

GOLDEN-WINGED WARBLERS AND BLUE-WINGED WARBLERS: THE RELATIVE SUCCESS OF A HABITAT SPECIALIST AND A GENERALIST

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ABSTRACT.—Evidence of the decline of Golden-winged Warblers (*Vermivora chrysoptera*) in Tompkins County, New York is presented, which adds to other examples of decline elsewhere. This decline is temporally correlated with an increase in Blue-winged Warblers (*V. pinus*). In Tompkins County, the Golden-winged Warbler nests only in the shrub stage of successional habitat on large patches of abandoned farmland. Blue-winged Warblers use later stages of succession as well as the early stages. A small decrease in the amount of recently abandoned farmland in Tompkins County with a larger increase in the amount of land in later stages of succession helps explain the decrease in Golden-winged Warblers and the increase in Blue-winged Warblers. The large magnitude of decline in Golden-winged Warblers, however, suggests that there may also be some negative biological interaction with the recently arrived and increasingly abundant Blue-winged Warbler. *Received 19 May 1980, accepted 21 August 1980.*

THE Golden-winged Warbler (*Vermivora chrysoptera*) and the Blue-winged Warbler (*V. pinus*) are of particular interest because of their dynamic zone of secondary contact and the resultant genetic and ecological interaction between them. Changes in their range have been summarized by Short (1963) and especially Gill (1980), and the following synopsis is taken from their works.

The Golden-winged Warbler has been expanding its range northward and eastward in the eastern United States for about 175 yr. The Blue-winged Warbler was originally allopatric to the Golden-winged Warbler and was restricted almost entirely to areas west of the Alleghenies. The Blue-winged Warbler also has had a major range expansion, which began later than the Golden-winged Warbler's and is still continuing (e.g. Kibbe 1978). The Golden-winged Warbler is now allopatric only at its extreme northern range and at its highest nesting elevations in the Appalachian Mountains.

While the Golden-winged Warbler expanded northward and eastward during this century, it disappeared from much of its southern range. Regions first colonized by Golden-winged Warblers more than a century ago that are now devoid of nesting Golden-winged Warblers include southern New Jersey, coastal portions of Connecticut, Rhode Island, and southern Massachusetts, and the southern portions of the Hudson River valley (see Gill 1980 for details).

The principal goal of this study has been to gain a greater understanding of the reasons why the changes in range have occurred and especially why the Golden-winged Warbler has declined in some areas. Gill (1980) has shown that there is a close temporal relation between the arrival of Blue-winged Warblers and the local extinction of Golden-winged Warblers within 50 yr or less. It is logical to wonder whether competition between the two species or genetic introgression of the Golden-winged Warbler with the Blue-winged Warbler could account for the disappearance of Golden-winged Warblers. Unfortunately, there is no evidence that distinguishes competition from genetic introgression as a possible cause of the elimination of Golden-winged Warblers. In this paper we will present evidence that another, not

necessarily exclusive, reason helps explain the disappearance of Golden-winged Warblers. We suggest that the Golden-winged Warbler is a habitat specialist requiring early succession fields, while the Blue-winged Warbler is, relatively, a habitat generalist. We believe that the Golden-winged Warbler's habitat requirements have contributed and are continuing to contribute to its loss of range.

METHODS

In order to determine the kind of vegetation used by each species, territorial boundaries were determined by observing singing males in Tompkins County, New York during 1978. All maps were determined by at least five visits, and most territories were visited at least 10 times. All were visited over a period of at least 3 weeks. Because males occasionally took long flights well beyond the area most frequently used, we chose boundary lines only when males had been observed at a particular location on at least two separate instances.

Vegetation was measured at predetermined, random distances along three or four parallel transects for each territory. Distances between transects within a territory were approximately equal and, depending on the size of the territory, were about 20–40 m apart. All transects were run perpendicular to but extended into unusual features along the perimeter in order to avoid bias in our samples. Vegetation was measured at 20 sampling stations within each territory. At each sampling station the density of three layers of vegetation was estimated for an imaginary vertical cylinder of 15 cm diameter. The layers of vegetation were: herbs, shrubs and small woody trees up to about 4 m in height, and trees taller than about 4 m. At each station each layer of vegetation was assigned one of our values: 0 for no growth, 1 for sparse growth, 2 for moderate growth, and 3 for dense growth. Four territories were remeasured after our judgment about the four categories became more consistent. All measurements were conducted in late June or July, when summer growth was essentially complete. Statistical analyses were performed on the average of the 20 observations for each layer of vegetation for each territory.

