Butler University Botanical Studies

Volume 13 Article 14

Variations in Engineering Features of the Nests of Several Species of Birds in Relation to Nest Sites and Nesting Materials

Walter P. Nickell

Butler University Botanical Studies

(1929-1964)

Edited by

J. E. Potzger

The *Butler University Botanical Studies* journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana's vegetation in past decades. Authors were Butler faculty, current and former master's degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler's first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal's publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor's degrees and 75 master's degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner , included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

Requests for use of materials, especially figures and tables for use in ecology text books, from the *Butler University Botanical Studies* continue to be granted. For more information, visit www.butler.edu/herbarium.

VARIATIONS IN ENGINEERING FEATURES OF THE NESTS OF SEVERAL SPECIES OF BIRDS IN RELATION TO NEST SITES AND NESTING MATERIALS

by

WALTER P. NICKELL

Cranbrook Institute of Science
Bloomfield Hills, Michigan

During about thirty-five years of field work in bird ecology in eastern and central North America, I have examined in the field or collected and analyzed about 20,000 nests of 169 species of birds. This list represents nearly a third (31.3% of the 533 species listed by Pough for the entire region of eastern and central North America from southern Texas to central Greenland. All of my studies have been confined within the region between the latitude of 30° and 50° north and between the 100th meridian and the Atlantic Ocean. The largest amount of my field work and study has been done in five counties of southeastern Michigan and three counties of southwestern Ontario where 25,379 nesting records have been established for 143 species of birds by about fifty field observers of the Detroit Audubon Bird Survey in the last 12 years.

In the course of these studies, I have been impressed repeatedly by the ability of several species of birds to construct successful nests on sites which from a structural standpoint have exhibited considerable variability. When sites, nests and nesting materials are carefully examined, the facts suggest that most birds are unable to vary to any great degree from instinctive engineering activities and patterns of building. A breakdown of the nest types and sites of the 533 species listed by Pough, 1946, 1951, shows that 496 species (93.5%) build statant or standing nests either in trees, other vegetation, artificial sites, or on the ground. Of these statant nest-builders, about 51% construct nests on or in the ground, or lay their eggs on the ground without gathering nest materials. The remaining 49% of the statant nest-builders construct or use nests in trees, shrubs, or forbs. Of these species nesting above ground in vegetation about 60 species build nests that are attached to their sites by grasses, bark, lichens, spider webs, and other fibrous materials. About a third of the attached nests are usually pensile or pendulous. Twelve species of birds nest on floating mats of vegetation and three species build nests which are adherent to the perpendicular surfaces of cliffs, walls or chimneys.

The study of a large number of nests of all types in their original sites, and in numerous habitats, has revealed that significant engineering variations appear chiefly in those statant nests in vegetation above the ground, and to a lesser extent, those which are adherent. Another variation in statant nests is called saddling. About 40 species, or roughly 7% of the bird species of eastern North America, exhibit considerable variation in the engineering features of their nests.

Three important factors appear to be involved in the nest placement of species of birds which demonstrate engineering variations: 1. The type of nest, 2. the type of nesting materials used, and 3. the type of site on which the nest is built. The nighthawks and whippoorwills make no attempt to build elaborate nests but simply lay their eggs on the ground or on leaves of the forest floor. Some terns and shorebirds wallow out saucer-shaped depressions in the earth. These depressions may or may not be lined. The Prairie Horned Lark (*Otocoris alpestris*) and the Vesper Sparrow (*Pooecetes gramineus*) excavate cup-like depressions in the ground in which they construct nests as complex as those of many tree-nesting birds like the Mourning Dove (*Zenaidura macroura*) and the cuckoos. The mockingbirds, thrashers and the Catbird build bulky structures in vertical crotches of trees and shrubs, but sometimes build on horizontal branches. The grebes, the Black Tern (*Chlidonias niger*), Forster's Tern (*Sterna forsteri*), and occasionally the Common Terns (*Sterna hirundo*), build on floating vegetation. The woodpeckers, titmice, and nuthatches excavate cavities in trees to hold their eggs. Robins and Wood Thrushes build their mud-walled or leaf-mold structures either in upright crotches or saddle them over horizontal forks.

True statant nests either on the ground or above remain in place by the weight and bulk of the materials wedged inside enclosing uprights of vegetation or resting within surrounding walls of earth. It is evident that only those species which attach their nests by means of sufficiently strong fibrous materials or those which build adherent structures are able to use sites which vary from enclosed vertical positions or the broad-based horizontal positions to which the builders of completely statant nests are restricted. Builders of strongly attached nests are able to fasten nests in vertical crotches, with or without foundation materials upon which to rest the bottom of the nest; in horizontal forks, attached at the rim as in the nests of vireos and the Acadian Flycatcher (*Empidonax virescens*); saddled on arching branches as in the Ruby-throated Hummingbird (*Archilochus colubris*) and Blue-gray Gnatcatcher (*Polioptila cereulea*); or on diagonal bases varying at any degree from the horizontal or the vertical positions. Although the birds mentioned in this paper usually build attached nests characteristic for the species, the combination of site and nest pattern results in variations from the pendulous to the pensile, saddled, and attached-statant types.

Engineering variations in pendulous type nests:

The Baltimore Oriole (*Icterus galbula*) is the best example of a bird which usually constructs nests which are completely suspended from the drooping ends of the branches of larger trees of several species. However, I have found four variations from this position which are apparently as successful as the more typical. Five positions are shown Plate 1: Fig. 1 for the Baltimore Oriole. Typical nest fastened at the drooping ends of branches; Fig. 2. Nest fastened in twigs on the side of a horizontal branch; Fig. 3. Nest fastened at the rim within horizontal fork (vireo-like); Fig. 4. Nest either suspended in a vertical fork or attached to the sides like the nest of the Orchard Oriole (*Icterus spurius*); Fig. 5. Nest attached to small side branches on an upright branch, fastened at both the rim and on one side and either fastened to or resting on twigs immediately below. Actually, these nests represent the almost completely pendulous, and the pensile and attached (pendant) types, variations limited to only a few species of birds of eastern North America.

