

# POPULATION BIOLOGY OF CAVITY NESTERS IN NORTHERN ARIZONA: DO NEST SITES LIMIT BREEDING DENSITIES?<sup>1</sup>

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**Abstract.** Breeding densities of secondary (i.e., nonexcavating) cavity-nesting birds are often assumed to be limited by availability of nest sites. We investigated this assumption for species breeding in northern Arizona's ponderosa pine forests. In 1979, we installed nest boxes on three treatment plots that differed in habitat structure and monitored breeding densities of six species through the 1983 breeding season. The effect of nest boxes was evaluated by comparing breeding densities on three treatment plots from 1980 to 1983 with: (1) pretreatment densities (1973 to 1975, 1979), and (2) densities on control plots from 1980 to 1983.

We observed variation in the importance of nest-site limitation among treatment plots and species. Overall breeding densities (all species combined) increased significantly on only two treatment plots. Individual species' responses were influenced by habitat structure, and breeding densities of only three species were apparently limited by nest sites before boxes were installed; Violet-green Swallows (*Tachycineta thalassina*), Pygmy Nuthatches (*Sitta pygmaea*), and Western Bluebirds (*Sialia mexicana*). A given species' breeding density in northern Arizona is nest-site limited if it is locally common and reliant on dead trees for nest sites. Availability of food or foraging substrate and territoriality may determine an upper limit to breeding densities if nest sites are in ample supply.

**Key words:** Arizona; breeding densities; cavity-nesting birds; nest boxes; population biology; ponderosa pine forests; territoriality.

## INTRODUCTION

Population density is rarely static in time or space (von Haartman 1971, Begon and Mortimer 1986). Studies of animal population dynamics have identified the singular or interactive influence of predation, intra- and interspecific resource competition, parasites and disease, habitat availability, and weather (reviewed by den Boer and Gradwell 1970, Andrewartha and Birch 1984, Begon and Mortimer 1986). Sources of variation in abundance can also be diverse within relatively specific taxonomic groups (MacArthur 1972, Schoener 1986). Factors influencing bird populations, for example, vary in importance according to geographic area, food habits, and migratory status (Lack 1966, von Haartman 1971, van Balen 1980, Newton 1980). Thus, empirical evidence suggests that synoptic theories, while heuristic, have limited applicability (Soloman 1970, Enright 1976, Simberloff 1980, Strong 1986).

Nevertheless, the literature suggests that abun-

dances of secondary (i.e., nonexcavating) cavity-nesting birds (hereafter referred to as SCNs) may be controlled by one factor, the availability of nest cavities (von Haartman 1956, Cody 1985). Suitable nest cavities are usually present in dead trees (snags) but can be scarce due to man's silvicultural activities or natural processes, such as fire, that keep forest habitat in an immature condition (Haapanen 1965).

Nest-box experiments can assess the importance of cavity limitation on SCN populations, and boxes often seem to increase breeding densities (Froke 1983). Intraspecific variation in the degree of nest-site limitation is rarely estimated, however. Moreover, most nest-box studies have been conducted on a small number of species, notably, Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*). Secondary cavity-nesting birds are a diverse group, accounting for over 15% of passerines breeding in north-temperate zones and, in North America, are represented in 11 orders and 19 families (Scott et al. 1977). Further, accounts of nest-box experiments with adequate controls are uncommon (Brush 1983). Lack of controls can render apparent experimental effects (i.e., increases) open to alternative explanations such as density changes associated with variation in availability of food or

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TABLE 1. Silvicultural profiles of study plots.

Plot	Tree species	Criterion					
		Relative density	Relative dominance	Relative frequency	Importance value	Absolute density (trees/ha)	Number of snags
Open treatment	<i>Pinus ponderosa</i>	81	87	69	237	57	7
	<i>Quercus gambelii</i>	19	13	31	63	12	
Open control	<i>P. ponderosa</i>	68	65	62	198	52	9
	<i>Q. gambelii</i>	32	35	38	102	21	
Thinned treatment	<i>P. ponderosa</i>	92	94	82	268	209	21
	<i>Q. gambelii</i>	8	6	18	32	16	
Thinned control	<i>P. ponderosa</i>	89	91	79	259	217	18
	<i>Q. gambelii</i>	11	9	21	41	19	
Dense treatment	<i>P. ponderosa</i>	90	86	77	253	583	39
	<i>Q. gambelii</i>	8	8	19	36	54	
	<i>Juniperus deppeana</i>	2	6	4	11	9	

unusually favorable climatic conditions (Järvinen 1983).

We conducted a nest-box study in northern Arizona's ponderosa pine forests. Previous work in this habitat suggests that numbers of nest cavities influence SCN breeding densities (Balda 1975, Scott 1979, Cunningham et al. 1980). To our knowledge, no controlled nest-box experiments have been conducted within any coniferous forests of western North America. Our primary objective was to test the hypothesis that the availability of nest sites limits SCN breeding densities in northern Arizona's ponderosa pine forests. Our experimental design allowed direct evaluation of inter- and intraspecific (i.e., among habitat) variation in the importance of nest-site limitation.

