

CHAPTER ONE

Dynamic Distributions and Population Declines of Golden-winged Warblers*

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Abstract. Golden-winged Warblers (*Vermivora chrysoptera*) are among the most vulnerable and have one of the most steeply declining populations of North American songbirds, with an estimated breeding population in 2010 of 383,000 adults. The breeding distribution of Golden-winged Warblers has been highly dynamic, expanding and then contracting over the past 150 years in response to regional habitat changes, interactions with closely related Blue-winged Warblers (*V. cyanoptera*), and possibly climate change. To delineate the present-day breeding distribution and to identify population concentrations that could serve as conservation focus areas, we compiled survey data collected during 2000–2006 in 21 states and three Canadian provinces as part of the Golden-winged Warbler Atlas Project (GOWAP), supplemented by data from state and provincial Breeding Bird Atlas projects and more recent observations posted in eBird. Based on >8,000 GOWAP surveys for Golden-winged and Blue-winged Warblers and their hybrids, we also mapped occurrence of phenotypically pure and mixed populations in a roughly 0.5-min latitude–longitude grid across the two species' breeding distributions. Hybrids and mixed populations of Golden-winged and Blue-winged Warblers occurred in a relatively

narrow zone across Minnesota, Wisconsin, Michigan, southern Ontario, and northern New York. Phenotypically pure Golden-winged Warbler populations occurred north of the hybrid zone. The region is defined for conservation planning as the *Great Lakes breeding-distribution segment*, but the future of populations in the Great Lakes states and Canada where 90% of the species currently breeds remains highly uncertain because of continued northward expansion of Blue-winged Warblers and the threat of hybridization. A second, now-disjunct range of Golden-winged Warbler populations occurs in the Appalachian Mountains (*Appalachian Mountains breeding-distribution segment*) from southeastern New York to northern Georgia, where they are surrounded at lower elevations by Blue-winged Warbler populations. Concentrations of Golden-winged Warblers persist in the Allegheny Mountains region of West Virginia, the Cumberland Mountains of Tennessee, the Blue Ridge Mountains of western North Carolina, the Allegheny Plateau and Pocono Mountains of Pennsylvania, and the Hudson Highlands of southern New York. High-elevation Appalachian populations have escaped contact with Blue-winged Warblers until recently and represent potentially important refugia for conservation

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and management. In the 44-year period from 1966 to 2010, the total breeding population of Golden-winged Warblers declined by 66% (−2.3% per year; latest North American Breeding Bird Survey data), with much steeper declines in the Appalachian Mountains Bird Conservation Region (BCR 28; −8.3% per year, 98% overall decline). Despite increasing populations in the northwestern part of the breeding distribution (Minnesota, Manitoba), total population estimates continued to decline by 18% in the 8-year period between 1994 and 2002. If these trends persist, our population projection predicts a further decline to ~37,000 individuals by 2100. In addition, based on historical records and standardized surveys across the nonbreeding distribution, we identified

three regions of nonbreeding concentration: mid-elevations and Caribbean slopes from Guatemala and Belize to northwestern Nicaragua, middle elevations (both Caribbean and Pacific slopes) in Costa Rica and western Panama, and an arc of the northern Andes from central Colombia to northern Venezuela. The nonbreeding distribution may be shifting northwest, paralleling shifts in the breeding distribution. Future conservation efforts for Golden-winged Warblers need to include close monitoring of dynamic regional populations and of phenotypic and genetic distributional shifts.

Key Words: abundance, Blue-winged Warbler, conservation, hybridization, Neotropical migrants, population trends.

Over the last 150 years, the breeding distribution of Golden-winged Warblers (*Vermivora chrysoptera*) in North America has changed dramatically, and the species has experienced one of the steepest population declines of any forest songbird over the past four decades (Sauer et al. 2012). The troubling trends have led to the Golden-winged Warbler being designated as a species of high conservation concern by Partners in Flight (Rich et al. 2004, Berlanga et al. 2010), the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2008), and the International Union for the Conservation of Nature Red List: Near Threatened (BirdLife International 2012). Golden-winged Warblers have also been petitioned to be listed under protection of the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2011) and are designated as Threatened in Canada (COSEWIC 2011).

Golden-winged Warblers interbreed with Blue-winged Warblers (*V. cyanoptera*) and produce viable offspring (Parkes 1951, Ficken and Ficken 1968, Gill 1980, Confer 2005). Hybridization and apparent competitive interactions between these species have contributed to the overall population declines of both species (Buehler et al. 2007). Developing effective conservation strategies requires an understanding of limiting factors specific to Golden-winged Warblers, and how limiting factors may be affected by presence of Blue-winged Warblers and hybrids. Breeding distributions of these two species are highly dynamic and shifting, and understanding where

hybridization is currently occurring is an important first step in developing effective conservation strategies.

The nonbreeding season is the longest portion of the annual cycle and lasts up to seven months, but until recently little was known about the ecology and conservation status of Golden-winged Warblers during migration or at nonbreeding sites (Chandler and King 2011). Lack of information away from the breeding grounds has hindered conservation efforts because it has not been possible to identify nonbreeding concentration areas or high-quality habitats.

Herein, we summarize the current distribution and status of Golden-winged Warblers at their breeding and nonbreeding grounds. We describe historical data and recently documented changes in species distributions. We also consider the context of simultaneously shifting breeding distribution of Blue-winged Warblers, including present-day geographic areas of overlap and hybridization. Last, we summarize recent population trends, provide estimates of population size, and project future changes to regional populations of Golden-winged Warblers. Most of the earlier topics have been reviewed in part in various publications (Confer 1992, Buehler et al. 2007, Confer et al. 2011), but the synthesis presented here is the first comprehensive review of all current information relating to distribution and population status of Golden-winged Warblers. Our synthesis draws heavily on information compiled for

the Golden-winged Warbler Status Review and Conservation Plan (A. M. Roth et al., unpubl. plan), especially Chapter 1 of that document (D. A. Buehler et al. in A. M. Roth et al., unpubl. plan), including results of recent surveys, distribution modeling, extensive literature review, and expert opinion.

METHODS

Historical and Current Breeding Distribution

To examine changes in breeding distributions, we divided the last 140 years into three periods: the late 19th and early 20th Centuries representing historical distribution; the period of extensive change during the 20th Century associated with forest cutting, clearing for agriculture, and subsequent farm-field abandonment up to about 1980 (Confer et al. 2011); and the most recent period of breeding-distribution contraction during the last two decades (Buehler et al. in A. M. Roth et al., unpubl. plan). We base our inference about distribution during the 19th and early 20th Centuries on narrative accounts, whereas changes during the mid-20th Century are better supported by empirical evidence and (since 1966) by the North American Breeding Bird Survey (BBS). Numerous state and provincial breeding-bird atlas projects during the 1980s also helped define the late 20th-Century breeding distribution, as described by the American Ornithologists' Union (1983) and presented in Confer (1992). Only the 21st Century breeding-distribution contraction is well documented by systematic surveys.

In 1999, S. B. Swarthout et al. (unpubl. report) launched the Golden-winged Warbler Atlas Project (GOWAP) to map the current breeding distribution and to understand the geographic extent of present-day interactions between Golden-winged and Blue-winged Warblers. The GOWAP engaged volunteer birders and professional biologists to survey known and potential breeding sites from 1999 to 2006 using three standardized protocols (S. B. Swarthout et al., unpubl. report). More than 200 volunteers and collaborators in 21 states and three provinces conducted GOWAP population surveys to determine locations and numbers of breeding birds, population status, and general habitat characteristics at survey locations, using a combination of passive listening, searching, and standardized playback

of vocalizations of Golden-winged Warblers. The GOWAP also produced an atlas of phenotypic Golden-winged and Blue-winged Warblers and their hybrids, based on >7,200 point counts in 442 DeLorme Atlas (DeLorme Atlas Gazetteers 2014) pages in 17 states and two Canadian provinces from 1999 to 2005. Each page represents a rectangular grid cell, which varied in size across states, but averaged ~4,300 km² across most of the Golden-winged and Blue-winged Warbler breeding distributions. Observers selected 20 survey points by locating accessible patches of apparent Golden-winged Warbler habitat distributed across each DeLorme page, with five points in each quarter-page section. Each point count consisted of a 10-min standardized playback sequence. Observers visually confirmed the phenotype of each warbler detected using Type I and Type II songs of Golden-winged and Blue-winged Warblers, because both species sing the same Type II song and can sing each other's Type I song (Confer 1992). Complete description of the GOWAP survey protocols and detailed state-level results and maps can be found in S. B. Swarthout et al. (unpubl. report).

To account for the changing breeding distribution in the years since the GOWAP, we compiled presence and absence records obtained from other ongoing Golden-winged Warbler monitoring programs, locations of recent tissue sampling and other research by Golden-winged Warbler Working Group collaborators, and records in the rapidly increasing citizen science database, eBird (Sullivan et al. 2009, 2014). In addition, second-generation breeding-bird atlas projects completed by many states and Ontario in the past decade have helped document recent breeding distribution; results of the GOWAP will serve as a baseline to index breeding distribution and population size change. Using all of these data sources we define two *breeding-distribution segments* (see Results and Discussion section) that have been adopted as broad conservation regions by D. A. Buehler et al. (in A. M. Roth et al., unpubl. plan), and refer to *populations* below as clusters of breeding individuals dispersed, often patchily, within the two breeding-distribution segments.

Estimating Population Size and Trends

Population trends reported in this manuscript are based on the analysis of BBS data from 1966 to

2010 (Sauer et al. 2012). We present distribution-wide and regional population estimates for Golden-winged Warblers based on the Partners in Flight method described by Rosenberg and Blancher (2005) and reviewed by Thogmartin et al. (2006), using BBS annual indices of relative abundance (Sauer et al. 2011) for the decade from 1998 to 2007 (Blancher et al. 2013, Partners in Flight Science Committee 2013). We then compared population estimates with similar estimates using BBS relative abundance for the decade from 1990 to 1999 (Rich et al. 2004). Trends from BBS are now estimated with hierarchical Bayesian count models rather than estimating equations (Sauer and Link 2011, Sauer et al. 2012), and we calculated population size estimates from indices of abundance resulting from Bayesian count models and projected population size estimates to the year 2100.

