

Population trends in *Vermivora* warblers are linked to strong migratory connectivity

Gunnar R. Kramer^{a,1}, David E. Andersen^b, David A. Buehler^c, Petra B. Wood^d, Sean M. Peterson^e, Justin A. Lehman^c, Kyle R. Aldinger^f, Lesley P. Bulluck^g, Sergio Harding^h, John A. Jonesⁱ, John P. Loegering^j, Curtis Smalling^k, Rachel Vallender^l, and Henry M. Streby^a

^aDepartment of Environmental Sciences, University of Toledo, Toledo, OH 43606; ^bUS Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, University of Minnesota, St. Paul, MN 55108; ^cDepartment of Forestry, Wildlife, and Fisheries, University of Tennessee, Knoxville, TN 37996; ^dUS Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, WV 26506; ^eDepartment of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; ^fWest Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, WV 26506; ^gDepartment of Biology, Virginia Commonwealth University, Richmond, VA 23284; ^hVirginia Department of Game and Inland Fisheries, Henrico, VA 23228; ⁱDepartment of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118; ^jAgriculture and Natural Resources Department, University of Minnesota, Crookston, MN 56716; ^kAudubon North Carolina, Boone, NC 28607; and ^lCanadian Wildlife Service, Environment and Climate Change Canada, Gatineau, QC, K1A 0H3 Canada

Edited by Robert E. Ricklefs, University of Missouri–St. Louis, St. Louis, MO, and approved January 30, 2018 (received for review October 31, 2017)

Migratory species can experience limiting factors at different locations and during different periods of their annual cycle. In migratory birds, these factors may even occur in different hemispheres. Therefore, identifying the distribution of populations throughout their annual cycle (i.e., migratory connectivity) can reveal the complex ecological and evolutionary relationships that link species and ecosystems across the globe and illuminate where and how limiting factors influence population trends. A growing body of literature continues to identify species that exhibit weak connectivity wherein individuals from distinct breeding areas co-occur during the nonbreeding period. A detailed account of a broadly distributed species exhibiting strong migratory connectivity in which nonbreeding isolation of populations is associated with differential population trends remains undescribed. Here, we present a range-wide assessment of the nonbreeding distribution and migratory connectivity of two broadly dispersed Nearctic–Neotropical migratory songbirds. We used geolocators to track the movements of 70 *Vermivora* warblers from sites spanning their breeding distribution in eastern North America and identified links between breeding populations and nonbreeding areas. Unlike blue-winged warblers (*Vermivora cyanoptera*), breeding populations of golden-winged warblers (*Vermivora chrysoptera*) exhibited strong migratory connectivity, which was associated with historical trends in breeding populations: stable for populations that winter in Central America and declining for those that winter in northern South America.

animal tracking | conservation | geocator | limiting factor | migration

Populations of migratory species can be limited by factors throughout their annual cycle. The degree to which spatially isolated breeding populations use geographically distinct areas during the nonbreeding period (i.e., migratory connectivity) affects the potential for regionally specific factors to influence population trends (1–3). Tracking migratory animals to link breeding populations with nonbreeding areas has primarily focused on the migratory behaviors of large mammals and large birds, which have been studied for decades, and even centuries (4–9). However, following recent technological advances, it is now possible to track all but the smallest migratory species across time and space (10–12). The value of tracking species throughout the annual cycle is manifold. Identifying the migratory pathways by which animal populations navigate between breeding and nonbreeding areas can reveal population-level differences in route or space use that may explain differential breeding population trends (13) or signal tradeoffs in life-history strategies (14–16). In migratory birds, the distribution of breeding populations during the nonbreeding period has the potential to be the primary driver of population trends as many long-distance migrant species spend more time on nonbreeding sites than in any

other location during the annual cycle (17). Furthermore, environmental conditions experienced during the nonbreeding period can have both direct (18) and indirect effects (19) on individuals, and can consequently influence population trends. As such, describing the spatial structure and level of dispersion of a migratory species during the nonbreeding period can identify potential areas that may limit some populations but not others (20–22), provide insight into the evolutionary history of migratory species (23–25), and aid in the identification of important areas that may be targeted for conservation (18, 21, 26–30).

Despite a growing body of information on the behaviors and connectivity of migratory birds, detailed range-wide studies investigating the nonbreeding distribution and migratory connectivity of entire species remain rare (20, 21). Weak migratory connectivity is most commonly reported in studies of long-distance migratory bird species worldwide (31–35). Weak connectivity results in nonbreeding areas that are inhabited by

Significance

Identifying drivers of population trends in migratory animals is difficult due to their reliance on different geographic regions throughout the annual cycle. Populations of Nearctic–Neotropical migratory birds are often thought to be limited by spatial variation in factors affecting reproduction and survival during the breeding season. We tracked individual songbirds from a two-species complex of New World warblers and discovered unequivocal evidence of a system in which strong associations between breeding areas and nonbreeding areas (i.e., migratory connectivity) is concordant with breeding population trends. The strong migratory connectivity we documented is associated with differential rates of land-use change in population-specific nonbreeding areas. Our results suggest that other migratory species with similar population trends may also exhibit strong migratory connectivity.

