Nest-Site Habitat of Cavity-Nesting Birds at the San Joaquin Experimental Range[1]

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Abstract

Detailed information about the nesting habitats of birds, including those needed for successful nesting, can provide a better understanding of the ecological factors that permit coexistence of different species and may aid in conservation efforts. From 1989 through 1994, we studied the nesting habitat of secondary cavity-nesting birds in oak woodlands at the San Joaquin Experimental Range, Madera County, CA. We measured habitat surrounding nests and examined similarities and differences in nesting habitat used by eight species to evaluate overlap in nesting habitat use and possible competition. Nesting habitat of Bewick's Wrens (*Thryomanes bewickii*) was unique among the species studied. Their nests were the lowest and located in the densest habitat on the steepest slopes where interior live oaks (*Quercus wislizenii*) were abundant. Nesting habitat was similar among European Starlings (*Sturnus vulgaris*), Western Bluebirds (*Sialia mexicana*), and Violet-green Swallows (*Tachycineta bicolor*). These species all nested in open areas with the highest density of blue oaks (*Quercus douglasii*), the lowest densities of live oaks and snags, and the lowest basal area of trees. Nests of White-breasted Nuthatches (*Sitta carolinensis*) were similar to the above three species, differing only in being lower compared to nests of European Starlings. Ash-throated Flycatcher (*Myiarchus cinerascens*) nesting habitat was characterized by dense stands of trees with a high density of live oaks and snags. Oak Titmouse (*Baeolophus inornatus*) nests were low and located in high-density stands of live oaks on steep slopes. House Wrens (*Troglodytes aedon*) nested in dense stands of trees. Successful Ash-throated Flycatcher and Oak Titmouse nests had higher basal area of live trees compared to unsuccessful nests and, compared to other species, habitat surrounding their nests had high basal area. European Starling nests were highest, and nests located high in trees had higher nest survival. Consequently, these three species tended to select nest sites in habitats where they had higher nest success. We recommend management activities that maintain habitat diversity, including areas that differ in tree species composition and density, to promote species diversity.

Keywords: Competition, European Starling, nest success, nest-site habitat, oak woodlands, secondary cavity-nesting birds, Sturnus vulgaris.

Introduction

Habitat features can influence nest-site quality and reproductive success (Martin and Roper 1988). Because nest-site selection in birds is closely tied to fitness, habitat features of nest sites that influence productivity should be under strong selection pressure. Habitat features that influence productivity can also influence the coexistence of species, as well as nest-site quality and reproductive success (Martin and Roper 1988). Species that overlap in nest-site selection criteria, for example, have been shown to experience higher predation rates, and such costs can favor use of nests sites that differ (Martin 1988, 1996). Processes such as competition and predation determine how many and which species coexist. Therefore, differences in

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nest sites among species may reflect selection for coexistence of species with nest sites that differ (Martin 1988, 1996). Understanding the nesting habitat requirements of coexisting species should provide a better understanding of the ecological factors related to the abundance and distribution of species and the ability of species to coexist.

Competition for limited nest sites may force use of suboptimal sites (Li and Martin 1991). Cavities are often limiting for cavity-nesting species (Brush 1983, Stauffer and Best 1982), although this is not always the case. When European Starlings (*Sturnus vulgaris*), a non-native species known to compete for nest sites with native cavity-nesting species, invade new habitats, their presence can contribute to nest-site limitation (see Wiens 1989, for review). Koenig (2003) found little evidence that the invasion of European Starling in North America has severely affected numbers of native cavity-nesting birds (Koenig 2003), although he recommended additional studies at the population level to confirm these results.