Nonbreeding Distribution and Survey Methods

Our assessment of the current nonbreeding distribution and migration routes was based on a combination of data sources, including a distribution model based on historical records, an occupancy model based on recent survey data from part of the nonbreeding distribution, specimen records from natural history collections, and additional records in eBird. Museum specimen records and other observational records contributed through Priority Migrant eBird (Barker Swarthout et al. 2008) formed the basis for a preliminary predictive model of the potential nonbreeding distribution of Golden-winged Warblers in the Neotropics (M. Moreno, unpubl. data) using MAXENT (Phillips et al. 2006). In 2008, the Golden-winged Warbler Working Group established survey sites in Honduras, Nicaragua, Costa Rica, Panama, Venezuela, and Colombia using a 100-km² grid and selecting locations in grid cells with ≥ 0.08 probability of occurrence for Golden-winged Warblers, based on a preliminary occupancy model (M. Moreno, unpubl. data). The resulting survey was implemented during four field seasons (December to early March of 2009–2012), with 4,856 surveys conducted at 1,499 locations. At each location, trained surveyors conducted 20-min point counts up to three times per field season. Survey effort varied greatly among countries and among field seasons. Venezuela received the least effort, with only 35 locations visited (three times each) during the 2009–2010 field

season. Honduras was only surveyed during the 2010–2011 (47 locations visited three times each) and 2011–2012 field seasons (126 locations visited three times each).

Surveys consisted of a 10-min passive observation period followed by 10-min of broadcasting vocalizations of Golden-winged Warblers. In addition, we divided observation periods during the entire 20-min survey into eight, 2.5-min intervals to estimate probability of occurrence while accounting for variation in probability of detection among observers in each country. The possibility of geographic segregation of male and female Golden-winged Warblers, and the potential for differences in detection probability between sexes, motivated us to model occurrence probability separately for males and females. For each sex, we developed a set of competing models including linear and quadratic terms for effects of precipitation, temperature, elevation, latitude, and longitude. We included linear terms to represent directional changes in resource use and quadratic terms to represent nonlinear trends in resource use. We produced distribution maps by model-averaging predictions of occurrence probability from each model. We fit models using methods described by Chandler et al. (2011) and implemented in the R package *unmarked* (Fiske and Chandler 2011). Subsequent to this analysis, we conducted 371 additional surveys in Panama in January 2015, using the same protocol, except with a 5-min broadcast of Golden-winged Warbler vocalizations.

To delineate the nonbreeding distribution of Golden-winged Warblers, we combined the results from the surveys and models described earlier with additional records in eBird, and we reviewed published literature for each country with records of Golden-winged Warblers during the nonbreeding season. Although Golden-winged Warblers are not breeding throughout most of the year, the nonbreeding season is defined here and throughout this volume as the period when most Golden-winged Warblers maintain a territory in Central and South America (Chandler 2011). Herein, we define the nonbreeding distribution as that used by Golden-winged Warblers during the nonbreeding season when they are resident in Central and South America, excluding areas only used during migration or by transients. Golden-winged Warblers have been observed in Central and South America from mid-September through

early April, but to eliminate including possible transients or migrants we only considered records from 1 November to 15 March to delineate the nonbreeding distribution. Between these dates, most individuals within the nonbreeding distribution maintain a territory (Chandler 2011), and we considered observations of Golden-winged Warblers outside the breeding distribution and outside of this period to be of transients or migrants. In total, we compiled and mapped 3,533 unique georeferenced occurrence records of Golden-winged Warblers during the nonbreeding season (as defined earlier) south of the U.S. Based on this information, we provide our best qualitative assessment of relative abundance and concentration of Golden-winged Warblers within their nonbreeding distribution. We also reviewed records, mostly from eBird, from the spring and fall migration seasons and provide a qualitative assessment of migration timing, routes, and potential stopover areas for Golden-winged Warblers.

RESULTS AND DISCUSSION

Breeding Distribution (1850–1900)

Due to a paucity of records prior to 1850, the pre-European settlement of North America breeding distribution of Golden-winged Warblers remains largely speculative. Most published maps of the historical breeding distribution may underestimate its eastern and northern extent and overestimate its southern extent, and errors have been carried forward to estimates of recent distribution (Confer 1992, Confer et al. 2011). Some records from the late 19th and early 20th Centuries already suggested presence in certain portions of the northeastern U.S., suggesting that even the historical breeding distribution of Golden-winged Warblers may have been dynamic.

In the Upper Midwest, Golden-winged Warbler breeding distribution during the late 1800s and early 1900s likely extended from southwestern Ontario (Speirs 1985, McCracken 1994) across southern Michigan (Berger 1958) and Wisconsin (Robbins 1991) to at least southeastern and central Minnesota (Roberts 1932), and south to northeastern Illinois, northern Indiana, and northern Ohio (Figure 1.1). Barrows (1912) did not report Golden-winged Warblers from the northern part of the Lower Peninsula or from the Upper

Peninsula of Michigan. Although sometimes described as a recent breeding bird in Manitoba (Confer et al. 2011), Golden-winged Warblers were first observed near Winnipeg in 1887 (Batchelder 1890). Five additional sightings from 1905 to 1928 and a small breeding population discovered east of Winnipeg in 1932 (Taylor 2003) suggest that Golden-winged Warblers may have been more widely distributed at the northern edge of their historical breeding distribution than previously reported (Confer 1992; Figure 1.1).

Farther south, Mumford and Keller (1984) claimed that almost every large swamp in northern Indiana had a pair of nesting Golden-winged Warblers during the late 1800s, and they were described as locally common in the early 1900s in northwestern Ohio but rare elsewhere in the state (Peterjohn and Rice 1991). South of our mapped historical breeding distribution (Figure 1.1), Roberts (1932) claimed that Golden-winged Warblers formerly bred south to southern Iowa, although Kent and Dinsmore (1996) reported only three nest records in Iowa, one in southeast (1888) and two in central Iowa (1898). In Missouri, there is one confirmed 1890 nesting record in the southeast and unconfirmed reports in 1884 from the northeast (Robbins and Easterla 1992). In the late 1800s, Ridgway (1889) reported Golden-winged Warblers breeding in southern Illinois, and Butler (1897) reported breeding in the Mississippi River bottoms, but it seems unlikely that Golden-winged Warblers bred regularly in the tallgrass prairie portions of Iowa, Illinois, and Indiana (Graber and Graber 1963). It is unclear, therefore, whether the historical breeding distribution was ever continuous between populations in the Great Lakes region and populations farther east in the Appalachian Mountains region and New England.

Golden-winged Warblers were first documented in southeastern New York in 1867, but breeding was not confirmed until 1897 (Andrle and Carroll 1988). By the early 1900s, Eaton (1914) described the species as common on western and northern Long Island and in the lower Hudson Valley, uncommon or local on southern and eastern Long Island and the central Hudson and Delaware valleys, and extremely rare in central and western New York. Golden-winged Warblers are widely thought to have expanded their distribution into southern New England during the late 1800s and early 1900s (Veit and Peterson 1993). Brewster (1906) first recorded Golden-winged Warblers

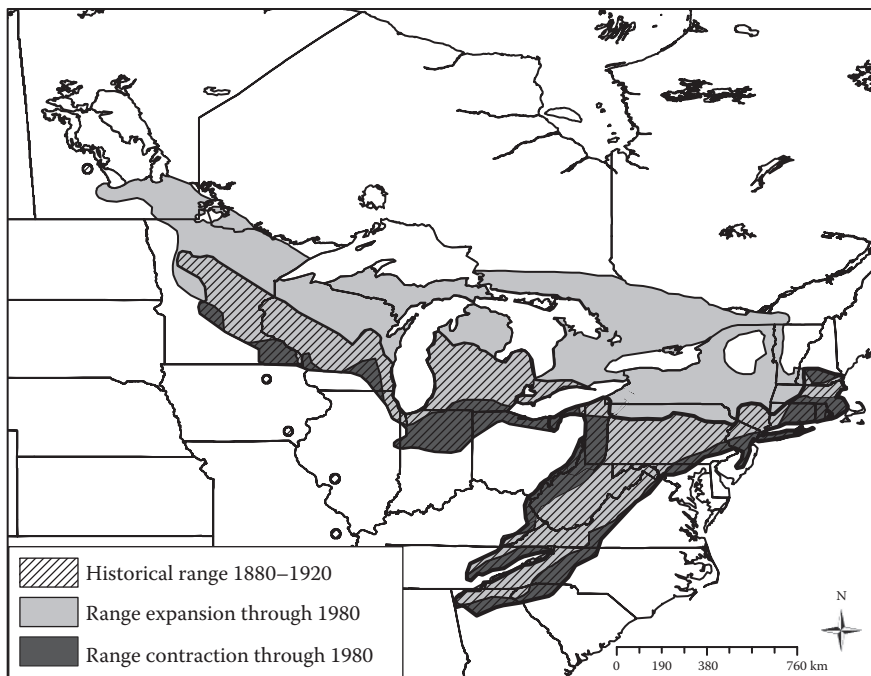


Figure 1.1. Golden-winged Warbler breeding distribution from ~1880 through 1980. Estimated distribution (hash marks) for 1880–1920 was derived largely from state ornithological accounts. Mid-1900s expansion in the north is shown in gray and contraction in the south and east in dark gray. Open circles represent additional early historical records that have previously been included in breeding-distribution maps, but which we regard as questionable (see text).

breeding in eastern Massachusetts in 1874, but J. A. Allen in Bent (1953) already considered the species to be common there by the 1860s. Golden-winged Warblers were first reported in Vermont in 1893 (Stearns and Coues 1893), and in southeastern New Hampshire they occurred as far north and west as Manchester and Concord by 1930 (Foss 1994). The first Connecticut breeding record was in 1875 near the Massachusetts border, followed by observations during the late 1800s of populations scattered throughout northern and southern Connecticut (Gill 1980, Bevier 1994), and in northeastern Rhode Island.

