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CAVITY-NESTING BIRDS AND THE CAVITY-TREE RESOURCE IN PLAINS COTTONWOOD BOTTOMLANDS

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Abstract: Densities of, and potential nesting substrates for, cavity-nesting birds were examined in a mature plains cottonwood (*Populus sargentii*) community in northeastern Colorado. Although snag (dead tree) densities were low (0.66/ha), the cavity-nesting guild included 7 species with densities ≤463 birds/100 ha. This finding suggests that cavity nesters are not limited by snag densities. Most (94.2%) of the nest substrate for cavity-nesting birds was provided by live trees with large, dead limbs (≥10 cm in diam). Both total dead limb length and the number of trees with dead limbs were highly correlated ($P < 0.001$) with the number of cavities excavated. Large trees (>55 cm in diam at breast ht [dbh]) and dead limbs 15–30 cm in diameter were preferred for cavity excavation. Because snags were a minor component of potential nest substrate, snag management may not be a useful concept for cavity-nesting birds in cottonwood bottomlands, and snag retention aspects of habitat models would be relatively unimportant for this forest type. Live-tree management is recommended.

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Birds nesting in tree cavities usually comprise 30–45% of forest bird communities (Scott et al. 1980). Densities have been linked to a number of characteristics associated with vegetative structure and composition including tree diameter, understory vegetation, overstory basal area, density, height, and composition (Anderson and Shugart 1974, Conner and Adkisson 1976, Smith 1977, McClelland et al. 1979, Raphael and White 1984, and others). The most important limiting factor is usually the availability of nesting substrate (Haartman 1957), often in the form of snags (dead trees) for cavity excavation and foraging substrates. Haapanen (1965), Balda (1975), and Scott (1979) recorded higher densities of cavity-nesting species in forests with snags than in those without snags.

The dead portions of live trees (often the tops) also may be used for nesting. Raphael and White (1984) found 19% of all cavity-nesting birds' nests in dead tops of live trees in California's old-growth pine (*Pinus* spp.)-fir (*Abies* spp.) forests. Carey (1983) reported 84% of all cavity trees in West Virginia's oak (*Quercus* spp.)-hickory (*Carya* spp.) forests were partially alive. Cavities in live parts of living trees also may be used as nest sites. Scott et al. (1980) reported 42% of cavity nests in a quaking aspen (*P. tremuloides*) community occurred in live parts of the trees.

This paper describes the relationship between nest substrate and cavity-nesting birds in a cottonwood riparian community in northeastern Colorado. Our objectives were to determine densities of the cavity-nesting bird species, densities of potential nest substrates for cavity-nesting birds, and patterns of bird use of potential nesting substrates by overstory size class of the cottonwood population.

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STUDY AREA

We studied the relationship between cavity-nesting birds and available nesting substrates along 30 km of the South Platte River near Crook, Colorado (Logan County). Elevations ranged from 1,116 to 1,149 m. Riparian vegetation was 500–1,000 m wide and was bounded by uplands of sand sagebrush (*Artemisia filifolia*)–mixed prairie (Harrington 1954) and tilled lands. Grazing by domestic cattle occurred on the river bottom before it was purchased by the Colorado Division of Wildlife in 1949 as the South Platte Wildlife Management Area (SPWMA). Grazing ceased in 1951.

Plains cottonwood dominated the riparian overstory. Peachleaf willow (*Salix amygdaloides*) comprised most of the remaining overstory with boxelder maple (*Acer negundo*), Siberian elm (*Ulmus pumila*), and red ash (*Fraxinus pennsylvanica*) being minor overstory components. The understory shrub layer was comprised primarily of western snowberry (*Symphoricarpos occidentalis*), coyote willow (*Salix exigua*), sandbar willow (*S. interior*), common poison-ivy (*Toxicodendron radicans*), and Woods rose (*Rosa woodsii*); all of these species usually occurred in discrete patches. Frost grape (*Vitis vulpina*) and Virginia creeper (*Pathenocissus quinquefolia*) were common vines. Common grasses and forbs included prairie cordgrass (*Spartina pectinata*), common reed (*Phragmites communis*), witchgrass panicum (*Panicum capillare*), cheatgrass brome (*Bromus tectorum*), hemp dogbane (*Apocynum cannabinum*), poison hemlock (*Conium maculatum*), curly dock (*Rumex crispus*), gaura (*Gaura parviflora*), and common cocklebur (*Xanthium strumarium*).