## METHODS

### STUDY PLOTS AND EXPERIMENTAL DESIGN

Fieldwork was conducted on five 8.0-ha study plots in northcentral Arizona on the Beaver Creek Watershed, Coconino National Forest. All plots contained ponderosa pine forest habitat which, in northern Arizona, is dominated by ponderosa pine (*Pinus ponderosa*) and varying densities of Gambel oak (*Quercus gambelii*). Plot elevation ranged from 2,100 to 2,300 m. Average annual precipitation and temperature on the Beaver Creek Watershed are about 64 cm and 22°C, respectively (Turkowski 1980).

We installed 60 nest boxes on each of three treatment plots after the 1979 breeding season. Two other plots served as controls for the nest-

box experiment. The boxes were spaced evenly throughout the treatment plots and placed at various heights (from 5 to 11 m) and exposures (see Brawn and Balda [1983] for details of box installation).

Boxes were constructed from a mixture of concrete and wood chips and identical (approximate volume = 1,900 cm<sup>3</sup>) except for diameter of entrance holes. We used two diameters, 38 and 32 mm, and installed 30 boxes with each size on each plot. SCNs are selective in regard to entrance hole diameter (Dhondt and Eyckerman 1980) and the sizes we used were considered to accommodate all species of SCNs, except raptors, that breed in northcentral Arizona (Balda, pers. observ.).

The three treatment plots had different habitat structures owing to different silvicultural histories (Table 1). The Dense-treatment plot had not been harvested for approximately 60 years and had relatively high pine and oak foliage volume, numerous snags, and a sparse understory due to a thick layer of pine duff. The Thinned-treatment plot had been moderately thinned in the 1970s of medium-sized pine stems and snags, resulting in a mixture of openings, mature pines, and thickets of young pine with a patchy herbaceous understory. The Open-treatment plot had been severely thinned in 1969 of all snags and about 75% of its original pine and oak foliage volume.

The two control plots corresponded in habitat structure to the Thinned- and Open-treatment plots. The Thinned-control plot had been moderately cut like the Thinned-treatment plot. The Open-control plot had been heavily thinned of

live pine and pine snags in the 1960s but contained more live oak than the Open-treatment plot (Table 1). The controls were located about 3.3 km from their respective treatment plots. No control was used for the Dense-treatment plot due to time constraints in censusing birds. We used the plotless point-quarter method to measure live vegetation (see Szaro and Balda 1979) and counted snags on all plots (Table 1).

#### ESTIMATION OF BREEDING BIRD DENSITIES

Breeding densities of SCNs were estimated using the spot-map census method (Robbins 1970). Beginning in mid-May, eight to 10 census visits were made on each plot each year. Census visits began at daybreak and each lasted 2 to 3 hr, during which we systematically traversed a plot using grid markers. All visual and auditory contacts with birds were mapped. We also searched for nests in natural cavities to clarify the reproductive status of singing males, location of breeding pairs detected on the control plots, or pairs not using nest boxes on the treatment plots. Breeding densities derived from the censuses and nest searches were standardized to number of pairs/40 ha to facilitate comparisons with other workers' density estimates (Szaro and Balda 1979, Cunningham et al. 1980).

#### ANALYSES OF EXPERIMENTAL EFFECTS ON SCN BREEDING DENSITIES

We analyzed effects of nest boxes on SCN breeding densities in two ways: (1) within-plot, pretreatment vs. posttreatment comparisons; and (2) within-year, treatment-control plot comparisons. "Treatment" refers only to the installation of nest boxes, not silvicultural activity. Within-plot comparisons were possible for all treatment plots. Four years of pretreatment breeding density data were available: 1973 to 1975 (all from Szaro and Balda 1979) and 1979 (Balda, unpubl. data). Pretreatment SCN densities were also estimated with the spot-map method. Treatment-control plot comparisons contrasted SCN densities from 1980 through 1983. Breeding densities on the two control plots were estimated only from 1980 to 1983.

Within-plot and within-year comparisons were analyzed by analysis of variance (ANOVA) with a repeated measures design. All density data were square root transformed owing to results of diagnostic variance-mean plots (Box et al. 1978).

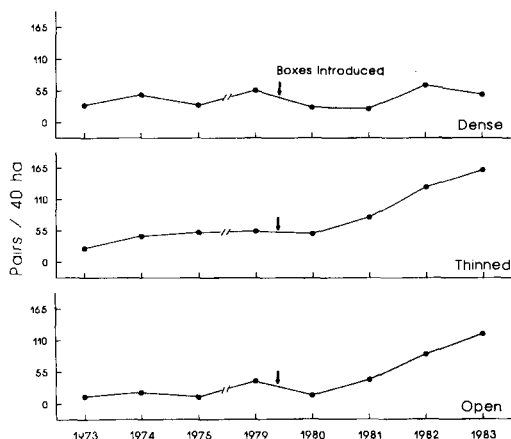


FIGURE 1. Pretreatment and posttreatment breeding densities of secondary cavity nesters (six species combined) on Dense-, Thinned-, and Open-treatment plots.

