LACK OF NEST SITE LIMITATION IN A CAVITY-NESTING BIRD COMMUNITY

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Abstract: We examined the relationship between nest site availability and density of secondary cavity-nesting birds by blocking cavities in an oak-pine (*Quercus* spp.-*Pinus* sp.) woodland. In 1986 and 1987 we blocked 67 and 106 cavities, respectively, on a 37-ha plot. The combined density of secondary cavity-nesting birds did not decline in either year by a greater proportion on the treatment plot than on a control plot, indicating that cavities were not limiting. In habitats where timber management has not substantially reduced availability of natural cavities, managers should not assume nest site limitation; natural nest site availability should be evaluated before implementing nestbox programs designed to increase populations of secondary cavity-nesting birds.

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Knowledge of factors that limit species' abundances is needed to formulate management guidelines and to predict effects of habitat alteration. Nest site limitation of secondary cavity-nesting birds (SCNB), i.e., cavity nesters that do not excavate their own cavity, is often assumed rather than hypothesized (e.g., von Haartman 1957, Hilden 1965, Thomas et al. 1979). In his paper on the evolution of the cavity-nesting habit in birds, von Haartman (1957: 339) stated, "In the case of hole-nesters it seems obvious that the number of holes, and not the amount of food, mostly acts as an ecological limiting factor, determining the maximum number of nesting pairs."

Much of the evidence indicating nest site limitation has come from European nestbox studies (see von Haartman 1971 for review). Bruns (1960) reported that densities of some European SCNB species have been increased 5-20 times by adding nestboxes. Natural nest site availability throughout much of Europe, however, has been substantially reduced by long-term intensive forest management (Bruns 1960, Haapanen 1965, Slagsvold 1978).

Many North American studies have documented nestbox use (e.g., Hamerstrom et al. 1973, McComb and Noble 1981, Savard 1988). However, we are aware of few controlled nestbox experiments, i.e., studies in which pre- and posttreatment densities were estimated from both treatment and control plots (Brush 1983, Brawn and Balda 1988). Dahlsten and Copper (1979) also used nestboxes to study population characteristics of SCNB's, but they did not obtain premanipulation estimates of abundance on nestbox and control plots. Nestbox use does not necessarily indicate nest site limitation; use can be merely compensatory rather than additive (see van Balen et al. 1982, Nilsson 1984a, Gauthier and Smith 1987).

Our objective was to test the hypothesis that breeding densities of SCNB's are limited by nest site availability at a site where the number of cavities was essentially unaffected by man. Rather than test the hypothesis by increasing nest site availability with nestboxes, we reduced nest site availability by blocking cavities.

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STUDY AREA AND METHODS

Research was done at the San Joaquin Experimental Range (SJER), located in the western foothills of the Sierra Nevada, 32 km north of

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Table 1. Vegetation characteristics on the control and treatment plots, San Joaquin Experimental Range, California, 1985-87. The *P* values from 2-sample t-tests (assuming unequal variance) are given.

Variable	Control plot $\bar{x}$	Control plot SE	Treatment plot $\bar{x}$	Treatment plot SE	*P*
Trees/ha	54.1	9.25	54.1	6.39	0.999
Blue oaks/ha	7.5	1.93	10.3	2.63	0.395
Live oaks/ha	14.9	2.96	25.8	3.71	0.025
Digger pines/ha	30.2	8.01	15.9	4.20	0.119
California buckeyes/ha	1.6	1.01	2.2	1.40	0.719
Snags/ha[a]	0.57		0.65		
Canopy cover (%)	27	4	29	3	0.608
Shrub cover (%)	21	2	6	1	0.000

[a] Estimated from total count on each plot. All other variables were estimated from a sample of 40 systematically-located 0.08-ha circular plots.

Fresno, California. Vegetation was characterized as oak-pine woodland. Three tree species were common: blue oak *(Quercus douglasii)*, interior live oak (*Q. wislizeni)*, and digger pine *(Pinus sabiniana)*. The SJER has never been managed for timber production, and most mature blue oaks are over 150 years old (R. Standiford, Univ. Calif., Berkeley, unpubl. data).