Nest-site selection can be thought of as operating on two spatial scales: the nest site, characteristics within the immediate vicinity of the nest, and the nest patch, characteristics of the habitat surrounding the nest (Martin and Roper 1988). Munro and Rounds (1985) found that nest box properties were more important than habitat variables in differentiating habitat use among species, but Holt and Martin (1997) found that vegetation structure surrounding the nest was important in determining occupation when nest sites were less limiting. Nest-site selection in Hermit Thrushes (*Catharus guttatus*) appeared to be a function of both nest site and nest patch characteristics (Martin and Roper 1988). Selected sites had a large number of potential nest sites in the surrounding area that predators would have to search to find a nest, thereby reducing predation risk.

If nest-site preferences are adaptive, nests located in preferred sites should be more successful. Use does not necessarily reflect preference, and nest-site selection may not be adaptive if nest sites are not equally available to all individuals. Competition for nest sites may result in niche shifts to minimize overlap with other species that lead to use of less than optimal conditions. Examination of associations between selected and successful nest sites can shed light on how processes such as competition and predation affect species' viability and coexistence.

In this study, we examined similarities and differences in nesting habitat of eight species of secondary cavity-nesting birds, including the European Starling. For three species, we examined differences between successful and failed nests to examine whether nest sites used were those in which individuals were most successful.

Methods

Study Area

The San Joaquin Experimental Range (hereafter SJER) is located in the western foothills of the Sierra Nevada, in Madera County, CA. It has an area of approximately 1,875 ha and ranges in elevation from 215 to 520 m. The climate is characterized by cool, wet winters and hot, dry summers. Annual precipitation averages 48.6 cm, with most falling as rain between November and March.

Habitat at SJER is classified primarily as blue oak-foothill pine (Mayer and Laudenslayer 1988). The sparse overstory is dominated by three tree species: blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus* *sabiniana*), but buckeye (*Aesculus californica*) and desert elderberry (*Sambucus mexicana*) also occur. Shrubs grow as scattered individuals or in denser clumps, and include wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), Mariposa manzanita (*Arctostaphylos viscida mariposa*), holly-leaf redberry (*Rhamnus ilicifolia*), and coffeeberry (*R. tomentella cuspidata*). In areas without shrubs, annual grasses and forbs dominate the understory. In some areas, the habitat is classified as blue oak woodland (Mayer and Laudenslayer 1988) where the overstory is primarily blue oak with a fairly open understory. SJER has been lightly to moderately grazed by cattle for approximately 100 years. A 29-ha research natural area has been ungrazed since 1934.

Fieldwork

We located and monitored nests of all species from 1989 to 1994. Two 30-ha plots, matched for total canopy cover, were searched most intensively. One of the plots was in grazed pastures and the other was in the research natural area. In 1992 to 1994, other areas within SJER were searched in addition to the two study plots to increase sample sizes and the range of habitats studied.

In 1989 to 1991, nests were checked every four to seven days using an automotive inspection mirror and a small light bulb. Nests were checked by using an extension ladder. Nests that could not be accessed with the extension ladder were observed from the ground. In 1992 to 1994, nests were checked every four to five days. We climbed to nests using various climbing techniques except when nests were in unstable substrates. Contents of nest cavities were observed with a fiberscope (Purcell 1997).

Nest age, or the number of days a nest was active at a given visit, was determined by extrapolating from identified events, such as the beginning of incubation, hatching, or fledging, and the appearance of nestlings. We were not able to determine the age of some nests, which were excluded from analyses of nest survival.

We examined habitat variables that we predicted would vary among species based on previous studies. Nest height has commonly been shown to differ across species and to influence nest predation rates in some species (Burhans and others 2002, Hatchwell and others 1999, Hooge and others 1999, Li and Martin 1991, Nilsson 1984). Because European Starlings are known to nest in open, relatively flat habitat dominated by blue oaks (Purcell and others 2002), we predicted that nesting habitat would vary among species in tree density, slope, and relative abundance of tree species and snags. Accordingly, the habitat variables we analyzed included nest height, basal area of live trees, numbers of blue oaks, live oaks, and snags surrounding the nest, and percent slope. For each active nest, nest height was measured using a clinometer and tape measure. Field crews recorded the number and species of trees and snags in a 0.04-ha plot (11.3 m radius) centered on the nest. This is a long- and widely-established plot size that allows comparisons among studies (James and Shugart 1970, Martin and others 1997). Basal area of live trees was measured with a basal area prism, and the slope of the nest plot was measured using a clinometer.