Author contributions: G.R.K., D.E.A., D.A.B., P.B.W., and H.M.S. designed research; G.R.K., D.E.A., D.A.B., S.M.P., J.A.L., K.R.A., L.P.B., J.A.J., J.P.L., C.S., R.V., and H.M.S. performed research; G.R.K., D.E.A., and H.M.S. analyzed data; and G.R.K., D.E.A., D.A.B., P.B.W., S.M.P., J.A.L., K.R.A., L.P.B., S.H., J.A.J., J.P.L., C.S., R.V., and H.M.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

Data deposition: Data used for this study are freely and publicly available on the Data Repository for the University of Minnesota (<https://conservancy.umn.edu/handle/11299/193202>).

¹To whom correspondence should be addressed. Email: gunnarrkramer@gmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1718985115/-DCSupplemental.

individuals from multiple, widely dispersed breeding populations. Strong migratory connectivity, resulting in geographic isolation during the nonbreeding period, is required for differential population trends of geographically distinct breeding populations to be driven by factors away from the breeding grounds. Although the theoretical implications of strong connectivity have been addressed and discussed (2), rarely are species' breeding population trends decisively linked to individual populations' occurrence at isolated nonbreeding areas, and this information can be particularly important for the conservation of declining and threatened species. Identifying species with populations that might be independently limited by factors outside of the breeding period will contribute to the understanding of the ecological and evolutionary implications of strong migratory connectivity, and why it appears to be uncommon among migratory birds.

We investigated the migratory connectivity of *Vermivora* wood-warblers (Parulidae), a species complex composed of two extant species of obligate Nearctic-Neotropical migrant warblers that are extremely closely related (36). Golden-winged warblers (*Vermivora chrysoptera*) and blue-winged warblers (*Vermivora cyanoptera*) breed and migrate throughout deciduous forests of eastern North America and occur throughout Central America, with golden-winged warblers also occurring in northern South America during the nonbreeding period, and recent evidence suggests golden-winged warblers may exhibit strong, range-wide migratory connectivity (29, 37). On the breeding grounds, golden-winged warblers and blue-winged warblers have overlapping distributions and regularly hybridize to produce viable young (38). Recent genomic evidence suggests overlap and hybridization has occurred for >1,000 y and that these two species may constitute a single, polymorphic species with differences in their genomes primarily associated with different plumage traits (36). That said, detailed information on the genetic structure of *Vermivora* populations is lacking (36, 39). Furthermore, there is little evidence of costs to producing hybrid young in this system (38, 40). Both species of *Vermivora* and two recognized hybrid phenotypes breed in a similar habitat, often with overlapping territories; sing songs with overlapping characteristics; and exhibit nearly identical foraging and reproductive strategies (41, 42).

Despite remarkable genetic, behavioral, and natural history similarities, regional populations of *Vermivora* have experienced starkly contrasting population trajectories since standardized monitoring began in 1966 (43, 44). Golden-winged warblers breeding throughout the Great Lakes region have maintained historical abundances, whereas golden-winged warblers breeding throughout the Appalachian Mountains region have declined steadily (44) (Fig. 1 *C* and *D*). To date, declines in the Appalachian Mountains have amounted to a loss of 98% of historical abundance and resulted in regional extirpations from many areas where golden-winged warblers were once common (41). Hypotheses about the cause of these declines have focused on breeding-grounds factors, namely, habitat loss and hybridization (i.e., genetic swamping), as the primary drivers of declines in Appalachian Mountains populations of golden-winged warblers (41). However, habitat loss and hybridization fail to parsimoniously explain the stationary population trends of Great Lakes populations of golden-winged warblers and the stationary population trends of blue-winged warblers throughout their distribution, including in the Appalachian Mountains, where they co-occur with historically declined populations of golden-winged warblers (42). Previous investigations into the migratory connectivity of *Vermivora* warblers have focused exclusively on golden-winged warblers and are equivocal. Assessments of stable isotopes in feathers of golden-winged warblers collected during the nonbreeding period showed a possible overlap between Appalachian and Great Lakes populations in Central America (46), whereas a smaller scale, light-level geolocator study found no evidence of nonbreeding population overlap between golden-winged warblers at Great Lakes

and Appalachian breeding sites (29). Populations of blue-winged warblers, including those breeding sympatrically with declining golden-winged warblers in the Appalachian Mountains region, have remained numerically stable (44) (Fig. 1 *E–G*). This suggests that the limiting factor primarily driving declines of Appalachian golden-winged warblers is likely experienced somewhere outside the breeding period at a time or location that exclusively affects golden-winged warblers that breed in the Appalachian Mountains.

Here, we present the results of a large, range-wide study (Fig. S1) tracking individual songbirds and describe the migratory connectivity of two hybridizing migratory species. We used light-level geolocators (hereafter, geolocators; *Materials and Methods* and *SI Materials and Methods*) to track individual *Vermivora* warblers throughout their annual cycle and determine links between breeding and nonbreeding areas. Based on differences in breeding population trends (Fig. 1) that are not explained by breeding-grounds factors, we predicted that golden-winged warblers would exhibit strong migratory connectivity, with declining populations occurring disparately from numerically stable populations. If there is strong migratory connectivity and isolation among populations during the nonbreeding period, we further predicted that nonbreeding areas used by historically declining populations will have experienced disproportionate rates of forest loss that coincide with population trends. We discuss the implications of the observed migratory connectivity of *Vermivora* warblers in ecological and evolutionary frameworks. Lastly, we identify species that share similar nonbreeding distributions with *Vermivora* and exhibit varied regional population trajectories akin to those seen in golden-winged warblers that we hypothesize may have similarly strong migratory connectivity driving those species' regional population trends.