Overall plot effects (i.e., changes in total SCN densities) were analyzed using plot and species as the two ANOVA grouping variables. Individual species' density changes were assessed with *F*-tests using variance estimates from one-way linear contrasts as the numerator and combined (i.e., all species and treatment plots) plot-species interaction variance estimates as the denominator (see Milliken and Johnson 1984). Insufficient degrees of freedom prevented separate analyses of individual species' densities within each treatment plot.

## RESULTS

#### EFFECTS OF NEST BOXES ON OVERALL SCN BREEDING DENSITIES

*Comparisons of pretreatment and posttreatment breeding densities.* Subsequent to installation of nest boxes, SCN breeding densities increased on the Thinned- and Open-treatment plots, but not on the Dense plot (Fig. 1). Overall SCN breeding densities (i.e., all species summed) on the Thinned-treatment plot increased on average from 46 pairs/40 ha (pretreatment) to 108 pairs/40 ha during the posttreatment years ( $F = 17.2$ ,  $df = 1, 5$ ,  $P < 0.01$ ). On the Open-treatment plot, overall average densities also increased significantly from 21 pairs/40 ha to 64 pairs/40 ha ( $F = 6.9$ ,  $df = 1, 5$ ,  $P < 0.05$ ). Pretreatment ( $\bar{x} = 41$  pairs/40 ha) and posttreatment densities ( $\bar{x} = 43$  pairs/40 ha) were not significantly dif-

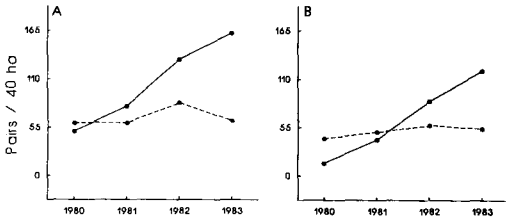


FIGURE 2. Overall breeding densities of secondary cavity-nesting birds on treatment (solid line) and control (dashed line) plots from 1980 to 1983. (A) Thinned habitat. (B) Open habitat.

ferent on the Dense-treatment plot ( $F = 0.2$ ,  $df = 1, 4$ ,  $P > 0.60$ ).

Breeding densities on the Thinned- and Open-treatment plots increased during each successive treatment year (Fig. 1). From 1980 through 1983, SCN densities on the Thinned-treatment plot increased 230% from 50 to 168 pairs/40 ha. On the Open-treatment plot, the 4-year increase was approximately 760% from 14 to 120 pairs/40 ha. Breeding densities in 1983 on the Thinned- and Open-treatment plots were more than three times those found within either plot during any pretreatment year. Posttreatment SCN densities on the Dense plot increased only between 1981 and 1982 and did not greatly exceed pretreatment densities observed in 1979.

From 1980 through 1983, over 90% of the SCN nests located on the Thinned- and Open-treatment plots were in boxes. Population densities on both plots increased concomitantly with increases in percent use of nest boxes ( $r = 0.85$ ,  $df = 6$ ,  $P < 0.05$ ). In contrast, on the Dense plot about 30% of located nests were in boxes and annual variation in densities was unrelated to box occupancy ( $r = 0.13$ ,  $df = 5$ ,  $P > 0.70$ ).

Overall breeding densities increased steadily on the Thinned- and Open-treatment plots because more pairs/species nested in boxes each year and, generally, more species used the boxes each year. For example, in 1980 on the Thinned-treatment, we found only three Western Bluebird (*Sialia mexicana*) and three Pygmy Nuthatch (*Sitta pygmaea*) nests in boxes; whereas in 1983, we found 14 Violet-green Swallow (*Tachycineta thalassina*), four Mountain Chickadee (*Parus gambeli*), two White-breasted Nuthatch (*Sitta carolinensis*), four Pygmy Nuthatch, two House Wren (*Troglodytes aedon*), and nine Western Bluebird nests in boxes.

*Comparisons of treatment and control plot breeding densities.* Overall breeding densities of SCNs during the posttreatment period were significantly greater on the Thinned-treatment plot than the Thinned-control (Fig. 2A,  $F = 5.9$ ,  $df = 1, 5$ ,  $P < 0.04$ ). Differences between these plots increased in each successive treatment year as densities on the Thinned-control were relatively stable (control  $\bar{x} = 69$  pairs/40 ha). The same SCN species were present in all treatment years on both plots; therefore, differences in overall breeding densities were caused by the number of pairs/species.