METHODS

Permanent stakes ($N = 155$) distributed across 10 16-ha plots (14–16 stakes/plot) served as points from which live-tree and snag densities were sampled. Stakes were placed 100 m apart in grids of varying shapes depending on river bottom width. Tree and snag densities were calculated using the point-centered quarter technique (Cottom and Curtis 1956). Measurements of tree dbh were made to determine basal areas and dbh size structure of forest overstory. We restricted our analysis to cottonwoods because they comprised >88% of all trees and contained almost all of the cavities.

In April 1984, while the trees were without leaves, a ground estimate of potential nesting substrate (PNS) was recorded as meters of dead limbs ≥10 cm in diameter for each tree in the sample used to determine cottonwood densities ($N = 547$). We recorded the number of cavities (any opening 3–12 cm in diam) that appeared to be usable (or used) as nest holes for each cottonwood. We measured tree and cavity heights with a clinometer and visually estimated diameter of the limb or bole at each cavity. We also estimated diameter of the cavity entrance to the nearest centimeter, periodically checking our estimates by actual measurement.

Populations of breeding birds that nest in cavities were censused using the variable circular-plot technique (Reynolds et al. 1980). Stakes used to determine tree densities also served as centers of circular plots from which bird populations were surveyed. Four observers each censused all 155 stations 1 time over a 10-day period in late May 1982 and 1984 (the community was not surveyed in 1983 due to extensive flooding). At each stake, an observer stood motionless for a 1-minute equilibration period and then counted all birds seen during a 10-minute interval. Daily surveys were conducted from sunrise to 1000 hours. Avian density estimates were determined by using program TRANSECT (Burnham et al. 1980) modified for point transect data (K. P. Burnham, pers. commun.). We pooled data from all 155 stations and used the Fourier series estimator to calculate densities. Standard errors (SE) were calculated using the indirect estimation method of program TRANSECT.

RESULTS AND DISCUSSION

Bird Densities

Ten species of cavity-nesting birds were present on the SPWMA but only 7 in sufficient numbers to calculate density estimates (Table 1). These included 3 primary excavators—northern flicker (*Colaptes auratus*), downy woodpecker (*Picoides pubescens*), and red-headed woodpecker (*Melanerpes erythrocephalus*); 3 secondary users—American kestrel (*Falco sparverius*), house wren (*Troglodytes aedon*), and European starling (*Sturnus vulgaris*); and the black-capped chickadee (*Parus*

atricapillus), which may excavate cavities when the substrate has reached an advanced stage of decay. Wood ducks (*Aix sponsa*) definitely nest on the study area and great crested flycatchers (*Myiarchus crinitus*) probably do, but both are at low densities. Eastern screech-owls (*Otus asio*) also are present but were not detected during surveys.

Total density of cavity-nesting birds was 463 birds/100 ha in 1982 and 247 birds/100 ha in 1984 ($\bar{x}$ presented/100 ha after Gullion 1985). These densities compare to 95–163 birds/100 ha in the Sierra Nevada (Raphael and White 1984), 240 birds/100 ha in Colorado subalpine habitat (Scott et al. 1978), and 15–365 birds/100 ha in the Douglas-fir (*Pseudotsuga menziesii*) region of western Oregon (Mannan et al. 1980). Cavity nesters comprised 32–43% of the total avian density in the 2 years, which is typical of most forest bird communities (Scott et al. 1980).

Species richness on our study area was 7.0 in both years (counting only those species present in numbers sufficient to calculate density estimates). For comparison, a mean of 6.4 ± 0.4 (SE) was recorded from 20 breeding bird censuses published in *American Birds* from 1973 to 1984 in areas where cottonwoods dominated or codominated the mature, riparian overstory (counting only those species with ≥1 territory). Densities of cavity-nesting birds for the 20 censuses ranged from 27 to 1,050 birds/100 ha ($\bar{x}$ = 396 ± 63.5 [SE]). House wrens were the dominant species on the SPWMA and in 16 of the 20 censuses in *American Birds*. Species equitability (Krebs 1972:507) ranged from 0.54 to 1.0 among those 20 studies, and for the SPWMA it was 0.52 in 1982 and 0.42 in 1984. We concluded that our cavity-nesting bird population was viable, and densities of cavity nesters fell within the range of normal limits suggested by other reports of cottonwood riparian populations.

