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CAVITY USE BY SECONDARY CAVITY-NESTING BIRDS AND RESPONSE TO MANIPULATIONS

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ABSTRACT.—I studied secondary cavity-nesting birds in riparian habitat along the lower Colorado River, Arizona, to determine whether the birds were limited by availability of nest sites in relatively undisturbed habitat. Species differed in cavity use on the basis of size and time, and cavities were a limiting factor on only one of three study areas. However, birds were responsive to cavity manipulations. Numbers of breeders decreased after cavities were blocked on a plot with many cavities, while breeders increased on a nest-box plot where few natural cavities were available. Breeding numbers remained stable on an unmanipulated plot, despite increased European Starlings (*Sturnus vulgaris*). Some cavity-related aggression occurred, but did not affect breeding numbers or success, because alternate nest sites were available.

Von Haartman (1957) and Hilden (1965) were among the first to suggest that cavity-nesting birds were limited by the availability of nest sites. Cavity-nesting birds are good ecological test species because nest sites are accessible and can be manipulated easily. Studies of cavity-nesting birds have often supported hypotheses of nest-site limitation. Some studies have counted snags or cavities and assessed their use (Gysel 1961, Balda 1975, McEllin 1979) while others have investigated changes in bird numbers and resource use presumably caused by changing availability of nest sites. Populations may decline following removal of nest sites (Scott 1979, Mannan et al. 1980) or rise following introduction of nest boxes (Lack 1966, Enemar and Sjostrand 1972, Hogstad 1975).

Several aspects of many of the above-mentioned studies weaken the conclusion of nest-site limitation. First, many of the nest-box studies (e.g., Lack 1966) were conducted in intensively managed forests, which were unnaturally devoid of nest sites. Second, pre-manipulation densities were seldom known, and comparisons were made between areas that may have differed in other ways (Dahlsten and Copper 1979). Third, snag removal also involves loss of foraging substrates for many cavity-nesters, especially bark-gleaners, bark-probers, flycatchers and raptors. Studies should be designed to manipulate only one factor at a time, in order to understand more fully the importance of each habitat component.

Anderson and Ohmart (1978) showed a strong correlation between abundances of snags and cavity-nesting birds in the lower Colorado River valley, suggesting that the birds were limited by nest-site availability. Therefore, I decided to test the nest-site limitation hypothesis in relatively undisturbed habitat along the lower Colorado River. My main question was: are cavity-nesting birds limited by the availability of nest sites? If so, do birds compete for cavities? I predicted that: (1) if suitable nest sites are limiting, use should approach saturation; (2) breeding numbers should increase if nest boxes are provided; (3) populations should decline if nest sites are removed; and (4) if cavities are limiting and population densities are high, birds should compete for nest sites.

I concentrated on secondary cavity-nesting species because cavities are easier to manipulate than snags. The Ash-throated Flycatcher (*Myiarchus cinerascens*), the most widespread secondary cavity-nester in the lower Colorado River valley, was the principal study species. I also collected data on Lucy's Warbler (*Vermivora luciae*), which is common but difficult to study because of its secretive nesting habits. Data were also collected on four other cavity-nesting species—Gila Woodpecker (*Melanerpes uropygialis*), Ladder-backed Woodpecker (*Picoides scalaris*), Brown-crested (Wied's Crested) Flycatcher (*Myiarchus tyrannulus*) and European Starling (*Sturnus vulgaris*)—since they either provide nest sites for Ash-throated Flycatchers or are potential competitors for them (pers. observ.). These species breed at the same time, increasing the chances of competition (Rosenberg et al. 1982).

METHODS

The study was conducted from March 1978 to July 1980. All study areas (abbreviated SA) were between Ehrenberg and the Bill Williams River delta, western Yuma Co., Arizona.

SA I, the cavity-blocking plot, was 14 km north of Ehrenberg, and was a 20-ha stand of honey mesquite (*Prosopis glandulosa*), with a patchy understory of saltbush (*Atriplex* spp.).

TABLE 1. Dimensions of cavities and cavity trees used as nest or roost sites, lower Colorado River valley.