Differences between the Open-treatment and control plots were less distinct than those between the Thinned-habitat plots (Fig. 2B). Breeding densities on the Open-control were relatively constant from 1980 to 1983 ( $\bar{x} = 50$  pairs/40 ha) but greater on the Open-treatment only in 1982 and 1983. In 1980, overall densities were greater on the control plot; thus, SCN densities were not significantly different on Open-habitat plots during the posttreatment period (ANOVA,  $F = 0.01$ ,  $df = 1, 5$ ,  $P > 0.90$ ).

The same SCN species were not found on the Open-habitat plots within each breeding season. For example, House Wrens were absent on the treatment plot in 1980 but found on the control in all treatment years. Violet-green Swallows bred on the treatment plot only in 1982 and 1983 and, conversely, on the control plot in only 1980 and 1981 (see Appendix).

The disparity between the Open-habitat plots in 1980, when the boxes had little effect (5% occupancy), was due to plot-plot differences that partially confounded our experimental design, specifically, the aforementioned difference in densities of oak trees (Table 1). Gambel oak often have hollowed-out branch scars, used as nest sites by White-breasted Nuthatches, House Wrens, and Western Bluebirds (Brawn, pers. observ.). Accordingly, we found eight SCN nests in oaks on the control in 1980 (4-year range = 4–9). Therefore, oaks somewhat reduced the validity of the control for the Open-treatment plot with respect to comparisons based on breeding densities. To compensate, we also analyzed annual changes (e.g., change between 1980 and 1981) in SCN densities on the Open-habitat plots and found that between-year changes in breeding densities were significantly greater on the treatment plot ( $F = 6.7$ ,  $df = 1, 5$ ,  $P < 0.04$ ).

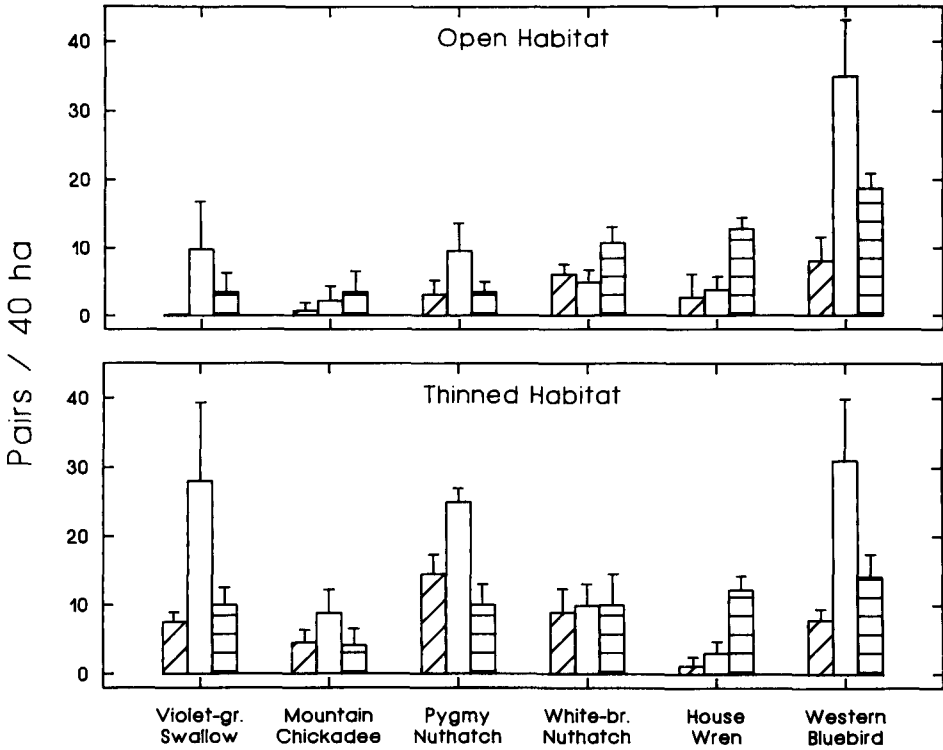


FIGURE 3. Breeding densities ( $\bar{x} + 1$  SE) of six secondary cavity-nesting species on Thinned- and Open-habitat study plots. (▨) = pretreatment densities, (□) = posttreatment densities, (▤) = control densities.

#### RESPONSES OF INDIVIDUAL SPECIES TO NEST BOXES

We observed considerable interspecific variation in response to the nest boxes. No species increased on the Dense plot; therefore, the following results consider only the Thinned- and Open-treatment plots.

