactions between habitat structure, nest-site selection, and nesting success in Song Sparrows (*Melospiza melodia*) nesting in restored, mature, and young naturally regenerating stands of riparian forest. We found that stand types differed markedly in structure, and that habitat structure influenced both nest-site selection and rates of nest loss to predation. Comparison of habitat structure among the three stand types indicated that restored stands offered fewer acceptable nest sites and poorer protection from nest predation. Concordant with those differences in habitat structure, Song Sparrows showed trends toward less density in restored stands than in mature forest, and had poorer nesting success as a result of predation. *Received 26 August 1999, accepted 27 November 2000.*

Riparian habitats support high diversity and density of both plants and animals, and provide important breeding areas for many obligate riparian species and critical stopover habitats for migrant birds (Knopf and Samson 1994, Knopf et al. 1988). Unfortunately, human activities have greatly diminished the extent of riparian habitat in the United States (Knopf et al. 1988). In the state of California alone, 89% of riparian areas have been lost in the last 150 years, and many of those remaining are degraded (Katibah 1984, Katibah et al. 1984). Consequently, restoring riparian habitats has become a priority among conservation practitioners (Warner and Hendrix 1984).

Several studies have found that birds respond favorably to riparian forest restoration, showing increases in both species diversity and density (Anderson et al. 1989, Farley et al. 1994, Dobkin et al. 1998, S. Laymon unpubl. data).

However, the ecological reasons why some species respond well to restoration, whereas others do not, are poorly understood. Moreover, that a species occurs at the same densities in both restored and natural areas may not be indicative of equivalent habitat quality because similar densities may result from source–sink dynamics (Van Horne 1983, Pulliam 1988, Robinson et al. 1995). Recently, a number of studies have shown a lack of correlation between density and reproductive success (Van Horne 1982, Vickery et al. 1992, Purcell and Verner 1998). Thus, understanding how species respond demographically to specific ecological variables in restored sites should help lead to better approaches to restoration.

Habitat structure is an important factor affecting species diversity and density (MacArthur and MacArthur 1961, Karr and Roth 1971). It can influence nest-site selection and reproductive success (MacKenzie and Sealy 1981, Martin and Roper 1988, Martin 1993), and consequently plays a significant role in response of various species to restoration. In this study, we examine nest-site selection and reproductive success in Song Sparrows (*Melospiza melodia*)

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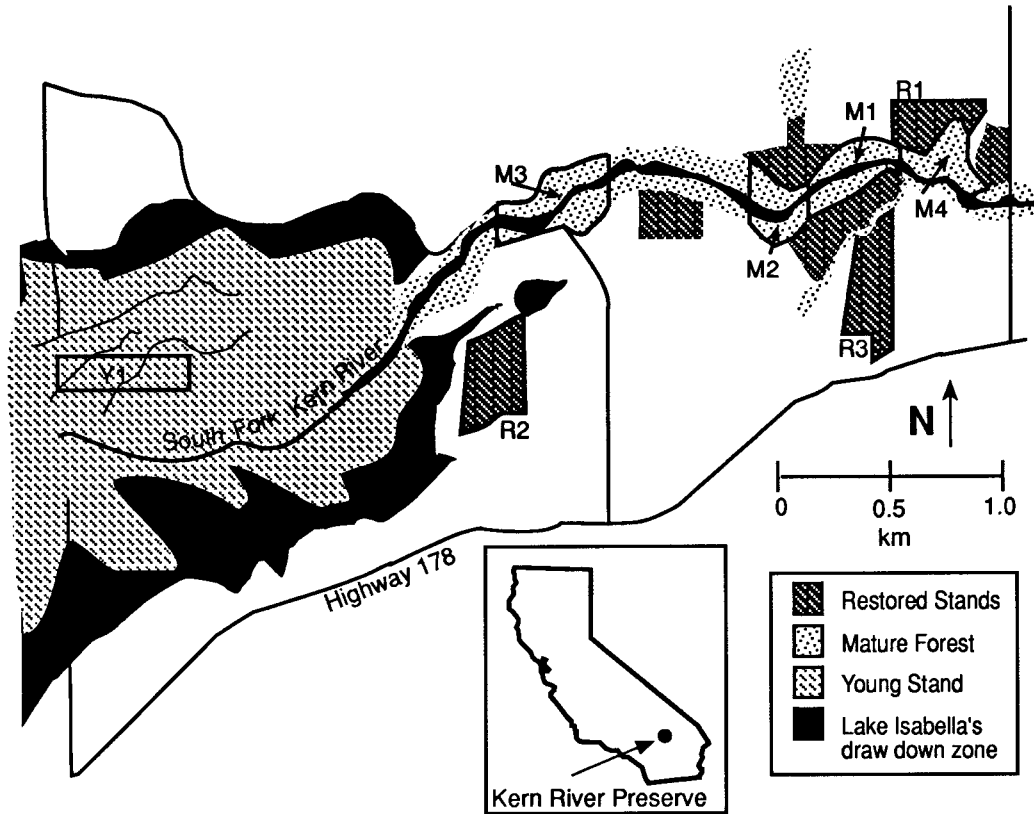[5] Present address: P.O. Box 1236, Weldon, California 93283, USA