	Cavity size								
	Large			Medium			Small		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
Entrance diameter[a]	5.4[b]	.09	7	3.8[b]	.05	11	4.1	.22	7
Cavity depth	26.4	.23	5	16.5	.35	11	7.1	.73	7
Cavity height (m)	1.5[c]	.08	6	1.6	.07	11	1.7	.19	7
	10.3[d]	.12	16						
Tree height (m)	3.8[c]	.23	6	4.2	.14	11	4.8	.50	7
	15.2[d]	.16	16						
Limb diameter	18.6[e]	.16	16	17.8[e]	.39	11	16.3	.54	7

[a] Measurements are in cm, unless noted otherwise.
[b] Significantly different; $t = 16.6$, df = 16, $P < .001$.
[c] Honey mesquite habitat.
[d] Cottonwood-willow habitat.
[e] Not significantly different; $t = 1.79$, df = 25, $P > .05$.

This plot was surrounded by similar habitat for 1.5 km in all directions, and was 85 m above sea level. SA II, an unmanipulated plot, also 20 ha, was 6 km east of Parker Dam, in the Bill Williams delta. Fremont cottonwood (*Populus fremonti*) and Goodding willow (*Salix gooddingii*) dominated the plot, with a dense understory of salt cedar (*Tamarix chinensis*) and cattails (*Typha* sp.). The plot was bounded to the west and north by similar habitat and to the east by regenerating, burned riparian habitat. To the south, beyond a narrow, incomplete border of honey mesquite and arrowweed (*Tessaria sericea*), was Sonoran desert scrub, composed of palo verde (*Cercidium microphyllum*) and a few saguaro (*Cereus giganteus*). SA III, 16 ha of honey mesquite, was 1 km east of SA I. This was the nest-box plot.

Study Areas I–III were censused at least three times per month during the breeding season (March–July), with occasional visits during the rest of the year. SA I was censused in 1979 (20 visits, 100 h) and 1980 (23 visits, 115 h). SA II was censused in 1978 and 1979 (17 visits, 111 h and 25 visits, 92 h, respectively), but was unusable in 1980 owing to a flood. SA III was censused only in 1980 (15 visits, 75 h). I used a modified version of Williams' (1936) spot map method. I determined bird use of SA III in 1979 (pre-manipulation) by carefully inspecting trees for nests. On 8–9 February 1980 I inspected all trees for cavities and nests, which was possible because of the open nature of the plot. Cavity use was determined by the presence and physical condition of the nesting materials—it was possible to identify nests to year and species in this way. Because of possible second broods, this method might overestimate the 1979 breeding population.

I looked for nests on each visit to a study area. Nests were then checked on each subsequent visit until activity ceased. Breeding activity was defined by the presence of eggs, nestlings or incubating adult, by an adult entering with food, or by active nest defense. For some inaccessible nests on SA II, I used the behavioral criteria of Jackson (1976) to determine nest status. I defined a nest as successful if at least one fledgling was produced.

Cavities on SA I were counted completely in September 1979, parts of SA II were searched in 1978 and 1979, and I checked SA III in February 1980. Dimensions, placement and use of cavities were recorded. All cavities found on SA I and SA III were investigated with a nest-checker, made of 2.5-cm diameter PVC pipe, with attached mirror and light. On SA II, I recorded a cavity as containing a nest if it was entered by a bird. Vegetation density and cavity height probably influenced count efficiency. I feel confident that I found all cavities on the open SA III, and all large and medium cavities on SA I. I probably missed some well-hidden small cavities on SA I, and some cavities of all sizes on SA II. At each cavity I measured foliage density using the board technique (MacArthur and MacArthur 1961).

Species-specific nest boxes for Ash-throated Flycatchers and Lucy's Warblers were used to augment the existing supply of cavities on SA III. Dimensions of each type of box were based on measurements of active nest cavities (Table 1, medium for Ash-throated Flycatchers, small for Lucy's Warblers). Nest boxes were built from 2.5 × 15 cm unstained, split redwood fenceboard, with ventilation holes in the sides and bottom. When possible, I placed boxes under the tree canopy with the entrance facing north, for shading.

