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SECONDARY CAVITY NESTING BIRDS OF TENNESSEE

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Abstract

This paper reviews the concepts of primary and secondary cavity nesting, identifies the cavity nesting species of birds of Tennessee, compares advantages and disadvantages of cavity nesting, and suggests some directions for future research with secondary cavity nesting species.

Introduction

The purposes of this paper are to describe the different categories of cavity nesting birds, compare advantages and disadvantages of cavity nesting, discuss adaptations of cavity nesting species, and use this information as background to present some research possibilities with secondary cavity nesters.

Species that excavate their own nest cavities are referred to as "primary cavity nesters." The term "secondary cavity nester" refers, in its most restricted sense, to those birds that normally nest in cavities that have been excavated by other species. Common usage of secondary cavity nester does not restrict the term to birds using cavities excavated by other birds but includes those species that nest in any type of preformed cavity, regardless of whether the cavity was formed by another bird or some other element of nature.

Half of the avian orders have cavity nesting species; in some orders, such as Coraciiformes (kingfishers et al.), Psittaciformes (parrots), and Piciformes (woodpeckers), all species nest in cavities (Gill 1989). In eastern North America about 17% of the nesting species use cavities (von Haartman 1957). Approximately 170 species of birds nest in Tennessee, and at least 34 (20%) of these use cavities for nesting. I have divided the cavity nesting species into five groups as follows:

(1) Exclusively primary cavity nesting—species that normally excavate their own nest cavity:
- Belted Kingfisher, *Ceryle alcyon*
- Red-headed Woodpecker, *Melanerpes erythrocephalus*
- Red-bellied Woodpecker, *Melanerpes carolinus*
- Yellow-bellied Sapsucker, *Sphyrapicus varius*
- Downy Woodpecker, *Picoides pubescens*
- Hairy Woodpecker, *Picoides villosus*
- Red-cockaded Woodpecker, *Picoides borealis*
- Northern Flicker, *Colaptes auratus*
- Pileated Woodpecker, *Dryocopus pileatus*
- Bank Swallow, *Riparia riparia*
- Red-breasted Nuthatch, *Sitta canadensis*

(2) Both primary and secondary cavity nesting—species that can excavate their own nest cavity but frequently use a preformed cavity:
- Black-capped Chickadee, *Parus atricapillus*
- Carolina Chickadee, *Parus carolinensis*
- Brown-headed Nuthatch, *Sitta pusilla*

(3) Secondary cavity nesting, narrow tolerance—species that do not excavate their nest cavity, but do use a cavity; the cavity must meet one or more restrictive requirements in terms of such features as height, internal dimensions, substrate material, and habitat:
- Wood Duck, *Aix sponsa*
- Hooded Merganser, *Lophodytes cucullatus*
- American Kestrel, *Falco sparverius*
- Eastern Screech-Owl, *Otus asio*
- Great Crested Flycatcher, *Myiarchus crinitus*
- Purple Martin, *Progne subis*
- Tree Swallow, *Tachycineta bicolor*
- Northern Rough-winged Swallow, *Stelgidopteryx serripennis*
- Tufted Titmouse, *Parus bicolor*
- White-breasted Nuthatch, *Sitta carolinensis*
- Eastern Bluebird, *Sialia sialis*
- Prothonotary Warbler, *Protonotaria citrea*

(4) Secondary cavity nesting, wide tolerance—species that do not excavate their nest cavity, but use a great diversity of cavities:
- Barn Owl, *Tyto alba*
- Carolina Wren, *Thryothorus ludovicianus*
- Bewick's Wren, *Thryomanes bewickii*
- House Wren, *Troglodytes aedon*
- European Starling, *Sturnus vulgaris*

(5) Opportunistic secondary cavity nesting—species that can nest either in cavities or outside of cavities:
- Barred Owl, *Strix varia*
- Common Grackle, *Quiscalus quiscula*
- House Sparrow, *Passer domesticus*

