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Los Angeles County Museum
Los Angeles 7
California
August, 1946

BREEDING HABITATS OF CERTAIN WOOD WARBLERS IN THE UNGLACIATED APPALACHIAN REGION

BY MAURICE BROOKS

THE unglaciated Appalachian Mountain region, from Pennsylvania southward, has long been noted, among ornithologists, for the breeding here of many species of birds generally associated with more northern regions. It has not been so well recognized that a good number of such species nest in the region in habitats which often differ radically from those usually occupied in other portions of their ranges.

Although there are other bird groups which show a tendency to occupy, locally, habitats at variance with their more common practices, this behavior is best illustrated by the wood warblers, Family Compsothlypidae. Wood warblers in the region display a great deal of plasticity in their choice of nesting sites. Most of the original timber which clothed the mountain slopes and high plateaus has been removed. From many of the mountains the spruce-fir forest of high elevations has practically disappeared. To a lesser degree, the birch-beech-maple forests, and the birch-hemlock forests have been destroyed or greatly disturbed. The oak-hickory-chestnut forest has undergone a profound transformation with the death, from the chestnut bark disease, of the chestnut, a dominant species in many areas.

Despite abrupt changes in the character of the forests, most warbler species have shown an amazing power of adaptation to new surroundings. The mountains have lost, in the time of ornithologists at least,

no species, and there are some species whose ranges have been considerably extended. This plasticity, resulting in the ability to occupy habitats and find nesting sites which, in other portions of the birds' ranges, would be considered unusual, can best be shown through specific examples.

GOLDEN-WINGED WARBLER, *Vermivora chrysoptera.*—In the unglaciated Appalachian region this is a characteristic bird of the oak-chestnut forests. It is most common on dry, brushy ridges between 2000 and 3000 feet elevations, where dead chestnut stubs are still standing. Males regularly select dead chestnuts as their singing perches. In the openings where the mature chestnuts have died, and where the abundant sprouts alternately grow and die of blight, the birds find nesting sites. They are seldom found in the river valleys, even where there are swamps and marshes. I have referred to this sprout growth (Brooks, 1940) as the "chestnut-sprout association," since it is a definite, widespread community, with a highly interesting bird life. Odum and Burleigh (1946) have discussed it at some length, and have written of the birds which find nests in this disclimax growth.

PARULA WARBLER, *Compsothlypis americana.*—The northern and southern races of the Parula Warbler meet and overlap territories in the unglaciated Appalachian region. Throughout the south, the southern race habitually nests in long moss (*Tillandsia*). In the north, the bird selects clumps of the superficially similar lichens, *Usnea* and *Cladonia usneoides,* in which to construct its nests.

The southern Appalachian region has no long moss, and relatively little *Usnea,* yet the birds are widely distributed, and often abundant, throughout the region. Nor are they restricted to coniferous or evergreen forests. They nest in southern mixed hardwoods, oak-chestnut-hickory, oak-pine, in the so-called "Appalachian forest," in northern hardwoods, in white pine, in hemlock, and at the borders of the red spruce forests. As is indicated by their occurrence in a wide variety of timber types, they nest at practically all elevations throughout the region save, perhaps, on some of the highest peaks. Although they may be somewhat more abundant in hemlock forests, they often nest in pure deciduous stands, and I have found nests in dense clumps of leaves at the ends of white oak and sycamore branches.

MAGNOLIA WARBLER, *Dendroica magnolia.*—This is another species which makes a wide choice of nesting habitats. It occurs in the mountains from the summits down to about 1200 feet, breeding in spruce-fir, northern mixed, and somewhat more sparingly in the northern

hardwood and oak-hickory-chestnut forests. Where the high ridges are covered with chestnut sprouts, however, the bird is common, making its nests in the dense clumps of dead chestnut twigs. In many cases the communities selected have no coniferous trees of any kind.

BLACK-THROATED BLUE WARBLER, *Dendroica caerulescens.*—This species, including the southern race, Cairns's Warbler, is a frequent companion of the Magnolia Warbler, occurring in every timber type occupied by the latter species. It is a characteristic bird of the "chestnut sprout association," and often nests well removed from any conifers.

BLACK-THROATED GREEN WARBLER, *Dendroica virens.*—Customarily associated with hemlock woods, this bird is notable in the Appalachian region for its wide choice of nesting sites and habitats. It breeds from elevations of 500 feet to the highest mountain peaks, and it occurs in every timber type in the region. On dry oak-hickory ridges, far removed from any conifers, it is often a characteristic species. I have seen nests placed in white oak and beech trees, and fastened to a wild grape vine.

BLACKBURNIAN WARBLER, *Dendroica fusca.*—Although very common in coniferous stands, the Blackburnian Warbler is also common on the dry chestnut ridges, where, like the Golden-winged Warbler, it frequently sings from the top branch of a dead chestnut or oak tree.