*Violet-green Swallows.* Swallows did not nest in boxes until 1981 on the Thinned plot and 1982 on the Open plot. Despite this lag in box use, by 1983 Violet-green Swallows had increased substantially on both treatment plots (Fig. 3). On the Thinned plot, swallow densities went up each treatment year and increased nearly six-fold from 1980 (2.5 pairs/40 ha) through 1983 (50 pairs/40 ha). Swallow densities increased sharply on the Open-treatment plot between 1981 and 1982 but decreased approximately 20% between 1982 and 1983. Swallow densities recorded after boxes were available were significantly greater than those observed during the pretreatment years ( $F = 9.21$ ,  $df = 1, 11$ ,  $P < 0.02$ ). Posttreatment breed-

ing density of swallows on the Thinned-treatment plot was, on average, approximately 266% higher than during the pretreatment period. Swallows were never recorded breeding on the Open-treatment plot before 1982, suggesting that a shortage of natural nest sites on that plot during the pretreatment period had caused a local extirpation. Control plot densities remained relatively stable (Thinned) or decreased (Open) during the posttreatment years and were significantly less than those on the treatment plots ( $F = 11.3$ ,  $df = 1, 11$ ,  $P < 0.01$ ).

*Mountain Chickadees.* We observed a relatively moderate density response to the boxes by Mountain Chickadees that appeared to be influenced by habitat structure (Fig. 3). Chickadees nested in boxes beginning in 1981 and 1982 on the Thinned- and Open-treatment plots, respectively. Chickadee densities during the pretreatment and posttreatment periods were not significantly different, however ( $F = 1.6$ ,  $df = 1, 11$ ,  $P > 0.50$ ). The average posttreatment density on

the Thinned plot was about 4 pairs/40 ha greater than that recorded during the pretreatment years. Pretreatment densities of chickadees on the Open plot averaged less than 1 pair/40 ha, and about 2.5 pairs/40 ha after boxes were available. Similarly, chickadee densities were not significantly different on the treatment plots and controls between 1980 and 1983 ( $F = 1.4$ ,  $df = 1, 11$ ,  $P > 0.25$ ).

*Pygmy Nuthatches.* Nest boxes promoted increased Pygmy Nuthatch densities on both treatment plots (Fig. 3). Pygmy Nuthatches nested in boxes on the Thinned plot during each treatment year and on the Open plot beginning in 1981. Average posttreatment densities were significantly higher than those during the pretreatment years ( $F = 9.8$ ,  $df = 1, 11$ ,  $P < 0.01$ ). On the Thinned plot, densities increased from a pretreatment average of 15 pairs/40 ha to a posttreatment mean of 25 pairs/40 ha. We observed over a 200% increase on the Open plot where densities increased, on average, from 3 to 10 pairs/40 ha. Breeding densities on the treatment plots were also significantly greater than control plot densities from 1980 through 1983 ( $F = 11.4$ ,  $df = 1, 11$ ,  $P < 0.01$ ).

*White-breasted Nuthatches.* White-breasted Nuthatches exhibited little response to the boxes (Fig. 3). This species nested in boxes only three times on the Thinned plot and twice on the Open plot. Moreover, White-breasted Nuthatches were the only species on the treatment plots that nested more frequently in natural cavities (i.e., in oaks) than in boxes. Nuthatch densities were equivalent during the pretreatment and posttreatment periods on both treatment plots ( $F = 0.42$ ,  $df = 1, 11$ ,  $P > 0.50$ ), equal on the Thinned-treatment and control, and greater on the Open-control than on the Open-treatment. The difference between Open-habitat plots was, again, attributable to differences in densities of Gambel oak on the plots. Treatment-control plot densities were not significantly different ( $F = 1.1$ ,  $df = 1, 11$ ,  $P > 0.25$ ).

*House Wrens.* Wrens nested in boxes less frequently than any other species, once on the Open, and twice on the Thinned plot. Pretreatment and posttreatment wren densities (Fig. 3) were equivalent on both treatment plots ( $F = 1.4$ ,  $df = 1, 11$ ,  $P > 0.25$ ). House Wrens were also exceptional because their densities were significantly greater on the control plots ( $F = 6.1$ ,  $df = 1, 11$ ,  $P < 0.05$ ).

*Western Bluebirds.* Western Bluebirds nested in boxes on both treatment plots during each treatment year and were the most common box occupant. Bluebird densities during the posttreatment period were significantly greater than pretreatment levels (Fig. 3,  $F = 11.0$ ,  $df = 1, 11$ ,  $P < 0.01$ ). Density increases of bluebirds on the treatment plots were the highest of any species (Fig. 3). Pretreatment mean densities on both treatment plots were approximately 8 pairs/40 ha, whereas posttreatment mean densities were 31 pairs/40 ha on the Thinned treatment and 35 pairs/40 ha on the Open treatment. Bluebird densities on the treatment plots were also significantly greater than those on controls from 1980 to 1983 ( $F = 17.1$ ,  $df = 1, 11$ ,  $P < 0.005$ ).

## DISCUSSION

We observed increasing densities on two of three treatment plots; thus, availability of nest sites can influence the population biology of SCNs in Arizona's ponderosa pine forests. Nonetheless, manifold density changes among treatment plots and species suggest that other factors also influence SCN breeding densities.