Table 1. Mean avian densities (birds/100 ha) in a plains cottonwood riparian community, South Platte Wildlife Management Area, Colorado, 1982 and 1984.

Species	1982 $\bar{x}$	1982 SE	1984 $\bar{x}$	1984 SE
Cavity nesters				
House wren	333	13.0	198	13.5
Black-capped chickadee	62	6.5	16	3.5
Northern flicker	17	2.5	6	2.0
Downy woodpecker	16	4.0	7	2.5
Red-headed woodpecker	16	3.0	9	2.0
European starling	14	2.5	9	3.0
American kestrel	5	1.0	2	1.0
Total cavity nesters	463		247	
(%)	(42.9)		(31.8)	
Other birds	617		530	
(%)	(57.1)		(68.2)	

Live-Tree and Snag Densities

Cottonwood density ($\bar{x}$ = 23.9 trees/ha) and basal area ($\bar{x}$ = 3.5 m²/ha) were low compared to other cottonwood bottomland studies where densities ranged from 37 to 191 trees/ha, and basal areas ranged from 4.8 to 13.9 m²/ha (Kapustka 1972, Johnson et al. 1976, Crouch 1979, Lindauer 1983). The frequency distribution of cottonwoods by dbh size class was normal but was skewed slightly to older age classes (J. A. Sedgwick and F. L. Knopf, unpubl. data). A few trees occurred in many of the larger size classes, but trees <24-cm dbh comprised only 20% of the total. Trees 24–52-cm dbh accounted for >50% of all cottonwoods. Population structure represented by this distribution, plus low tree density and basal area, were indicative of a decadent overstory community. A large average dbh ($\bar{x}$ = 43.1 ± 1.1 [SE] cm) also suggests an aging overstory.

Given the apparent decadence of the cottonwood community, we expected snag density to be relatively low. Live-tree density and, consequently, snag density decline as communities age (Cline et al. 1980, Carey 1983). Additionally, the relative length of time snags remain standing in cottonwood bottomlands probably is short due to loose, sandy soils (U.S. Dep. Agric. and Colo. Agric. Exp. Stn. 1977), frequent high winds, and bank erosion during spring flooding. Snag density was especially low on our study area ($\bar{x}$ = 0.66 snags/ha), and snags comprised only 2.7% of all cottonwoods. In contrast, Scott et al. (1980) reported snag densities of 34.1/ha in quaking aspen, 11.6/ha in ponderosa pine (*Pinus ponderosa*), and 43.7/ha in spruce (*Picea* spp.)-fir in Colorado. Snag densities in maple-beech (*Fagus* spp.)-birch (*Betula* spp.) forests in West Virginia ranged from 22.4 to 55.1/ha (Carey 1983), whereas in Oregon Cline et al. (1980) reported densities of 17.3–100.6 snags/ha in Douglas-fir depending on the forest

Table 2. Mean dead limb length by tree diameter at breast height (dbh) size class of plains cottonwoods, South Platte Wildlife Management Area, Colorado, 1984.

N trees	Midpoint of dbh size class (cm)	Limb length (m) ($\bar{x}$)[a]
79	10	0.04 A
127	25	0.95 A
141	40	1.91 A
99	55	3.65 AB
46	70	6.43 B
30	85	6.47 B
12	100	6.25 B
9	115	7.67 B
2	130	6.50 B
2	145	8.00 B

[a] Values with different letters are different at $P = 0.05$ (Duncan's multiple range test).

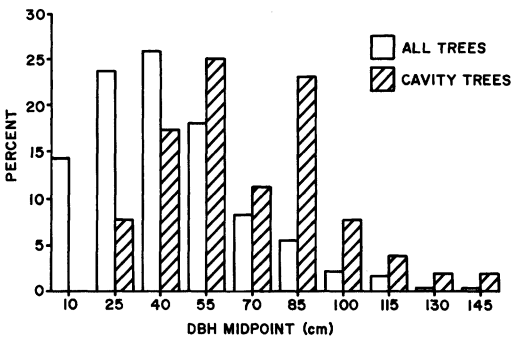

Fig. 1. Distribution of all trees and cavity trees by diameter at breast height (dbh) size class, South Platte Wildlife Management Area, Colorado, 1984.

age class. Based only on snag density, the SPWMA should support a low density population of cavity-nesting birds.