Engineering variations in pensile type nests:

Pensile type nests are built by ten species of vireos, two species of kinglets, seveu species of blackbirds, the Parula Warbler (*Compsothlypsis americana*) and the Acadian Flycatcher. The number of engineering variations likely to most builders of pensile nests apparently is slightly less than for birds which build pendulous nests. Three major factors appear to be involved: 1. A tendency by the builders of pensile nests to utilize weaker and shorter kinds of binding materials because of the scarcity of the longer and stronger materials in woodland habitats; 2. A more limited choice of horizontal forks in trees which meet the basic requirements of the nest pattern; 3. The mode of attaching the nest at the rim. In my experience the species which exhibits the greatest number of engineering variations in this category is the Red-winged Blackbird (*Agelaius phoeniceus*). I have found four departures from the so-called typical nest placement in this species. Fig. 1. The more usual nest is attached at the sides in clumps of cattails, reeds or coarse grasses where the individual stalks are growing close together. Often the bottom of the nest rests in the saddle made by the vegetation as it converges downward, so that it is only partially suspended. Nests built after this fashion on floating mats and in other windswept areas occasionally result in a series of unlined nests superimposed one upon the other, making a total structure a foot or 18 inches in height. These large structures are nearly always found in living cattails or reeds which sway outward with the wind, forcing the attached nest downward along the smooth stalks. Fig. 2. Many nests of the redwing are built in grass hummocks both in marsh areas and in dry fields. Most of these rest solidly on the tops of the hummocks, enclosed by masses of stalks and are attached firmly at the sides and rims as in the wholly pensile nests. However, some of these nests are poorly attached and occasionally one is not attached at all. Fig. 3. Redwings nesting in upright forks of shrubs in swamps or nearly dry fields usually attach the nests at the sides and rims so that they are partially suspended from two to four uprights like nests of the Orchard Oriole. Fig. 4. A variation from Fig. 3 is accomplished by the builders when they fill the bases of the fork with foundation material upon which the nests rest as in No. 2 while being enclosed by uprights and attached at both rims and sides. This type of redwing nest should be called attached-statant and probably represents the most secure anchorage possible. Fig. 5. Occasionally, redwings build in grape and Virginia creeper vines and in horizontal forks of shrubs. In such situations nests are attached at the rims, forming a pensile type similar to the nests of vireos and the Acadian Flycatcher.

I have found four positions for nests of the Red-eyed Warbling and Yellow-throated Vireos (*Vireo olivaceus*), (*Vireo gilvus*), and (*Vireo flavifrons*), numbered in the order of their prevalence: Fig. 1. Probably more than 90% of the nests of these vireos found are in horizontal end forks where the twigs are usually no more than one-fourth inch in diameter. Nests are built in the narrow ends of the Y-shaped horizontal forks and fastened by wrapping over each prong. These wrappings form the rims of nests and their sole support. Fig. 2. The most common variation from the first position are nests built in U-shaped horizontal crotches formed by two twigs which have grown at right angles to a larger branch two to three inches apart. This position permits the nest to be attached over the rim at the back and two sides. I believe that sites of this type with spacing suitable to vireo nest size are much less common in woodlands than Y-shaped forks at or near the ends of branches, hence, fewer nests are found in this position. Fig. 3. This position differs from No. 1 in that the Y-shaped fork is formed by three hranches—one being below the other two—so that the bottom of the nest is supported by the third prong. Nests in this position are of the attached-statant category. Fig. 4. The fourth position is uncommon because the branching habits of most trees at or near the ends of horizontal branches are such that upright forks are not usually formed. A red-eyed Vireo nest, No. 1624 from the Royal Ontario Museum of Zoology, is attached to one upright and one horizontal branch at such an angle that it is pendant. I have found two other nests of this species attached in the same position. Nests of the Acadian Flycatcher exhibit the first three variations shown in nests of the vireos, but apparently, not that shown in Fig. 4. Nests of this species are attached at the rims, but the materials of the basket and somerimes the lining extend beyond the supporting forks so that the structures are partially saddled at both sides. These nests are usually not more than one and one-quarter inches to two inches in total depth as compared with a depth of two and ooe-half to three inches for nests of the vireos. The outer diameters of the flycatcher's and varieos' nests all average slightly over two and one-half inches. One of the major functions of the rather stiff lining of all these nests is to serve as inner braceworks which hold the shapes of total structures and in the nests of Acadian Flycatchers serve as cantilevers to support the centers of the nests.

Engineering variations in pendant nests:

The nests of the Phoebe (*Sayornis phoebe*) and Barn Swallow (*Hirundo rustica*) may be : Fig. 1. Pendant (adhesive; Fig. 2. Saddled—adhesive; Fig. 3. Partially statant—adhesive, and Fig. 4. Statant according to the particular site upon which the birds build. All types of variations except, perhaps, that of Fig. 2 are found in cave mouths and under overhanging rock ledges. Originally these species nested entirely in such situations, but now probably nest more commonly on man-made sites. With natural or man-made conditions, nests of the type in Fig. 1 are adherent to broken-and-irregular or slightly downward-sloping vertical surfaces where the mud used by both species holds the nests in place. Top and side views of nests in vertical positions show them to be crescent-shaped and tapered toward the bottom. These nests are usually deeper than nests partially resting on some projection. Nests of the type shown in Fig. 2 are adherent to vertical walls and saddled over insulators, wires, plumbing fixtures or wires and steel rods projecting from the walls beneath concrete bridges. These nests often have the same form as in that of Fig. 1, but are much more securely anchored. The nest illustrated in Fig. 3 is found on the tops of door frames, stripping and other building trim where the weights of nests rest so that they remain more firmly in place than do completely adhesive nests. These nests are not as deep as the two preceding and are more blunt at the bases. Nests of the form shown in Fig. 4 are found on wide-based ledges, rafters, steel braces under bridges, and on shelves placed for these birds by man. The backs of nests are either against or adherent to vertical surfaces but rest on the flat bases as securely as do statant nests. In such situations the original builders in successive nestings over several seasons and/or later builders often amass tall super-structures of as many as ten nests up to a foot in height. The habitat and nesting requirements of these two species often coincide to the extent that either species builds upon the nest of the other.