Statistical Analysis

We analyzed differences and similarities of nest habitats used by the nonexcavator species with MANOVA and Scheffe's multiple comparison procedure, controlling for Type I error rates (SAS Institute, Inc. 2004). Variables were examined for nonlinearity with generalized additive models using cubic spline smoothing (GAM; R Development Core Team 2003). Transformations suggested by GAM to describe the functional shapes of variables were obtained by trying logarithmic, quadratic, and square root functions. Results suggested the use of linear forms for nest height, number of snags surrounding the nest, and percent slope; logarithmic forms were suggested for basal area of live trees, number of blue oaks, and number of live oaks surrounding the nest.

We compared successful and failed nests for three species of secondary cavity nesters with sample sizes > 40 to examine whether the nesting habitat used by a species differed from the habitat where they were most successful. We used the logistic exposure method (Shaffer 2004) to investigate the importance of nesting-habitat variables to nest survival. This method allows evaluation of a broad array of covariates, evaluation of competing models, and does not require the assumption of constant daily survival rates or any assumptions about when nest failure occurs within an interval. Analysis is based on generalized linear models, assuming a binomial distribution and a logit link function. Analyses were done using Proc GENMOD (SAS Institute, Inc. 2004). Each visitation interval is treated as an observation.

Nest survival may change in relation to time-specific variables such as nest initiation date and stage of development. To control for potentially confounding effects of time-specific factors, we first considered linear, quadratic, and cubic effects of nest age; linear and quadratic effects of date; and a categorical effect of year, following Grant and others (2005). We evaluated 24 models that included a constant daily survival model (null model) and all combinations of age, date, and year effects. The most-supported time-specific model was included in subsequent analyses to control for potentially confounding effects of age, date, and year as the base model.

We examined 22 models containing all one- and two-variable combinations of the six variables included in the MANOVA and the base model. Models were ranked and compared using ΔAICc and Akaike weights (Burnham and Anderson 2002). Models with lower AICc scores are considered closer to the true model. Because ΔAICc is the difference between the best fitting model and model "i," models with low ΔAICc values have more support. Akaike weights can be interpreted as the probability that model "i" is the best model for the data at hand, given the set of models considered. Effective sample size, based on the total number of days that each nest was known to survive plus one day for each interval that ended in failure (Rotella and others 2004), was used to calculate AICc. We used model averaging to address model selection uncertainty. Variance estimates based on weighted averages of parameter estimates across all models reflect both uncertainty in parameter estimates and uncertainty in selecting that model. The relative importance of each variable was assessed by summing the Akaike weights over all models in which that variable appeared. This was possible because each variable occurred in the same number of models (6). Model fit of the global model was assessed with the Hosmer-Lemeshow decile of risks test (Hosmer and Lemeshow 2000). In all cases, the global model fit the data well (Ash-throated Flycatcher: $\hat{C}$= 3.51, P = 0.89, Oak Titmouse: $\hat{C}$ = 2.49, P = 0.96, European Starling: $\hat{C}$ = 5.91, P = 0.66).

Results

Nesting habitat differed across the eight nonexcavator species (*table 1*). Bewick's Wrens differed most from the other species and had extreme values for five of the six variables. Their nests were the lowest and were located in the densest habitat on the steepest slopes, where live oaks were abundant and blue oaks were sparse.