Results and Discussion

Geolocator-marked golden-winged warblers ($n = 41$) occurred at sites from Guatemala and southern Mexico to northern Venezuela during the nonbreeding period (Fig. 2*A*). Individuals from historically stable Great Lakes breeding populations [bird conservation region (BCR) S12: Boreal Hardwood Transition; *Materials and Methods* and Fig. 1] were dispersed broadly and almost exclusively throughout Central America during the nonbreeding period [28 of 29 (97%); Fig. 2 *B* and *C*], although one individual from a breeding site in central Ontario, Canada, occurred in northern South America (Fig. 2*A*). Golden-winged warblers from historically declining breeding populations in the Appalachian Mountains (BCR S28: Appalachian Mountains, $n = 12$) occurred at sites exclusively in northern South America, primarily in northern Venezuela (Fig. 2 *D* and *E*), during the nonbreeding period. Blue-winged warblers ($n = 25$), which exhibit historically stable population trends throughout their breeding distribution (BCRs S23, S24, and S28: Prairie Hardwood Transition, Central Hardwoods, and Appalachian Mountains, respectively; Fig. 1), occurred almost exclusively in Central America during the nonbreeding period [24 of 25 (96%); Fig. 2*F*]. Only one blue-winged warbler from a northern Appalachian Mountains breeding population occurred in northern South America. Phenotypic hybrids ($n = 4$) from breeding populations in the Great Lakes region ($n = 2$) occurred in northern Central America during the nonbreeding period (Fig. 3*B*), whereas hybrids from breeding populations in the Appalachian Mountains ($n = 2$) occurred in northern South America (Fig. 3*C*). Golden-winged warblers from Great Lakes breeding populations and blue-winged warblers overlapped extensively in Central America during the nonbreeding period (Fig. 2 *B*, *C*, and *G–J* and Fig. S3). However, historically declining Appalachian Mountains populations of golden-winged warblers were isolated from historically stable populations of both golden-winged warblers and blue-winged warblers during the nonbreeding period (Fig. S2).

Regional breeding populations of blue-winged warblers (i.e., populations identified by their BCRs) did not occur in isolation