Farther south, the earliest records suggest that Golden-winged Warblers occurred historically throughout most of their current breeding distribution in the Appalachian Mountains region, although some expansion of the breeding distribution may have occurred prior to 1920. During the late 1860s, Golden-winged Warblers were reported as a rare to uncommon breeder throughout Pennsylvania, with most birds concentrated in western Pennsylvania (McWilliams and Brauning 2000). The species was first documented breeding in Maryland in 1895, but

by the early 1900s was reported as an increasingly common breeder in western Maryland (Eifrig 1904, Robbins and Blom 1996). In the central and southern Appalachian Mountains, breeding populations were thought to be limited to scattered summits higher than 850 m prior to European settlement (Mengel 1965). Historical status in Virginia is unclear, but the first description of a nest of a Golden-winged Warbler came from Greenbrier County in 1837 (Bent 1953). Golden-winged Warblers were considered rare by early ornithologists in Tennessee in the late 1800s, occurring in the southern Blue Ridge Mountains and eastern Cumberland Escarpment (Nicholson 1997). Brewster (1885, 1886) reported Golden-winged Warblers to be abundant in the second-growth forests and open oak (*Quercus* spp.) woodlands of western North Carolina at elevations between 600 and 1,200 m. The species was formerly considered a fairly common summer resident in northern Georgia (Burleigh 1958), and was reported from three counties in the mountains of northwestern South Carolina in the late 1800s (Loomis 1890, 1891; Sprunt and Chamberlain 1949; Post and Gauthreaux 1989).

20th-Century Breeding-Distribution Changes (1900–1980)

Golden-winged Warblers experienced a substantial breeding-distribution expansion during the early and mid-1900s in response to extensive forest clearing in the Upper Midwest and a period of extensive farm abandonment in the northeastern U.S. (Figure 1.1). By 1980, however, Golden-winged Warblers had begun to disappear from many portions of their historical and expanded breeding distribution, especially in southern parts of the Upper Midwest, in New England, and at lower elevations in the Appalachian Mountains.

Golden-winged Warblers were rediscovered near Riding Mountain National Park in western Manitoba in 1967 (Artuso 2008) and confirmed as breeding elsewhere in Manitoba in 1978 (Koes 2003). In Minnesota, the species expanded its breeding distribution to the Canadian border sometime after 1930 (Janssen 1987), and in Wisconsin expanded throughout the northern portion of the state but receded from areas where Golden-winged Warblers bred historically in the south (Cutright et al. 2006). Golden-winged Warblers were reported from the Upper Peninsula of Michigan in 1921 (Wood 1951, Payne 2011), and by the mid-1980s bred throughout most of the Upper Peninsula and most of the Lower Peninsula, with the exception of the southern two tiers of counties (Brewer et al. 1991). In general, since 1950, there has been a marked shift in breeding distribution away from the developed southern portions of Minnesota, Wisconsin, and Michigan to the extensively forested, wetland shrub communities farther north (D. A. Buehler et al. in A. M. Roth et al., unpubl. plan). In Ontario, breeding populations of Golden-winged Warblers continued to expand northeastward in the 1930s, were considered fairly common throughout the Bruce Peninsula and northward to Sudbury by the 1970s (Speirs 1985, McCracken 1994), and were common in eastern Ontario by the 1980s (Peck and James 1983).

Breeding-season records of Golden-winged Warblers in northern Illinois continued through the 1980s (Bohlen 1989, Kleen et al. 2004; BBS data), but there are no contemporary records from southern Illinois (Robinson 1996). By the 1980s, Golden-winged Warblers were reported as very rare summer residents in northern Indiana, with

nesting records up until 1983 (J. Castrale, pers. comm.). Breeding populations of Golden-winged Warblers were probably already declining in Ohio by the late 1930s, and there were no confirmed breeding records in the 1980s (Peterjohn 1989, Peterjohn and Rice 1991) or more recently (P. Rodewald, pers. comm.).

In response to extensive farm abandonment, maximum abundance and breeding-distribution extent of Golden-winged Warblers peaked in the northeastern U.S. between 1930 and 1950 (Confer 1992). By 1950, the species was moderately abundant throughout central and western New York but had disappeared from Long Island and the Lower Hudson Valley (Andrle and Carroll 1988). Numbers continued to increase through the 1980s in the Eastern Ontario Plain, Indian River Lakes, and St. Lawrence Plains regions (Confer et al. 1991, McGowan and Corwin 2008). In the mid-1900s, Golden-winged Warblers persisted as rare and local breeders near the southern tip of Lake Champlain and the Connecticut River in Vermont (Laughlin and Kibbe 1985) and in the coastal lowlands of New Hampshire (Foss 1994). Golden-winged Warbler populations increased throughout eastern Massachusetts through the early 1900s (Veit and Peterson 1993). By the 1950s, most breeding records came from eastern Massachusetts (except Cape Cod and adjacent islands) or the Berkshires, where the species was still increasing in abundance (Bailey 1955). After the 1950s, the number of breeding Golden-winged Warblers declined in Massachusetts (Veit and Petersen 1993), with the last breeding populations documented in Essex and Berkshire counties (Petersen and Meservey 2003). Through the 1980s, the breeding distribution continued to shift northward in New York (Confer et al. 1991) and into portions of adjacent Quebec, where Golden-winged Warblers were first detected in 1957 (Gauthier and Aubry 1996).

In Pennsylvania, Golden-winged Warblers remained scarce at higher elevations in the mid-1950s, but bred throughout the Ridge and Valley Region; by 1980 they had expanded through northern Pennsylvania, but were absent at low elevations in the southwest and southeast parts of the state (Brauning 1992). By the mid-1980s, Golden-winged Warblers continued to breed in the mountains of western Maryland (Robbins and Blom 1996) and throughout most of southern and central West Virginia (Buckelew and Hall 1994).

Golden-winged Warblers likely expanded their breeding distribution in southeastern Kentucky and Tennessee following strip-mine reclamation and logging in the early 1900s; Stupka (1963) reported Golden-winged Warblers as fairly common at low and middle elevations in Great Smoky Mountains National Park into the 1950s, and they occurred along the eastern Cumberland Escarpment through the 1980s. A small population persisted through the 1980s in northern Georgia, but disappeared from South Carolina prior to 1980.

Recent Breeding-Distribution Changes and Current Breeding Distribution (1980 to Present)

The 1990s were a period of continued rapid change in breeding distribution and population status of Golden-winged Warblers, leading to their recognition as a species of high conservation concern, especially in the eastern parts of their breeding distribution (Rich et al. 2004, Buehler et al. 2007). Based on GOWAP surveys from 1999 to 2006 (S. B. Swarthout et al.,

unpubl. report), collaborative research and monitoring efforts of the Golden-winged Warbler Conservation Initiative, records and data from the BBS (1966–2012), state and provincial breeding bird atlases, and observations reported in eBird, we derived our estimate of the current (ca. 2013) breeding distribution of Golden-winged Warblers (Figure 1.2). The current distribution map was adopted for use in the Golden-winged Warbler Status Review and Conservation Plan (A. M. Roth et al., unpubl. plan). Golden-winged Warblers have been extirpated from Illinois, Indiana, and Ohio, and no longer breed consistently throughout central New York. Thus, Golden-winged Warblers now occur in two disjunct regions—a Great Lakes and an Appalachian Mountains breeding-distribution segment. The *Great Lakes breeding-distribution segment* extends from the eastern edge of Saskatchewan eastward to the Champlain Valley of northeastern New York and adjacent Vermont. The *Appalachian Mountains breeding-distribution segment* extends from northern Georgia and the Cumberland Mountains of Tennessee to southeastern New York and extreme northwestern

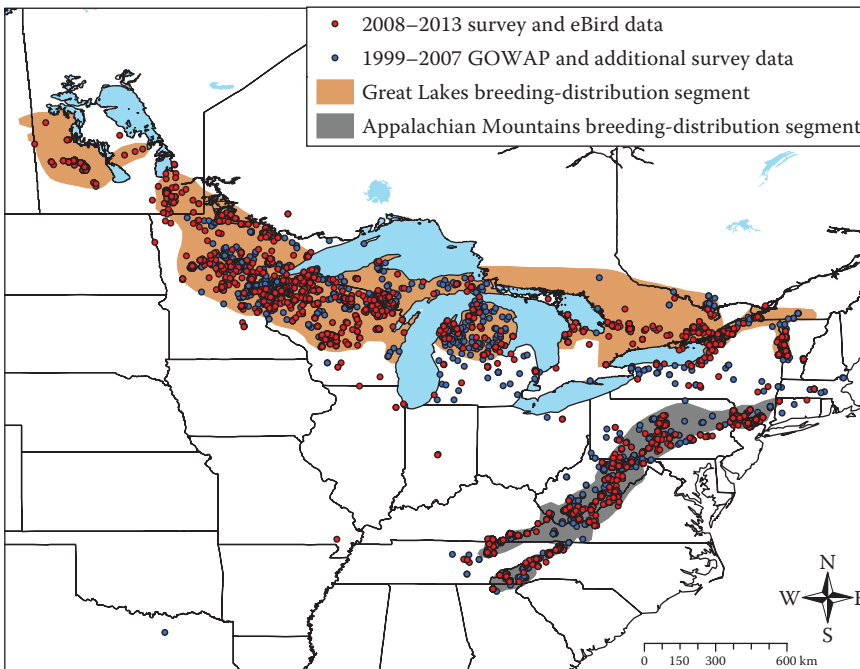


Figure 1.2. Current breeding distribution of Golden-winged Warblers in 2013, as determined by the Golden-winged Warbler Working Group based on all available survey and observational data. The Ontario Breeding Bird Atlas data are not shown on this map but were used to estimate current breeding distribution. Areas with only sporadic occurrence and areas without breeding records since 2008 were not included within the two breeding-distribution segments (shaded regions).

Connecticut (Figure 1.2). These two breeding-distribution segments are treated separately within the Golden-winged Warbler Conservation Plan (A. M. Roth et al., unpubl. plan) and are referred to throughout this volume.