A few species are not easy to categorize; while some are virtually always primary cavity nesters and others are normally secondary cavity nesters, species such as the chickadees may be either primary or secondary cavity nesters. Common Grackles are typically open nesters (i.e., do not use cavities), but under certain conditions they readily use cavities (Spero and Pitts 1984). Thus any classification of cavity nesting birds is somewhat subjective, and different authors might establish slightly different lists. I have arbitrarily excluded Black Vultures (*Coragyps atratus*), Turkey Vultures (*Cathartes aura*), and Chimney Swifts (*Chaetura pelagica*) from the lists because, though these species may nest in enclosed sites, such sites are generally not called cavities. In spite of the arbitrary content of some of the categories, I believe such attempts at descriptive subdivision are useful. The absence of a clear dichotomy among species as either primary or secondary cavity nesters is obvious. For example, the range of nest site characteristics that is acceptable to each species is made more apparent by including a "primary and secondary" category. For example, classifying Carolina Chickadees as primary cavity nesters (or, equally incorrect, calling them secondary cavity nesters), with no indication of their flexibility in nest site selection, would be misleading. Anyone involved in management of this species or investigation of its nesting biology would benefit from the knowledge that Carolina Chickadees can, depending on some unknown set of circumstances, be either primary or secondary cavity nesters.

ADVANTAGES AND DISADVANTAGES OF CAVITY NESTING

Most bird nests provide advantages other than simply supporting and retaining the eggs and developing young. Additional functions of nests may include protection of the adults, eggs, and young from predators, and protection from adverse weather. Nest construction in many species is a key element in the complex process of courtship and pair bond formation.

Based on a survey of many studies of nesting birds, Nice (1957) calculated that in cavity nesting species approximately 66% of the eggs produced fledglings, whereas in open nesting species the corresponding figure was approximately 49%. Though considerable variation in nest success of a particular species may occur between years, in different habitats, or in diverse climates, recent studies (e.g., Alerstam and Hogstedt 1981) have reinforced Nice's conclusion. Benefits resulting from cavity nesting may include better concealment from predators; decreased accessibility to predators; and better protection from wind, rain, and temperature fluctuations. Disadvantages (or costs) of cavity nesting vary. Cavity excavation requires considerable time and energy, though I know of no studies that have compared the expenses for construction of open nests versus cavities. The cavity must be defended from competitors, and the familiar scene of European Starlings ousting Northern Flickers from a recently completed cavity is but one example of this necessity. Many other competitors, such as insects, reptiles, and mammals, are constantly searching for suitable cavities. Secondary cavity nesters must locate a suitable cavity and then defend it from both intraspecific and interspecific competitors. Numerous researchers (e.g., von Haartman 1957) have concluded that a shortage of suitable cavities plays a major role in determining the population levels of secondary cavity nesting species. Van Balen et al. (1982) found that 54-93% of the natural cavities on their study sites were occupied each year; some pairs of secondary cavity nesters were unable to find a suitable cavity and consequently either did not nest, or moved away from their territories in search of cavities. Mortality due to competition may be greater than mortality due to predators; von Haartman (1957) thought that more Pied Flycatchers (Ficedula hypo*leuca*) were killed by Great Tits (*Parus major*) (a larger and stronger competitor for cavities) than by birds of prey. In Tennessee, one of the factors influencing Eastern Bluebird use of nest boxes is the local population level of House Sparrows (Pitts 1979); bluebirds in turn dominate Carolina Chickadees and influence their use of nest boxes (pers. observ.).

Another problem sometimes faced by secondary cavity nesters is the residue of parasites from former occupants. Nest cavities may contain thousands of parasites which may induce abandonment of nest sites by the parent birds, or early departure and even death of the young birds (Boyd 1951). The green, aromatic leaves added to nests by species such as House Sparrows, European Starlings, and Purple Martins are thought by some writers (e.g., Wimberger 1984, Clark and Mason 1985) to repel parasites. In addition to parasites, McComb and Noble (1982) found that cavities, especially nest boxes, frequently housed various other invertebrates such as paper wasps that nesting birds would have to contend with.