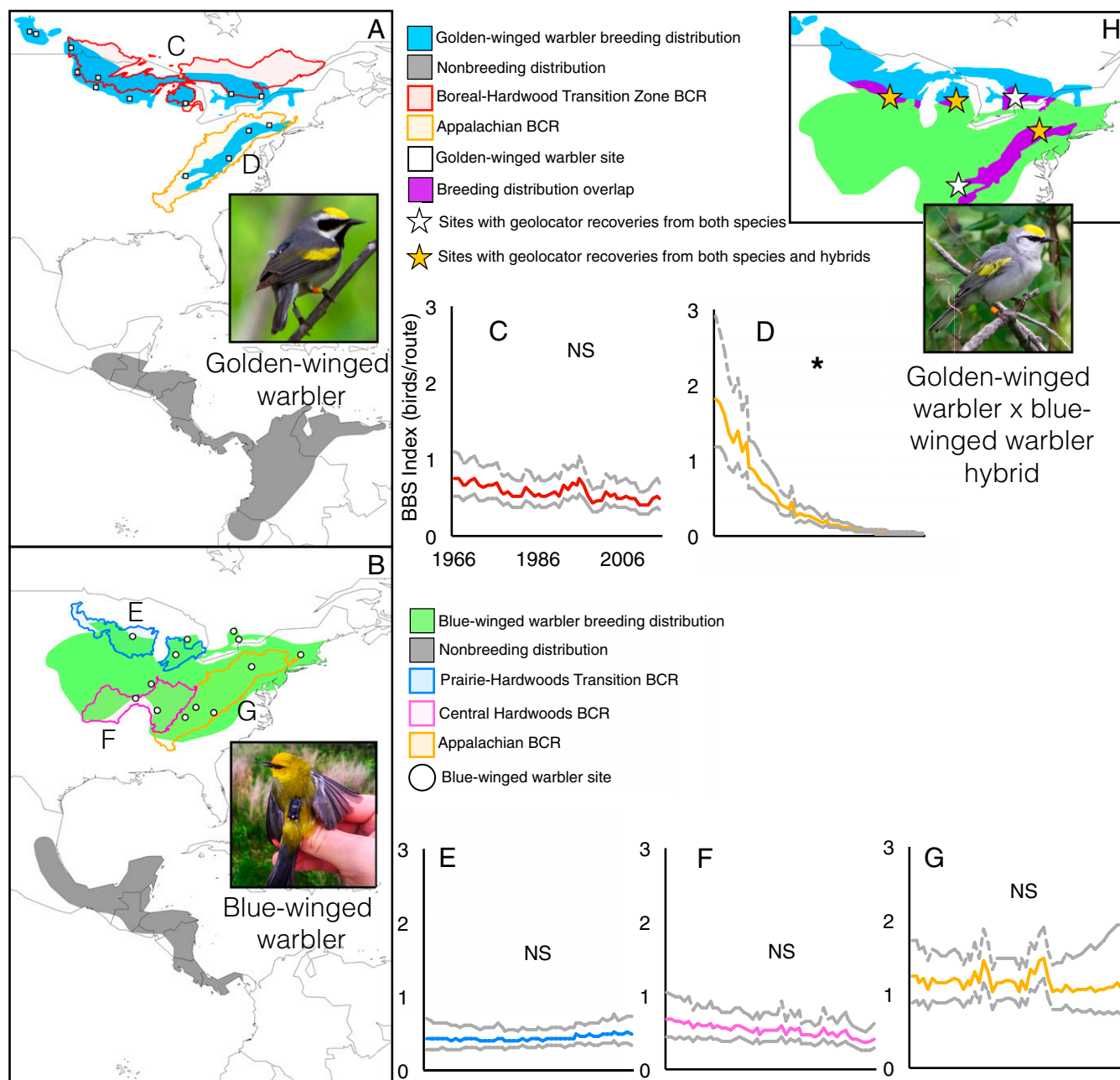


Fig. 1. Breeding and nonbreeding distributions of golden-winged warblers (A) and blue-winged warblers (B) with relevant BCRs outlined and study sites identified (keys are provided for details). Historical population trends of each species are provided for each relevant BCR from 1966 to 2015 [Breeding Bird Survey (44)]. In trend graphs, solid-colored lines represent annual indices of golden-winged warblers (C and D) and blue-winged warblers (E–G) (44) derived from hierarchical model analysis. Dashed gray lines represent 95% credible intervals around annual indices. Populations are noted as exhibiting nonsignificant trends [i.e., numerically stable (NS)] or significant trends [increasing or declining (*)] depending on whether the 95% credible interval around the trend estimate (from 1966 to 2015) includes zero. Note that all trend graphs have the same axis scales. (H) Breeding distribution overlap between golden-winged warblers and blue-winged warblers is presented. Range map information is adapted from BirdLife International (45), and nonbreeding ranges are buffered by 100 km.

from one another during the nonbreeding period (one-way ANOVA: $F = 1.3$; $df = 3, 20$; $P = 0.3$; Fig. S3). However, individual blue-winged warblers that spent the nonbreeding period in Central America exhibited a pattern such that individuals from more easterly breeding longitudes tended to occur farther east during the nonbreeding period (Fig. S3). Conversely, regionally isolated breeding populations of golden-winged warblers maintained their separation during the nonbreeding period, with the Great Lakes population of golden-winged warblers occurring farther west during the nonbreeding period, on average, than

Appalachian Mountains breeding populations ($F = 213.4$; $df = 1, 39$; $P < 0.0001$; Figs. S2 and S3). Unsurprisingly, this pattern remained when we considered the relationship between individual breeding longitude and nonbreeding longitude within and between populations of golden-winged warblers (Fig. S4).

We found strong evidence to support our hypothesis that population trends of *Vermivora* warblers were associated with the distribution and isolation of historically stable and declining populations during the nonbreeding period. Historically stable populations of golden-winged warblers from breeding sites in the