Twenty nest boxes for each species were placed on SA III in a rectangular grid pattern. Two nest boxes, one of each type, were placed at each corner of a 75-m grid cell, at least 10 m apart and out of sight of each other, to avoid interference. No interference was observed. Nest-box densities equalled maximum bird densities obtained from censuses in the lower Colorado River valley (Anderson and Ohmart

TABLE 2. Cavity availability before manipulation.[a]

Study area	Large		Medium		Small	
	Avail.	Used	Avail.	Used	Avail.	Used
I	0	–	12	6	8	6
II	30	21	12	11	0	–
III	0	–	0	–	3	3

[a] See text for methods of determining availability and use.

TABLE 3. Cavity dimensions and characteristics for used and unused medium cavities, SA I.

	Unused		Used[a]	
	Mean	SD	Mean	SD
Entrance diameter (cm)	3.9	0.6	3.9	0.3
Cavity depth (cm)	14.6	4.1	18.0	3.2
Cavity height (m)	1.3	0.7	2.0	1.1
Percent live foliage (canopy)	63.8	39.0	36.7	42.3
Sample size	6		6	

[a] Active nest in 1979.

1978). SA III extended 75 m out from edge nest boxes, for censusing purposes.

All known cavities on SA I were blocked between 1 February and 5 March 1980, before the spring arrival of secondary cavity-nesters, by nailing doubled lawnchair webbing over cavity entrances. Cavities were re-opened on 1 June 1980.

RESULTS

ABUNDANCE AND USE OF CAVITIES

Cavities were grouped according to size and excavator/user species. Large cavities were those excavated and/or used by Gila Woodpeckers, and also used by Brown-crested and Ash-throated flycatchers and starlings (Table 1). Medium cavities were those used and/or excavated by Ladder-backed Woodpeckers and also used by Ash-throated Flycatchers. Small cavities were either natural knotholes or unfinished Ladder-backed Woodpecker holes, and were used by Lucy's Warblers.

Table 2 summarizes cavity data for the three study areas. Although the plots had different numbers of cavities, use patterns did not differ significantly (SA I vs. SA II: $\chi^2 = 2.32$, $n = 62$, $P > .05$; Fig. 1). SA III had three small cavities, all of which were used by Lucy's Warblers. Birds used 73.9% of all cavities, significantly less than full use ($\chi^2 = 19.6$, $n = 65$, $P < .001$). I found no clear-cut physical differences between used and unused medium cavities on SA I. Used cavities averaged somewhat deeper, and higher above the ground, but there was extensive overlap (Table 3). Limbs that contained unused cavities had no noticeable excessive decay and unused cavities did not contain droppings or other litter that might have made them unsuitable. Vegetation around the cavities did not change noticeably during the study, and vegetation density was not significantly different around used and unused cavities (Table 4). Similar comparisons could not be made on SA II since I was unable to reach those cavities.

Nest-cavities were often re-used, indicating that they remain suitable for more than one year. Nine of 13 cavities used on SA II in 1978 were re-used in 1979. Three of the remaining four old cavities were unusable due to treefall. Two of 12 medium cavities used on SA I in 1978 were re-used in 1979. An additional cavity used by Ash-throated Flycatchers in 1980 (after cavities were re-opened) was used as a roosting site by a Ladder-backed Woodpecker later in summer 1980.

CAVITY-BLOCKING

Blockage of cavities caused the number of breeding cavity-nesters on SA I to decline significantly between 1979 and 1980. Total number of pairs declined from 13.5 to 8 ($T = 32$, $n = 9$, $P < .05$; Fig. 2). Decreases in individual species could not be tested for significance, but Ash-throated Flycatchers, declining from five pairs to none, accounted for most of the decline. Ladder-backed Woodpeckers declined slightly, from 2.5 pairs to 2, because a 1979 partial territory on the western edge of the grid was not re-used in 1980. Three pairs of flycatchers, or 60% of the breeding population, were observed in May 1980 investigating blocked cavities, with two pairs simultaneously checking and fighting over the same cavity. One pair of flycatchers returned after cavities had been re-opened and nested unsuccessfully. While two Lucy's Warbler territories occupied in 1979 were abandoned in 1980, apparently due to local lack of cavities, total warbler numbers did not change.