Availability of Potential Nesting Substrate

Snag densities alone did not reflect accurately the availability of nesting substrates for cavity-nesting birds on the SPWMA. Older cottonwoods, apparently otherwise healthy, often had limbs or sections of limbs that were dead. Many of these dead limbs were ≥10 cm in diameter, a measure commonly accepted as the minimum necessary for cavity nesters (Evans and Conner 1979, Thomas et al. 1979). Of all cottonwoods limb trees (trees with ≥1 m of dead limbs ≥10 cm in diam) made up 47% of the population (11.3/ha) and provided PNS. Mean dead limb length was 5.5 ± 0.3 (SE) m/limb tree (62.2 m dead limbs/ha). Larger trees were more important than smaller trees as PNS because mean dead limb length gradually increased from 0.04 m for trees in the smaller dbh size classes to 8 m for cottonwoods in the largest size classes ($P < 0.001$, Table 2). The importance of large trees in providing PNS also is reflected in the frequency distribution curves of both limb trees and the total length of dead limbs by dbh size class. Both curves are shifted towards older trees relative to the overall cottonwood distribution curve. Most limb trees (86%) and total dead limb length (83%) occurred in 25–85-cm dbh size classes.

Although snag densities were low, snags frequently were used as nest trees. More snags (20.0%) contained cavities than live trees (9.2%). Therefore, snags present on the SPWMA are important to cavity nesters; however, low densities of snags diminish their overall importance as PNS.

Characteristics of Cavity Trees

Cavity trees comprised 9.5% of the total cottonwood population with a density of 2.3 cavity trees/ha. This density compares with 4–9 cavity trees/ha in oak-hickory forests in West Virginia (Carey 1983), 6.4/ha in ponderosa pine in Arizona (Scott 1978), and 0.7–0.9 cavity trees/ha in Douglas-fir in Oregon (Mannan et al. 1980). Most cavity trees on the SPWMA were alive (94.2%); only 3 of 52 (5.8%) were snags. Similarly, most cavities (95.8%) were in live trees, and only 4 of 96 (4.2%) were in snags. Cavity trees were taller ($P < 0.0005$) than non-cavity trees ($\bar{x} = 12.8 \pm 0.4$ [SE] m vs. 10.9 ± 0.2 [SE] m), had a greater ($P < 0.0001$) mean dbh (68.5 ± 3.8 [SE] cm vs. 40.5 ± 1.1 [SE] cm), and had a greater ($P < 0.0001$) length of dead limbs than trees without cavities (6.3 ± 0.7 [SE] m vs. 2.2 ± 0.2 [SE] m). Distribution of cavity trees vs. all available trees by dbh size class indicated that birds preferred trees ≥55-cm dbh (Fig. 1). A disproportionate number of trees this size and larger had cavities relative to their availability.

Cavity density was 4.2 cavities/ha; each cavity tree had an average of 1.8 ± 0.2 (SE) cavities. Most trees with cavities had 1 cavity (61.5%), 23.1% had 2 cavities, and 15.4% had 3–9 cavities. Larger trees had more cavities than smaller trees ($P < 0.0009$), ranging from a mean of 1.0/145-cm-dbh trees to 0.0/10-cm-dbh trees (Table 3). The frequency distribution of cavities by dbh size class was correlated with that of dead limb length ($r = 0.89$, $P < 0.001$) and

number of limb trees ($r = 0.92$, $P < 0.001$). Therefore, limb length and limb trees appear to be good measures of suitable nesting substrate for cavity nesters. The importance of large trees to cavity-nesting birds was evident as 83% of all cavities were in trees 40–90-cm dbh.