The northward expansion of the Golden-winged Warbler breeding distribution has continued recently into northern New York, eastern and northwestern Ontario, southwestern Manitoba, and even farther west in Canada with one confirmed and several possible breeding records for Saskatchewan (Smith 1996). Monitoring efforts and sightings of Golden-winged Warblers have increased in recent years across Manitoba, with more than 395 territorial birds recorded in 2008 and 2009; observers believed there were >1,000 pairs in Manitoba in the late 2000s. It is unclear, however, whether the number of breeding Golden-winged Warblers in Manitoba is increasing, or whether local populations have only recently been adequately surveyed.

Golden-winged Warblers had virtually disappeared as a breeder by the 1990s from southern Minnesota (Janssen 1987) and southern Wisconsin (Cutright et al. 2006). Recent GOWAP surveys and eBird records show the highest concentrations in north-central and east-central Minnesota and adjacent northwestern Wisconsin. Smaller areas of concentration are located in the Black River State Forest area and in northeastern Wisconsin near the border with Michigan's Upper Peninsula (Figure 1.2). The most recent Michigan Breeding Bird Atlas (BBA) documented continued contraction of the breeding distribution of Golden-winged Warblers in southern Michigan (Payne 2011). The GOWAP surveys found Golden-winged Warblers largely restricted to the northwestern portions of Michigan's Lower Peninsula, and although Golden-winged Warblers have been recorded breeding throughout the Upper Peninsula (Payne 2011), few were detected during the GOWAP. None have been reported at Ottawa National Forest in the western part of the Upper Peninsula, in spite of recent surveys of apparently appropriate habitat (B. Bogaczyk, pers. comm.).

Except for a few sites near Long Point and the Niagara Escarpment, breeding Golden-winged Warblers have vanished from southwestern Ontario. The latest Ontario BBA (2001–2005) found that the recent breeding-distribution expansion had not continued beyond the Canadian

Shield region, and the breeding distribution in eastern Ontario had contracted by 27% since the 1980s (Cadman et al. 2007). Scattered breeding locations persist along the Ottawa River, on the Bruce Peninsula, and along the northern shore of Georgian Bay (but not Lake Superior), and a potentially new breeding location has been identified in far western Ontario in the Lake of the Woods area. The breeding distribution in Quebec also appears to have contracted since its peak in the 1980s (Gauthier and Aubry 1996), and was limited to the southwestern corner of the province and the area near Ottawa by 2002.

No breeding Golden-winged Warblers were found in Illinois, Indiana, or Ohio during the GOWAP or more recently. In New York, the largest concentration of Golden-winged Warblers still exists (ca. 2013) in the St. Lawrence Valley, but their breeding distribution is now contracting from the south and does not seem to have expanded farther to the north or east. A few breeding Golden-winged Warblers also persist in the Lake Champlain Valley on both the New York and Vermont sides. Breeding Golden-winged Warblers are now virtually absent from the Finger Lakes region; a few breeding individuals persisted along the south shore of Lake Ontario until about 2005 (McGowan and Corwin 2008), but subsequently this population has also become extirpated.

During the 1990s, Golden-winged Warblers disappeared as a breeding bird from the coastal plain of New Hampshire but continued to breed in the central Connecticut Valley near Hanover. Breeding Golden-winged Warblers have since disappeared from that region and may now be extirpated from New Hampshire (Suomala 2005). Similarly, there have been only four confirmed breeding records in Massachusetts since 1990, and breeding Golden-winged Warblers are now thought to be extirpated in that state. During the 1980s, Bevier (1994) reported confirmed breeding only from northwestern Connecticut but Golden-winged Warblers subsequently disappeared from most of these areas and were known to breed at only three locations by 2009. In Rhode Island, breeding Golden-winged Warblers are now extirpated and are only rarely observed during migration. Note that in this entire zone of recent breeding-distribution contraction, from southern Wisconsin through central New York to New England, reports persist as of 2013 of isolated individuals, including singing males,

but no evidence indicates that Golden-winged Warblers consistently breed south or east of the mapped boundary for the Great Lakes breeding-distribution segment (Figure 1.2).

The Appalachian Mountains breeding-distribution segment also has contracted significantly since 1990, and a major focus of the GOWAP was to clearly define its present-day southern boundary. In contrast to the Great Lakes region, Golden-winged Warblers in the Appalachian Mountains have not shifted their breeding distribution geographically through time, but rather have contracted their breeding distribution to refugia, often at higher elevations, as Blue-winged Warblers have expanded their breeding distribution into surrounding lower elevations. At the northern end of the Appalachian Mountains breeding distribution, a population of Golden-winged Warblers persists in the Hudson Highlands of southeastern New York, but the extent of this population's distribution has shrunk by more than 75% since the 1980s (McGowan and Corwin 2008). Golden-winged Warblers may now be restricted to a few sites in and around Sterling Forest State Park. In adjacent New Jersey, an estimated 80–90 Golden-winged Warbler pairs were present in the northwestern part of the state as recently as 2000–2002 (S. Petzinger, pers. comm.). By 2008, however, only a single male remained in the Delaware Water Gap-Kittatinny Ridge area, and the last small cluster of breeding individuals in the state persists in the New Jersey Highlands adjacent to Sterling Forest State Park in New York.

By the 1990s, breeding Golden-winged Warblers had disappeared throughout much of Pennsylvania with the exception of higher elevation sites above 600 m within the Valley and Ridge and Pocono regions, and in more forested landscapes of the mountainous Allegheny High Plateau (Brauning 1992). The GOWAP (1999–2006) and more recent surveys indicated that breeding Golden-winged Warblers remained common in these three, high-elevation regions. Populations in south-central Pennsylvania are contiguous with populations in western Maryland, where the species persists primarily in Garrett County (Ellison 2010), and in the Allegheny Mountains of northeastern West Virginia, which is currently the largest population in that state. In the Allegheny Mountains, breeding Golden-winged Warblers remain at elevations primarily between 850 and 915 m but are virtually absent above 1,200 m,

even in apparently suitable deciduous forest cover types (Canterbury 1997; Gill et al. 2001; P. Wood, pers. comm.; R. Bailey, pers. comm.). In other parts of West Virginia, the number of breeding Golden-winged Warblers has declined rapidly (Canterbury et al. 1993, Canterbury and Stover 1999); relatively large numbers persisted into the 1990s in the coalfields of southern and central West Virginia (McDowell, Wyoming, and Raleigh counties), almost entirely on reclaimed narrow strip benches ≥ 610 m in elevation, but these populations have nearly disappeared since 2003 (J. Larkin, pers. comm.). A similar pattern has occurred in southeastern Kentucky, where >50 Golden-winged Warbler breeding territories were studied on reclaimed mines as recently as 2004–2005, but breeding Golden-winged Warblers disappeared rapidly from most sites by 2009 (Patton et al. 2010).

Surveys of the historical Golden-winged Warbler breeding distribution in Virginia detected only 50 males and 6 females in 2006, primarily in Bath and Highland counties (Wilson et al. 2007). In Tennessee, >200 pairs continued to breed in the Cumberland Mountains and in several locales in the southern Blue Ridge Mountains in far northeastern Tennessee through the late 2000s. A few breeding pairs also remained at higher elevations on the Cumberland Plateau until about 2000 (Welton 2003). Across western North Carolina, Golden-winged Warblers remained through 2013 as a locally common summer resident at middle and high elevations (600–1,600 m), largely contiguous with the breeding distribution in Tennessee. In 2006, GOWAP surveys located ~ 100 breeding pairs in North Carolina, and more recent observations through 2013 have come from 13 western counties in that state (C. Smalling, pers. comm.; eBird records). In the mountains of northern Georgia, Golden-winged Warblers remained a rare summer resident through the late 1990s, but after five years (1999–2003) of surveying potential breeding areas on public and private lands within the historical Georgia breeding distribution, Klaus (2004) found <20 territorial males. A small population breeding in regenerating forest following clear-cutting within the Cherokee National Forest reported during the 1990s had disappeared (Klaus 1999), as did a breeding population previously reported from the adjacent Great Smoky Mountains National Park in Tennessee (Nicholson 1997).

Geographic Overlap and Hybridization with Blue-winged Warblers

Changes in the distribution and abundance of Golden-winged Warblers are widely believed to be, at least in part, the result of interactions with Blue-winged Warblers, its closely related sister species. A divergence of 3% (cytochrome B) to 4.5% (NDII) between the mtDNA of Golden-winged and Blue-winged Warblers (Gill 1997, Dabrowski et al. 2005) suggests that isolation of ancestral populations occurred one to two million years before present (BP). In the absence of a fossil record, Short (1963) speculated that the advance and retreat of glaciers during the Wisconsin Glacial Episode (12,000 years BP) led to isolation and left Golden-winged Warblers restricted to the southeastern coastal plain of North America and Blue-winged Warblers to west of the Mississippi Embayment, a water barrier stretching several hundred km from present-day Illinois to the Gulf of Mexico. Following warming climate and retreat of glaciers, breeding distributions of both species likely moved northward but remained isolated until after European settlement (Short 1963). Extensive forest clearing in the Great Lakes region and Appalachian Mountains during the late 1800s and early 1900s undoubtedly increased habitat abundance and distribution for both species in those regions.

As Golden-winged Warblers expanded their breeding distribution northward during the early and mid-20th Century, Blue-winged Warblers also expanded their breeding distribution northward and eastward. Where Blue-winged Warblers colonize areas occupied by Golden-winged Warblers, hybridization is frequent and Golden-winged Warblers have typically been extirpated within 50 years (Gill 1980); species replacement has occurred in the Great Lakes region east to New York and southern New England. Secondary contact has created a dynamic zone of overlap and hybridization that has moved steadily northward as the breeding distributions of the two species shifted (Gill 1980, Gill et al. 2001). In New York, the rate of movement of the hybrid zone was estimated at 3–6 km/year through the mid-20th Century (Confer and Larkin 1998). Blue-winged Warblers also expanded their breeding distribution eastward during the 20th Century, but because of steep elevational relief in the Appalachian Mountains, distributional overlap and interactions

with Golden-winged Warblers have been more complex. Remaining mostly at lower elevations, Blue-winged Warblers expanded their breeding distribution north and east along major river valleys and around mountain ridges, extending to central New York, southern New England, eastern Pennsylvania, and New Jersey in the north and to northern Alabama, northern Georgia, and southwestern North Carolina in the south. Blue-winged Warblers remained uncommon, however, on the eastern side of the Appalachian Mountains south of the Maryland Piedmont (Gill et al. 2001).