NEST-BOX PLOT

Addition of nest boxes to SA III resulted in an increase in breeding numbers, from three to six pairs of secondary cavity-nesters (Fig. 2). My method of determining 1979 densities was conservative but I should have detected all breeding pairs (see Methods). Sample size was too small to test the significance of this 100% increase, but the increase in Ash-throated Flycatchers (0 to 3 pairs) was responsible. Lucy's Warbler numbers remained stable at three pairs, and they used only natural cavities. Birds used proportionately fewer nest sites after manipulation (7% vs. 100%, $\chi^2 = 12.8$, $n = 46$, $P < .001$; Fig. 1).

TABLE 4. Mean foliage density at used and unused medium cavities, SA I, expressed as m^2/m^3. Density differences were not significant (ANOVA: $F_{5,5} = 0.0$, $P > .5$).

Height (m)	Cavity status	
	Unused	Used[a]
0.15	0.024	0.027
0.6	0.030	0.032
1.5	0.082	0.111
3.0	0.069	0.064
4.5	0.027	0.019

[a] Active nest in 1979.

UNMANIPULATED PLOT

Breeding bird numbers on SA II were relatively stable in 1978–1979, increasing by four pairs (20%) in 1979, owing to the addition of four pairs of starlings (Fig. 2). Sample size was too small to test statistically. The increased number of starlings had no effect on breeding numbers of other cavity-nesters.

COMPETITION AND AGGRESSION

I saw little competition for nest sites, in the sense of density reduction or reproductive failure of the "losing" species. Two cases did appear to involve competition: on SA I, a pair of Ash-throated Flycatchers displaced an incubating Ladder-backed Woodpecker pair; while on SA II a Brown-crested Flycatcher pair defeated an Ash-throated Flycatcher pair for a cavity. This was competition since in neither case did the losing pair nest on the study area.

Most conflicts did not involve competition. On SA II in 1978, I noted two cases of prolonged aggression between incubating Gila Woodpeckers and Brown-crested Flycatchers. This resulted in sequential use—the woodpeckers successfully defended their nests and fledged young, while the flycatchers nested in those cavities after the fledglings were gone. A similar instance of sequential use occurred on SA II in 1978, without aggression. Thus 60% (3 of 5) of the Brown-crested Flycatcher population on SA II showed this behavior. In other cases of aggression, in 1979 three pairs of starlings ousted Gila Woodpeckers from cavities used by the latter in 1978. Aggression occurred early (February) and the woodpeckers found alternative nest sites. The same territories remained occupied and new holes were excavated, without any period of absence, suggesting that the same pairs remained on their territories. In four isolated instances, nesting Ash-throated Flycatchers chased intruding Brown-crested Flycatchers from within 15 m of the cavity. Overall, aggression had little effect on nesting success, as 58 of 63 nests (92%) were successful, with most nest failures caused by predation.

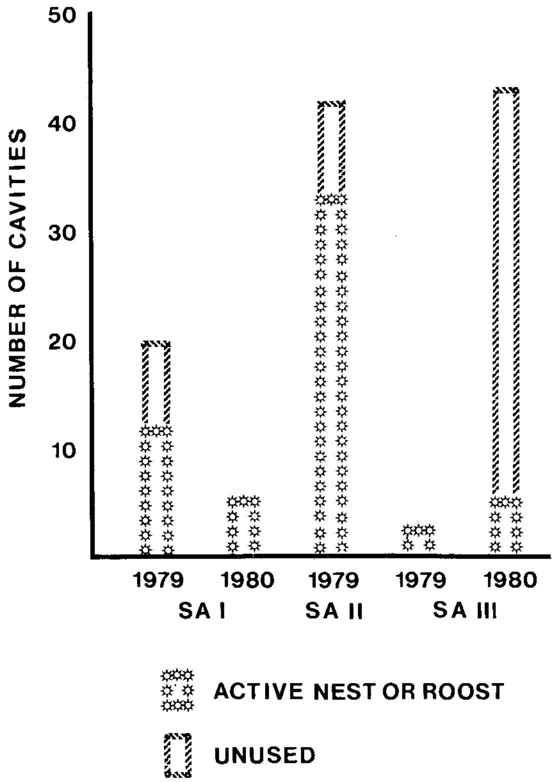

FIGURE 1. Cavity use by cavity-nesting birds and response to manipulations. See text for statistics.