Two 20-ha rectangular plots were established by Verner and Ritter (1985). These were selected from aerial photographs based on similarly in relief and canopy cover. The plots were about 350 m in elevation and about 1.6 km apart. Each plot was originally gridded into 30-m intervals. We added grid markers to expand the gridded area of each plot to 30 ha (450 x 660 m). One plot had been lightly to moderately grazed by cattle for ≥80 years, but no grazing had occurred on the other plot since 1934. The grazed plot was arbitrarily chosen as the treatment plot. The ungrazed plot served as the control. To compare woody vegetation on the 2 plots, we sampled vegetation in 40 systematically-located 0.08-ha circular plots (32-m diam) on each plot. Variables included number of trees (grouped by species and dbh size class), canopy cover, and shrub cover.

During the winter of 1985-86, we mapped the locations of all cavity trees found within the 30-ha gridded area and within an additional 30-m-wide strip on all sides of each plot. Thus, the total area censused at each plot was 37 ha. At each cavity tree we recorded tree species, number of suitable excavated cavities (created by woodpeckers), and number of suitable nonexcavated cavities (not created by woodpeckers). Suitable cavities were defined as those with entrance diameters 2.5-15 cm and depths between I5 and 50 cm. These measurements were equal to the minimum and maximum values from a sample of 80 active nests of cavity-nesting birds located in 1985 (Waters 1988). Most cavities could be reached with an 8-m aluminum ladder. A few, primarily cavities in the taller digger pines, were inaccessible, and their suitability was estimated from the ground.

1986 Experiment.-During April 1985 we censused breeding birds on each plot using the spot-mapping method (Robbins 1970, Verner 1985). We searched for active cavity-nesting bird nests during and after spot-mapping visits and mapped their locations. Effort in locating nests varied among years but was equal between plots within each year. In late winter 1986, just prior to the breeding season, we blocked cavity entrances on the treatment plot with dead tree branches and twigs. Each cavity that had contained a known SCNB nest in 1985 was blocked as were all other cavities in that tree; 67 cavities (45 excavated and 22 nonexcavated) were blocked. The same observer censused both plots again during spring 1986. We unblocked cavities at the end of the breeding season.

In 1986 we also monitored nest success at all accessible SCNB nests found within each plot. An 8-m ladder, cavity light, and 2.5-cm-diameter mirror were used to inspect nest contents once or twice a week throughout the nesting cycle and more frequently near fledging.

1987 Experiment.-Because preliminary data analysis indicated that total SCNB density was not adversely affected by the 1986 experiment, we blocked more cavities in 1987. Cavity trees were randomly selected rather than conditioning selection on previous use of a nest tree as in 1986. We blocked all cavities in each selected cavity tree; 106 cavities (62 excavated and 44 nonexcavated) were blocked. The 2 plots were again censused by spot-mapping. Two observers (different from the observer that censused the

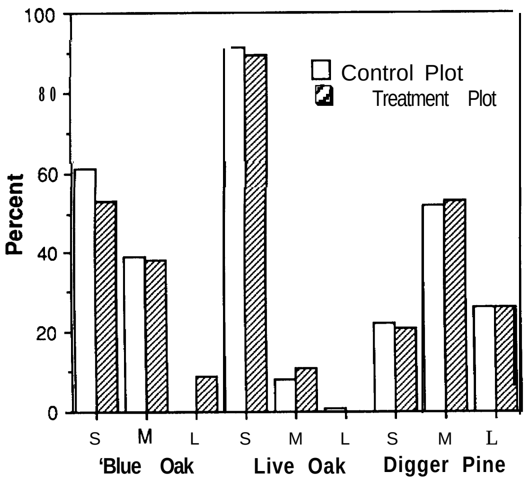

Fig. 1. Percent distribution of tree stems in 3 dbh size classes (S = 8-23 cm, M = 23-53 cm, L = >53 cm) at the San Joaquin Experimental Range, California, 1985-87.

plots in 1985 and 1986) contributed equal censusing effort on each plot to balance observer variability.

RESULTS

Comparison of Control and Treatment Plots

Tree density and canopy cover did not differ significantly between the 2 plots (Table 1). Live oak density, however, was significantly greater on the treatment plot. Shrub cover was significantly greater on the control plot, reflecting both the lack of cattle grazing and differences in soil and bedrock conditions. Diameter size class distribution of the 3 common tree species (Fig. 1) did not differ significantly between plots (blue oak: $x^2 = 2.97$, $P = 0.234$; live oak: $x^2 = 1.28$, $P = 0.533$; digger pine: $x^2 = 0.03$, $P = 0.985$). The large standard errors for the variables (Table 1) reflect the patchy spatial distribution of trees and shrubs on these plots.

