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## Selectivity and Ecological Consequences of Cavity Nesters Using Natural vs. Artificial Nest Sites

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Secondary cavity nesters will use nest boxes in lieu of tree cavities in managed forests (Bellrose et al. 1964, van Balen et al. 1982). Information on use of artificial vs. natural cavities is fragmentary, but preference for boxes is sometimes observed (e.g. Eadie and Gauthier 1985, Korpimäki 1987). This may indicate variation in quality of nest sites regarding expected reproductive success (van Balen 1984; Nilsson 1984a, b). I observed nest-site choice by breeding birds in northern Arizona and offer an alternate hypothesis for nest-site preference.

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I examined occupancy of artificial and natural cavities on 3 8.0-ha study plots in ponderosa pine (*Pinus ponderosa*) forests. I observed 5 species: Violet-green Swallow (*Tachycineta thalassina*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), Pygmy Nuthatch (*Sitta pygmaea*), and Western Bluebird (*Sialia mexicana*). The plots, referred to as "Dense," "Thinned," and "Open," differed in habitat structures. The Dense plot had 637 live trees/ha (583 Ponderosa pine, 54 Gambel's Oak [*Quercus gambelii*]), and 39 dead trees (total); the Thinned plot had 225 live trees/ha (209 pine, 16 oak) and 21 dead trees; and the Open plot had 69 live trees/ha (57 pine, 12 oak) and 7 dead trees. I installed 60 nest boxes on each plot before the 1980 breeding season (see Brawn and Balda 1983). All boxes were identical except for entrance-hole diameter; half the boxes on each plot
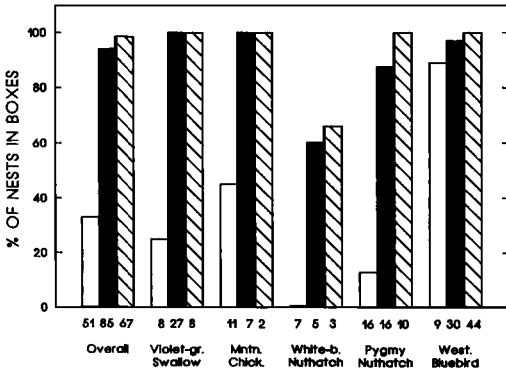
Fig. 1. Proportion of located nests in boxes on Dense (open bars), Thinned (solid bars), and Open (hatched bars) study plots. Sample sizes (i.e. all nests from 1980–1983 breeding seasons combined) are given at bottom of bars.

had small (32 mm) entrances, and half had large (38 mm). Average box heights were similar among the plots ($\bar{x} = 8.0$ m, SE = 0.2) and exposures were selected randomly.

Woodpeckers observed breeding on or near the plots (i.e. Acorn Woodpecker [*Melanerpes formicivorus*], Hairy Woodpecker [*Picoides villosus*], Three-toed Woodpecker [*Picoides tridactylus*], and Northern Flicker [*Colaptes auratus*]) commonly excavate nest cavities in dead ponderosa pine or decayed parts of otherwise sound Gambel's Oak (pers. obs.). Therefore, densities of dead trees and oaks approximate differences among plots in numbers of natural cavities available to secondary cavity nesters. I inspected nest boxes and searched for active nests in natural cavities on each plot throughout each breeding season from 1980–1983. A box was occupied if it contained eggs. Natural cavities were deemed occupied after observation of feeding visits (to nestlings or incubating adults) or removal of fecal sacs.

Overall, nest boxes were apparently preferred over natural cavities on the Thinned and Open plots, but not on the Dense plot (Fig. 1). Nearly all nests located on the Thinned and Open plots were in boxes. Natural cavities on these plots were largely ignored by breeding birds after nest boxes became available. In contrast, no boxes were used on the Dense plot in 1980, and 65–70% of all nests located thereafter were in natural cavities. The proportion of nests in boxes on the Dense plot was significantly lower than that on the other plots (ANOVA, $F_{2,12} = 9.6$, $P = 0.003$).

The difference among plots in box or natural-cavity occupancy stemmed from intraspecific variation in selection of nest type. All species selected boxes over natural cavities on the Thinned and Open plots where, except for White-breasted Nuthatches, over 85% of each species' nests were in boxes (Fig. 1). On the

Dense plot, only Western Bluebirds apparently preferred nest boxes. Within species, except bluebirds, the proportion of nests in boxes on the Dense plot was significantly less than that observed elsewhere (Kruskal-Wallis test, $H = 8.3$, df = 2, $P = 0.016$).