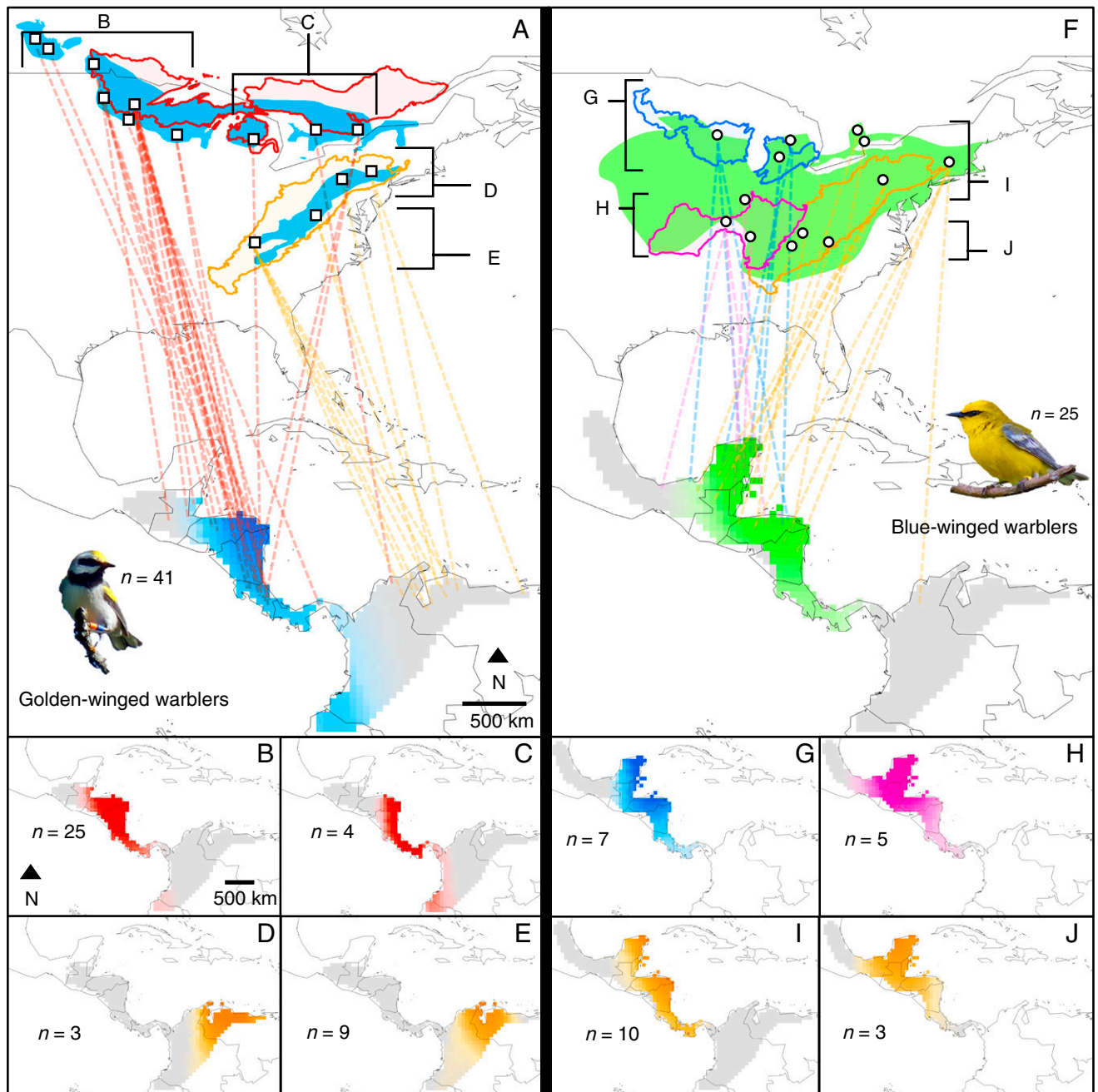


Fig. 2. Species-level average nonbreeding probability density function of golden-winged warblers (A) and blue-winged warblers (F). Dashed lines link individual warblers from breeding sites to their highest probability nonbreeding area. Colors correspond to BCRs in Fig. 1. Lines do not represent migration routes. Brackets define sites used to create population-level average probability density functions of golden-winged warblers (B–E) and blue-winged warblers (G–J). In all probability density functions, darker colors correspond to higher probability of use and the bottom 50% of probabilities are shown in gray to aid in visualization of core use areas. Range maps are adapted from BirdLife International (45). A description of BCRs is provided in Fig. 1.

Great Lakes region occurred throughout Central America during the nonbreeding period, whereas historically declining populations from breeding sites in the Appalachian Mountains region occurred in northern South America. Notably, blue-winged warblers from breeding sites in the Appalachian Mountains region (i.e., the same region in which golden-winged warblers are declining) occurred in Central America during the nonbreeding period alongside historically stable Great Lakes populations of golden-winged warblers. The remarkable similarities between these two species on the breeding grounds (e.g., nearly identical

habitat use, phenology, life-history) and co-occurrence in geographical space suggest that the differential population trends observed between populations of golden-winged warblers and blue-winged warblers breeding in the Appalachian Mountains region are likely driven by factors outside of the breeding period.

Intraspecific migratory connectivity between populations of golden-winged warblers was strong (i.e., individuals from distinct breeding populations used different areas during the nonbreeding period), and we are not aware of any other report of similarly strong connectivity from a range-wide study of distinct breeding

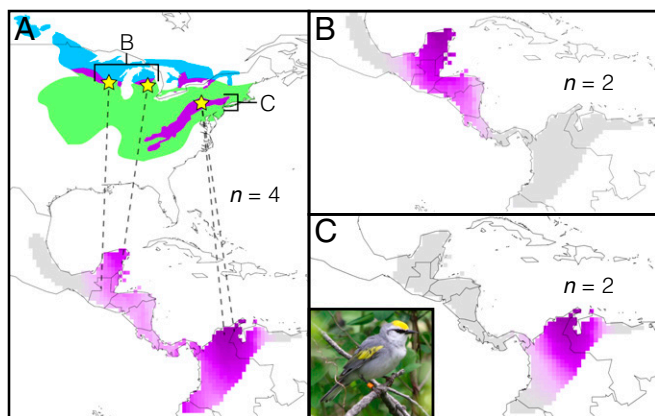


Fig. 3. Average nonbreeding probability density function of all phenotypic *Vermivora* hybrids ($n = 4$; A) and average nonbreeding probability density functions of hybrids from distinct breeding regions in the Great Lakes (B) and Appalachian Mountains (C) regions. Darker colors correspond to higher probability of use, and probabilities $<50\%$ of the maximum shown in gray to aid in visualization of core use areas. Lines represent links between individuals' breeding sites and areas of most probable nonbreeding sites but do not represent migration routes. Range maps are adapted from BirdLife International (45).

populations in another species of migratory songbird. Blue-winged warbler populations exhibited weak connectivity (i.e., individuals from distinct and isolated breeding areas co-occurred during the nonbreeding period) and occurred throughout Central America alongside golden-winged warblers from Great Lakes populations. We found weak connectivity (or high levels of dispersion) within Great Lakes golden-winged warblers and blue-winged warblers range-wide. For example, individual golden-winged warblers from breeding sites in Minnesota, where $\sim 50\%$ of the global population of golden-winged warblers breed (41), were dispersed throughout Central America, occurring from southern Mexico to Panama (maximum distance between two individuals was $>1,500$ km) during the nonbreeding period. Similarly, blue-winged warblers from breeding sites in Massachusetts were dispersed during the nonbreeding period from the Yucatan Peninsula, Mexico, to northern Colombia (maximum distance between two individuals was $\sim 2,000$ km). Without considering the individual that migrated to Colombia, Massachusetts blue-winged warblers were still broadly dispersed (maximum distance between two individuals was $\sim 1,000$ km). Conversely, populations of golden-winged warblers from breeding sites throughout the Appalachian Mountains were more concentrated in a relatively small area in northeastern Colombia and northwestern Venezuela during the nonbreeding period (maximum distance between two individuals from the same breeding site was ~ 600 km).