DISCUSSION

CAVITY USE UNDER NATURAL CONDITIONS

Cavities were not fully used and did not limit breeding numbers on two of three plots, SA I and SA II. On SA II even the increased starling density and displacement of Gila Woodpeckers did not cause a reduction in breeding numbers or success. Broken-top snags were abundant and provided numerous sites for cavity excavation (pers. observ.). On SA I, unused cavities were as physically suitable as used cavities, suggesting that some other factor limited breeding numbers. However, the simultaneous absence of medium cavities and Ash-throated Flycatchers on SA III, and the full use of small cavities there, indicate that nest sites were limiting on SA III.

Re-use and sequential use of successful nest cavities on SA II suggest that riparian cavity-nesters were site-faithful, but do not indicate that cavities were limiting. However, these behaviors might prove useful to birds in cases where nest sites were limiting.

EFFECTS OF CAVITY-BLOCKING

I conclude that cavities became a limiting resource on SA I for Ash-throated Flycatchers, since cavity blocking was followed by failure of flycatchers to nest on the plot. The fact that

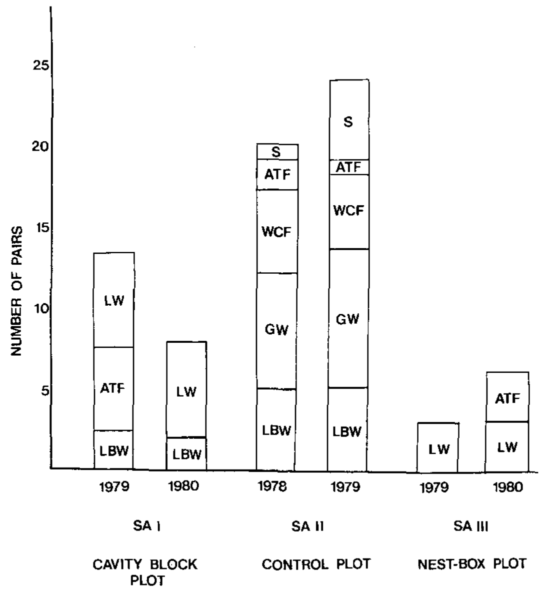

FIGURE 2. Effects of manipulation of cavity availability on breeding numbers of cavity-nesting birds, lower Colorado River valley. LBW = Ladder-backed Woodpecker, ATF = Ash-throated Flycatcher, LW = Lucy's Warbler, GW = Gila Woodpecker, WCF = Brown-crested (Wied's) Flycatcher, S = European Starling. See text for statistics.

flycatchers responded quickly to both blocking and re-opening of cavities also indicates that nest sites were a crucial resource. The different responses of Ash-throated Flycatchers and Lucy's Warblers on SA I were probably due to my varying success in locating nests. Lucy's Warbler nests were more hidden by branches or foliage, and I was seldom able to follow birds back to the nest.

I know of no studies in which natural cavities were blocked. Slagsvold (1978) blocked the entrances of all nest boxes that were not being used by Great Tits (*Parus major*) on his plot. This resulted in complete exclusion of Pied Flycatchers (*Ficedula hypoleuca*) from the plot, as they cannot oust Great Tits from cavities. In my study, Ash-throated Flycatchers did not use or attempt to obtain unblocked Lucy's Warbler cavities. These species use cavities of very different sizes (see Results and Table 1).

NEST BOXES

Results from SA III clearly showed that Ash-throated Flycatchers had been limited by cavity availability before manipulation. There were no medium cavities on the plot and thus no nest sites for the flycatchers. Ash-throated Flycatchers use a wide variety of natural and artificial cavities (Bent 1942; pers. observ.), so it is not surprising that nest boxes were used.

I do not know what factors limited Lucy's Warblers on SA III. The fact that they did not use nest boxes suggests either that cavities were not limiting or that the boxes were unsuitable. However, pre-manipulation full use of cavities by these warblers indicates that nest sites were limiting. This species has not been reported to use nest boxes.