Table 1—*Means (sd) and results of MANOVA and Scheffe's multiple-comparison procedure to examine differences in nest habitat of nonexcavators. Wilks' lambda = 0.5395, df = 42, 1560.7, P < 0.0001. For each variable, species with the same letter did not differ.*

Species	*N*	**Nest height (m)**	**Basal area of live trees (m^2/ha)**	**Number of blue oaks**[1]	**Number of live oaks**[1]	**Number of snags**[1]	**Slope (percent)**
Ash-throated Flycatcher	43	3.8 (1.7) ab	10.9 (6.5) b	1.1 (1.6) a	7.6 (7.5) b	2.0 (2.5) b	12.7 (6.7) ab
Violet-green Swallow	24	4.9 (2.0) bc	6.3 (3.4) ab	2.4 (1.7) b	1.0 (2.3) a	0.1 (0.6) a	14.6 (6.7) b
Oak Titmouse	80	3.8 (1.9) b	11.2 (7.6) b	1.4 (1.8) ab	6.6 (8.1) b	1.3 (2.1) ab	13.8 (5.9) b
White-breasted Nuthatch	35	4.3 (1.7) b	9.5 (5.8) ab	1.6 (2.0) ab	3.9 (5.9) ab	0.7 (1.2) ab	11.9 (6.2) ab
Bewick's Wren	17	1.3 (1.7) a	13.8 (12.2) b	0.4 (1.2) a	7.9 (7.1) ab	1.3 (1.8) ab	16.4 (8.6) b
House Wren	40	4.5 (1.9) b	10.3 (6.7) b	1.5 (2.9) ab	4.6 (1.5) ab	1.5 (2.2) ab	12.2 (5.7) ab
Western Bluebird	31	4.0 (1.5) ab	5.6 (3.5) a	1.6 (1.5) ab	1.4 (3.1) a	0.3 (0.8) a	13.1 (6.1) ab
European Starling	85	7.4 (4.9) c	6.7 (5.7) a	1.8 (2.5) b	2.0 (4.9) a	0.4 (1.2) a	9.8 (4.3) a

[1] The number of blue oaks (*Quercus douglasii*), interior live oaks (*Q. wislizenii*) and snags in a 0.04 ha circular plot surrounding the nest tree.

Nesting habitats of starlings, bluebirds, and swallows were similar. All three species nested in open areas with low basal area of live trees, where blue oaks were abundant, and live oaks and snags were sparse. Starling nests were the highest and were found in the most level areas. Swallow nests were second in height after starling nests and were found on steeper slopes compared to starlings. Bluebird nests were intermediate in height, significantly lower than starling nests, and occurred in areas with the lowest tree density.

White-breasted nuthatch nests were intermediate in most respects and were similar to the above three species. They differed only in nest height from starling nests.

Ash-throated Flycatcher nesting habitat was characterized by dense stands of trees that included predominantly live oaks, and the greatest number of snags.

Oak Titmice nested lower than all other species except Bewick's Wrens, although only significantly lower than starlings, and their nests were located in dense stands with abundant live oaks on fairly steep slopes.

House Wren nests were intermediate in nest-habitat characteristics. Their nests tended to be fairly high and they were found in denser stands of trees.

Nest Survival

Sample sizes for examining correlates of nest success were adequate for three species: Ash-throated Flycatcher, Oak Titmouse, and European Starling. Nest survival was not constant over the nest period for any of the three species. The most-supported time-specific model for Ash-throated Flycatchers included a cubic effect of nest age. For Oak Titmice, the best model included a linear effect of nest age and a quadratic effect of nest date. Nest survival of European Starlings was best explained by a model that included quadratic effects of nest age.

Nesting habitat variables did not appear to be strong predictors of nest survival for Ash-throated Flycatchers (*tables 2 and 3*). The base model was the most-supported model and age of the nest was an important predictor of nest survival. Basal area of live trees had the highest relative importance value (*table 3*), suggesting that successful Ash-throated Flycatcher nests had higher basal area of live trees.