Engineering variations in attached-saddled nests:

The Ruby-throated Hummingbird, the Blue-gray Gnatcatcher and the Eastern Wood Pewee (*Myiochanes virens*) are probably the best known eastern North American species which build the attached-saddled type of nest. Of these species the hummingbird undoubtedly exhibits the greatest number of adaptations of material to position of nest site. I have found nine different combinations of attachment and saddling in nests of this species. This ability to saddle successfully such tiny nests over branches often steeply inclined and ranging from one-eighth of an inch to more than one inch in diameter cannot be wholly the result of the small size of the nest and the use of spider silk as a binding material. For the hummingbird also uses glue-like saliva to hold the nest in place. Herrick (1935:157-158) superbly described the various steps followed in nest-building by female hummingbirds. He wrote that "The ruby-throated hummingbird fixes its diminutive and exquisitely wrought nest to a small twig, placing it at a fork, perhaps, or for greater security, extending the base of the nest around the stem, and always building up one side of the nest to compensate for whatever inclination the twig may have. The birds first spread a small wafer of inspissated saliva (Fig. 84) on the chosen twig and, building upon this, literally glue their nest to its support, after the common habit of the swifts. Whether this is an invariable custom in their nest-building or used only when the need is imperative, I cannot say."

Plate 1, Fig. 1 for the hummingbird illustrates a nest sitting astride a one-inch branch with the materials of the nest extending only part way down its sides. Fig. 2 shows a nest in which the wrappings completely encircle a one-quarter-inch twig. Fig. 3 varies from 2 in being attached at the side to a diagonal twig as well as encircling the branch below. Fig. 4 sits astride a larger branch between two uprights to which the nest is attached at the sides. Fig. 5 shows a nest which is saddled on and completely encircles, at the bottom, a diagonal branch. Fig. 6 varies from 5 in being built on so steep a diagonal that both tbe binding materials at one side and part of the bottom of the nest encircles the twig at such an angle that the nest becomes nearly pendant. Fig. 7 differs from 6 in being saddled over (encircling) a branch at the bottom of the nest and encircling the diagonal as well. Fig. 8, apparently, is found only in trees like the oaks, the smaller branches of which grow in a gnarled and crooked pattern. The nest is deeply saddled and encircles the two diagonals for most of its depth. Fig. 9 closely resembles the placement common to the Eastern Pewees' nests. The nest encircles the fork and its shaft of the horizontal branch with only the outer part of the nest unsupported at the bottom. Nests of the Blue-gray Gnatcatcher and the Eastern Pewee, because of their greater size and lack of the additional feature of glue-fastening characteristic of the hummingbird, show fewer engineering variations. Obviously, the two-inch diameter nests of the Gnatcatcher and the three-inch diameter, flat nests of the Pewee could not be adapted to horizontal branches less than one and one-half inches in diameter for the former and two to two and one-half inches for the latter. Nests of these birds would be inadequate if built on steeply inclined branches of any size unless strongly supported horizontally, because neither bird adequately saddles the branch.

The Blue-gray Gnatcatcher. I have found only three variations in nest position for the Gnatcatcher. Fig. 1 shows the commonest position for the nest of this species. The bottom of the nest is saddled over a horizontal branch of an inch or more in diameter and attached to the side of an upright. Fig. 2 shows a nest saddled over a horizontal branch without side support. Fig. 3 shows a nest position which has been reported only a few times. I have found two nests with this placement (Nickell: 159-160), at Aurora, Indiana, and in Oakland County, Michigan. All nests in vertical forks which have been reported have been at low elevations after the fashion of the Alder Flycatcher (*Empidonax traillii*), Yellow Warbler (*Dendroica petechia*) and Goldfinch (*Spinus tristis*).

The Eastern Wood Pewee. The common placement of nests of this species is represented by Fig. 1, for Wood Pewee. The nests are saddled over one or both forks of a horizontal branch and extend back along the shaft. They are attached by outliers of finely shredded bark and plant downs bound in place by spider silk. Fig. 2 illustration shows a saddled nest over a larger horizontal branch attached to an upright branch at the side. Sometimes a nest is found in an upright crotch which is wide enough and sufficiently flat at the base to accommodate a nest (Fig. 3).