### COMPARISON OF OVERALL SCN DENSITY CHANGES AMONG TREATMENT PLOTS

Availability of natural nest cavities in snags may partially account for the differential effect of boxes on the treatment plots. A comparatively high number of snags (Table 1), infrequent use of boxes, and absence of density increases suggest that availability of nest sites was not influencing breeding densities on the Dense plot. On the Open- and Thinned-treatment plots, however, silvicultural management had affected limitation of breeding densities by nest sites.

Prior to provision of boxes, average overall SCN breeding densities were highest on the Thinned plot, slightly lower on the Dense plot, and lowest on the Open plot. After boxes were available, overall SCN densities were, on average, highest on the Thinned plot, considerably lower on the Open plot, and lowest on the Dense plot (Fig. 1). The largest pretreatment to posttreatment increase occurred on the Thinned plot, where 62 pairs/40 ha were added (combined 4-year average). Forty-three pairs/40 ha were added to the Open plot and only two on the Dense plot (Fig. 1). These data prompt two questions: (1) why were density increases higher on the Thinned-treatment plot than the Open-treat-

ment plot where, before boxes were installed, fewer nest sites were available; and (2) assuming nest sites were not limiting on any plot after boxes were provided, why did SCN densities on the Thinned- and Open-treatment plots attain levels much higher than those observed on the Dense plot?

Habitat requirements of the SCNs, independent of nest sites, may explain the higher increase on the Thinned- vs. Open-treatment plots. Density of live trees was considerably greater on the Thinned plot (Table 1). Four of the six SCN species considered in this study (Mountain Chickadees, Pygmy Nuthatches, White-breasted Nuthatches, and House Wrens) are foliage or bark gleaners during the breeding season (Szaro and Balda 1979). These species' combined pretreatment to posttreatment increase was 18 pairs/40 ha on the Thinned-treatment but only 7 pairs/40 ha on the Open-treatment plot. Therefore, the magnitude of nest-site limitation on foliage/bark gleaners appears to be contingent upon the availability of foraging substrate.

Enoksson and Nilsson (1983) report an inverse relationship between food availability and size of European Nuthatch (*Sitta europaea*) territories. We estimated the size of Pygmy Nuthatch territories at the onset of the nesting period on the Thinned- and Open-treatment plots from 1981 through 1983. Territories were significantly larger on the Open-treatment plot (ANOVA,  $F = 9.4$ ,  $df = 1, 23$ ,  $P < 0.01$ ). Moreover, after boxes were installed, nuthatches increased, on average, by 11 pairs/40 ha on the Thinned-treatment plot but only 5 pairs/40 ha on the Open-treatment. We are uncertain, however, about the role of territoriality during the breeding season in controlling population densities (see following discussion of territoriality).

During the breeding season, Violet-green Swallows and Western Bluebirds are aerial feeders and ground/aerial feeders, respectively. Violet-green Swallows also increased more on the Thinned- than the Open-treatment plot (Fig. 3). Swallows typically forage above tree canopy or lower in canopy openings and greater foliage volume may enhance food resources within their foraging zone. We did not quantify aerial insect densities.

About 60% of Western Bluebird foraging attempts on our plots were "drops" from low perches onto the ground (Brawn, unpubl. data). The amount of ground cover as live vegetation

(grasses and forbs) was similar on the Thinned- (34%) and Open-treatment plots (39%). We estimated ground-insect biomass on both plots (1,200 net sweeps/plot/year) in 1982 and 1983 and, based on dry mass, the plots were equivalent (2-year  $\bar{x}$  [SD]: Thinned plot = 114 g [234]; Open plot = 103 g [118]). Thus, density responses to nest boxes were similar in magnitude on the Thinned- and Open-treatment plots for the one species whose foraging substrate and food resources were apparently unaffected by habitat structure.

Availability of foraging substrate can only partially explain the aforementioned change in relative SCN densities on the treatment plots. The Dense-treatment plot is seemingly poor breeding habitat for only House Wrens and Western Bluebirds. Wrens have never been recorded on the Dense plot. Bluebirds are found on this plot; however, the closed canopy on much of the Dense plot has resulted in a thick layer of pine duff covering about 50% of the ground. Pine duff appears to support relatively low insect biomass (Brawn, pers. observ.) and is likely poor foraging substrate for bluebirds. Only 12% of ground cover on the Dense plot was live vegetation.

We are uncertain why densities of the other SCN species were not higher on the Dense plot. Productivity is known to decrease in ponderosa pine forests as they approach "senescent," closed-canopy conditions (Schubert 1974), suggesting that quality of foraging substrate as well as quantity may influence SCN habitat choice and breeding densities. Comprehensive sampling of foliage gleaner foraging efficiency and abundances of arboreal insects would evaluate this hypothesis.