European migratory bird species that disperse broadly during the nonbreeding period are less likely to be declining than species with restricted distributions during the nonbreeding period compared with their breeding distributions (47, 48). We observed this trend at the population level, with greater nonbreeding dispersion among numerically stable populations (i.e., golden-winged warblers breeding in the Great Lakes and all populations of blue-winged warblers) compared with declining breeding populations (e.g., golden-winged warblers breeding in the Appalachian Mountains), suggesting that migratory diversity (i.e., within-population variation in migratory routes and/or destinations) may be linked to population trends at both species and population levels. Tracking additional individuals may uncover greater dispersion, but golden-winged warblers from Appalachian Mountains breeding populations were overrepresented in our sample based on estimated population size [29% of golden-winged warbler sample but only $\sim 5\%$ of the global population (41)];

therefore, we believe additional sampling will likely confirm low dispersion in this population.

The differential population trends observed in *Vermivora* warblers using Central American vs. South American nonbreeding areas may be caused by a variety of factors. The complexity of the ecological relationships and resource requirements that exist throughout the annual cycle of a migratory species makes it unlikely that there is a single driver of these trends. However, the identification of spatial isolation between these populations of *Vermivora* warblers suggests that the drivers of historical declines in populations of Appalachian Mountains-breeding golden-winged warblers are linked to their nonbreeding distribution in northern South America or the migratory pathways they use between breeding and nonbreeding locations. The cause of the precipitous declines of golden-winged warblers that use this region during the nonbreeding period need not be tied to a single factor, but may be the result of a reliance on a region that has experienced extensive anthropogenic exploitation and changes in land use over the past century (49–52).

Aerial photographs and/or satellite imagery covering the entire nonbreeding distribution of *Vermivora* are not available for the period when Appalachian Mountains populations of golden-winged warblers experienced their steepest declines [~ 1970 – 1980 (44)]. Furthermore, it is unlikely that golden-winged warblers in the Appalachian Mountains region began declining in 1966, the first year of the Breeding Bird Survey (41). Therefore, clearly identifying a mechanism related to these declines is challenging. Using modeled estimates of historical land-use and land-cover change (HYDE 3.1) (53–55) (*SI Materials and Methods*, in which a detailed description of the analysis is provided, and Fig. S5) for the region, we found that forest-dominated landscapes at appropriate elevations for golden-winged warblers [i.e., 200–2,400 m above sea level (41)] were converted to other, nonforest land uses in northern South America at a disproportionate rate compared with Central America (53–55) (Fig. 4). The loss of the forest-dominated landscape within the appropriate elevation envelope for golden-winged warblers in northern South America began in the early- to mid-1940s and continued through 1980 (Fig. 4). Based on our description of the migratory connectivity of *Vermivora*, these dramatic regional shifts in land use would likely affect primarily golden-winged warblers from Appalachian Mountains breeding populations (Fig. 2). Simple linear regressions reveal that these predicted changes in the amount of forest-dominated land in population-specific nonbreeding ranges explain significant variation in the breeding population trends of all three groups [(i) blue-winged warblers range-wide, 1966–2010: $F = 16.3$; $df = 1, 8$; $P = 0.004$; (ii) Great Lakes populations of golden-winged warblers, 1966–2010: $F = 13.5$; $df = 1, 8$; $P = 0.006$; and (iii) Appalachian Mountains populations of golden-winged warblers, 1966–1990: $F = 77.7$; $df = 1, 4$; $P = 0.0009$] (Fig. 4). This evidence provides a parsimonious and temporally synchronized explanation for the observed differences in breeding population trends among these three groups of *Vermivora* warblers.

Certainly, the loss of appropriate humid mid-elevation tropical forest cover types caused by changes in land use, or other consequences of human activities, may have direct effects on the survival of nonbreeding golden-winged warblers (56). However, habitat fragmentation, reduced habitat quality, and habitat loss may have nonlethal effects that lead to lower reproductive success and survival of individuals that return to North America to breed (19, 57). Additionally, golden-winged warblers migrating to northern South America from northern Appalachian Mountains breeding sites travel $>5,000$ km farther than golden-winged warblers migrating between Central America and Great Lakes breeding sites each year (29). Therefore, northern Appalachian breeding populations of golden-winged warblers may be more sensitive to declines in available food resources, phenology mismatches during migration, and/or higher risk of encountering