Secondary cavity nesters may experience a higher rate of predation than primary cavity nesters, though I am aware of no data conclusively demonstrating this. Some nest predators, such as raccoons (Procyo*n lotor*) and rat snakes (*Elaphe obsoleta*), may return to sites where they have previously taken eggs, nestlings, or adults. Sonerud (1985) felt that Tengmalm's Owl (A*egolius funereus*) preferred to nest in new boxes because its main predator, the pine marten (*Martes martes*), revisited sites where it had earlier found food. Some primary cavity nesters that use nest sites for extended periods have evolved defensive strategies. For example, Red-cockaded Woodpeckers maintain a pine gum barrier around the nest cavity entrances; the gum effectively reduces rat snake predation (Jackson 1974).

Why so few cavity nesters?

If cavity nesters are more successful than species building open nests, why do only 20% of Tennessee's bird species use cavities? Birds exhibit a tremendous diversity of morphological and behavioral adaptations that enable them to occupy various niches. Some of these modifications are compatible with cavity nesting. Alerstam and Hogstedt (1981) noted that birds usually adopt one of three options in order to avoid nest predation: active nest defense, nest concealment and camouflage, or sheltered nests (i.e., in cavities or similarly protected and relatively inaccessible sites). Large birds such as Bald Eagles (Hali*aeetus leucocephalus*) are capable of nest defense against many potential predators, but the morphological adaptations of eagles for a predatory style of life preclude these birds from excavating cavities. Cavities of a suitable size for eagles are probably scarce, partly as a result of the absence of any other species of animal that excavates cavities that could be used by eagles. Species such as Killdeer (Ch*aradrius vociferus*) and Eastern Meadowlarks (*Sturnella magna*) occupy habitats that offer few opportunities for cavity nesters, yet by the use of camouflage and concealment these species are successful. In contrast, species (such as woodpeckers) with structural features that can be used for both feeding and nest cavity excavation are more logical candidates for primary cavity nesting.

Alerstam and Hogstedt (1981) hypothesized that cavity nesting ("sheltered nesting" in their terminology) should be more common in nonmigratory species and migrants with exposed feeding niches. They reasoned that nonmigrants would be favored because of their ability to lay prior claim to cavities in short supply, and migrants with exposed feeding niches would more likely be cavity nesters than migrants that forage in less exposed habitats because exposed feeding would increase the probability of visually-hunting predators finding nests. Cavities, even though detectable to such predators, might render the contained eggs or young inaccessible.

Though the higher success rate of cavity nests is well established, other factors also influence population levels. To the extent that individuals of a secondary cavity nesting species are prevented from nesting by a shortage of suitable cavities, the population level of that species will be depressed in spite of a high rate of nest success for those individuals that do nest. The most abundant species of breeding birds in Tennessee, such as Indigo Bunting (Passe*rina cyanea*) and Red-winged Blackbird (*Agelaius phoeniceus*), are not cavity nesters. A multitude of factors determines avian population levels, and ultimately the success or demise of a species; nest success rate is only one of those factors. Birds as a group are successful because of their ability to occupy a diversity of niches. Cavity nesting is only one dimension of some of those niches.