RESULTS

Abundance.—Based on our observations during 1976–1978 (Confer and Knapp 1979), we were fairly optimistic about the future abundance of Golden-winged Warblers in Tompkins County. Observations during the summer of 1979 and information that has only recently become available now lead us to suspect a greater rate of decline of Golden-winged Warblers. During the summer of 1979, we observed only 2 territorial male Golden-winged Warblers where we found 4–8 males in each of the preceding 2 yr. In Broome County, New York, which is immediately south of Tompkins County, a banding station with permanent net locations banded 11 Golden-winged and 3 Blue-winged warblers from 1961 to 1968 but banded 2 Golden-winged and 14 Blue-winged warblers from 1976 to 1979 (H. Marsi, pers. comm.). From another location in Broome County the field records of other observers indicate a change from common Golden-winged/rare Blue-winged warbler to rare Golden-winged/common Blue-winged warbler during the 1970's (J. and A. Baldwin, pers. comm.). The Golden-winged Warbler is declining in this area of New York just as Gill (1980) has demonstrated for many other areas of eastern United States.

Habitat.—Golden-winged and Blue-winged warblers usually nest in loose aggregations or colonies that in our experience have up to 10 pairs. Most of the area of a colony is at the same stage of succession. One such colony, Varna or South Monkey Run, in the Ithaca, New York area has been censused periodically from 1950 to 1978. Censuses of this colony show the continual increase in the proportion of Blue-winged Warblers from the 1950's up to today (Short 1962, Ficken and Ficken 1968, Confer and Knapp 1979). Golden-winged Warblers seem to have disappeared from this colony, with no residents in 1978 and only one Golden-winged out of 29 known

TABLE 1. The mean value and variance for herbs, shrubs, and trees for 16 Blue-winged Warbler and 8 Golden-winged Warbler territories in Tompkins County, New York.

Vegetation type	Blue-winged		Golden-winged	
	\bar{x}	s^2	\bar{x}	s^2
Herbs	2.09	0.107	2.18	0.119
Shrubs	1.46	0.170	1.36	0.256
Trees	0.99	0.509	0.38	0.021

resident individuals from 1976 to 1978 (Confer and Knapp 1979). These data by themselves are compatible with two hypotheses: Blue-winged Warblers eliminate Golden-winged Warblers, because the former are better competitors; or Blue-winged Warblers eliminate Golden-winged Warblers by genetic introgression. Other information from Tompkins County, however, suggests that there are colony to colony differences in the ratio of these two species and that competition or genetic assimilation are inadequate explanations for site-specific differences in the ratio of these two species. We found 16 different resident Golden-winged Warblers, which comprised 18% of the censused Blue-winged Warblers, Golden-winged Warblers, and their hybrids from 1976 to 1978 in Tompkins County, excluding the Varna colony. This distribution is significantly different from random only at the 90% confidence level (Chi-square 2×3 value is 4.71). The observation suggests that characteristics of specific colony sites may influence the proportion of these two species.

The Varna site has not been altered by man during the last three decades, and during this time succession has produced a forest canopy over much of the area. Observations like this during 1977 led us to hypothesize that Golden-winged Warblers in Tompkins County do not nest in habitat that has reached older stages of succession. Consequently, we measured the density of herbs, shrubs, and trees in the territories of 8 Golden-winged and 16 Blue-winged warblers that we located in 1978. Table 1 shows that the herb and shrub cover for the territories of the two species are indistinguishable by our methods. The values for tree cover differ in two respects, however. The mean tree value for the 8 Golden-winged Warbler territories is less than half as large as the mean tree value for the 16 Blue-winged Warbler territories. The variances for the tree values differ by even more, so that the Golden-winged Warbler value is less than 5% as large as the Blue-winged Warbler value. Both of these differences have important biological implications.

For the Golden-winged Warbler the mean tree value was only 0.38. Because an unbroken forest canopy would have a value of 3.0 and a pure grassland would have a value of 0.0, the values for the Golden-winged Warbler territories indicate habitat with few trees, although sometimes there was moderate tree growth along the perimeter. In our 3 yr of observation, all but one Golden-winged Warbler territory were located in an early stage of secondary succession in which tree-sized vegetation was just appearing. The one exceptional territory was in a forest clearing created by a seepage area where soil moisture prevented tree growth. Wetness, however, was not a requisite for Golden-winged Warbler territories, because some of the territories were on dry, well-drained slopes. For the Blue-winged Warbler the mean tree value of 0.99 is indicative of areas with a considerable amount of tree growth. The mean values for herbs, shrubs, and trees were tested for statistical differences using a discriminant analysis that standardizes each variance to unity. After standardization of the variances, the univariate F -ratio ($df = 1,22$) for the between-