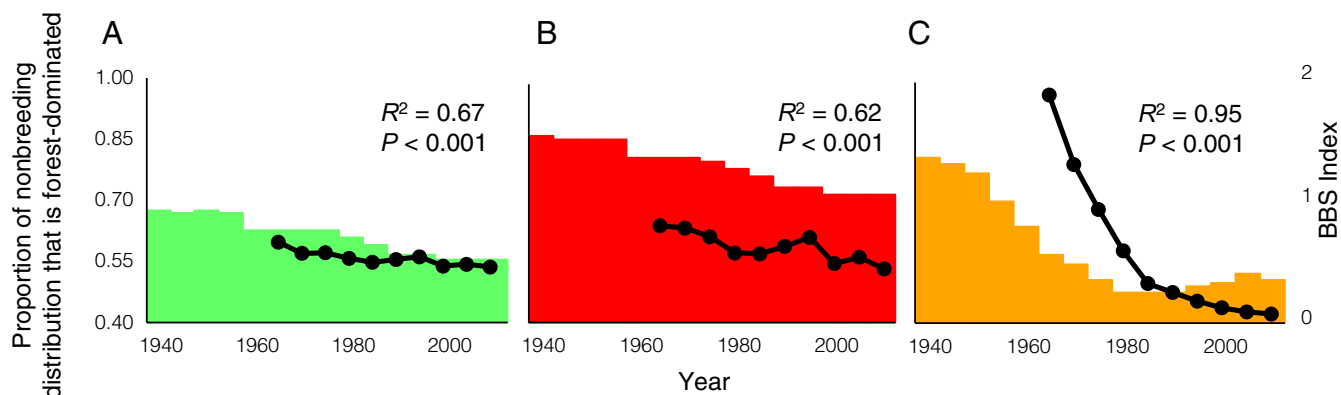


Fig. 4. Bar charts showing the modeled proportion of forest-dominated land cover at 200–2,400 m above sea level in the nonbreeding distribution of blue-winged warblers (A; Central America, southern Mexico), Great Lakes breeding populations of golden-winged warblers (B; Central America), and Appalachian Mountains breeding populations of golden-winged warblers (C; northern South America). Overlaid lines show breeding population trends (44) of each group over the same time scale. Axes for the proportion of forest (left y axis) and the Breeding Bird Survey (BBS) index (right y axis) are the same for all respective plots. Summary statistics of simple linear relationships of BBS index as a function of the proportion of forest-dominated land cover are presented. Regressions in blue-winged warblers (A) and Great Lakes breeding populations of golden-winged warblers (B) use all available years. The regression for Appalachian Mountains breeding populations of golden-winged warblers used the period 1966 to 1990 during the steepest decline and before the population was effectively reduced to near zero. Land-use data are from the HYDE 3.1 database (53–55).

predators or other obstacles during migration (16, 17, 57–59). Conversely, *Vermivora* that occur in Central America during the nonbreeding period migrate shorter distances to nonbreeding sites and are more widely dispersed during the nonbreeding period such that the effects of potentially limiting factors are not likely to be experienced by all individuals of a population. A future productive research focus may be identifying potential limiting factors during migration so as to assess the impact of differential migration strategies on population trends of *Vermivora* warblers.

We did not observe intermediate nonbreeding site affinity in probable first-generation hybrids [identified based on plumage characteristics (60)]. Hybrids with intermediate migratory traits have been described in other species (61), but the hybrids we monitored did not occur in areas that we could differentiate from one of the parental types (e.g., hybrids from the Appalachian Mountains did not occur in Panama). However, if hybrids and parental types used nonbreeding areas separated by short distances (i.e., <250 km), we would be unlikely to differentiate those sites due to the spatial resolution of geolocator data. Future research with higher resolution technology (i.e., satellite-enabled markers, global positioning system-enabled markers) may be useful in determining if hybrids exhibit intermediate phenotypes in nonbreeding site affinity that are unable to be identified with geolocators. It is challenging to identify meaningful patterns in the nonbreeding distribution of two hybrids captured in the Great Lakes portion of the breeding distribution as there is little differentiation in the nonbreeding ranges of blue-winged warblers and golden-winged warblers breeding in that region. However, the two phenotypic hybrids we tracked from the Appalachian Mountains wintered in northern South America, where golden-winged warblers from the Appalachian Mountains occur during the nonbreeding period. We note, however, that our sample of hybrids may be influenced by ascertainment bias in that we only captured and attached geolocators to hybrids that returned to breeding areas after successfully migrating to and from nonbreeding locations, reducing any opportunity to identify migration to poor-quality or inappropriate nonbreeding locations that negatively influenced survival or breeding propensity (13). It is likely that the hybrid individuals we captured and tracked originated from interspecific pairings or extrapair copulations between parental species in the Appalachian Mountains region. Given the results of this study, the hybrid offspring of these pairings likely received genetic information from a blue-winged warbler that wintered in Central America and a golden-winged warbler that wintered in

northern South America. If a subset of hybrid individuals produced in the Appalachian Mountains with a genetic predisposition to migrate to Central American nonbreeding areas does not survive (possibly due to a multitude of reasons, including a recombination of alleles that results in maladaptive migratory orientation or another postzygotic barrier), disperses to breeding areas that are outside the Appalachian Mountains (i.e., nonbreeding site affinity and breeding site affinity are genetically linked), or does not exhibit breeding behavior, our sample of hybrids would likely be biased. Further research is required to fully account for the behaviors of hybrid *Vermivora* warblers during their first migration and winter and to identify specific genomic regions associated with different migratory phenotypes (62).

It is unlikely that golden-winged warblers are the only broadly dispersed Nearctic-Neotropical migrant songbird species that exhibits strong migratory connectivity and shows population trends consistent with being limited by nonbreeding factors. Our results confirm that migratory connectivity and the nonbreeding distribution of species can be linked to breeding population trends. However, range-wide geolocator studies are expensive and logistically challenging, and being able to identify potential candidate species that may exhibit these similar relationships without mounting a continent-wide study would be valuable. We therefore identified 25 species of Nearctic-Neotropical migrant passerines that have similar nonbreeding distributions to *Vermivora* warblers and broadly dispersed breeding distributions (*Materials and Methods*, Fig. S6, and Table S2). Of those 25 species, we identified 16 (64%) that showed structured differences in regional breeding population trajectories that could be caused by nonbreeding factors (Table S2). Six of those species showed similar patterns in range-wide population trends as golden-winged warblers (declines from 1966 to 1990, followed by stable trends from ~1990 to 2015). Without detailed knowledge of the factors affecting population trends of these species, we predict their regionally distinct breeding population trends may be linked to migratory connectivity and nonbreeding distribution similar to what we observed in golden-winged warblers. The Kentucky warbler (*Geothlypis formosa*) stands out as one of the most likely candidates to exhibit strong migratory connectivity based on these assumptions (Fig. S6 and Table S2). Kentucky warblers exhibit a dichotomous north-south pattern in their breeding population trends and occur in the same regions as golden-winged warblers during the nonbreeding period. In addition, range-wide declines starting in 1966 have leveled off and

global population trends have been stable since ~1990, similar to golden-winged warblers. Kentucky warblers may be another species that exhibits strong migratory connectivity, and like golden-winged warblers, signals of strong connectivity (e.g., coinciding population declines) may be shared among species that occupy similar regions and are affected by similar limiting factors during the annual cycle.