Adaptations of Cavity Nesters

Birds nesting in cavities differ from open nesting species in several ways. In most secondary cavity nesters the males establish and defend a territory only after locating a suitable cavity (von Haartman 1957). In most other territorial species the male defends some suitable habitat, and the female then selects the actual nest site. Competition for the scarce supply of nest cavities has resulted in the year-round defense of such cavities by territorial individuals or pairs in many species. The high mortality of Eastern Bluebirds in severe winters is one example of a consequence of year–round defense of a cavity (Pitts 1978). Bluebirds typically are nonmigratory at latitudes where winter survival is likely; at higher latitudes (e.g., central Illinois) winter weather varies from year to year but allows survival in some years. In mild winters the non-migrating individuals survive and, consequently, retain control of the best cavities; in such years the migrating individuals are selected against because of their limited access to cavities. In severe winters, mortality of nonmigrants will be high (even approaching 100%) and the returning migrants will be at an advantage, especially if they return earlier than other competitors. Consequently, there is continual selection pressure at low and middle latitudes for non-migrating bluebirds, and for early returning migrants at higher latitudes; both strategies carry great risks.

A second correlate of cavity nesting is the inclusion of cavity demonstration as a part of courtship. Males defending territories with suitable nest cavities typically concentrate their courtship activities around the nest cavity and, in many species, include movements into and out of the cavity as part of courtship. Krieg (1971) noted that pair bonding in Eastern Bluebirds involved nest cavity demonstration by males and acceptance of the cavity by females.

A third correlate of cavity nesting is the disappearance of eggshell pigments. Lack (1958), in his analysis of egg color in thrushes, found that certain colors were closely associated with specific types of nest sites, a situation long recognized by egg collectors. Those species nesting in deep holes had the lightest colored (i.e., whitest) eggs. Lack (1958) speculated that the white eggs of hole nesters were not simply the result of a lack of predation pressure (due to the fact that the eggs were rarely seen by predators) but that the light color was an adaptation to increase their visibility to the parents in the dim light of the cavity. I am not aware of any studies that have tested the advantages of white eggs, or the disadvantages of colored eggs, in dark cavities. Von Haartman (1957) felt that the occurrence of blue eggs or other non-white eggs in cavity nesters was probably related to the length of time the species had been using cavities. He pointed out that primary cavity nesters evolved earlier than secondary cavity nesters, and consequently have had more time for adaptations such as changes in egg color to occur.

A fourth correlate of cavity nesting is an increase in the length of time the young remain in the nest (von Haartman 1957). Whereas this is more pronounced in primary cavity nesters, it occurs in many secondary cavity nesters. As one example, among the nesting thrushes of Tennessee the open nesting American Robin (Turdus migratorius) and Wood Thrush (*Hylocichla mustelina*) usually have nestling periods of 13 days (Howell 1942, Nolan 1974) while Eastern Bluebirds have nestling periods of 16-18 days (Pitts 1976). The young of open nesters normally leave the nest before all of their feathers are fully developed and before they are capable of flight. Nolan [1974] estimated that young Wood Thrushes could fly only about 0.3 m at the time they fledged. The young of cavity nesters have more complete feather development and are normally capable of sustained flight at the time of fledging; I have observed maiden flights of Eastern Bluebirds of 100 m. The more advanced development of the young of cavity nesters at fledging is attributable to their longer nestling period, not to a faster rate of development. The longer nestling period of cavity nesters is thought to have evolved because of the increased safety of the cavity (von Haartman 1957) as compared to an open nest, and perhaps also because it facilitated one-site feeding of the brood by the parents for a few more days which, it seems, would be more efficient than feeding a scattered brood at several sites around the nest.

Other suggested, but less clearly demonstrated or less widespread, correlates of cavity nesting include increased polygamy, the production of hissing notes by nestlings, and differences in the stimuli releasing the gaping reaction of nestlings (von Haartman 1957).

Research and Management Opportunities

Several species of secondary cavity nesting birds readily accept nest boxes and as a result have been intensively studied. Examples include Wood Ducks and Eastern Bluebirds. Other species, such as Great Crested Flycatchers and Tufted Titmice, use nest boxes less frequently. One of the primary tools of Wood Duck, bluebird, and Purple Martin management is construction and placement of nest boxes. Though thousands of boxes have been placed for such species and much research concerning them has been published, many questions remain unanswered; the opportunities for research and the application of findings to management are varied and numerous.