ENGINEERING VARIATIONS IN ATTACHED-STATANT NESTS

The three species of Eastern North American birds which demonstrate the greatest variety of engineering features in their nest placements are the Alder Flycatcher, Yellow Warbler, and the Goldfinch. Approximately 7,000 nests of these three species have been collected and examined. Although each species is in a different family, these birds commonly nest in the same types of habitats where available nest sites and nesting materials are basically similar or, in many instances, the same. In particular these birds use the same fibrous materials with which the baskets of their nests are constructed and attached in the nest sites. These birds have overlapping nesting seasons, in southeastern Michigan beginning with the Yellow Warbler in mid-May, the Alder Flycatcher by June 10 and continuing with the Goldfinch by mid-July, ending in late September, and they either gather the bark fibers of the Swamp Milkweed (*Asclepias incarnata*) and other fibrous plants bit by bit, or they commonly dismantle each other's nests to obtain these materials. Moreover, these birds are comparable in size and the nests, which are of the same type, overlap in dimensions to an extent that occasionally birds of each species may superimpose their nests over those of the others. All of the three species show the same variations io engineering features to varying degrees. Fig. 1 is a nest representing the commonest form. The narrow lower part of the vertical crotch is filled with foundation material so that the upper part, attached at the sides, rests upon it. In Fig. 2 the nest is built without foundation so that it is held in place by the attachments at the sides. Fig. 3 shows a nest built in a horizontal branch with one or two uprights to which the side or sides of the nest are attached. It is usually saddled, also. In Fig. 4 the nest is saddled over a horizontal branch so that the bottom of the nest completely encircles its support. Fig. 5 represents nests encircling inclined stems of shrubs and attached to a side branch. Fig. 6 shows an upright stem to which the nest is attached and a lateral branch which is saddled and encircled by the bottom of the nest. Fig. 7 shows a nest attached at the rim to a lateral branch wrapped at one side to an upright stem, making a pendant form. In Fig. 8 the nest is attached at the sides between two uprights and is unsupported at the bottom. In Fig. 9 the nest is attached at the rim to a horizontal fork so that it forms a pensile type like the nests of vireos. I have seen the nests of both the Yellow Warbler and the Alder Flycatcher built in nests of Red-eyed Vireos.

ENGINEERING VARIATIONS IN SOME STATANT NESTS

The Robin (*Turdus migratorius*) and the Wood Thrush (*Hylocichla mustelina*) usually build statant nests which are unattached to their sites. The rigid nest cups of Robins' nests are usually built of heavy mud, occasionally of muck or leaf-mold. Wood Thrush nests cups usually contain only the lighter weight leaf-mold or muck. I have found four engineering aspects in the nest of these species. Fig. 1 illustrates the most abundant form of the nests of the Wood Thrush and the Robin in wild nature. The Wood Thrush is still largely restricted to its usual habitat, but the Robin in modern times has adapted to man-made situations so that its most abundant nest sites are probably represented in Fig. 4. In Fig. 1 the nest is in upright crotches of trees or the larger shrubs, enclosed by two to four uprights. Nests rest solidly in the bottoms of the crotches by their own weight and often partially saddle the uprights in narrower crotches. Fig. 2 shows nests built over horizontal crotches and saddled. Fig. 3 shows a nest found on branches which droop to form inclines. Nests in this position are thickened on the lower sides by built-up foundation materials which permit the nest to stand in a level position. Fig. 4 shows the nest of the Robin around human habitations This type of nest is found on window ledges, rafters, steps, niches in walls and chimneys, nesting shelves, transformer boxes, tops of fence posts and on brace flanges under bridges.

THE BRANCHING HABITS OF TREES, SHRUBS AND FORBS AS FACTORS IN BIRD NEST SITE CHOICE

Most species of birds which nest above ground must select sites in some kind of vegetation which afford them opportunity to build their characteristic types of nests. That birds do select, within the framework of instinct, the sites on which they build their nests, cannot be doubted because of the high percentage of nests which are successfully placed to fulfill their functions as compared with those which are failures because of faulty construction or anchorage. There is evidence in the pre-nesting behavior of many species of birds that some degree of experimentation is followed before a final choice of site is made. In some cases the male birds which do not later participate in nest construction, may either choose the nest site or influence the female in her choice. The male robin's molding activity on or in a variety of crotches or bare branches, some completely unsuitable for robin nest placement, is practically identical with the activity of the female when pressing mud in molding the well-formed nest cup. The male catbird carries twigs to one or more crotches while being followed closely by the female. Later, the female may accept his choice and build upon his beginnings, or choose another site leaving the forgotten twigs unused. Further evidence of experimentation is suggested by frames found on different sites built by several species of birds before an actual nest is completed. I have observed this behavior in the Red-eyed Vireo, Red-winged Blackbird, Yellow Warbler, Barn Swallow, Phoebe, Goldfinch, Cardinal (*Richmondena cardinalis*), and Catbird (*Dumetella carolinensis*). A considerable percentage of these abortive attempts at nest building may be due to the birds having first chosen sites which are unsuitable for their types of nests and their modes of attachment. Several nest frames I have examined have been in forms too narrow to accommodate nests of the dimensions required by the birds. Other sites of abortive nesting attempts may have failed to satisfy the instinctive requirements for stability. Field studies I have made of the species of vegetation in which several species of birds have nested in the Southeastern Michigan Region during the last 20 years have shown that three aspects of vegetation appear to be important factors for nest sites and nesting materials of birds: 1. The branching habits and other characters of individual plant species; 2. Abundance, distribution and growth stage, and 3. Availability of plants with bark, fibers, twigs, rootlets, leaves and downs suitable for nest construction. I have found that some species of trees and shrubs are almost never used as nest sites by any species of birds in this region while others are used abundantly by several species. Good examples of trees and shrubs which are not commonly used as nest sites by birds are sumacs, poplars, ashes, hickories, wild cherries, birches, and others, probably because of open branching habits, smoothness of bark, brittleness of twigs and other characters which render them largely unsuitable for secure nest anchorage for most birds.