The GOWAP hybrid atlas surveys from 1999 to 2005 documented a relatively narrow zone of overlap and hybridization between Golden-winged and Blue-winged Warblers extending from central and northern New York west through southwestern Ontario, the middle Lower Peninsula of Michigan, and central Wisconsin, to east-central Minnesota (Figure 1.3). By 2005, the only large phenotypically pure Golden-winged Warbler populations appeared to exist north of this hybrid zone in northern Minnesota and Manitoba. The GOWAP assessment also indicated a second contact zone throughout the Appalachian Mountains, where breeding Golden-winged Warblers persisted, usually at high elevations, surrounded by areas dominated by breeding Blue-winged Warblers (Figure 1.3). Only 4% of the roughly 2,800 individuals detected as part of the GOWAP were phenotypic hybrids, observed in 95 grid cells throughout both zones of overlap. In an additional 80 grid cells, Golden-winged and Blue-winged Warblers were both observed, but no hybrids were detected, suggesting that hybrids are relatively rare even in zones of overlap.

Phenotypic Golden-winged Warbler populations in far northern Minnesota remain outside the expanding breeding distribution of Blue-winged Warblers (Shapiro et al. 2004), but Vallender et al. (2009) found Blue-winged Warbler mtDNA evidence of cryptic hybrids among the phenotypic Golden-winged Warblers in this region. Golden-winged Warblers in Manitoba and eastern Saskatchewan comprise possibly the only nonintrogressed Golden-winged Warbler population anywhere within their breeding distribution (Vallender et al. 2009). The discovery of a Brewster's Warbler (hybrid) in Manitoba in 2008 and the recent identification there of cryptic hybrids indicates that this population may currently be experiencing introgression

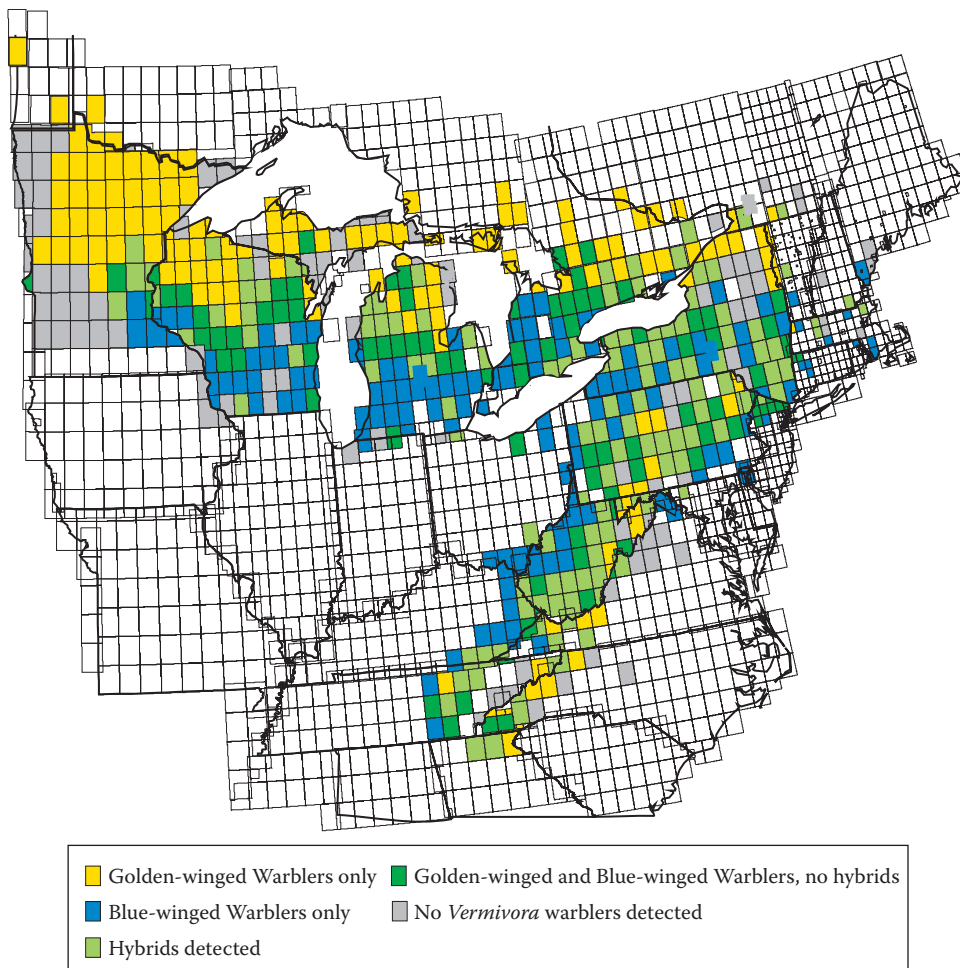


Figure 1.3. Distribution of phenotypic Golden-winged Warblers (GWWA), Blue-winged Warblers (BWWA), and zone of hybridization based on 1999–2005 data from the Golden-winged Warbler Atlas Project (S. B. Swarthout et al., unpubl. report). Each shaded grid cell represents a page from a DeLorme Atlas (DeLorme Atlas Gazetteers 2014) ~4,300 km² each.

(Vallender et al. 2009; Chapter 4, this volume), and that genetic monitoring of this population is warranted. Blue-winged Warblers or hybrids were detected during the GOWAP throughout central and eastern Wisconsin, leaving phenotypically pure Golden-winged Warblers only in the northwestern part of that state. Similarly, Blue-winged Warblers and hybrids were found throughout the Lower Peninsula of Michigan, interspersed with a few grid cells where only Golden-winged Warblers were detected. The GOWAP did not sample Ontario, but the second Ontario BBA indicated an expansion of the breeding distribution of Blue-winged Warblers throughout southwestern Ontario, replacing Golden-winged Warblers at all

but a few sites (Cadman et al. 2007). Even along the Canadian Shield, where a large population of Golden-winged Warblers existed in the 1990s, Blue-winged Warblers and hybrids began to appear and increased in abundance after 2001. A similar, rapid replacement of Golden-winged Warblers by Blue-winged Warblers occurred in the St. Lawrence Valley of New York, where the first hybrid warblers were detected in the late 1990s. The advancing front of Blue-winged Warbler breeding distribution passed through the well-monitored Fort Drum area by 2005. By 2008, J. Bolsinger (pers. comm.) found a mixed population of 50% Golden-winged Warblers, 32% Blue-winged Warblers, and 17% phenotypic hybrids at that site.

In the Appalachian Mountains, interactions between Golden-winged and Blue-winged Warblers have been more complex, and importantly, several areas exist where both species co-occurred for long periods, mediated by ecological gradients in elevation, vegetation types, or both. For example, in the western portion of the Hudson Highlands in southeastern New York, both species co-occurred for over a century (Eaton 1914, Frech and Confer 1987, Scully 1997, Confer and Tupper 2000). However, Dabrowski et al. (2005) questioned the continuing co-occurrence of these two species in the Hudson Highlands due to increased genetic introgression. Similarly, breeding Golden-winged and Blue-winged Warblers co-occurred in the New Jersey Highlands for almost a century (Confer and Larkin 1998, Confer and Tupper 2000). By 2010, breeding Golden-winged Warblers in that state only persisted in the Newark Watershed within the New Jersey Highlands. Blue-winged Warblers expanded their breeding distribution through the Delaware River Valley in the late 1900s (Gill 1997), and between 2003 and 2008 rapidly replaced breeding Golden-winged Warblers throughout northwestern New Jersey after a brief period of hybridization (S. Petzinger, pers. comm.).

In Pennsylvania, Blue-winged Warblers and hybrids were detected nearly throughout the state during 1999–2006 GOWAP surveys. The breeding distribution of Blue-winged Warblers in Pennsylvania expanded at elevations below 600 m during the late 1900s, but contracted overall in the state since 1990 because of reduction in the extent of early successional forest (Wilson et al. 2012). In adjacent Maryland, the breeding distribution of Blue-winged Warblers also contracted overall since the 1980s and has not expanded to higher elevations in mountainous areas in western Maryland (Ellison 2010). High-elevation, extensively forested areas in Pennsylvania and in the adjacent Allegheny Mountains of western Maryland and West Virginia currently support the largest breeding populations of Golden-winged Warblers within the Appalachian Mountains breeding-distribution segment, and this population of Golden-winged Warblers remains largely isolated geographically from Blue-winged Warblers. High elevation sites therefore represent important conservation areas where management to increase the amount of breeding habitat is especially critical (A. M. Roth et al., unpubl. plan).

A similar situation exists at high elevations in the Blue Ridge and Cumberland mountains of western North Carolina and northern Georgia, where Golden-winged Warblers remain isolated from Blue-winged Warblers. A few hybrids were detected during the GOWAP within areas occupied by Golden-winged Warblers, but with little evidence of extensive hybridization. These areas also currently serve as refugia where management to increase habitat quantity and quality to increase populations is critically needed to avoid extirpation (Percy 2012).

In contrast, the breeding distribution of Blue-winged Warblers expanded rapidly into southeastern Kentucky after 2000, including some high-elevation areas where Golden-winged Warblers had previously been found consistently. Hybrids were commonly observed in these areas after 2005, and breeding Golden-winged Warblers had all but disappeared from Kentucky by 2009 (Patton et al. 2010; S. Vorisek and J. Larkin, pers. comm.). West Virginia supported the largest number of breeding Golden-winged Warblers in the Appalachian Mountains as recently as the 1990s, but GOWAP surveys indicated the presence of both species or hybrids in 20 of 32 grid cells (Figure 1.3), with only Blue-winged Warblers detected in the western third of the state. Since 1995, Blue-winged Warblers replaced Golden-winged Warblers throughout the coalfield region of southern and central West Virginia; only isolated Golden-winged Warbler breeding sites were thought to remain as of 2009. By 2013, Golden-winged Warblers persisted only at middle elevations in the Allegheny Mountains of eastern West Virginia (K. Aldinger, pers. comm.; J. Larkin, pers. comm.). Last, surveys in a 40-county area of western Virginia in 2006 documented the expansion of Blue-winged Warblers into 10 of 11 counties where breeding Golden-winged Warblers were still present; hybrids were detected in 7 of these counties (Wilson et al. 2007).