FIG. 1.   Map of study area. Nests were located throughout the mature forest area shown. The three restoration sites (R1, R2, R3), four mature forest sites (M1, M2, M3, M4), and the young forest monitoring site (Y1) are shown in heavy outline in the figure. The Kern River flows from east to west in this region.

nesting in restored and natural riparian forest areas in southern California. To evaluate restored habitat, we compared reproductive success of Song Sparrows in mature and restored stands, using a young, naturally regenerating stand for comparison. Specifically, we (1) determine how forest structure differs among stand types, (2) compare Song Sparrow density and reproductive success among stand types, and (3) investigate how habitat structure affects nest-site selection and nest predation.

METHODS

Study sites and study species.—The study took place on The Nature Conservancy's Kern River Preserve in Kern County, California, from 1989 to 1994 (Fig. 1). The study area is located in the South Fork Kern River Valley (800 m elevation) at the southern end of the Sierra Nevada. The vegetation is characterized by willow–cottonwood riparian forest surrounded by uplands of desert scrub and oak woodland. Al-

though much of the original forest in the region was logged (Fleshman and Kaufman 1984), the remaining riparian forest is one of the most extensive in California. Since 1986, The Nature Conservancy has been restoring riparian habitat at the Preserve for the express purpose of increasing breeding habitat for obligate riparian birds.

Restored stands are located in secondary flood plain bordering mature forest (Fig. 1). Past agricultural use had resulted in substantial habitat degradation, including deforestation and introduction of alien grasses and forbs. Restoration efforts have involved planting native Fremont cottonwood (*Populus fremontii*), red willow (*Salix laevigata*), and a small amount of mule fat (*Baccharis salicifolia*). No revegetation of the understory has been attempted in most restoration areas, and winter grazing occurs in some years. Restoration areas remain dominated by alien grasses and forbs. We examined three, 14–20 ha restored stands in our study (Fig. 1); one (R1) was studied in both 1993 and 1994, and two (R2 and R3) were added in 1994. R1 was planted in 1991, R2 in 1989, and R3 in 1992.

The mature forest extends for several miles along the Kern River and had historically been grazed, but never deforested. In 1981, grazing ceased in the mature forest with the exception of winter grazing on a 20 ha area. Although not pristine, those habitats are much less degraded than other nearby ones and are dominated by native plant species in both the under- and overstory. Fremont cottonwood and red willow are the dominant tree species. Song Sparrow nests were monitored in four, 12–20 ha areas of the mature forest (Fig. 1). M1 is a mix of willow and cottonwood with understory of native herbs including stinging nettle (*Urtica dioica holosericea*), goldenrod (*Solidago spectabilis*), California mugwort (*Artemisia douglasiana*), and milkweed (*Asclepias fascicularis*). Interspersed are areas dominated by mulefat, and low marshy areas dominated by bulrush (*Scirpus* sp.) and cattails (*Typha* sp.). M2 is similar to M1, but is still grazed each winter. M3 is a marsh dominated by willow. M4 is dominated by cottonwood.

The young, naturally regenerating stand (hereafter referred to simply as the young stand) is in an area periodically inundated by a nearby reservoir, Lake Isabella. Riparian forest in that area had originally been cleared for agricultural use. Since 1986, the forest has been regenerating naturally and consists mostly of native Goodding's black willow (*Salix gooddingii*), the only willows able to withstand the frequent deep flooding by the reservoir. We monitored nests from a 16 ha area (Fig. 1) located in the U.S. Forest Service's South Fork Wildlife Area.

Song Sparrows were chosen for this study because they are among the first species to use restored stands, and because they are common enough in all stand types to enable us to gather enough data for comparative purposes. Additionally, in that arid region, they are dependent on riparian habitat for reproduction. Like many riparian obligate breeders, they are open-cup nesters that nest in forest understory, and are therefore subject to similar microclimatic factors, as well as predation from a similar suite of predators.