Staghorn Sumac. One of the most abundant and widely distributed shrubs of this area is Staghorn Sumac (*Rhus typhina*), yet it is not often used as nest sites by any species of bird, and wherever it is used, then only when individual branching arrangements depart from the usual growth habit or are supplemented by several species of grapes, Virginia Creeper (*Parthenocissus* *quinquefolia*) and other vines which are twined around them. The parallel growth of the upright terminal branches furnish no enclosing crotches to support statant nests of Catbirds, Brown Thrashers, Robins, Cedar Waxwings (*Bombycilla cedrorum*), and Kingbirds (*Tyrannus tyrannus*) although the habitat is suitable, as indicated by nests in other species of shrubs and trees growing in the midst of Sumac colonies. Occasionally, a Goldfinch will build a nest in a Sumac shrub which has a two-pronged, Y-shaped, upright terminal sufficiently wide to accommodate its nest, but only because the structure is securely attached at two sides and wedged in the bottom of the fork. In a 20-year study (1934-1953) of the Catbird, I found 3,939 nests which were built in 116 species of trees and shrubs of which 54% were in the first five species, all shrubs or low much-branched trees, listed in Table 2. Only seven nests were found in Staghorn Sumac and all were supplemented by vines climbing on the sumac. In a six-year Goldfinch study (1950-1955) 4,084 nests were found in 80 species of trees and shrubs. Over 74% of these nests were in the first five species (Table 2), also, all shrub or shrub-like. Twenty nests were in Staghorn Sumac (Table 1).

Quaking Aspen. Quaking Aspen like Staghorn Sumac is not often used by tree-nesting birds, yet it is abundant and widely distributed in both wet and dry situations. The irregular distribution of branches along the trunks, the scarcity of enclosing uprights, the smoothness of its bark on both trunk and branches, the brittleness of its small twigs and its lack of foliage density all appear to render it unfit for nest sites for most birds which build completely statant nests. As abundant as it is in the generalized habitats of Catbirds, I have found only five of 3,939 of these statant nests in its branches in 20 years. Again, as in Staghorn Sumac, the Goldfinch was able to use the Quaking Aspen because of its smaller attached nest. One hundred and fifty-seven (3.8%) of 4,084 nests of the Goldfinch found in six years were in Aspen, (Table 1). However, the Goldfinch is the only species which more than rarely uses Aspen for nest sites in the southern Michigan region. Table 1 lists eight species of trees and one shrub which are distributed over the habitats of the Goldfinch and the Catbird in numbers which should place them among those more commonly used as nest sites. A comparison with Table 2 shows them to be much less used than one might expect considering their commonness. The structure of these plants render them less suitable as nesting sites.

A comparison of the numbers of attached-statant nests of the Goldfinch and the statant nests of the Catbird found in eight common species of shrubs in Southeastern Michigan is shown in Table 2. Both the Goldfinch and the Catbird are among the most abundant nesting birds in Southeastern Michigan as the 8,023 records for the two species show. Both species exhibit a considerable degree of tolerance in habitats which they will occupy, and these habitats overlap at many points.

Gray Dogwood. It will be noted in Table 2 that Gray Dogwood as a nesting shrub occupied first place for both species of birds in their over-all habitats. Gray Dogwood has the same rank as a valuable shrub for nesting four other species of birds also. These species are the Yellow Warbler, Alder Flycatcher, Cardinal, and Field Sparrow (*Spizella pusilla*), all common species, but with somewhat more restricted habitats than the two preceding. Gray Dogwood and the Hawthorns are undoubtedly among the most abundant and widely distributed shrubs in Southeastern Michigan and Southwestern Ontario. The habitats of both show considerable overlapping largely, apparently, because of the tolerance of Gray Dogwood for both wet and dry situations. Billington (1949:243) stated that, "The Panicled Dogwood is one of our most common shrubs. It grows abundantly along the roadsides and in fence rows bordering our fields and woods. It grows on the banks of streams, and everywhere it makes a beautiful appearance when in flower."

TABLE 1

FREQUENCY OF USE OF NEST SITES IN NINE SPECIES OF TREES AND SHRUBS BY THE GOLDFINCH (304 nests) AND THE CATBIRD (28 nests) COMPARED TO EIGHT MORE COMMONLY USED TREES AND SHRUBS LISTED IN TABLE 2.

PLANT SPECIES	Goldfinch Number of Nests	Catbird Number of Nests
Quaking Aspen (*Populus tremuloides*)	157	5
Wild Black Cherry (*Prunis serotina*)	49	9
Cherry Birch (*Betula lenta*)	20	0
Staghorn Sumac (*Rhus typhina*)	20	7
White Ash (*Fraxinus americana*)	19	0
Choke Cherry (*Prunus virginiana*)	13	3
Black Ash (*Fraxinus nigra*)	13	0
Paper Birch (*Betula papyrifera*)	11	1
Shagbark Hickory (*Hicoria ovata*)	2	3

The branching habit of Gray Dogwood, when thinly distributed in wet or dry situations, and at the edges of dense thickets of this species, is near optimum for nest sites of several species of our small birds. Its upright branching pattern, with terminals somewhat evenly distributed around each central axis, furnishes two to eight (average four) points of attachment for attached-statant nests and enclosing baskets for statant nests. Reference to Table 2 will show that Goldfinches using Gray Dogwood built about one nest in a horizontal position to every 172 nests built in vertical crotches. The greater number of Catbird nests in horizontal positions (about one to 20 in vertical

TABLE 2

COMPARISON OF EIGHT GENERA AND SPECIES OF TREES AND SHRUBS AS SITES OF 5,491 NESTS OF THE GOLDFINCH AND THE CATBIRD WITH EMPHASIS ON THE FIRST FIVE UNDER EACH SPECIES OF BIRD