We counted more cavity trees and cavities on the treatment plot (Table 2). Numbers of blue oak and digger pine cavity trees were similar between plots, but the treatment plot had about twice as many live oak cavity trees. No cavities were found in California buckeyes *(Aesculus californica)*.

Table 2. Cavity trees, excavated cavities, and nonexcavated cavities found on 37-ha control and treatment plots, San Joaquin Experimental Range, California, 1985-87.

Tree species	Control plot: Cavity trees	Control plot: Cavities: Excavated	Control plot: Cavities: Nonexcavated	Treatment plot: Cavity trees	Treatment plot: Cavities: Excavated	Treatment plot: Cavities: Nonexcavated
Blue oak	27	51	18	31	68	17
Live oak	28	17	28	61	21	58
Digger pine	6	10	1	9	10	0
Snag	2	1	1	2	2	0
Subtotals	63	79	48	103	101	75
Totals		127			176	

Changes in Densities of Breeding SCNB's

Eight diurnal SCNB species bred on 1 or both plots during the study: European starling *(Sturnus vulgaris)*, plain titmouse *(Parus inornatus)*, western bluebird *(Sialia mexicana)*, house wren *(Troglodytes aedon)*, ash-throated flycatcher *(Myiarchus cinerascens)*, white-breasted nuthatch *(Sitta carolinensis)*, violet-green swallow *(Tachycineta thalassina)*, and Bewick's wren *(Thryomanes bewickii)*.

1986 Experiment. -The combined density of the 8 SCNB species in 1985 was 45.9 territories per 30 ha on the control plot and 41.6 territories per 30 ha on the treatment plot. Following cavity blocking in 1986, combined density of SCNB's on the treatment plot declined by 17% to 34.7 territories per 30 ha. Combined SCNB density on the control plot, however, declined by 29% to 32.7 territories per 30 ha. None of the 8 SCNB species declined by a greater proportion on the treatment plot (Fig. 2). Both plots showed a decrease in SCNB density primarily because the number of house wrens declined dramatically throughout the entire study area in 1986.

1987 Experiment. - Combined SCNB density increased on both plots between 1986 and 1987. On the control plot, SCNB density increased from 32.7 territories per 30 ha in 1986 to 38.9 territories per 30 ha in 1987-an increase of 19%. On the treatment plot SCNB density increased 27%; total density increased from 34.7 territories per 30 ha in 1986 to 44.1 territories per 30 ha in 1987. Only ash-throated flycatcher density declined by more on the treatment plot than on the control plot between 1986 and 1987 (Fig. 2), but the difference between plots was small.

Reproductive Success

In all 3 years the ratio of the number of SCNB nests found divided by the combined SCNB density estimate for that plot was similar be-

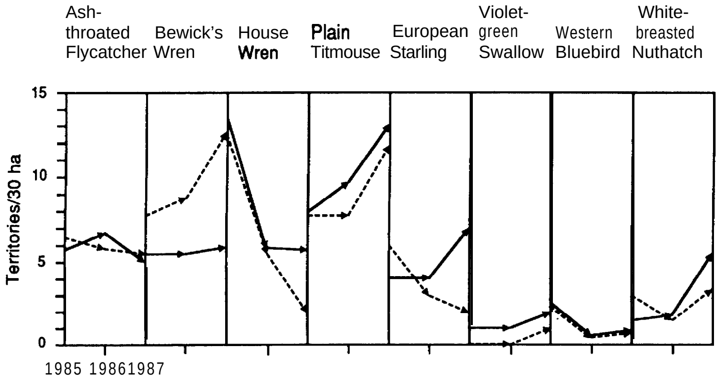

Fig. 2. Changes in densities of secondary cavity-nesting birds on the treatment plot (solid arrow) and control plot (dashed arrow) between 1985 and 1986 and between 1986 and 1987.

tween plots. In 1985 this ratio was 0.57 on the control plot (26 nests found/45.9 territories) and 0.58 on the treatment plot (24 nests found/41.6 territories). In 1986 the ratio was 0.70 (23 nests found/32.7 territories) on the control plot and 0.69 (24 nests found/347 territories) on the treatment plot. In 1987 search effort was low on both plots; the ratio was 0.39 (15 nests found/38.9 territories) on the control plot and 0.43 (19 nests found/44.1 territories) on the treatment plot. Of the 16 SCNB nests monitored on the control plot in 1986, 11 were successful (fledged ≥ 1 young). On the treatment plot, 11 of 14 were successful. These proportions were not significantly different (P = 0.272, Fisher exact test).