Quantification of habitat structure.—We compared habitat structure among stand types using random plots previously established to monitor changes in vegetation. To investigate the effect of habitat structure on nest-site selection, we compared habitat around nests ($n = 100$; 39 mature, 27 restored, and 34 young) to habitat in random plots ($n = 93$; 35 mature, 29 restored, and 29 young). Additionally, habitat surrounding successful nests was compared to habitat surrounding depredated nests to examine influence of habitat on nest predation. We included only first-known nesting attempts in analyses.

We characterized habitat structure at large and small scales relative to nests, referred to here as nest patch and nest site, respectively (sensu Martin and Roper 1988). Eleven variables at the scale of the nest patch, and seven variables at the scale of nest site were measured.

We characterized habitat structure of nest patch within 0.04 ha plots, centered either on a nest or a random point. Each plot had nine sampling points; one at the center, and one at 5 and 10 m intervals on each of four sampling lines radiating out at right angles to each other. Sampling lines were placed in four cardinal directions for the first plot and then shifted by 10° as we worked through the site. Habitat structure was measured at each sampling point, and points averaged to produce a single value for each plot. Variables include canopy cover, ground cover, foliage height, lateral cover at three levels (between 0 to 1 m, 1 to 2 m, and 2 to 3 m), number of trees in two size classes (8–50 cm diameter at breast height [DBH], and >50 cm DBH), and percentage cover of three major classes of understory plants—grasses, forbs, and shrubs. Canopy and ground cover were quantified using an inverted monocular with a 10-cell grid inscribed on a plastic prism, by counting the number of cells at least half filled with foliage (Laymon 1970). Foliage height was measured using a 3 m pole, marked in 0.1 m intervals. If the top of the foliage was above 5 m, we estimated height visually. Lateral cover quantifies the cover observed looking out from the nest to the edge of the nest patch. It was estimated using a white canvas cloth (0.5 m wide × 3 m high), divided vertically into three, 1 m high sections (0 to 1 m, 1 to 2 m, and 2 to 3 m). Each section was divided into a grid of 50 squares for ease of estimating cover. The cloth was placed 11.3 m from the nest, at the edge of the plot along each sampling line, and an observer at the center recorded percentage of squares at least half obscured in each vertical meter (Noon 1981).

Variables quantifying habitat structure at the nest-site scale included foliage cover within three vertical layers (between 0 to 1 m, 1 to 2 m, and 2 to 3 m), the number of saplings (3–8 cm DBH) within 5 m of the nest, and (for nests only) nest height, substrate, and concealment. Foliage cover was measured using a 3 m pole marked at 0.1 m intervals, with data recorded at the nest (or center of a random plot), and at 1, 2, and 3 m from the nest along four sampling lines. If foliage occurred within a radius of 0.1 m of the pole within a 0.1 m segment, we counted one hit. Hits were averaged for each vertical meter. All saplings within a radius of 5 m were counted. Nest concealment was measured using a 0.25 m radius cloth circle held directly in front of the nest. Concealment was the percentage of the circle visible 1 m from the nest, in four horizontal directions from the nest, and directly above (Martin and Roper 1988).

Density and reproductive success.—Numbers of avian breeding pairs were determined by the Kern River Research Center from spot counts conducted from early May to late June. Four observers rotated through 10 surveys per site. Locations of singing

males were supplemented by other types of vocalizations and visual sightings (Verner 1985). Densities were estimated in restored stands from 1989 to 1994, and mature forest from 1991 to 1994, whereas estimates for the young stand were obtained only in 1994. Number of sites surveyed varies among years because number of restored stands increased with planting, and not all mature sites were surveyed each year due to funding constraints.

In mature forest and restored stands, we estimated reproductive success over two seasons, May–August 1993 and April–August 1994. In the young stand, we monitored reproductive success during April–August 1994. Nests were monitored every three to four days (Martin and Guepel 1993). Nests surviving to the seventh day after hatching were considered successful and, to minimize disturbance, not monitored further. Song Sparrows fledge at approximately 10 days (Nice 1964), thus our estimates of success may be slightly elevated. Clutch size, number of young fledged, and nestling size were recorded for each nest. We used those measures of reproductive success to compare nests in restored stands to those in nearby mature forest, and nests in restored and mature stands to those in the young stand to control for differences due to forest age.

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) was common in the study area, and was much higher in mature than in restored stands in 1993 (Larison et al. 1998), but distributed more evenly among stand types in 1994. For that reason, only data from 1994 were used to compare clutch size and number of young raised among stand types. Clutch size could not be determined for nests parasitized prior to clutch completion. Additionally, cowbirds may remove host eggs either a few days before or on the same day as parasitizing a nest (Sealy 1992). For that reason, clutch size could not be determined for nests parasitized within two days after we found them. Such nests were excluded from analysis of clutch size. Parasitized nests were also excluded from analysis of number of young fledged. Nestlings were banded, measured, and weighed on the seventh day after hatching. Because mass is correlated with nestling and fledgling survival (Tinbergen and Boerlijst 1990, Hochachka and Smith 1991), mean nestling mass in nonparasitized nests was compared among stand types.