Variation in nest survival of Oak Titmice nests was best explained by basal area of live trees. The model containing only basal area received the most support, basal area was included in six of the seven top models (*table 2*), and it had a relatively high importance value (*table 3*). Successful Oak Titmice nests had higher basal area of live trees.

European Starling nests located high in trees had higher nest survival. Nest height alone was the most-supported model, it was included in the top six models (*table 2*), and it had a high importance value in relation to the other variables (*table 3*).

Table 2—*Model selection results for logistic-exposure models of daily survival rates for Ash-throated Flycatcher, Oak Titmouse, and European Starling nests. Twenty-two candidate models were considered that included all one- and two-variable combinations of nest height (Nest ht), basal area of live trees (Basal area), the number of blue oaks (Blue oak), interior live oaks (Live oak), and snags (Snag) in a 0.04-ha circular plot surrounding the nest tree, and slope (Slope).* $Log_e(L)$ *is the value of the maximized log-likelihood function, K is the number of parameters in the model,* AIC_c *is Akaike's information criterion corrected for small samples,* ΔAIC_c *is the difference between the best fitting model and model i , and* $\mathbf{w_i}$ *is the Akaike weight and indicates the relative likelihood that a model is the best model of those considered. All models included the best time-specific model (Base) for each species. Only models with* $\Delta AIC_c \leq 2.0$ *and the base model are shown. The effective sample sizes are as follows: Ash-throated Flycatcher - 828 exposure days, based on 44 nests; Oak Titmouse – 2,557 exposure days, based on 99 nests; European Starling – 1,895 exposure days, based on 76 nests.*

Model	**K**	**$Log_e(L)$**	**AIC_c**	**ΔAIC_c**	**w_i**
		Ash-throated Flycatcher			
Base[1]	4	-47.0	102.0	0.0	0.13
Basal area	5	-46.1	102.3	0.3	0.11
Live oak	5	-46.5	103.1	1.1	0.07
Snag	5	-46.6	103.3	1.3	0.07
Basal area + Slope	6	-45.8	103.6	1.6	0.06
Slope	5	-46.9	103.9	1.9	0.05
Basal area + Blue oak	6	-45.9	104.0	2.0	0.04
		Oak Titmouse			
Basal area	5	-88.8	187.6	0.0	0.14
Base[2]	4	-90.0	188.1	0.47	0.11
Basal area + Blue oak	6	-88.4	188.9	1.28	0.08
Basal area + Slope	6	-88.5	189.0	1.39	0.07
Basal area + Live oak	6	-88.6	189.2	1.62	0.06
Nest ht + Basal area	6	-88.7	189.4	1.78	0.06
Basal area + Snag	6	-88.7	189.4	1.81	0.06
		European Starling			
Nest ht	4	-65.3	138.6	0.0	0.24
Nest ht + Live oak	5	-64.9	139.9	1.3	0.12
Nest ht + Basal area	5	-65.2	140.5	1.9	0.09
Nest ht + Slope	5	-65.3	140.6	1.9	0.09
Nest ht + Blue oak	5	-65.3	140.6	2.0	0.09
Nest ht + Snag	5	-65.3	140.6	2.0	0.09
Base[3]	3	-67.8	141.7	3.1	0.05

[1] The base model for Ash-throated Flycatcher included a cubic effect of nest age.

[2] The base model for Oak Titmouse included a linear effect of nest age and a quadratic effect of nest date.

[3] The base model for European Starling included a quadratic effect of nest age.