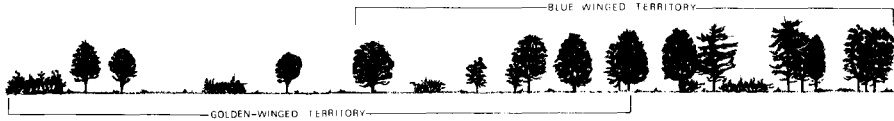


FIG. 1. A 570-m transect through two real territories showing typical vegetation cover. The horizontal scale is reduced twice as much as the vertical scale. A few Blue-winged Warbler territories had fewer trees than this Golden-winged Warbler territory, but no Golden-winged Warbler used areas as densely wooded as this Blue-winged Warbler territory.

species tree value was 5.89, which is significantly different at the 95% confidence level. The values for herbs and shrubs were not significantly different.

The difference in the mean values for trees may not be as significant biologically as the difference in the range of tree values for territories chosen by Blue-winged and Golden-winged warblers. For the Golden-winged Warblers the range was only 0.15–0.60. In contrast, the range for Blue-winged Warblers was 0.10–2.70. This includes the kind of habitat chosen by Golden-winged Warblers but also includes territories with a nearly unbroken forest canopy, which Golden-winged Warblers do not use. The variances for the tree values differ by a multiple of 23. Bartlett's test for nonhomogeneity of variances yields a corrected Chi-square value of 13.45, which is highly significant. These data show that in Tompkins County, Blue-winged Warblers are relative habitat generalists, while Golden-winged Warblers are relative habitat specialists. In our experiences in Tompkins County, Golden-winged Warblers nest almost exclusively in areas that are about 10–30 yr into secondary succession. Blue-winged Warblers can nest in active pasture land with low levels of grazing and a forest edge and also in areas perhaps 60–70 yr into secondary succession. Consequently, much less land is potentially suitable for the Golden-winged Warbler than for the Blue-winged Warbler.

Another attribute of the vegetative structure of Golden-winged and Blue-winged warbler territories is suggested by Fig. 1. We have located more than 60 territories in 3 yr of observation, and in all cases the vegetation of these territories was composed of patches of plants. Figure 1 shows a transect through two, real, overlapping territories, with the position of the plants based on real measurements and the horizontal scale reduced twice as much as the vertical scale. The horizon has been foreshortened so that trees would appear on the line. The same Golden-winged Warbler male utilized the area with fewer trees for two successive years, while the same Blue-winged Warbler female with a different male Blue-winged Warbler utilized the same area for two consecutive years. The distribution of herbs and shrubs is clumped, as suggested by the illustration. The trees are less clumped than the herbs and shrubs but still do not appear to be randomly arranged. In Tompkins County, only abandoned farmland, either cropland or pasture, produces habitat suitable for both Blue-winged and Golden-winged warblers. Succession on clearcuts in central New York does not produce patches of vegetation. The accumulation of dormant seeds in the forest floor rapidly produces dense growth of saplings after clearcutting, which is not suitable habitat for these warblers. Severe forest fires might have produced suitable patchy habitat in the past, but such fires in eastern deciduous forests are now rare.

Furthermore, it is our experience that territories are almost always located in large tracts of suitable habitat of 10–50 ha, although the territories occupy only part of

the entire tract. We found only one territory, the forementioned Golden-winged Warbler territory in a forest clearing, that was located in a small, isolated area. There are many small areas that appear suitable in Tompkins County, but they are not used. Thus, the tendency for several birds to nest in loose aggregations presents an additional habitat requirement for large tracts of abandoned cropland or pastureland.

Human land use.—The preceding suggests that the current breeding sites of Golden-winged Warblers in New York are restricted to recently abandoned farmland. The following suggests that the historical rise and decline of the abundance of Golden-winged Warblers in Tompkins County is paralleled by the rise and decline in the local abundance of this kind of habitat.

We have examined an incomplete collection of the unpublished field notes for 1900–1917 of H. D. Reed and of A. A. Allen, which is in the Cornell Archival Collection. The extensive records of these active observers did not include any note about the presence of Golden-winged Warblers in Tompkins County during this time. By 1927 the manual prepared by A. A. Allen for his ornithology course listed the Golden-winged Warbler as irregular in the area in and around Tompkins County. By 1937 the weekly compilation of reports by several observers assembled by A. A. Allen showed that the Golden-winged Warbler was reported frequently (Temple and Temple 1976).

Agricultural settlements by Europeans did not begin in Tompkins County until General Sullivan virtually eliminated the local Indians by his war of destruction just before the 19th century. Farming expanded rapidly thereafter, and by 1880 73% of Tompkins County was improved farmland (Caslick 1975). From then on, there has been a continual abandonment of farmland in and around Tompkins County. Caslick (1975) reported that by 1938 only 53% of Tompkins County was in active agriculture. About 24,000 ha of abandoned farmland began the process of secondary succession in Tompkins County from 1880 to 1938. Thus, the Golden-winged Warbler arrived and became well established during the time that about 20% of the land in Tompkins County ceased being farmed.