Statistical methods.—Factor analysis was used to examine habitat differences among stand types using patch scale variables. Although principal components analysis is more commonly used for exploratory data analysis, factor analysis explained more of the variance, using fewer factors, than did principal components analysis, and factor analysis was more appropriate for our data because it assumes that values of variables differ from each other by ratios consistent among samples (Manly 1986). Prior to analysis, variables were arcsin transformed to improve normality, and data were checked for linearity among pairs of variables and outliers. Variables that remained severely non-normal after transformation, lacked linearity in relation to other variables, or caused numerous cases to be outliers, were excluded from the analysis. Varimax rotation was then used after extraction of factors to obtain factor loadings. Factor scores were used to test for differences among stand types using one-way ANOVAs with Bonferroni post-hoc tests.

Logistic regression (Hosmer and Lemeshow 1989, Trexlor and Travis 1993) was used to examine nest-site selection using the program STATA 4.0 (StataCorp. 1995) for the Macintosh computer. Variables were analyzed univariately for inclusion in analysis ($P < 0.15$ for inclusion; Hosmer and Lemeshow 1989), and logistic regressions were run manually in a forward stepwise manner, using likelihood ratio tests to help determine which variables should be added or dropped. Models for nest-site selection and nest predation were constructed on the basis of significance of the logistic model, parsimony, and tests of goodness-of-fit (Hosmer and Lemeshow 1989). Because some factors associated with nest-site selection differed among stand types, stand type was added to the logistic regression for nest-site selection using three binary indicator variables (Hosmer and Lemeshow 1989).

To further examine suitability of the three stand types for nesting sparrows, we examined availability of nest sites on the basis of the foliage characteristics that most strongly influenced their choice of nest site. To do that, we used the mean value of foliage cover at Song Sparrow nests to separate random plots into those that were better or poorer than average, for each variable, and compared stand types using contingency table analyses.

Song Sparrow densities were compared between restored and mature stands using a Mann-Whitney *U* test (Sokal and Rohlf 1995). Because there was only one young stand, density differences between it and other stand types could not be tested. To determine whether restored stands provided adequate nesting habitat for sparrows, we first estimated daily nest survival rates and standard errors using the program Mayfield (Hines 2000), which is based on methods described in Bart and Robson (1982). We then used the program CONTRAST (Hines and Sauer 1989) as described by Sauer and Williams (1989) to compare daily survival rates among stand types. Clutch size, number of young fledged per successful nest, and mean nestling mass were tested using one-way ANOVA or Kruskal-Wallis, depending on whether data satisfied assumptions of normality and homogeneity of variances (Sokal and Rohlf 1995).

RESULTS

Habitat structure in the three stand types.—The three stand types differed significantly in hab-

TABLE 1. Factor loadings for habitat variables.

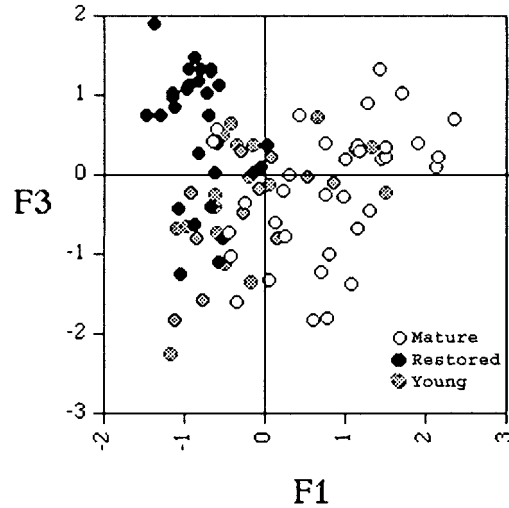| Variable	F1	F2	F3
Percent of Variance			
Explained	53%	26%	21%
Percent canopy cover	0.90	0.22	0.02
Percent ground cover	−0.69	0.01	0.02
Foliage height	0.85	0.14	−0.11
Percent lateral cover,			
0 to 1 m	−0.01	0.57	−0.41
Percent lateral cover,			
1 to 2 m	0.25	0.85	−0.07
Percent lateral cover,			
2 to 3 m	0.10	0.78	0.05
Percent grass cover	−0.51	−0.02	0.67
Percent forb cover	−0.10	0.06	−0.81