GOLDFINCH—PLANT SPECIES	No. of Nests	Nos. in horizontal positions	Nos. in vertical positions	Percentage in each species	Average height in feet above ground
1. Gray Dogwood (*Cornus racemosa*) . . .	1203	7	1196	29	4.6
2. Hawthorns (*Crataegus* spp.)	579	92	487	14	5.4
3. Shrub Willows (*Salix* spp.)	529	7	522	12.9	6.2
4. Red Osier Dogwood (*Cornus stolonifera* . . .	450	3	447	11	4.2
5. Elms (*Ulmus* spp.	266	33	233	6.5	6.6
6. American Elder (*Sambucus canadensis* . .	89	4	85	2.1	4.8
7. Wild Grapes (*Vitis* spp.) . .	14	3	11	34	5.6
8. Tartarian Honeysuckle (*Lonicera tartarica*)	9	0	9	22	5.8
CATBIRD—PLANT SPECIES					
1. Gray Dogwood	581	29	552	14.8	5.2
2. Tartarian Honeysuckle.	543	143	400	13.8	5.4
3. Hawthorns.	448	28	420	11.3	5.4
4. Wild Grapes . . .	326	114	212	8.2	6.0
5. American Elder . . .	229	32	197	5.8	4.6
6. Red Osier Dogwood	99	27	72	2.5	4.6
7. Shrub Willows.	94	6	88	2.4	4.8
8. Elms	32	3	29	0.8	5.4

positions) is largely explained by the tendency of this bird to nest in denser growth where crossing horizontal branches and vines form the hammock-like sites used.

The Hawthorns. Although the Hawthorns have a considerably different branching pattern from the Gray Dogwood, they are nevertheless as suitable for nest sites. The general arrangement of Hawthorn branches tends to be a combination of upright and horizontal growth with interlacing diagonals and cross-branches which furnish many good sites in either vertical or horizontal positions. The ratios of horizontal positions to vertical positions used by the Goldfinch and the Catbirds in the Hawthorns are about 1.2 to 6.3 and 1 to 16 (Table 2). The greater proportion of Catbird nests in vertical positions is explained by this bird's tendency to build near the centers of shrubs in the main trunk crotches while Goldfinches more often choose smaller shrubs and the outer parts of the larger shrubs. The number of branches forming crotches for nest sites average 3.3 per shrub.

Tartarian Honeysuckle. Tartarian Honeysuckle is a shrub which was introduced into Southeastern Michigan for landscaping large estates, probably 50 years ago. It forms dense hedges along roads, paths, woods edges, and beside buildings and old stoue walls, most favorable habitats for Catbirds but scarcely used by Goldfinches. Goldfinches use Tartarian Honeysuckle when it occurs as scattered shrubs in open areas where its seeds have been dropped by birds. The high rank it occupies as a nesting shrub for Catbirds is due to its great suitability and abundance in the area where my studies were most intensive. Its growth pattern consisting of up to eight upright terminal branches in the younger growths and its habit of falling to a nearly recumbent position from the center of clumps when it is mature, creates both horizontal and vertical sites for Robins, Brown Thrashers, Catbirds, Cuckoos, Mourning Doves and Song Sparrows (*Melospiza melodia*). The ratio of 1.3 nests in horizontal positions to 3 8 nests in vertical positions for nests of the Catbird is probably one of the closest approximations to even distribution between the two positions found in any shrub or tree which is commonly used as nest sites. Uprights around the terminals or the central stems average 4 per shrub.

Shrub Willows. Several species of Shrub Willows occupying third place for nest sites of the Goldfinch have branching patterns similar to that of Gray Dogwood. The habitats of these shrubs, however, are confined chiefly to wetter situations which are not commonly chosen by the Catbird for nesting. Moreover, the upright crotches of the majority of these shrubs are narrow, hence more suitable for the smaller, attached nests of Goldfinches than for the much larger, unattached nests of Catbirds. Goldfinch nests were 5.6 times as numerous as nests of Catbirds in these shrubs and averaged over one foot higher above ground. Good horizontal sites are not common in Shrub Willows.

Red Osier Dogwood. This species is a native shrub found generally in marshes, bogs, along streams and other wet situations. This limitation gives it a status comparable to that of the Shrub Willows as nest sites for both the Goldfinch and the Catbird. Upright terminals forming the crotch average 3.1, but are usually evenly spaced. Its growth in the more open situations renders it more suitable for Goldfinches than for Catbirds.

The Elms. The majority of the Elms used as nest sites by the Goldfinch and the Catbird are saplings which are three to 35 feet in height. Nearly all Goldfinch nests are placed in the top trunk forks of smaller trees or in tufts along the horizontal branches of larger saplings. Practically all Catbird nests are placed in the lower main trunk crotches of saplings of medium size, as few horizontal elm branches are suitable for holding their statant nests. These crotches average 3.6 uprights and 5.4 feet above the earth. The average height of nests of the Goldfinch was over one foot higher (6.6 feet) because of their greater number of high nests in horizontal positions (Table 2).

American Elder. This shrub is common in moist situations where both the Goldfinch and the Catbird nest. Its habitat limitations confine its growth largely to stream banks, flood plains, and edges of bogs and marshes so that it is not nearly as widely distributed as most of the foregoing species. However, its branching pattern renders it moderately suitable for nest sites for several species of birds. This branching pattern is loose and open so that many of its horizontal branches are unsuitable as sites for either attached or statant nests unless supplemented by branches of other vegetation. The central crotches, formed by an average of four branches, are flaring so that they are usually more adaptable to the larger nests than to the smaller nests of Goldfinches, Alder Flycatchers, and Yellow Warblers, although these smaller birds, which attach their nests, do find a moderate number of crotches which fit their needs. The ratio of horizontal positions used by the Goldfinch and the Catbird in 282 nests in this shrub was 1:8. The ratio of horizontal sites used by the Goldfinch to vertical sites was about 1 to 21, while the Catbird's ratio of horizontal sites used to vertical sites was 1 to 7. The number of Catbirds' nests found in Elder was two and one-half times that of the Goldfinch. The average heights of nests above the ground was almost the same: 4.8 feet for the Goldfinch and 4.6 feet for the Catbird.