Our observation of between-plot variation in box use and consequent population changes agrees with results from other nest-box experiments. Utilizing an experimental design similar to ours, Higuchi (1978) installed boxes on plots with "secondary successional" and "mature broadleaved" habitats. Box use and population increases were relatively high on the successional plots where natural nest sites were scarce. Within the mature habitat, where natural cavities were numerous, box usage was low and densities were not enhanced. Järvinen (1978) placed boxes on several plots within mountain birch forest habitat in Finland. Natural cavities were scarce on all of Järvinen's plots; but, over a 10-year period, densities of Pied Flycatchers and European Redstarts (*Phoenicurus phoenicurus*) increased more

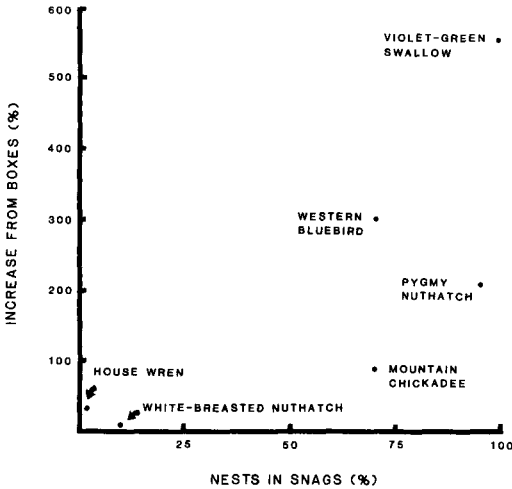


FIGURE 4. Relationship between dependence on snags for nest sites (from Cunningham et al. 1980) and density increase after nest boxes were installed. Density increases are average increases over pretreatment densities on Thinned- and Open-treatment plots.

within comparatively "productive" habitats. Similarly, Enemar (1980) found that redstarts (a foliage gleaner) will not use nest boxes in certain habitat types and concluded that factors other than the supply of nest sites can limit their population densities.

Newton (1979, cited in Village 1983) concluded that breeding densities of cavity-nesting raptors are limited by nest sites or food, whichever is in shortest supply. Our results suggest that this conclusion is applicable to certain cavity-nesting passerines in northern Arizona.

#### INTERSPECIFIC VARIATION IN POPULATION RESPONSE TO NEST BOXES

The species considered here separate into three groups concerning response to the box experiment: High—Violet-green Swallows, Pygmy Nuthatches, and Western Bluebirds; Intermediate—Mountain Chickadees; and Low—White-breasted Nuthatches and House Wrens. Three factors may account for the differential responses; reliance on snags for nest sites, local population densities, and, possibly, territoriality. Other studies have found that interspecific competition for nest sites can negatively influence SCN breeding densities (Slagsvold 1978, van Balen et al. 1982, Minot and Perrins 1986). We did observe interspecific interactions near

nest boxes; however, from 1980 through 1983, pairwise correlations of density changes among the SCNs were positive (Brawn 1985).

A study of SCN nest-site selection in northern Arizona (Cunningham et al. 1980) found pronounced interspecific variation in use of snags for nest sites; certain species are reliant on snags, while others rarely nest in snags. For example, nearly all Violet-green Swallow ( $n = 41$ ) and Pygmy Nuthatch ( $n = 34$ ) nests, but only one of 12 White-breasted Nuthatch nests were in snags. Furthermore, an experiment in ponderosa pine habitat that removed snags (Scott 1979) indicated that some species' densities are sensitive to snag abundance, but others are not. The patterns of interspecific variation in use of snags found by Cunningham et al. (1980) and use of nest boxes on the Thinned- and Open-treatment plots were concordant (Fig. 4,  $r = 0.81$ ,  $df = 4$ ,  $P < 0.05$ ).

Cunningham et al. (1980) also documented SCN breeding densities in ponderosa pine forests throughout northern Arizona. Density data from eight plots (derived using the spot-map method) indicated that, regardless of variation in availability of snags and foraging substrate, Mountain Chickadees, White-breasted Nuthatches, and House Wrens are often relatively uncommon. Therefore, the more common species were those that increased the most after provision of nest boxes.

Limitation of SCN populations by nest sites may require a critical level of local abundance. The presence of surplus or floater individuals, that would breed if more nest sites were available, is unlikely if a species is regionally rare. Low densities in northern Arizona may explain why Mountain Chickadees, a species that uses snags (Fig. 4), did not increase more on the treatment plots. A study on Mountain Chickadees in California, where local densities are higher, recorded significant density increases subsequent to installation of boxes (Dahlsten and Copper 1979). Alternatively, low ambient densities may simply retard density increases subsequent to installation of boxes.

The importance of intraspecific territoriality during the breeding season in our study is unclear. Mountain Chickadees, White-breasted Nuthatches, and House Wrens are territorial at the onset of the breeding season but, again, these species are comparatively rare and their territories were never contiguous. Violet-green Swal-



lows were common but do not maintain feeding territories (Brawn, pers. observ.).