Breeding Population Trends and Changes in Population Size

Sauer et al. (2012) estimated that the global breeding Golden-winged Warbler population declined from 1966 to 2010 at an average annual rate of -2.6% (95% Credible Limits: -3.5% to -1.6%): one of the steepest declines observed for any North American forest songbird. Extremely steep population declines

occurred in the Appalachian Mountains Bird Conservation Region (BCR) (-8.5% per year), whereas more moderate declines occurred in the Prairie Hardwood Transition BCR (-2.9%) and the Boreal-Hardwood Transition BCR (-1.1%).

Using indices of abundance resulting from the Bayesian analysis of BBS data, we estimated that the number of Golden-winged Warblers declined from roughly 1.25 million breeding adults (95% CL: 950,000; 1,700,000) in 1966 to 386,000 (95% CL: 290,000; 520,000) in 2000 and 383,000 (95% CL: 275,000; 565,000) in 2010 (Figure 1.4). Using the population estimate for 2010 and assuming the 45-year BBS trend and the observed variability in that trend will continue, we predict a population of 37,000 breeding adults (95% CL: 27,000; 67,000) by 2100. This evaluation represents a reduction in population size of 1.2 million birds (97%) in 135 years. Note that the apparent leveling off of the overall trend in recent years could be the result of recent stabilization of Golden-winged Warbler populations, which is not suggested by our distributional analysis, or could result from a low detection rate of Golden-winged Warblers on BBS routes in areas where the species has become rare, and therefore the low power of the BBS to detect further changes. If populations have truly begun to stabilize, applying the 45-year trend will result in a lower future population projection than may actually occur.

Based on regional estimates of population size, we estimate that $>80\%$ of breeding Golden-winged Warblers currently occur within the Boreal-Hardwood Transition BCR (BCR 12) and nearly 90% of the total population occurs within the area we defined as the Great Lakes breeding-distribution segment (Table 1.1). In contrast, only about 5% of the current breeding population occurs within the Appalachian Mountains BCR (BCR 28), which corresponds with the Appalachian Mountains breeding-distribution segment. Ongoing reduction in Golden-winged Warbler population size in the Appalachian Mountains BCR is especially alarming—a 97.8% population decline from 1966 to 2010 and a 61.7% decline between our average estimate for the 1990s and our average estimate for the 2000s decades (Table 1.1). The change also represents a proportional change, in that the Appalachian Mountains BCR was estimated to support nearly 10% of the total population of breeding Golden-winged Warblers during the decade of the 1990s, but only 5% of the total population during the 2000s. The 1,740% increase in estimated population size in the Boreal Taiga Plains BCR between the 1900s and 2000s is based on relatively few records, such that the credible interval is extremely broad (Table 1.1). Buehler et al. (in A. M. Roth et al., unpubl. plan) used these same estimates of population trends and changes in regional population size to predict

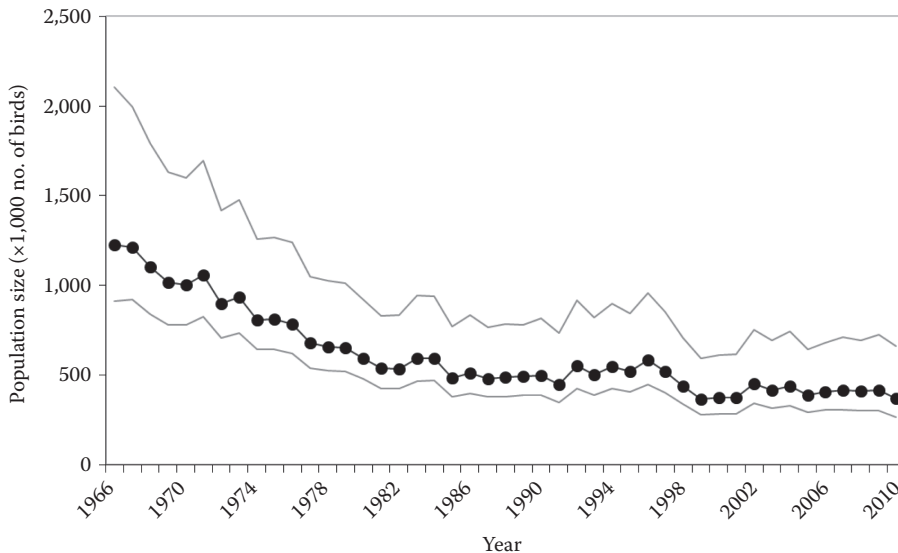


Figure 1.4. Annual breeding population size of Golden-winged Warblers (with 95% credible limits [CL]) estimated with a hierarchical Bayesian analysis of North American Breeding Bird Survey data (1966–2011).

TABLE 1.1

Estimated percent of total Golden-winged Warbler population and change in population size by Bird Conservation Region (BCR) over the entire period (1966–2010) of the North American Breeding Bird Survey (BBS) and between average estimates for the decades of the 1990s vs. the 2000s (see Blancher et al. 2013).

Bird Conservation Region	Percent of population	1966–2010	1990s vs 2000s (average for each decade)
Boreal Hardwood Transition (BCR 12)	80.2	-27.5 (-30.3, -25.9)	-16.3 (-17.8, -15.2)
Prairie Hardwood Transition (BCR 23)	9.8	-70.7 (-76.8, -46.3)	-11.8 (-27.0, 25.9)
Appalachian Mountains (BCR 28)	5.3	-97.8 (-97.9, -97.7)	-61.7 (-63.7, -60.5)
Great Lakes–St. Lawrence Plain (BCR 13)	4.0	-16.0 (-18.1, -10.9)	0.9 (-5.5, 8.2)
Boreal Taiga Plains (BCR 6)	0.6		1,740 (850, 946,620)
Total Population Change		-66.2 (-67.0, -65.5)	-17.9 (-20.3, -15.4)

Trend estimates are derived from the BBS (Sauer et al. 2011). Numbers in parentheses are 95% credible limits; significant change (0.95 probability that the percent change differs from zero) is indicated in bold font.

probability of Golden-winged Warbler population persistence in portions of the species' breeding distribution.

Nonbreeding Distribution

Nonbreeding-season point-count surveys during December–early March 2009–2012 resulted in 543 detections of male Golden-winged Warblers and 76 detections of females. Because of the low number of female detections, we modeled only occurrence of males. Probability of male occurrence was lower in Colombia and Venezuela

than in northern Central America (Figure 1.5). Note that these results were based on few survey points in Venezuela; few detections of Golden-winged Warblers in Colombia; and no survey data from Guatemala, Belize, or Mexico. Throughout the modeled distribution, probability of occurrence was greatest at intermediate elevations (700–1,400 m) and was lowest (<0.05) in the lowlands of South America (<500 m), above 3,000 m throughout the estimated nonbreeding distribution, and in the tropical dry forests of Costa Rica, Nicaragua, and Honduras (Figure 1.5). Female Golden-winged warblers were detected

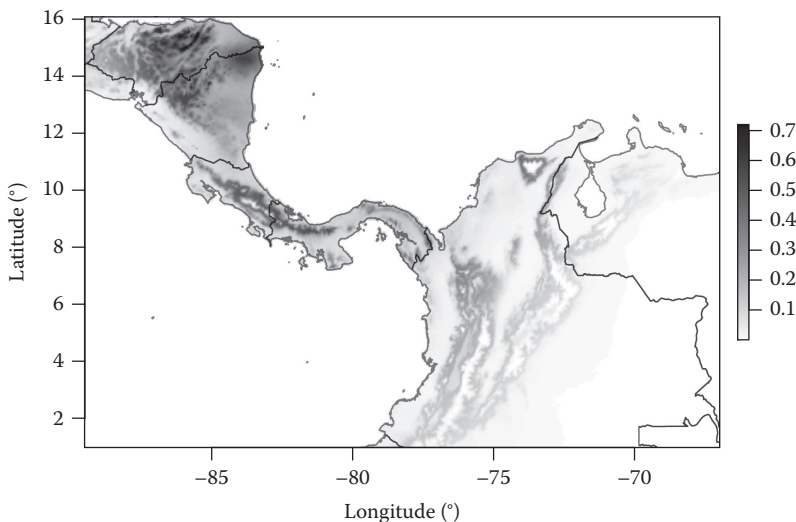


Figure 1.5. Estimated probability of occurrence of male Golden-winged Warblers, based on survey data from December to mid-March, 2009–2012. We modeled probability of occurrence as a function of annual precipitation, temperature, elevation, longitude, and latitude.

throughout the geographic distribution of males, providing no evidence for latitudinal segregation between males and females. Habitat associations for females, however, did suggest some spatial segregation, with females occupying lower elevations and drier areas than males.

Combining our model results with a qualitative assessment of 3,533 specimen and observational records from 1 November to 15 March, we estimated that the nonbreeding distribution (excluding areas used only by migrants or transients) of Golden-winged Warblers extends from southeastern Mexico and Belize south and east through the highlands and Caribbean slope of Guatemala, El Salvador, and Honduras to northwestern Nicaragua, in humid lowlands and middle elevations on both Caribbean and Pacific slopes in Costa Rica and Panama, and in an arc of the northern Andes from northwestern Venezuela to central Colombia (Figure 1.6). Smaller numbers of Golden-winged Warblers regularly occur during the nonbreeding season farther north in eastern Mexico, including the Yucatan Peninsula, in the Santa Marta and Perijá Mountain regions of northern Colombia, and farther south in the western Andes to northwestern Ecuador. Scattered records from the Pacific lowlands of Central America, and in the Greater Antilles, Virgin Islands, and Trinidad may indicate rare but regular occurrence during the nonbreeding season in those regions. Based on high predicted occupancy and frequency of observations, the largest numbers of Golden-winged Warblers during the nonbreeding season likely occur at middle elevations (700–1,400 m) from Honduras to western Panama and possibly in the Andes of central Colombia.