CHESTNUT-SIDED WARBLER, *Dendroica pensylvanica.*—As might be expected, this species is the most common and characteristic warbler of the "chestnut sprout association," being found practically throughout the region at elevations of 1500 feet or more. The brushy second growth which now clothes so many of the Appalachian slopes is, apparently, exactly suited to the needs of this species, although it nests about openings in the spruce stands as well.

MOURNING WARBLER, *Oporornis philadelphia.*—Reaching its southern breeding limits in Virginia and West Virginia, this is a characteristic, and often abundant, species in the "chestnut sprout association" above 3000 feet. It breeds also in the spruce forest openings, but is generally more common in deciduous stands.

CANADA WARBLER, *Wilsonia canadensis.*—This species is most common in rhododendron tangles under spruce or hemlock forests, but it is also often found in the dense sprouts and brier stands of the "chestnut sprout associations." In such situations it is frequently far removed from any conifers today, although there may be stands of *Kalmia* and other broad-leaved evergreens in such situations.

To recapitulate, every one of the warblers which I have listed, save the Parula, is at least locally common in the "chestnut sprout asso-

ciation," and all are found today in habitats entirely disssociated from coniferous stands or remnant conifers.

Having stated the facts as they are known, it seems desirable to enter the field of pure theory in an attempt to explain a situation which will seem highly aberrant to most northern bird students. I believe that the explanation may lie in the conditions which prevailed during the Pleistocene. At least four times during this recent geologic period, advancing ice sheets effectively barred great sections of the North American continent to land-nesting birds. As glacial ice advanced, there must have been, just south of the ice mass, a cumulative piling up of birds which had habitually nested northward.

Of perhaps equal importance in unsettling the breeding habits of many species were the spectacular climatic fluctuations which occurred during interglacial periods. It has been shown that presently existing lakes in northern Ohio and Indiana were, at such times, completely dried up on two occasions, the lake beds being covered over with mesophytic forest. The Dismal Swamp in Virginia has undergone similar fluctuations. The piling up of great numbers of birds just south of the ice mass, followed by comparatively rapid recession of the ice, with resultant changes in the vegetation, must have led to constantly shifting bird populations, with resultant breakdown of breeding habits and territorialism.

It may be pointed out that birds accustomed to nest in the coniferous forest had larger areas of such forests in which to breed during times of glacial advance. To a limited extent, this was doubtless true, since there is evidence that the spruce-fir forest extended along the mountains at least as far as South Carolina. On the other hand, the great mixed-mesophytic Tertiary forest of the Allegheny and Cumberland plateaus seems not to have been greatly modified by glaciation, and it may be presumed that there were forests of oak-hickory-chestnut and oak-pine, as well as northern hardwoods, during Pleistocene times not far south of the line of glacial ice.

There is some evidence to show that enforced piling up of birds of any given species in an area will result in a greatly increased breeding population within that area. There is a wealth of evidence, moreover, to show that some individuals within a given species are sufficiently plastic in their breeding habits to adapt themselves to new sites and new breeding conditions.

If this theory be tenable, therefore, we might expect that birds forced out of their traditional breeding grounds, and coming into competition with others of their kind in a new territory, would find homes in new vegetational types, wherever unoccupied niches pre-

sented themselves. As we have seen, this is precisely the condition which obtains today for many northern warblers in the southern Appalachian region.

Perhaps the key to this situation lies in varying degrees of plasticity among individuals of the same species. This individual variation need not be too surprising in the light of Chimney Swift behavior since the coming of the white man. Many of these birds have moved to the city or the village to occupy man-made structures, but others, rugged individualists, have quite literally clung to the hollow trees of their ancestors.

We may postulate, therefore, that the conservatives among the wood warblers moved northward as the ice receded, to reoccupy nesting sites in the traditional coniferous forests of their ancestors. Pioneering individuals, however, having learned that it was possible to nest in deciduous forests of various types, may have remained over wide areas of the unglaciated Appalachian highlands, carrying on and extending the new behavior pattern.

This ability to adapt readily to new conditions may explain the striking association of warblers in chestnut sprout areas in the southern highlands. These birds are biologically sound, a sort of avian "left wing," undismayed by change and ready to use it, when it comes, to their own advantage.

SUMMARY

1. This paper discusses the breeding of certain wood warblers in the unglaciated Appalachian region, where they are to be found in habitats radically different from those occupied northward.

2. Many of these warblers breed in areas of chestnut sprouts which have followed the death from blight of mature chestnut trees.

3. The theory is propounded that crowding of birds in the area just southward of glacial ice, coupled with rapid and marked climatic fluctuations in interglacial periods, led to changed breeding habits among certain individuals, and that these habits have persisted to the present time.

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Division of Forestry
West Virginia University
Morgantown, West Virginia