Breeding territoriality was therefore potentially relevant only with Pygmy Nuthatches and Western Bluebirds. Intraspecific interactions appeared to exclude some individuals of these species from breeding on the Thinned- and Open-treatment plots. In early spring, we often noted color-marked birds (first-year males that fledged from boxes) attempting to gain possession of a nest box; however, these birds were usually displaced by adults and not subsequently observed breeding on the plots (Brawn 1984). Territorial behavior is deemed to be most important when densities are at the highest possible level (Lack 1966, Klomp 1980, Patterson 1980); thus, in our study, generally consistent annual density increases obfuscate the issue. Once densities do "stabilize," a removal experiment, like that performed by Village (1983), will assess the effects of territoriality. Village found nest sites to be a limiting influence on European Kestrel (*Falco tinnunculus*) populations; however, territoriality was the proximate factor causing the shortage of nest sites.

Events outside the breeding season may also influence the magnitude of nest-site limitation, especially within permanent resident species. Territoriality or food could locally limit populations during the fall or winter (van Balen 1980, Klomp 1980), thereby reducing numbers of floaters during the breeding season and diminishing the direct influence of nest-site availability. Our observation that the strongest response to nest boxes occurred within migratory species (swallows and bluebirds) circumstantially supports this possibility. Removal experiments of individuals within rare and common species throughout the year would clarify the processes underlying interspecific variation in nest-site limitation.

## CONCLUSIONS

The widely held belief that nest sites limit SCN breeding densities appears only partially correct. Our experiments demonstrate that SCNs in northern Arizona, as a group, can indeed be limited by nest sites; but, importantly, only three of six species demonstrably increased. A given SCN population appears limited by nest sites if sufficiently common during the breeding season and dependent upon snags as a source for nest sites. Furthermore, within species that are nest site limited, the magnitude of such limitation is mit-

igated by habitat structure. Our results are consistent with the growing realization that ecological phenomena are best viewed from a pluralistic perspective (MacArthur 1972, Simberloff 1980, Schoener 1986).

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APPENDIX. Breeding densities (pairs/40 ha) of secondary cavity-nesting birds on treatment and control plots.

Species	Plot	Year							
		1973	1974	1975	1979	1980	1981	1982	1983
Violet-green Swallow	Dense treatment	9.0	9.0	7.5	17.5	5.0	3.8	12.5	7.5
	Thinned treatment	6.0	9.0	7.5	7.5	2.5	12.5	45.0	50.0
	Thinned control <sup>a</sup>	—	—	—	—	10.0	10.0	15.0	5.0
	Open treatment	0	0	0	0	0	0	21.8	17.5
	Open control <sup>a</sup>	—	—	—	—	11.3	2.5	0	0
Mountain Chickadee	Dense treatment	0	7.5	3.0	5.0	0	3.8	10.0	7.5
	Thinned treatment	0	6.0	4.5	7.5	1.3	11.3	7.5	15.0
	Thinned control	—	—	—	—	0	2.5	7.5	6.3
	Open treatment	1.5	0	1.5	0	0	0	4.4	4.4
	Open control	—	—	—	—	0	1.3	6.3	3.8
White-breasted Nuthatch	Dense treatment	3.0	10.5	3.0	10.0	6.3	2.5	10.0	7.5
	Thinned treatment	3.0	7.5	15.0	10.0	10.0	3.8	10.0	16.0
	Thinned control	—	—	—	—	10.0	5.0	8.8	16.3
	Open treatment	5.2	9.0	6.0	4.3	3.3	4.4	3.3	8.7
	Open control	—	—	—	—	6.3	7.5	15.0	13.8
Pygmy Nuthatch	Dense treatment	13.5	15.0	13.5	23.7	15.0	10.0	25.0	18.8
	Thinned treatment	7.5	15.0	18.0	17.5	21.5	22.5	30.0	25.0
	Thinned control	—	—	—	—	18.8	17.5	16.3	11.3
	Open treatment	0	2.3	1.5	8.7	0	8.7	12.0	17.5
	Open control	—	—	—	—	0	5.0	3.8	5.0
House Wren	Dense treatment	0	0	0	0	0	0	0	0
	Thinned treatment	2.3	0	0	2.5	5.0	1.3	2.5	6.0
	Thinned control	—	—	—	—	12.5	13.8	15.0	7.5
	Open treatment	0	0	0	10.9	0	4.4	4.4	6.6
	Open control	—	—	—	—	10.0	13.8	17.5	10.0
Western Bluebird	Dense treatment	4.5	6.0	3.0	0	0	3.8	7.5	7.5
	Thinned treatment	5.2	8.3	7.5	10.0	10.0	27.5	37.0	50.0
	Thinned control	—	—	—	—	8.8	11.3	20.0	16.3
	Open treatment	6.0	8.3	3.0	15.2	10.9	23.9	40.0	65.0
	Open control	—	—	—	—	15.0	20.0	18.8	21.0

<sup>a</sup> Breeding densities on the control plots were estimated only from 1980 to 1983.