WAS THERE COMPETITION?

Competition was not found to be important, despite extensive overlap in habitat and nesting seasons. Conflicts occurred but they generally consisted of cavity defense or displacements, rather than complete exclusion from breeding or reduction in breeding success. Gila Woodpeckers displaced by starlings had time to excavate new cavities and breed successfully. Brown-crested Flycatchers were delayed somewhat, but nestlings still fledged in July. As there is strong evidence that food is superabundant in late June and July (Rosenberg et al. 1982), later fledglings would not face harsher conditions in this riparian habitat.

Sequential use of cavities may be an adaptation to avoid aggression and interference with nesting, as might the partial segregation of cavity use based on size. Limiting factors undoubtedly vary among places and years. My study areas had high populations of cavity-nesters, although the habitats were not typical in numbers of nest sites (Brush et al., unpubl.). The potential for interference competition seems great in habitats where nest sites are few in number.

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RECENT PUBLICATIONS

A Guide to Bird Behavior, Volume 1.—Donald W. Stokes. 1983. Little, Brown and Co., Boston. 336 p. Paper cover. $8.95. This is a paperback reprint of the novel and still unique guide to understanding the behavior of 25 species of common North American birds (noticed in Condor 82: 148). Ideal for birders who want to go beyond identification and listing.

Managing Wetlands and Their Birds/A Manual of Wetland and Waterfowl Management.—Edited by D. A. Scott. 1982. International Waterfowl Research Bureau, Slimbridge, England. 368 p. Paper cover. £6.00. Source: I.W.R.B., Slimbridge, Glos. GL2 7BX, England. This manual deals with the *active* management of wetlands and the populations of birds ecologically dependent on them, in contrast to passive management—the straightforward protection of sites and species. The outcome of a 10-year effort by the I.W.R.B., it presents the 44 papers given at a 1982 conference held in West Germany. The papers are grouped thematically: management of wetlands, creation of artificial nesting sites, farming for waterfowl, predation, environmental contamination and disease, endangered species, regulation of hunting, and sanctuaries. Most of the papers concern ducks and geese, but some treat flamingoes, gulls, and other waterbirds. Geographically, they emanate from Europe, North America, and the Soviet Union. Reporting on a wide variety of management practices that have been tried, they offer encouragement and many ideas for wildlife biologists. Illustrations, references.

A Review of Some Important Techniques in Sampling Wildlife.—A. R. Sen. 1982. Occasional Paper No. 49, Canadian Wildlife Service. 15 p. Paper cover. Source: Minister of Supply and Services, Ottawa, Canada. Catalogue No. CW69-1/49E. "This paper reviews some of the important methods for estimating animal numbers or densities based on (*i*) direct counts of population units as used in quadrat, strip, line-transect, and line-intercept sampling and (*ii*) indirect counts and indices, such as capture-mark-recapture, change-in-ratio, and catch-effort methods, and indices based on track, call, roadside, and pellet-group counts." Sen concisely explains each method and points out its assumptions, applicability, and limitations. References.

Elliott Coues/Naturalist and Frontier Historian.—Paul Russell Cutright and Michael J. Brodhead. 1981. University of Illinois Press, Urbana. 509 p. $28.50. Elliott Coues's name and his major publications are still honored by taxonomically inclined ornithologists, yet his life has been forgotten. Strangely, the story of this colorful, influential, and enormously productive scientist has been hitherto neglected. We now have this first-rate biography of him, based on the literature and a vast collection of previously unpublished material, in particular Coues's own handwritten "Book of Dates." The book is consequently crammed with revealing details and quotations from his letters and publications. It follows his life closely without attempting to view him in a broad context. The authors explain matters wherever necessary yet refrain from much commentary or speculation. They portray Coues as a brilliant and extraordinary man: Army surgeon, systematic zoologist, editor, historian, lexicographer, and "general scientific gadfly." He also took active roles in Theosophy, the occult, and the fight for womens' rights! The book closes with lists of the new birds and mammals described by Coues, a list of his memberships in learned societies, and a full bibliography of literature about and by him. This last is ample evidence of Coues's status as one of the greatest ornithologists ever. Photographs, index.