For more recent times Caslick (1975) has determined the proportion of Tompkins County land covered by various densities of woody vegetation. From 1954 to 1968 the proportion of land with more than 2% but less than 50% woody vegetation decreased from 17 to 14%. This represents a decrease in the kind of habitat that might be suitable for both Golden-winged and Blue-winged warblers. On the other hand, Caslick found that the area with more than 50% but less than a complete canopy tripled from 3 to 9% during the same time. This represents an increase in the kind of habitat that might be suitable for Blue-winged Warblers but would have too many trees for Golden-winged Warblers. Thus, from 1954 to 1968 the sum of the two vegetation categories suitable for Blue-winged Warblers increased, while the one category suitable for Golden-winged Warblers decreased.

The Golden-winged Warbler declined in Tompkins County from 1955 to 1965, according to the analyses of A. A. Allen's weekly reports by Temple and Temple (1975). During this same period, Temple and Temple found that Blue-winged Warblers showed a major increase in their abundance. The change in abundance of both these species is consistent with the change in amount of land that could provide suitable habitat for each. In view of our preceding observations that the Golden-winged Warbler is a habitat specialist and that the Blue-winged Warbler is a habitat generalist, we suspect that these events have some causal relation.

DISCUSSION

The initial stages of the abandonment of farmland throughout the eastern United States probably provided the early succession habitat that was essential for the range expansion of Golden-winged Warblers. Today in some parts of eastern United States, practically all land is either completely reforested, in active agriculture, or under suburban and urban development. In such areas, where there are few if any large tracts of recently abandoned farmland, there is probably little habitat suitable for Golden-winged Warblers. This, by itself, could account for the present decline of Golden-winged Warblers throughout much of their former range (Gill 1980).

Even if the change in habitat is partially responsible for the decrease in Golden-winged Warblers, the data for Tompkins County are still puzzling. Temple and Temple (1975) reported about an 80% decrease in the frequency with which Golden-winged Warblers were reported, while Caslick (1975) reported less than a 20% decrease in the vegetation category that included habitat suitable for Golden-winged Warblers during the same period. The decrease in habitat that actually was suitable for Golden-winged Warblers cannot be determined from Caslick's analyses, yet it seems unlikely, even if feasible, that a 20% decrease in the vegetation category with potentially suitable habitat for Golden-winged Warblers would account for their 80% decrease. Golden-winged Warblers are decreasing in Tompkins County while there is still some habitat that appears suitable and while a congener, the Blue-winged Warbler, is rapidly increasing. The congener was allopatric until clearing the climax forests provided routes for the expansion of Blue-winged Warblers. We suggest that no single, simple explanation accounts for the observations in Tompkins County. Probably habitat loss and some factor associated with the recent sympatry with the Blue-winged Warbler combine to account for the rapid decrease in Golden-winged Warblers. Possibly this interaction of factors was the cause of the widespread loss of range in other areas in the past.

This discussion presents as many ideas that need documentation as it presents documentations of ideas. At this stage in the development of our understanding of the ecology of Golden-winged and Blue-winged warblers, it is instructive to recall the interpretation provided by more detailed studies of similar situations. We find the analogy between Golden-winged and Blue-winged warblers and the Kirtland's Warbler (*Dendroica kirtlandii*) to be strikingly similar (Mayfield 1960). Like the Kirtland's Warbler, the Golden-winged Warbler, at least in central New York, uses only a very specific kind of habitat, and the abundance of this habitat, like that of the Kirtland's Warbler, is highly influenced by man's activities. For both species, it seems that once man's use of land increased the amount of suitable habitat, whereas now his use is decreasing the amount of suitable habitat. Furthermore, it seems unlikely that man's future use of land will produce great quantities of large parcels of abandoned farmland with patches of herbs, shrubs, and trees. It seems inevitable that land use alone will result in a continuation of the loss of range for Golden-winged Warblers. Additionally, the Golden-winged Warbler may very well be highly adversely influenced by a rapidly expanding congener. To stretch our analogy to the Kirtland's Warbler one step further, the possible negative biological interaction between the Golden-winged Warbler and the Blue-winged Warbler is similar to the negative biological interaction between the Kirtland's Warbler and the Brown-headed Cowbird (*Molothrus ater*). The long-term maintenance of the Golden-winged Warbler population, as with the Kirtland's Warbler, may require both

habitat manipulation and localized elimination of a species with a negative biological interaction.

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