The Wild Grapes. The various species of wild grapes of this region grow mostly in moist or dry thickets and along fence rows where they attach themselves to other, supporting vegetation. They are found only sparsely in the more open areas in which Goldfinches most commonly nest, but are common in one of the more favored types of Catbird habitat. The interlacing network of crossing branches and tendrils which these shrubs form on shrubs, trees and fences, constitute good horizontal sites and the three (or four) upright terminals of smaller vines are arranged around the central axes, producing basket-like vertical sites. The ratio of Goldfinch nests to Catbird nests found in the grapes was 1 to 23. The ratio of nests of both species found in horizontal sites to those found in vertical sites was 1 to 2.

Herbaceous Plants. Forbs are not often used as nest sites by most species of birds which nest above the ground. Most of these plants are too weak to support the weights of nests except in clusters as in the nests of Long-billed Marsh Wrens (*Telmatodytes palustris*), Redwings and Least Bitterns (*Ixobrychus exilis exilis*) which attach their nests to cattails, reeds and other herbaceous marsh vegetation. Moreover, most larger forbs which could be used if suitably branched and sufficiently strong to support nests, have not reached their full growth by the time many birds are at the height of their nesting activities. A notable exception is the Goldfinch which begins its nesting about mid-July and nests again about mid-August. I have found 15 nests of this bird in Canada Goldenrod (*Solidago canadensis*) and two nests in Swamp Milkweed. Others have reported nests of this species in thistles. I have found one nest of the Catbird in Tall Meadow Rue (*Thalictrum polygamum*).

PLANT AND OTHER MATERIALS USED IN BIRDS' NESTS

The nesting materials of birds are usually found in the immediate vicinity of the nest site and their variety, when considered as a whole for all species nesting in any region, is almost as great as the plant species themselves. In addition such materials as mud, hair, feathers, spider silk, dried spittle of spittle bugs (Family Cercopidae), and man-made materials of many kinds are included in all parts of nests.

Again, as in choosing nest sites, birds instinctively select from their environment materials which fit the need of their own kinds of nests. The Baltimore Oriole usually nests in the vicinity of streams, lakes, swamps, and other wet situations where Swamp Milkweed grows in greater or lesser abundance. Its pendulous nesr frame is usually built of the milkweed's outer bark fibers which I have many times seen them gathering. If cotton wrapping-twine, yarn, or other strong, fibrous and flexible materials approximating the qnalities of the natural material is found, they will be used. The lining of the nests is of the long hair of cattle and horses, or finely shredded, spring-like bark of grapes and other vines. The apparent function of tbe linings in these nests is primarily to prevent their collapse from the weight of the adults, eggs, and young, as no appreciable amount of insulating materials is used. Obviously, the Baltimore Oriole would find it impossible to suspend its nest from slender branch ends if it attempted to make use of twigs, leaves, coarse tree bark, stiff weed stalks, tendrils, moss, mud, and many other materials used by several species of birds building statant nests. Just as obviously, the Catbird, Robin, Phoebe, or Hummingbird would fail if they should attempt to duplicate the Orioles' feat of engineering with the kinds of materials which they instinctively gather from their surroundings. Hence, each species must select the kinds of materials which meet the requirements of its nest pattern. Among birds building different types of nests and following different patterns of construction there are many points of similarity in the use of materials, but most birds indicate one or more points of specificity in selecting certain materials or good substitutes for them in constructing their nests. The Baltimore Oriole, Red-winged Blackbird, Yellow Warbler, Redstart, Alder Flycatcher, Goldfinch, Cedar Waxwing, Kingbird, and sometimes the Catbird, Phoebe, Red-eyed Vireo, Acadian Flycatcher, and others, representing pendulous, pensile, pendant, adherent, attached, and statant nest types will all use the outer bark fibers of Swamp Milkweed in their nests if it is abundant near at hand or if it can be obtained easily from abandoned nests of other species. This material is used as binding for other short loose materials and for the attachment of nests Only the first eight above listed species use milkweed fibers regularly; the others make use of it, apparently, when it is easily obtained or when other materials are not available near the nest site. Milkweed fibers in wild nature far from human homes are often almost the only available material with sufficient strength, length, and flexibility with which the Baltimore Oriole could build a secure, suspended nest. In this sense this material, then, becomes close to being specific for this bird. The other users of Swamp Milkweed fibers build their nests in such situations as enclosed forks or resting securely on foundations so that this material is useful to various degrees but becomes less than specific because they can and do use the shorter, weaker, and less easily obtained fibers of common milkweed (*Asclepias syriaca*) and other weeds, and a variety of plant downs and catkins which can be felted sufficiently to hold nests together.

Other apparent examples of specificity in nesting materials are found in the use of spider silk as a binder and a substance of attachment by the vireos, Eastern Wood Pewee, Blue-gray Gnatcatcher, and Ruby-throated Hummingbird. Due to their methods of saddling, encircling and attaching nests and the need for a fine but strong material which is commonly found in their habitats, probably no other type of substance will quite suffice. Another desirable quality of spider silk in both the attachment of the nests to sites and the fastening of lichens with which these nests are covered, is its stickiness when wet by the birds' saliva at the time it is used. Bits of lichens used on the outer walls of the nests of pewees, gnatcatchers, hummingbirds, Black-capped Vireos (*Vireo atricapillus*) and the Yellow-throated Vireo are held in place by these apparently irreplaceable spiders' silks. For the Robin, Barn Swallow, and Phoebe mud becomes a specific building material for which, apparently, there is no adequate substitute. The use of mosses by the Phoebe appears to be another example of specificity but examination of large numbers of nests in relation to the availability of this material shows that weed barks and other fibrous materials are used frequently to act as binders for the mud used in nests. Rootlets used as nest linings by Catbirds and Brown Thrashers appear to be the most constant feature of their nests. The daily familiarity of these birds with the rootlets of trees and shrubs which they uncover in feeding in thickets and on the forest floor may be a factor in their use. These rootlets which are moist and flexible when placed in the nests become like small wire springs when dry. In this dry state they serve as an inner bracework which preserves the shape of the nest baskets. In the final analysis it may be said that engineering variations found in the nests of some birds are the result of instinctive nest patterns in species which are adapted to mechanical variations in nest sites within the limitations imposed by nesting materials.