FIG. 2. Differences in habitat structure among three forest types on the basis of factor analysis. F1 corresponds to tree size, and F3 to understory foliage type.

itat structure (Table 1, Fig. 2). The first three factors explained 99% of variance, and reflected differences in tree age or size (F1), lateral cover (F2), and type of understory foliage cover (F3). All stand types differed significantly on F1 ($F = 46.9$, df = 2 and 90, $P < 0.001$; post-hoc tests $P < 0.002$ in all cases); restored stands had low canopy cover and low foliage height, whereas mature forest had high canopy cover and foliage height, and the young stand was intermediate. Stand types did not differ significantly from each other along F2 ($F = 0.85$, df = 2 and 90, $P < 0.44$). Restored stands scored highest on F3 ($F = 10.41$, df = 2 and 90, $P < 0.001$; post-hoc tests $P < 0.001$), but young and mature stands scored similarly (post-hoc test $P < 0.99$); restored stands had more grass cover and less forb cover than the natural stands.

Sparrow density.—Song Sparrow densities increased across years for both mature (Spearman's $\rho = 0.77$, $P = 0.005$) and restored stands (Spearman's $\rho = 0.37$, $P = 0.008$). Density of Song Sparrows appeared to be lower in restored stands than in mature forest for most years (Fig. 3). With only one data point for the young stand, it was only possible to test statistically for differences between mature and restored stands. Mann-Whitney *U*-tests were only marginally significant for two of three years with sufficient data, (1992: $P = 0.03$ and 1994: $P = 0.02$; P value required for significance = 0.016), and not significant in 1993 ($P = 0.17$). In 1994, Song Sparrow numbers in mature forest were more than twice those in restored stands, and on the young stand, sparrow numbers were more than twice those in mature forest. In 1991, only one mature forest site was

monitored, but numbers were four times those found on restored sites.

Nest-site selection.—Logistic regression showed that habitat structure at the nest-site scale was a significant factor in nest-site selection (Model $\chi^2 = 49.9$, df = 6, $P < 0.001$; Hosmer-Lemeshow goodness-of-fit: $\chi^2 = 5.5$, df = 6, $P < 0.48$). The probability of a site being selected for nesting in-
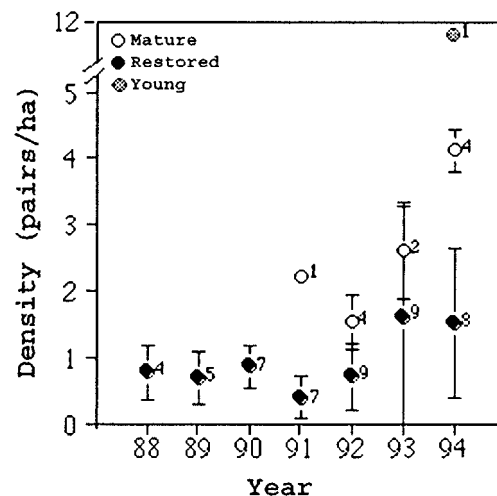

FIG. 3. Mean Song Sparrow densities in three riparian forest types from 1989–1994. Error bars represent standard deviations; numbers indicate sample size.
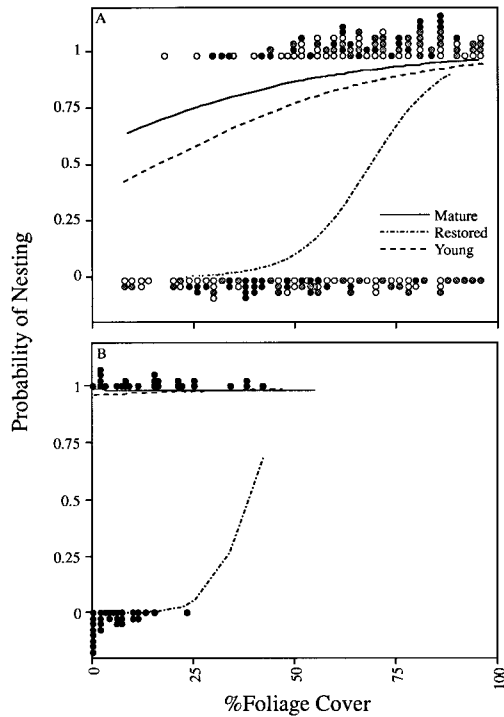
Fig. 4. Probability of Song Sparrow nest-site selection predicted from logistic regression on habitat structure. (A) Selection on foliage cover between 0 to 1 m. Individual plots are represented by small circles, with a probability of 0 for random points and 1 for nests. Open circles are from mature forest, gray from young forest, and black from restored forest. (B) Selection on foliage cover between 2 to 3 m. Individual plots are shown only for restored forest, the only forest type in which sparrows selected for that variable.