Table 3—*Model-averaged parameter estimates, unconditional standard errors (SE), and relative importance values from logistic-exposure models relating daily survival rates of Ash-throated Flycatcher, Oak Titmouse, and European Starling nests to time-dependent and nest-site variables. For continuous variables, the sign of the estimate (Est.) indicates the effect in relation to nest success. Standard errors reflect both uncertainty in parameter estimates from a given model and uncertainty in selecting that model. Relative importance values (Rel. imp.) are the sum of the Akaike weights over all models in which that variable appears and are a measure of the relative importance of the predictor variable to daily nest survival rate.*

	Ash-throated Flycatcher			Oak Titmouse			European Starling		
Parameter[a]	**Est.**	**SE**	**Rel. imp.**	**Est.**	**SE**	**Rel. imp.**	**Est.**	**SE**	**Rel. imp.**
Intercept	5.08	3.42		47.16	20.25		13.9	4.70	
Age	0.57	0.67		0.07	0.02		-0.9	0.41	
Age^2	-0.07	0.04					0.02	0.01	
Age^3	0.00	0.00							
Date				-0.77	0.38				
Date^2				0.00	0.00				
Nest height	-0.00	0.04	0.17	0.01	0.03	0.18	0.18	0.16	0.72
Basal area	0.24	0.04	0.34	0.23	0.30	0.59	0.02	0.08	0.16
No. blue oaks	0.02	0.09	0.19	0.04	0.09	0.21	-0.02	0.07	0.16
No. live oaks	0.04	0.08	0.23	-0.00	0.03	0.18	-0.04	0.08	0.21
No. snags	0.02	0.04	0.19	-0.00	0.02	0.17	0.01	0.05	0.15
Slope	-0.00	0.01	0.20	-0.00	0.01	0.19	-0.00	0.01	0.15

[a] Age, Age^2, and Age^3 represent linear, quadratic, and cubic effects of nest age. Date and Date^2 represent linear and quadratic effects of Julian date. Basal area, number of blue oaks, and number of live oaks were log transformed.

Discussion

While the eight species studied here differed in nest habitat selection, considerable overlap occurred among some species. We found extensive overlap among nesting habitats used by European Starlings, Western Bluebirds, Violet-green Swallows, and to a lesser extent, White-breasted Nuthatches. The patterns of overlap in nesting habitat found here were consistent with those found for nest-cavity characteristics (Purcell and Verner 2007).

Niche overlap provides only weak evidence of interspecific competition without evidence of limiting resources (Wiens 1989). Results of a cavity-blocking experiment done at SJER in the mid-1980s suggested that cavities were not limiting at that time (Waters and others 1990), but numbers of starlings have increased since that study was completed (Purcell and others 2002). We suspect that nest sites have become a limited resource following the increase in starling abundance, at least for some species, based on several lines of evidence (Purcell and Verner, in review). The most compelling of these are based on observations of nest usurpation by starlings of five native species and aggressive interactions between starlings and native cavity-nesting species at nest cavities (Olsen and others 2007).

A decrease in availability of a limiting resource promotes intensified competition, which is generally believed to result in a narrowing of niche breadth or niche shifts to minimize overlap (Schoener 1982, Wiens 1989). Western Bluebirds and Violet-green Swallows had the smallest niches relative to nest habitat characteristics, as gauged by the standard deviation and range of the habitat variables measured here, suggesting decreased niche breadth. Nest-cavity variables of bluebirds and swallows also had the lowest variability compared to other cavity-nesting species in a companion study (Purcell and Verner, in review). Studies of Tree Swallows (Tachycineta bicolor), a close relative of the Violet-green Swallow, have shown them to be less selective and more variable in nest-site selection compared to other species (Dobkin and others 1995, Munro and Rounds 1985, Parren 1991, Rendell and Robertson 1989), even though access to nest sites may have been limited by competition with starlings (Dobkin and others 1995, Peterson and Gauthier 1985, Rendell and Robertson 1989).

Habitat partitioning can favor coexistence of bird species, and divergence in nesting sites can reduce predation risk (Martin 1988, Martin and Roper 1988). Bewick's Wrens were the most divergent in their nesting habitat. They also had the highest reproductive success of 16 species nesting at SJER (Purcell 1995).

Are Nest Sites Adaptive?