In Mexico, Howell and Webb (1995) considered Golden-winged Warblers an uncommon to fairly common transient and visitor during boreal winter on the Atlantic slope of Chiapas, and rare elsewhere. Nonbreeding-season records in Mexico are clustered in the highlands of eastern Chiapas, but Golden-winged Warblers also regularly occur in the mountains of southern Veracruz and scattered across the wetter parts of the Yucatan Peninsula. In adjacent Guatemala, Land (1970) considered Golden-winged Warblers uncommon in the Caribbean lowlands, sea level to 1,750 m; most recent records are from the highlands of central Guatemala, with scattered additional records in the Petén Department in the north, in the Sierras of the Caribbean region,

and in the lower mountains and volcanoes closer to the Pacific Coast. However, recent surveys in Petén found very few individuals (R. E. Bennett, unpubl. data). Few historical records of Golden-winged Warblers during the nonbreeding season exist for Belize, and Jones (2003:201) described them as a “very uncommon winter visitor;” yet >50 recent eBird records as of December 2015 suggest that Golden-winged Warblers occur during the nonbreeding season throughout the country especially in the low, forested mountainous regions of Belize.

Honduras appears to support a considerable population of Golden-winged Warblers during the nonbreeding season, based on recent surveys and fieldwork. Monroe (1968) considered Golden-winged Warblers uncommon visitors during the nonbreeding season, from sea level to 1,800 m and most frequent on the Caribbean slope and interior highlands. The recent surveys at 503 sites during field seasons of 2010–2011 and 2011–2012 (Bennett 2012), plus additional recent eBird records, indicated that Golden-winged Warblers are widespread and fairly common on the northern Caribbean slope and at middle and upper elevations throughout the interior highlands. Golden-winged Warblers occupy a variety of forest types in Honduras, including humid broadleaf forest, mixed pine-broadleaf forest, and riparian forest corridors within highly disturbed landscapes (Bennett 2012). Golden-winged Warblers are generally absent from the Pacific slope below 1,000 m, and their status is uncertain in the eastern Caribbean lowlands (Mosquita Region).

In El Salvador, the first records of Golden-winged Warblers were from slopes of volcanoes near the Pacific Coast and in the northeast (Thurber et al. 1987), and recent eBird records come from those areas and the highlands near the Honduran border in northwestern El Salvador. It is likely that small numbers of Golden-winged Warblers occur during the nonbreeding season in highland regions throughout the country, although some records may be of migrants. Golden-winged Warblers are also common in the Central Highlands of northwestern Nicaragua, contiguous with the mountainous areas in Honduras; they were detected at 60% of 303 sites visited in that region during three recent field seasons (2009–2011). Martínez-Sánchez and Will (2010), summarizing records through 1993, considered Golden-winged

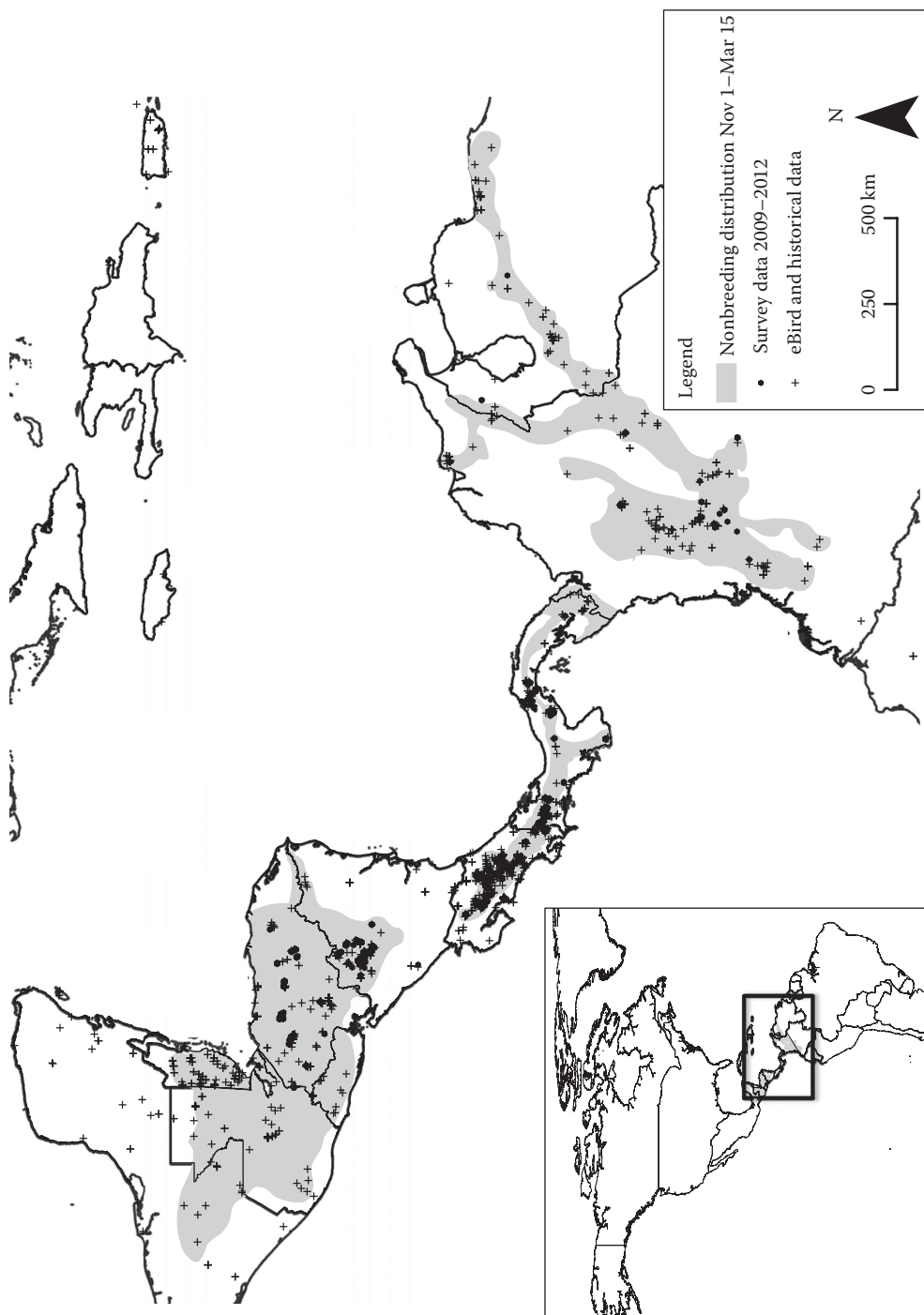


Figure 1.6. Nonbreeding distribution of Golden-winged Warblers in Central and northern South America. Dots represent specific locality records from historical specimens and other published records, standardized surveys conducted during 2009–2012, and additional 1 November to 15 March records from eBird.

Warblers only an uncommon transient and nonbreeding-season resident in Nicaragua, with only scattered records from the rest of the country, primarily from volcanoes near the Pacific Coast and the San Juan River region near the border with Costa Rica. As in Honduras, it is uncertain whether Golden-winged Warblers occur during the nonbreeding season in the extensive Caribbean lowlands where no recent surveys have been conducted.

Another major area used by Golden-winged Warblers during the nonbreeding season is in a mid-elevation zone in the highlands of Costa Rica and western Panama. Golden-winged Warblers are most numerous from 700 to 1,400 m on the Caribbean slopes of the Guanacaste, Tilaran, and Central Cordilleras, on both slopes of the Talamanca Cordillera, and in the lower Fila Costeña in southwestern Costa Rica (Slud 1964, Stiles and Skutch 1989; eBird). Smaller numbers of Golden-winged Warblers occur during the nonbreeding season regularly where forest remains in the lower foothills of the Caribbean slope, to near sea level in the southwestern Pacific lowlands from Carara to the Osa Peninsula, and possibly in the mountains of the Nicoya Peninsula. During recent surveys (2009–2012) at 486 sites, 184 Golden-winged Warblers were detected at roughly 30% of sites sampled, confirming continued presence at many areas previously used by Golden-winged Warblers during the nonbreeding season throughout Costa Rica although Golden-winged Warblers are apparently absent from the extensive Caribbean lowlands during the nonbreeding season.

In Panama, Golden-winged Warblers are most numerous in the foothills and lower Pacific slopes in the westernmost province of Chiriquí (Wetmore et al. 1984, Ridgely and Gwynne 1989; eBird). A large region of potential habitat exists on the Caribbean slopes of the Talamanca Mountains in La Amistad National Park, but few ornithological records exist for this region. In central Panama, records of Golden-winged Warblers are concentrated in several areas, including the Pacific slopes of El Valle volcano, near sea level in the Canal Zone, and in the Cerro Azul-Cerro Jefe region near Panama City. Golden-winged Warblers also occur regularly in eastern Panama in the mountains of Darien Province. Scattered additional historical and recent records in other parts of Panama suggest that Golden-winged

Warblers may be continuously distributed at lower and mid-elevations throughout the entire country, especially along the Cordillera Central and the San Blas Cordillera in eastern Panama. Recent surveys (2009–2012) at 340 sites in areas that appeared to be suitable for Golden-winged Warblers, however, resulted in only 32 detections (<10% of sites), mostly in Chiriquí and other areas with historical records of occurrence. Our recent surveys in Panama in 2015 revealed that female Golden-winged Warblers consistently occupy areas that receive less annual precipitation than males. Two sites were identified as important for female Golden-winged Warblers, despite the absence of males: the Parque Metropolitano in Panama City and the lowland secondary broadleaf forest around Meteti, Darien.