I believe a major gap exists in our understanding of how nest boxes affect target species. Nest boxes placed in appropriate habitat will attract Wood Ducks or bluebirds, and local populations of these species can be increased several fold as a result. Would these additional individuals have nested if the nest boxes had not been present? If so, where? Does placing nest boxes in one area deprive another area of nesting birds? What is the effect of nest boxes on the regional population of a species? By concentrating many nest boxes in small areas, are we causing population levels to rise beyond their optimum? Are parasites, predators, or disease organisms more prevalent in areas with high numbers of nest boxes than in areas with only natural cavities? The placing of nest boxes at appropriate intervals can be used as a tool for manipulating densities of some secondary cavity nesters (Brawn 1987), and this technique seems to have great potential for studying the effects of different population densities on clutch size, timing of nesting, nest success, survival of young and adults, and other features. Such studies will require careful planning and several seasons of field work to yield reliable data, but many questions relating to the effects of population density could be addressed.

Another area of concern is the validity of extrapolating generalizations based on data collected from birds using nest boxes to birds using natural nest cavities. Are data derived from nest box studies (such as measures of clutch size, nest success, etc.) really indicative of what is happening in the natural cavities these species have traditionally used? Does the availability of nest boxes result in better survival of certain age classes or phenotypes than if only natural cavities were available? A few researchers have tackled such questions. Pinkowski (1976) found that Eastern Bluebirds used a wide variety of natural cavities but preferred nest boxes, possibly because the nest boxes were closer to the preferred cavity size. Pinkowski (1977) found blow flies (Protocalliphora sp.) more abundant in nest boxes than in natural cavities. Nilsson (1986) found that birds nesting in natural cavities were less successful than those using nest boxes, and questioned the "fact" that cavity nesters were more successful than open nesters because he felt many of the studies of cavity nesters were biased because they were conducted with nest boxes. Robertson and Rendell (1990), comparing the ecology of Tree Swallows breeding in nest boxes and natural cavities, found that for some aspects such as clutch size, nest boxes did not accurately reflect what was happening in natural cavities. Soulliere (1990) summarized the available information on use of natural cavities by Wood Ducks and found that while 0-58% of the natural cavities in an area may be used, much additional research was needed.

Another area needing more research is snag management. Conner (1978) summarized much information pertaining to species using snags, and snag management, in southern forests. He emphasized the influence of snag availability on the abundance and diversity of cavity nesting birds, and he commented on the effects of various timber rotations and harvesting techniques on snag availability. Though this topic has received considerable attention in recent years (e.g., Davis et al. 1983) in many areas, especially privately-owned forests, there are no plans for snag management, and the most common way of dealing with snags is to remove them.

Whereas a few species of secondary cavity nesting birds have received much attention, others have received little. Carolina Chickadees are one of our most familiar birds, and I was surprised to learn that apparently only two studies (Brewer 1961, Mowbray and Goertz 1972) of its nesting biology are based on observations of more than three or four nests. One reason we know so little about chickadee nesting biology is that they frequently excavate their own nest cavity; yet they will occasionally use nest boxes. Drury (1958) suggested that nest boxes filled with peat moss and sawdust are more likely to be used by chickadees because excavation may be an essential and instinctive part of the nesting cycle that must be fulfilled. The genus Parus is one of the most intensively studied in the world, and many of the theories and models of clutch size determination and population regulation are based on its study; these hypotheses would be strengthened by the inclusion of more information on Carolina Chickadees.

The Great Crested Flycatcher is another species whose nesting biology is inadequately documented. Study of this species may now be especially timely because of the increased fragmentation of our forests and the loss of tropical forests where this species winters. Numerous other species, such as Rough-winged Swallows and Prothonotary Warblers, offer a variety of research possibilities. The existence of many publications on a species may not mean that research opportunities on that species have been exhausted: the opposite may be true—the more we learn about a species, the more unanswered questions we may raise.

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