Little information on reproductive success was obtained in 1987. Six of 7 nests monitored were successful on the control plot and 4 of 5 were successful on the treatment plot. Plain titmouse fledging success was apparently not substantially affected by blocking cavities, because we counted a similar number (6) of family broods on each plot during the postfledging period (early May).

DISCUSSION

We found no evidence that the breeding density of SCNB's on the treatment plot was limited by nest site availability. The lack of a negative effect on SCNB densities following substantial reductions in nest site availability suggests that nest sites were a relatively abundant resource. Because our treatment was not spatially replicated, we cannot make statistical generalizations to areas outside of our treatment plot. Biologists must always compromise between number of plots and plot size. Because of the relatively large size of our treatment plot, however, we believe our results were affected little by potential problems associated with small plot size (see Wiens et al. 1986).

Although we failed to locate many of the SCNB nests on the treatment plot, especially in 1987 when search effort was low, we do not think birds were forced to nest off the plot as a result of our manipulation. If this were true, the ratio of nests found to combined SCNB density should have been lower on the treatment plot than on the control plot in 1986 and 1987. This ratio was similar between plots in all 3 years. Large plot size also makes this possibility unlikely.

Clearly, more cavities were available on the treatment plot than were required to meet the immediate breeding demand of 1 cavity per pair. The cavity counts (Table 2) should be considered minimum estimates. Cavity censusing effort was intensive, and we probably located most excavated cavities. However, we undoubtedly missed cavities-especially smaller nonexcavated cavities that can be hard to detect. There were ≥109 (176 – 67) cavities available after blocking in 1986 and ≥70 (176 – 106) available after blocking in 1987. To sustain a SCNB population over the long term, however, numerous alternate cavities are probably necessary. For example, alternate cavities are needed so that birds can renest if their nest is lost to a predator or competitor (Short 1979, Nilsson 1984b). Availability of alternate cavities could also be important so that birds are not forced to nest in cavities that have acquired large parasite populations due to repeated use (Brown and Brown 1986, Nilsson 1986). Perhaps both a permanent and substantial reduction of nest site availability would have caused eventual decreases in SCNB populations

The majority of cavity-nesting birds are residents and use cavities year-round for roosting (von Haartman 1968, Short 1979). Because we did not block cavities during winter, we can make no conclusions about the possible effects on SCNB populations of reducing winter roost site availability.

We know of only 1 other study in which nest site availability was reduced by blocking natural cavities. Brush (1983) concluded that ash-throated flycatchers were limited by nest site availability because their density declined from 5 pairs to none after blocking all cavities on a 20-ha plot in Arizona. Scott (1979) showed that snag removal in a ponderosa pine *(Pinus ponderosa)* forest resulted in decreased cavity-nesting bird densities. In a Norwegian forest, Slagsvold (1978) blocked the entrances of all nestboxes on a plot except those used by great tits *(Parus major).* Pied flycatchers *(Ficedula hypoleuca)* were completely excluded from breeding on the plot; males fought aggressively but unsuccessfully with great tits for possession of nestboxes, and females emigrated from the area. We observed no interspecific aggression among SCNB species around cavities on the treatment plot during our study. The only aggressive intraspecific interactions observed were among ash-throated flycatchers. Most of these occurred away from the immediate vicinity of any potential nest cavities and occurred on both plots in all years.

Various factors influence cavity density. The most important are tree density, age of the trees, and tree species composition (van Balen et al. 1982). Age of the trees and tree species composition influence the amount and type of wood decay (Cartwright and Findlay 1958, Peace 1962), and cavity formation is strongly associated with wood decay. Nearly all of the nonexcavated cavities we found appeared to have developed through natural decay where a limb had died and fallen off. Indeed, the most common way decay fungi invade a tree's heartwood is through wounds left by dead limbs (Cartwright and Findlay 1958, Shigo and Marx 1977). Thirty-four percent of 277 SCNB nests found throughout our study area were located in nonexcavated cavities (Waters 1988). Excavated cavities are also associated with wood decay because woodpeckers prefer to excavate cavities in areas of the tree where the wood has been softened by decay (Conner et al. 1976, Miller and Miller 1980, Runde and Capen 1987).