Most references for South America depict the nonbreeding distribution of Golden-winged Warblers as including much of western Colombia and northwestern Venezuela (Ridgely et al. 2005, Ridgely and Tudor 2009). Our compilation of historical and recent records, however, suggests that the current nonbreeding distribution in these countries is much more narrow and restricted, and may possibly be shrinking in area. In Colombia, Hilty and Brown (1986) described Golden-winged Warblers as fairly common in the western Andes and less numerous eastward, mostly in foothills and lower slopes (700–2,000 m), south to Cauca and Huila in the western Andes and to Meta on the east slope of the eastern Andes. The records we compiled are scattered along the slopes of the Andean mountain chains but are concentrated on slopes facing the interior valleys of the Magdalena and Cauca rivers (Figure 1.5). Fewer records are from farther south in the western Andes including a few south to Mindo, Ecuador, in the more isolated Serranía de San Lucas, Sierra Nevada de Santa Marta, and Sierra de Perijá in northern Colombia, and possibly in the hilly region of the western Chocó. There are few records of Golden-winged Warblers on the eastern slope of the eastern Andes. Many Colombian records are from October, November, and March, and it is difficult to distinguish records of resident birds from those of migrants. During recent surveys in three field seasons (2009–2012) at 421 sites in Colombia, Golden-winged Warblers were detected at only 35 sites (<10%), mostly in the central portions of the central and western Andes; many potentially suitable areas throughout Colombia were not surveyed.

In northwestern Venezuela, Golden-winged Warblers occur during the nonbreeding season in an arc at intermediate elevations (950–2,400 m) along the slopes of the Andes and the Coastal Cordillera, east at least to the Caracas area, in the Sierra de Perijá at the Colombian border, and Sierra de San Luis in the far north (Hilty 2003). A few individuals have been recorded farther east in the Coastal Cordillera (Sucre and Monagas) and in the Tepui region (Sierra de Lema). Most records for Venezuela are from historical specimens collected in the early 20th Century, but it is unclear whether a lack of modern records reflects a lack of recent reports in databases such as eBird or a change in nonbreeding distribution. Of 35 sites surveyed in Venezuela during our 2010–2011 field season, only three Golden-winged Warblers were detected at two sites. We do not have enough recent data, therefore, to make conclusions about the current status of Golden-winged Warblers in Venezuela during the nonbreeding season.

The possibility that Golden-winged Warblers may be relatively less common during the nonbreeding season in South America today than they were historically is intriguing. For a low-density, hard-to-detect species that occupies dense forest canopy during the nonbreeding season, Golden-winged Warblers collected in Central and South America are relatively well represented compared with other migrant warblers in major museum collections, based on general collecting activity in the early 20th Century. Our recent surveys were not extensive, but it was difficult to find Golden-winged Warblers even in areas with high predicted probability of occurrence. In contrast, Golden-winged Warblers may be more numerous than previously thought in the northern part of their nonbreeding distribution in Central America. For example, Monroe (1968) reported only five specimens collected during the period we defined as the nonbreeding season from Honduras, and Belize was not included in many previously published maps or descriptions of the Golden-winged Warblers nonbreeding distribution (American Ornithologists' Union 1983, DeGraaf and Rappole 1995, Birdlife International 2012). Even in Nicaragua, where >300 Golden-winged Warblers were detected on recent surveys, Martínez-Sánchez and Will (2010) cited few definitive records prior to 1990. Considering the extent of the nonbreeding distribution is much greater from west to east than from north to south, and

the breeding distribution has shifted toward the northwest, it is possible that a concomitant shift in the nonbreeding distribution also has occurred.

Distributions of Blue-winged and Golden-winged Warblers during the period we defined as the nonbreeding season did not overlap, with Blue-winged Warblers distributed farther north in northern Central America and southern Mexico (Gill et al. 2001). Substantial overlap of these two species during the nonbreeding season may be limited to portions of Guatemala, Belize, and Honduras (Land 1970, Confer 1992, Gill et al. 2001; eBird records); records of Blue-winged Warblers are rare in Nicaragua (Martínez-Sánchez and Will 2010), Costa Rica (Stiles and Skutch 1989), and Panama (Ridgely and Gwynne 1989), and there are only two records from South America in northern Colombia and northern Venezuela. Golden-winged × Blue-winged Warbler hybrids have been found throughout the Central American nonbreeding distribution of both species, and there are a few records of hybrids from Colombia and Venezuela.

Migration Routes and Timing

Little is known about the migration of Golden-winged Warblers, especially south of the U.S. We examined 1,244 observation and specimen records from south of the U.S. and outside the period we defined as the nonbreeding season (1 November to 15 March). The locations of Golden-winged Warbler eBird records during migration suggest a looped, trans-Gulf of Mexico migration, with spring migration occurring farther west than fall migration. Elliptical migration is a common pattern observed in long-distance migrants breeding in eastern North America (La Sorte et al. 2014). In spring, most individuals cross the western Gulf of Mexico to Texas and Louisiana (or possibly farther north), arriving mostly in late April and early May (earliest, 10 April). The migration period appears to be short, with the latest spring records of Golden-winged Warblers in Nicaragua (17 April), Colombia (19 April), Guatemala (24 April), Honduras (25 April), and Costa Rica (1 May) in late April and early May. Spring migrants have been reported from late March to early May along the Caribbean coast (including offshore islands) from western Panama to Belize and southeastern Mexico (but not on Yucatan Peninsula),

indicating that some Golden-winged Warblers may move northward along the Central American coast, or may cross the western Caribbean Sea before crossing the Gulf of Mexico to the U.S. A paucity of spring records from Florida or anywhere in the southeastern Coastal Plain of the U.S. further suggests that some Golden-winged Warblers may fly directly from Central America to breeding grounds in the southern Appalachian Mountains.

Fall records (August–November) of Golden-winged Warblers in eBird also suggest a trans-Gulf of Mexico migration, but farther east, with a much greater concentration of records in Florida in early fall (late August through September) than in spring, but few records from along the Gulf of Mexico coast in Louisiana, Texas, or Mexico. Some fall migrants also likely cross the Caribbean Sea, as evidenced by records from offshore islands along the Central American coast and occasionally from Caribbean islands; a few records from Bermuda suggest that some individuals even may attempt to cross the western Atlantic Ocean to reach South America. Migrant Golden-winged Warblers have been detected in Yucatan and Belize in late August, and the first individuals arrive in Honduras and Nicaragua during the first week of September, and in Costa Rica, Panama, Colombia, and Venezuela by mid-September.

Implications for Conservation

The breeding distribution of Golden-winged Warblers has been highly dynamic, exhibiting among the largest shifts of any North American songbird. Our review of the historical breeding distribution suggests a continual shift northward by Golden-winged Warblers over the past 100 years in the Upper Midwest, but a geographically stable distribution in the Appalachian Mountains, despite steeply declining populations within the Appalachian Mountains breeding-distribution segment. This historical context suggests two different but complementary conservation strategies. Species population stability may best be addressed through land management aimed at creating dynamic forested landscapes (A. M. Roth et al., unpubl. plan) to support source populations in the Great Lakes breeding-distribution segment. At the same time, preservation of the remaining historical breeding distribution and potential genetic variability might best be addressed by focusing on maintenance of Golden-winged

Warbler populations in the Appalachian Mountains breeding-distribution segment.

The three northern states within the Great Lakes breeding-distribution segment currently harbor an estimated 76% of the total global population of breeding Golden-winged Warblers, with 5%, 24%, and 47% of the estimated population in Michigan, Wisconsin, and Minnesota, respectively (Blancher et al. 2013). These three northern states therefore hold the greatest stewardship responsibility for future conservation of Golden-winged Warblers. Wisconsin currently lists Golden-winged Warblers as a Species of Special Concern, and in Minnesota, Golden-winged Warblers were designated a species of greatest conservation need in 2013 based on their high stewardship value (D. Carlson, pers. comm.).

In contrast, the Appalachian Mountains breeding-distribution segment currently includes only 5% of the estimated global population of Golden-winged Warblers. The Appalachian Mountains represent a considerable portion of the historical breeding distribution, and include areas where Golden-winged Warblers remain geographically isolated from Blue-winged Warblers. Golden-winged Warbler populations in the Appalachian Mountains may also be important in terms of genetic diversity in the face of climate change, because these populations are presumably better adapted to warm climates (Hampe and Petit 2005). Within this region, Golden-winged Warblers are listed as endangered, threatened, or special concern by at least six states including Connecticut, New York, New Jersey, Kentucky, Tennessee, and Georgia, but do not have special protection status in the two states with the largest remaining populations: Pennsylvania and West Virginia. Overall, the traditional conservation paradigm of directing resources primarily to jurisdictions where a species is endangered makes it more difficult to focus conservation where larger populations provide greater potential for management success (Wells et al. 2010). The Appalachian Mountains breeding-distribution segment of Golden-winged Warblers has reached levels where BBS is becoming ineffective in tracking changes in distribution and relative abundance, and a new, targeted monitoring approach will be necessary there, such as the spatially balanced sampling design implemented by R. W. Rohrbaugh et al. (unpubl. report).

As with many Neotropical–Nearctic migratory birds, the extent of the nonbreeding distribution

is considerably smaller than during the breeding season, and loss of nonbreeding habitat could be an important factor limiting Golden-winged Warbler populations. Within the nonbreeding distribution of Golden-winged Warblers, conservation efforts are likely to be most effective by focusing on the retention of forested landscapes at intermediate elevations in Central American and the northern Andes (Chapter 11, this volume). The probable shift in the nonbreeding distribution to the north and west has important implications for the conservation of Golden-winged Warblers in northern Central America, especially Guatemala, Honduras, and Nicaragua. Conservation of forested, middle-elevation landscapes in these countries will be key to the successful retention of habitat used during the nonbreeding season for a large portion of the Golden-winged Warbler population (Chapter 2, this volume). If Golden-winged Warblers are becoming more numerous at the northern end of their nonbreeding distribution, interactions between Golden-winged and Blue-winged Warblers during the nonbreeding season also may play an increasing role in determining species interactions and hybridization during the breeding season. The recently completed *Wintering Grounds Conservation Plan for Golden-winged Warbler* presents a strategy for prioritized conservation action in each country within the nonbreeding distribution (R. E. Bennett et al., unpubl. report).

The complexity of changes in the breeding distribution, the genetic and ecological interactions with Blue-winged Warblers, and the apparent shifts in distribution and abundance during the nonbreeding season collectively pose unique challenges for the full-life-cycle conservation of Golden-winged Warblers. An aggressive and collaborative conservation strategy, incorporating the latest research results and management guidelines, will be necessary to reverse population declines and maintain healthy numbers of Golden-winged Warblers throughout their present-day distribution.

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