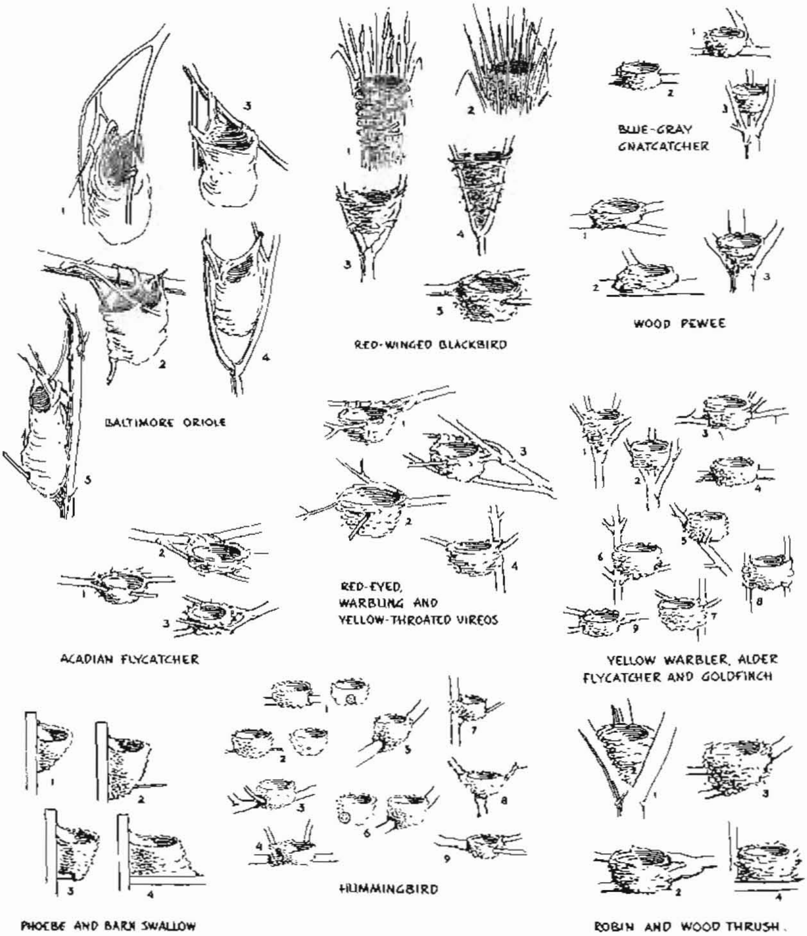
SUMMARY

During 35 years of examining in the field and collecting about 20,000 nests of 169 species of birds, I have collected a great mass of data on the nest sites and nesting materials of these birds and have noted the engineering variations from the so-called typical which have occurred for each species. My studies in the region of Eastern North America between 50° and 30° north latitude and between the 100th meridian and the Atlantic Ocean have indicated that only about seven per cent of the species listed in Eastern North America exhibit any great degree of variation from their usual nest placements.

Important factors involved in nest placement, which demonstrates engineering variations which I have found, occur in nests which are built above ground and all except a few have occurred in nests which are attached or adherent to their supports. Engineering variations are listed for the nests of 16 species of birds which are shown on Plate 1 accompanying the text. The types of nests listed as showing these variations are pendulous, pensile, pendant, attached-saddled, attached-statant, and statant

The branching habits of trees, shrubs and forbs are discussed in relation to nest site choice. Table 1 lists nine species of trees and shrubs which are common but not frequently used as nest sites and compares the ferquency of their use by the Goldfinch which builds attached-statant nests, and that of the Catbird which constructs statant nests. Also, this table compares the use of these shrubs with the frequency of use of eight other plant species which are most frequently used as nest sites in southeastern Michigan (Table 2). Table 2 lists eight species of trees, the first five of which under the Goldfinch and the Catbird show the greatest usage in 4,084 nests of the former and 3,939 nests of the latter. The abundance, distribution and usability of the various species listed is discussed in the text.

Forbs are shown to be largely unsuitable for nest sites for most species of



ENGINEERING FEATURES OF NESTS OF 16 BIRD SPECIES

birds because of not being available at the height of the nesting season and by being poorly branched and weak. Goldenrods, thistles, cattails, reeds, and marsh grasses are exceptions for the Red-winged Blackbird and the Goldfinch.

Nesting materials are discussed, their types and the specificity of their use by the bird species indicated. Some apparent specificity in the use of certain materials is shown to be only apparent, because of known substitutions which some species have made successfully.

Illustrations of Engineering Variations by Luella C. Schroeder

LITERATURE CITED

Billington, Cecil. 1949. Shrubs of Michigan. Cranbrook Institute of Science. Bloomfield Hills, Michigan. Bulletin 20. Second Edition.

Fernald, M. L. 1950. Gray's Manual of Botany, Eighth Edition. American Book Company, New York.

Herrick, Francis Hobart 1935. Wild Birds at Home. D. Appleton-Century Company, New York.

Nickell, Walter P. 1956. Vertical Nest Placement in the Blue-Gray Gnatcatcher. Wils. Bull. Vol 68:159-160

Pough, Richard H. 1946. Audubon Bird Guide. Eastern Land Birds. Doubleday and Company, Inc., Garden City, New York.

Pough, Richard H. 1951. Audubon Water Bird Guide. Doubleday and Company, Inc., Garden City, New York.