Although overall tree density and diameter size class distributions did not differ significantly between the 2 plots (Table 1 and Fig. l), cavity density was 39% greater on the treatment plot. Cavity density was greater on the treatment plot because oaks were more abundant, and the 2 oak species contained most of the cavities (Table 2). Digger pine is not as long-lived as blue and live oaks, but we believe there are other reasons why we found so few cavities in digger pines. The most striking difference between the 2 oaks and digger pine was the almost complete lack of nonexcavated cavities in digger pines (Table 2). This difference is probably related to certain physiological differences between hardwoods and conifers. When a hardwood limb dies, a protective layer of gum-filled cells develops at the base of the limb. This layer is limited to the sapwood (the living wood tissue), leaving the heartwood unprotected from invasion by decay fungi. Conifers also develop a protective zone of resin at the base of dead limbs. This resin is not limited to the sapwood but also spreads to the heartwood, providing greater protection against decay fungi (Peace 1962).

We compared cavity and cavity tree densities on our plots to estimates reported in the literature (Table 3). Comparisons are rough because few authors specified how they defined a cavity, and locating cavities can be difficult. Low tree density, small tree heights, and gridded plots greatly facilitated counting cavities on our plots. Cavity and cavity tree densities on our treatment plot were not exceptionally high compared to estimates from other habitats.

Other authors have noted that SCNB densities are not necessarily limited by nest site availability. Edington and Edington (1972) concluded that SCNB's were not limited by nest site availability because only 21% of the available cavities were occupied. Results of a simulation study led Raphael (1983) to conclude that cavities can sometimes build up to the point where their numbers do not limit SCNB populations. Raphael and White (1984) found a significant correlation between cavity density and SCNB density in the coniferous forests of the Sierra Nevada, suggesting densities were limited by nest site availability. They also found a significant negative correlation between cavity-nesting bird density and annual precipitation. They concluded that weather, primarily winter

Table 3. Estimates of cavity and cavity tree densities.

Cavities/ha	Cavity trees/ha	Forest type	Location	Study
4.8	2.8	Treatment plot	Calif.	This study
3.4	1.7	Control plot	Calif.	This study
6-7		Hardwood dominated	Europe	van Balen et al. (1982)
4.2	2.3	Hardwood dominated	wyo.	Sedgwick and Knopf (1986)
15		Hardwood dominated	Europe	Edington and Edington (1972)
4.4	2.8	Hardwood dominated	Colo.	Winternitz and Cahn (1983)
	4-9	Hardwood dominated	W.Va.	Carey (1983)
	4-17	Hardwood dominated	W.Va.	Carey (1983)
0.2-2.1		Hardwood dominated	Ariz.	Brush (1983)
5		Hardwood dominated	Europe	Ludescher (1973; cited in van Balen et al. [1982])
cl-3		Conifer dominated	Calif.	Raphael and White (1984)
1-1.5		Conifer dominated	Europe	Kneitz (1961; cited in van Balen et al. [1982])
	0.7-0.9	Conifer dominated	Oreg.	Mannan et al. (1980)
	6.4	Conifer dominated	Ariz.	Scott (1978)

weather, strongly affected abundance. Brawn and Balda (1988) added nestboxes to 3 plots in ponderosa pine forests of Arizona and concluded that SCNB's were limited by nest site availability on the 2 more intensively managed plots, but not on the least managed plot. The least managed plot contained many more oaks and snags than the more managed plots. Natural cavity availability was not reported but was probably greater on the least managed plot.

MANAGEMENT IMPLICATIONS

In areas where nest site availability has been decreased by man or where it is naturally low, adding nestboxes can be a useful mitigation technique to maintain or increase SCNB populations. It is important, however, that biologists do not simply assume that cavity-nesting birds are limited by nest site availability. Other factors like food abundance, winter mortality, and territoriality probably influence populations more in areas where natural cavities are abundant.

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