creased as foliage cover in the vertical layer between 0 to 1 m increased (Fig. 4A; Partial coefficient = 0.04, Wald's z = 5.0, P < 0.01). That relationship was found in all stand types, although the strength of the relationship was strongest in restored stands. Nearly all sparrows (99%) placed their nest within 1 m of the ground, so it is not surprising that sparrows selected greater foliage cover between 0 to 1 m. In restored stands, sparrows were increasingly likely to build on a site as foliage cover in the layer between 2 to 3 m increased (Fig. 4B; Partial coefficient = 0.15, Wald's z = 3.0, P < 0.04). Sparrows in young and mature natural stands, however, did not exhibit a similar preference (young P < 0.31, mature P < 0.88). The resulting model correctly classifies nests and random

plots 71% of the time. The significantly lower probability of nesting in restored stands when compared to mature (Fig. 4; Partial coefficient = 1.36, Wald's z = 2.2, P < 0.03), suggests that restored stands are less suitable for nesting Song Sparrows.

At patch scale, lateral cover in the layer between 0 to 1 m and foliage height appear to influence selection (Model χ^2 = 26.7, df = 6, P < 0.001). Probability of a patch being used for nesting increased in all stand types as lateral cover increased (partial coefficient = 0.05, P < 0.003). Response to variation in foliage height varied among stand types. The probability of a patch being used for nesting decreased with increasing foliage height in mature forest (partial coefficient = −0.18, P < 0.04), and increased as foliage height increased in restored stands (partial coefficient = 0.87, P < 0.02). The patch-scale model was slightly less predictive of selection (65%) than was the nest-site scale model (71%), and patch-scale variables were completely swamped by nest-site scale variables when combined in the analysis. Thus, factors at the nest-site scale appear to be most influential in nest-site selection.

Mean foliage cover at Song Sparrow nests was 67.8% between 0 to 1 m, and 13.1% between 2 to 3 m. The results of contingency table tests indicate that number of plots with above or below average foliage cover differed significantly among stand types (Fig. 5; foliage cover between 0 to 1 m, χ^2 = 10.6, df = 2, P < 0.005; foliage cover at 2 to 3 m, χ^2 = 6.9, df = 2, P < 0.03). Restored stands had significantly fewer plots with above-average foliage cover at 0 to 1 m and 2 to 3 m than both mature forest and the young stand (P < 0.04 in all cases), whereas mature and young stands did not differ (P > 0.57 in both cases).

Reproductive success.—A total of 164 nests were monitored; 39 in 1993 (20 mature, 19 restored), and 125 in 1994 (50 mature, 35 restored, 40 young). All but four nests in restored stands were found on R1. Although we added two restored areas in 1994, we found only four nests on R3, and failed to find any nests on R2, despite the fact that at least 45 person hours were spent searching in each area, and more than 20 Song Sparrow pairs were recorded in each area (the rate of nest location on R1 and in natural stands averaged 10 or more nests in the same number of hours).
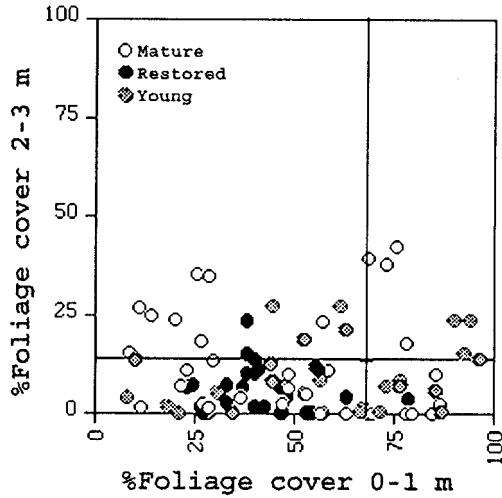
FIG. 5. Availability of above average nest sites in three forest types is examined by plotting random plots according to two aspects of foliage cover selected on by Song Sparrows. The horizontal and vertical lines represent mean of each variable at Song Sparrow nests. White circles represent mature forest, gray young forest, and black restored forest.

No significant differences in nesting success were found in 1993 ($\chi^2 = 1.80$, df = 1, $P = 0.18$) or 1994 ($\chi^2 = 1.19$, df = 1, $P = 0.55$), though the estimated probability of nesting success on restored sites was lower than that on natural sites by 50% in 1993, and 34–40% in 1994 (Fig. 6A). Nests were more likely to fail during incubation than during nestling stage in 1993, for both restored ($\chi^2 = 3.8$, df = 1, $P < 0.05$) and mature stands ($\chi^2 = 5.9$, df = 1, $P < 0.02$), but that difference was not observed in 1994 ($P > 0.5$ in all cases).