Among passerine secondary cavity nesters in Europe, clutch size and fledging success were correlated positively with volume of a nest cavity (Löhrl 1980; van Balen 1984; Nilsson 1984a, b). Further, in titmice (*Parus* spp.), breeding birds will "adjust" clutch size according to cavity volume (van Balen 1984). The proximate mechanism that underlies these phenomena may involve hyperthermia and resultant low survivorship of nestlings when cavity volume is too small for a brood. A relationship between reproductive success and cavity volume has been used to explain apparent preference for nest boxes or natural cavities (Nilsson 1984a) and for large boxes over small (van Balen 1984).

Variation in quality of nest sites relative to expected reproductive success may also stem from vulnerability to predation (Korpimäki 1987). For example, secondary cavity nesters in Sweden preferred nest sites that were relatively high and presumably less accessible to predators (Nilsson 1984b).

My observations are inconsistent with the hypothesis that variation in quality of nest sites determines preference for artificial or natural cavities. Near uniform occupancy of boxes was expected on the Open plot where few natural cavities existed. However, both nest types were available on the other plots. To account for my observations, the nest-site quality hypothesis requires that nest boxes on the Thinned plot were generally "better" than natural cavities, and the opposite relation on the Dense plot. Although I did not measure volumes of natural cavities, sizes of dead trees on the Thinned and Dense plots were not significantly different (mean height and dbh [±SE]; Dense plot, 19.4 m [±2.4] and 38.4 cm [±4.3]; Thinned plot, 18.9 m [±2.5] and 36.1 cm [±5.2]; *t*-tests, $P > 0.35$). Moreover, I observed the same species of woodpeckers on the 2 plots in similar numbers (Brawn et al. 1987). Thus, volume of natural cavities was probably not different on the Dense and Thinned study plots, yet 4 of 5 species demonstrated plot-specific selectivity. Preference for boxes by bluebirds on the Dense plot was exceptional. Additional field studies of clutch and brood sizes, cavity volumes, and breeding energetics are needed to further evaluate the nest-site quality-volume hypothesis for birds in northern Arizona.

Predation on nests in boxes was <5% on all plots (nests from 1980–1983 combined) and I detected no preference regarding height (Brawn 1985). Western Bluebird nests in natural cavities on another plot without boxes experienced similar predation rates (Brawn 1987). Therefore, vulnerability to predation also appeared unimportant.

An alternative hypothesis is that relative densities

of artificial vs. natural cavities can influence occupancy of a given nest type. Ratios of nest boxes to dead trees on the Dense, Thinned, and Open plots were approximately 1.5, 3.0, and 9.0, respectively. If boxes and natural cavities were used according to their availability, the frequency of box occupancy on the Dense and Thinned plots should have been similar. Yet, 94% of the nests on the Thinned plot were in boxes. I propose that prospective breeders "switch" to the most frequently encountered cavity type. About 70% of the boxes on the Dense plot were never occupied. Thick vegetation may have prevented their detection. Switching behavior could benefit birds attempting reproduction by reducing time spent searching for potential nest sites. Secondary cavity nesters, especially first-time breeders, often inspect many cavities prior to selection of a nest site (Eadie and Gauthier 1985, pers. obs.). How birds locate cavities merits investigation. Field experiments that vary the ratio of artificial to natural cavities within similar habitats could test the hypothesis that selectivity is frequency dependent.

Apparent preference for a certain type of nest site has potential ecological consequences. More boxes were occupied in successive breeding seasons (Brawn et al. 1987) on the Thinned plot where intra- and interspecific encounters at nest boxes also increased (Brawn unpubl. data). This was noteworthy because natural cavities were available as nest sites with, presumably, less potential interference. Natural cavities on the Thinned plot were evidently suitable as nest sites because all five species bred there before 1980 (Brawn et al. 1987).

In addition, overall breeding densities of secondary cavity nesters increased from 1980 through 1983 on the Open and Thinned plots, but not on the Dense plot (Brawn and Balda 1988). Selectivity for a certain type of nest may limit breeding densities at a level below that obtained if all types of cavities are used in proportion to their availability. Variation in breeding densities of secondary cavity nesters in northern Arizona cannot be attributed to one factor (Brawn and Balda 1988), but individual behavior may influence population-level dynamics (Hassell and May 1985, Martin 1986).

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