Characteristics of Cavities

Cavity entrances averaged 5.4 ± 0.2 (SE) cm in diameter. Over 90% of all cavity entrances were 3–7 cm in diameter, which corresponds to the size of cavities used by birds occurring on the SPWMA (3-cm holes: downy woodpecker, black-capped chickadee, and house wren; 5-cm holes: red-headed woodpecker; 7-cm holes: northern flicker) (Evans and Conner 1979, Raphael and White 1984). Some of the larger cavities (8–12 cm) may have been enlarged over time and are suitable for larger cavity nesters; e.g., wood duck, eastern screech-owl, and American kestrel.

Mean cavity height was 5.84 ± 0.21 (SE) m (range = 1.2–10.0 m). Over 50% of all cavities were 3.7–6.4 m aboveground. Mean diameter of the limb (or bole) at cavity height was 20.8 ± 0.7 (SE) cm. One cavity was in a limb only 8 cm in diameter, but all others were in limbs ≥12 cm in diameter; most (69.9%) were in limbs 15–30 cm in diameter.

CONCLUSIONS

Biologists have used snag densities as correlates of habitat quality for cavity nesters. Cunningham et al. (1980) and Raphael and White (1984), among others, reported high correlations between cavity-nester densities and snag densities. These correlations have fostered attempts to predict the number of snags required for various density levels of cavity-nesting birds, especially in coniferous forests (Balda 1975, Evans and Conner 1979, Thomas et al. 1979). Because snags are not the major component of PNS and are not correlates of habitat quality for cavity-nesting birds in mature cottonwood bottomlands, snag densities are not useful in terms of management of cavity-nesting birds in these areas. Carey (1983) also questioned the utility of snags as a management concept for deciduous forests in West Virginia. Similarly, with nearly 50% of all nests of cavity nesters in quaking aspen forests being in live trees (Scott et al. 1980), snag management alone does not appear to be a useful concept in that forest type. Management of deciduous forest stands to enhance populations of cavity-nesting birds is suggested as being primarily live-tree management. The importance of snag retention aspects (see Rasmussen and Ffolliott 1983) of habitat models for cavity nesters appears diminished in deciduous forests. However, snags may remain a useful management concept in selected deciduous stands or forest types, especially those that are relatively young and managed for timber (R. N. Conner, pers. commun.).

Table 3. Mean number of cavities by tree diameter at breast height (dbh) size class of plains cottonwoods, South Platte Wildlife Management Area, Colorado, 1984.

N trees	Midpoint of dbh size class (cm)	*N* cavities ($\bar{x}$)[a]
79	10	0.00 A
127	25	0.03 A
141	40	0.21 AB
99	55	0.25 AB
46	70	0.26 AB
30	85	0.42 AB
12	100	0.44 AB
9	115	0.47 AB
2	130	0.50 AB
2	145	1.00 B

[a] Values with different letters are different at $P = 0.05$ (Duncan's multiple range test).

MANAGEMENT IMPLICATIONS

Harvest of trees in cottonwood bottomlands on the Great Plains has been sporadic. In southern Colorado cottonwoods recently were removed as a phreatophyte control measure, and in Nebraska and Kansas thousands of hectares of cottonwoods were harvested for pulp in the early and mid-1970's (Borden 1978). Cottonwood is used extensively as commercial firewood at many localities in Colorado and Wyoming (W. D. Graul and R. Oakleaf, pers. commun.). Demand for wood may increase, and a better understanding of the cavity resource in cottonwood bottomlands will enable the coordination of potential harvest and control measures and management of cavity-nesting birds. Management guidelines for plains cottonwood on the western Great Plains should consider: (1) retaining trees ≥55-cm dbh, (2) retaining snags, (3) limiting the harvest of cottonwoods with dead limbs ≥10 cm in diameter and retaining cottonwoods with limbs >15 cm in diameter, (4) managing for a diversity of cavity-tree heights and diameters but maintaining a mean cavity-tree dbh of 68.5 cm (the current $\bar{x}$ value along the South Platte Riv-

ver), and (5) managing for current levels of cavity-tree densities (2.3 cavity trees/ha) to accommodate secondary cavity-nesting bird species. In view of the poor regeneration of plains cottonwood stands along the South Platte River of Colorado and elsewhere on the western Great Plains (J. A. Sedgwick and F. L. Knopf, unpubl. data), programmed efforts to preserve current stands are advised.

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