Clutch size in restored stands was significantly smaller than in mature forest (Fig. 6B; $F = 4.7$, df = 2 and 74, $P < 0.01$, Bonferroni adjusted post-hoc test $P < 0.01$), but was not significantly smaller than in the young stand ($P < 0.17$), although a similar trend is apparent. No difference in clutch size was apparent between young and mature stands ($P < 0.99$). No differences were found among stands in number of young raised per nest (Fig. 6C; Kruskal-Wallis estimated $\chi^2 = 0.47$, df = 2, $P < 0.79$, $n = 30$), or nestling mass (Fig. 6D; Kruskal-Wallis estimated $\chi^2 = 1.56$, df = 2, $P < 0.46$, $n = 30$).

Effect of habitat structure on nest predation.—Nest predation was affected by different aspects of habitat structure than was nest-site se-

lection. Before hatching, nests with higher forb cover were less likely to be depredated in all stand types (Partial coefficient = −0.02, $\chi^2 = 4.1$, df = 1, $P < 0.04$; Hosmer-Lemeshow goodness-of-fit $\chi^2 = 7.6$, df = 6, $P < 0.27$). A logistic regression model using only forb cover correctly classifies 75% of nests as depredated or not. None of the habitat variables we measured were significantly related to predation that occurred after hatching. Forb cover was significantly higher in natural stands than in restored stands (Kruskal-Wallis estimated $\chi^2 = 9.9$, df = 2, $P < 0.007$, see also Table 1, Fig. 2). Although forb cover was a significant factor in nest predation, it did not appear to be a significant criterion for nest-site selection. In univariate tests, forb cover influenced nest-site selection in restored stands ($P < 0.03$), but not in mature ($P < 0.51$) or young stands ($P < 0.35$), and was dropped from the nest-site selection model (likelihood ratio test, $P < 0.22$).

DISCUSSION

Our results show that habitat structure influences nest-site selection and nesting success in Song Sparrows, and suggest that habitat differences among stand types may lead to concordant differences in sparrow densities and reproductive success. Song Sparrows showed specific nest-site preferences. Average foliage cover at nests was 68% in the vertical layer between 0 to 1 m, and 13% in the 2 to 3 m layer. Most random sites in restored stands (90%) fell below both those averages, indicating that restored stands provided poorer nesting habitat than natural stands. That may have caused sparrows to reject restored stands, resulting in the observed tendency for lower Song Sparrow densities to occur on restored than on natural stands.