For nesting-habitat preferences to be adaptive, preferred sites must be more productive so that selection can act to favor preferences (Martin 1998). If successful nesting habitat differs from used nesting habitat, use might not reflect preference and could indicate niche shifts resulting from competition. Selection can only act on phenotypic variation in nest site choice if it has a genetic basis. We assumed that heritable genetic variation for habitat selection exists because a variety of evidence suggests that habitat preferences have a genetic basis (Jaenike and Holt 1991, Martin 1998).

Nesting-habitat selection by the three species examined appeared to be adaptive. Both Ash-throated Flycatchers and Oak Titmice nested and were more successful in areas with high basal area. European Starling nests were the highest of the eight species examined, and high nests were more successful, a finding in agreement with Nilsson (1984). It should be noted, however, that nesting habitat characteristics had little ability to predict nest survival of Ash-throated Flycatchers. Compared to results of a companion study examining nest-site characteristics (Purcell and Verner, in review), we found less evidence that nesting habitat was important to nest survival than were features specific to the smaller scale of the nest site. We found fewer nesting-habitat variables important in predicting nest survival and greater agreement between habitats where species nested and where they were more successful. These results suggest that optimal nesting habitat is either less limiting or less important than optimal nest sites, a question that deserves study.

Management Considerations

Habitats that are complex and heterogeneous can provide habitat requirements for greater numbers of species than simple, uniform habitats. Results of this study suggest that maintaining a diversity of habitats, including areas differing in tree density and species, can help foster wildlife species diversity. We suggest that spatially diverse and complex oak woodlands will best provide for the differing habitat needs of the species considered here.

If birds choose habitat features that increase the probability of nesting successfully, identification of these features is critical for effective management. Ash-throated Flycatcher and Oak Titmouse nests were more successful in habitat with high basal area, suggesting that high tree density and/or the abundance of large trees is important for these species. European Starlings that occupied high nests were more successful. A positive correlation between nest height and nest success has been found for a wide variety of species (Burhans and others 2002, Hatchwell and others 1999, Hooge and others 1999, Li and Martin 1991, Nilsson 1984). If species are competitively excluded from higher sites by starlings, more high-quality nest sites could be provided and competition reduced by increasing the availability of large trees. We recommend management practices that encourage maintenance of large, mature oak trees and recruitment of replacement oaks.

Although nest boxes can help reduce competition for limited nest sites, the target species and nest-box placement need to be considered. Nest boxes should be constructed to exclude starlings and monitored to assure that they are not used by non-native species. Results of this study suggest that nest boxes should be placed in appropriate habitat for each target species. A primary consideration is that not all species use nest boxes (*table 4*). The eight species considered here nested in areas that differed in tree densities and dominant tree species, and slope, and nest trees differed in species, size, and decadence (*table 4*). The needs of the entire native bird community and the potential effects of targeting a single species should be considered when augmenting existing cavities with nest boxes (Purcell and others 1997). Effects of nest box programs have rarely considered the potential effects of nest boxes on the rest of the bird community. We believe the question of community-wide effects and possible adverse impacts on other species deserves further study.

Table 4—*Summary of nesting habitat for eight cavity-nesting bird species at the San Joaquin Experimental Range.*

Species	Nest tree	Tree density	Dominant tree species	Slope	Uses nest boxes
Ash-throated Flycatcher	Large diameter live oaks	dense	Live oaks with snags	moderate	Yes
Violet-green Swallow	Tall, healthy blue oaks	medium	Blue oaks	steep	No
Oak Titmouse	Average oaks of both species	dense	Mixed	steep	Yes
White-breasted Nuthatch	Large diameter blue oaks	medium	Mixed	moderate	Rarely
Bewick's Wren	Variable	dense	Live oaks, pines, snags	steep	Rarely
House Wren	Large diameter, decadent oaks	dense	Mixed	moderate	Yes
Western Bluebird	Healthy blue oaks	sparse	Blue oaks	moderate	Yes
European Starling	Tall blue oaks	sparse	Blue oaks	level	No?

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