The tendency of Song Sparrows to exhibit poorer reproductive success (smaller clutch size and lower nest success) in restored stands is concordant with the results from habitat structure. Restored stands had less forb cover, and nests with lower forb cover were more likely to be lost to predation. Thus, nests in restored stands may have been more detectable by predators than those in natural stands (Martin and Roper 1988, Martin 1993). Additionally, restored stands may have failed to attract older, experienced individuals because of poor-qual-
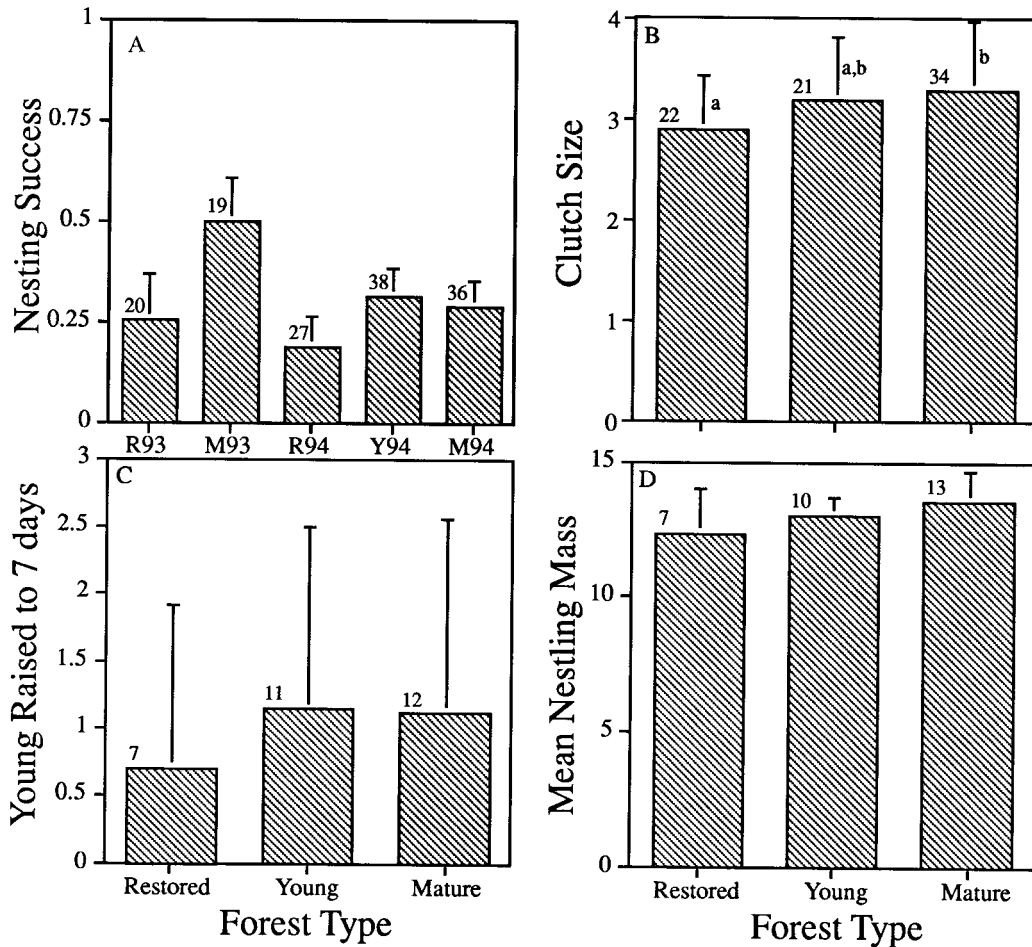
FIG. 6. Comparisons of reproductive success in Song Sparrows in three forest types. Error bars represent standard errors. Values to the left of error bars are sample sizes. Columns with different letters to the right of the error bars are significantly different from each other at the 0.05 level. (A) Mayfield estimates of nest success. For illustration, means and standard errors for a 21 day nesting period were calculated (Hensler and Nichols 1989). R93, R94 = restored stands 1993, 1994 respectively; M93, M94 = mature stands 1993, 1994, respectively; Y94 = young stand 1994. (B) Mean clutch size. (C) Number of young raised per nest. (D) Mean nestling mass.

ity habitat. Several studies have shown that young, inexperienced individuals may be out-competed for better sites by more mature individuals, and tend to have lower reproductive success than experienced birds (Nol and Smith 1987, Smith 1988, Sæther 1990). For example, Robertson and Rendell (1990) attributed lower reproductive success for Tree Swallows (*Tach-ycineta bicolor*) in natural cavities compared to nest boxes, in part, to a greater ratio of first-time to experienced breeders using natural cavities. Unfortunately, due to lack of long-term demographic studies at the site we were not able to assess the age structure of Song Sparrow populations during the course of this study. In addition to lower reproductive success, nest finding rates were lower in restored areas than in natural stands. We found only four nests on R3 and no nests on R4. There were typically lower densities of Song Sparrows on those two sites than on R1, but still enough birds that more nests would be expected. Insufficient data on habitat structure from those two areas precluded a test of differences in habitat structure, though such differences seemed apparent from casual observation. R2 had a

sparse understory composed mostly of dry weeds, whereas R3 consisted mostly of low grasses.

Other factors, unmeasured in this study, that could contribute to differential reproductive success and apparently lower habitat quality include (1) differences in predation rates due to edge effects or differences in predator assemblages (Wilcove 1985, Andrén and Angelstam 1988), and (2) lower food availability in restored stands, which can result in lower clutch size (Arcese and Smith 1988, Martin 1987) and increase parental foraging effort, thus reducing the time spent defending the nest (Arcese and Smith 1988, Martin 1992).

Results suggest that greater attention should be directed to restoration of the understory to increase cover, particularly of forbs. Furthermore, because cover and cover type influence nest-site selection and nesting success, data suggest that land-use practices such as grazing are likely not compatible with restoration. Recent studies have shown that grazing is associated with reduced cover and increased nest predation (Ammon and Stacey 1997, Dobkin et al. 1998), and it is therefore likely to have a negative effect on nesting success in riparian areas undergoing restoration. Examining demographic processes can provide valuable insights that may help to improve restoration practices. Whereas Song Sparrows have many things in common with other species that depend on riparian forests, other species may have different or more specialized habitat needs. Many species that depend on riparian forest are open-cup nesters and are therefore subject to microclimates and predation pressures similar to those experienced by Song Sparrows. Although sparrows may represent a valuable surrogate for assessing the success of restoration projects and improving the science of restoration, further research will be needed on additional species to examine those relationships.

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