More complex scenarios may explain the patterns in population trends exhibited by Kentucky warblers and the other species we have promoted as potential candidates to exhibit strong migratory connectivity. There also are factors (e.g., regionally specific breeding-ground factors) that could obfuscate or mask the purported signals that we used to identify species that may exhibit strong migratory connectivity. Identifying species with strong connectivity and understanding the implications of such strong connectivity are timely and important (63). If anthropogenic changes in land-use patterns in northern South America are identified as a key factor driving population declines of golden-winged warblers occurring in that region during the nonbreeding period, then the strong migratory connectivity we observed in golden-winged warblers may constitute an evolutionary trap (64). In this case, anthropogenic factors that are limiting populations may be occurring over a relatively short period and outpacing the natural ability of these populations to adapt. Understanding the implications (65, 66) and diversity (67–69) of patterns in the distribution of migratory species throughout the annual cycle will aid in predicting the effects of continuously changing anthropogenic factors on migratory species globally (70).

Conclusion

We provide details on the distribution and migratory connectivity of two closely related, Nearctic-Neotropical migrant songbird species, which recent genetic evidence suggests may be plumage morphs of a single-species complex. More importantly, we show through a thorough sampling of populations throughout these species' breeding ranges that strong connectivity leading to the isolation and segregation of populations during the nonbreeding period may be associated with patterns in breeding population trends. Unlike blue-winged warblers, golden-winged warblers exhibited strong migratory connectivity, with declining populations occurring exclusively in northern South America. Identifying the factors that led to the severe declines and local extirpation of golden-winged warblers in the Appalachian Mountains region will be critical for their long-term conservation. Our observations of migratory connectivity in *Vermivora* warblers represent a major advance in understanding the unique drivers shaping migration strategies; the distribution of populations throughout the annual cycle; and, ultimately, the evolutionary trajectories of migrants in the rapidly changing Anthropocene. Studies like ours may benefit future research focused on identifying genomic regions associated with specific migratory behaviors. Our findings highlight the value of collecting information about the annual movements of species across their distribution, and studies like ours can aid in the conservation of migratory species, such as *Vermivora* warblers, in the future.

Materials and Methods

Study Area and General Procedures. We studied golden-winged warblers, blue-winged warblers, and their hybrids across their breeding distributions in eastern North America from 2013 to 2017. A small portion of these results include a reanalysis of geolocator data (<https://conservancy.umn.edu/handle/11299/183086>) reported by Kramer et al. (29). Study areas were chosen based upon location (i.e., representing the greatest geographic distribution), density of *Vermivora* warblers, and ease of access. *Vermivora* warblers are diverse-forest species that are often associated with young, regenerating forest surrounded by a larger matrix of mature forest, and our study sites reflected the full range of land-cover types used by these species (71). We captured all warblers in mist nets using conspecific call and song broadcasts. Upon initial capture, we determined age and sex, assigned a phenotypic

species (i.e., typical golden-winged warbler, typical blue-winged warbler, hybrid) based on plumage traits (60), and weighed and banded each individual with a US Geological Survey/Canadian Wildlife Service aluminum band and one to three plastic color leg bands to aid in future identification. We attached geolocators (model ML6240, 2-min light-sampling regime; Biotrack Ltd.) to male *Vermivora* warblers that we determined to exhibit territorial or breeding behaviors (i.e., resident, nonmigratory behaviors) using an adapted leg-loop harness that was developed and tested on this species complex without any known negative effects (72–74). All birds were released after processing, and we monitored geolocator-marked birds for signs of stress during a brief (~1–15 min) acclimation period.

The year following deployment, we returned to the sites where we marked warblers with geolocators and attempted to recapture all marked birds that returned. *Vermivora* warblers exhibit high site fidelity when their breeding habitat is not altered or removed and often return to the same territories year after year (73, 75). Thus, we began searches for returning geolocator-marked birds at the site where they were marked the previous year. We expanded our search radius to include appropriate breeding cover types within ~1–3 km of the deployment site depending on the site and the surrounding landscape. We used the same methods as described above to lure returning geolocator-marked individuals into mist nets. We then removed the geolocator and released the warbler at its capture location. We attached new geolocators to a subset of individuals that successfully carried a geolocator in 2013 or 2014 in an attempt to understand whether individuals use different nonbreeding areas in different years (a discussion of how we treated individuals with multiple years of data is provided in the next section).

We captured and marked birds following Protocol 561, approved by the University of Tennessee Institutional Animal Care and Use Committee; Protocol 104A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee; Virginia Commonwealth University Institutional Animal Care and Use Committee Proposal 10230; and Protocols 07-0303 and 10-0201 approved by the West Virginia University Institutional Animal Care and Use Committee.

Geolocator Data Analysis. We downloaded and decompressed raw light-level data from geolocators using BASTrack software (Bastrack Ltd.). All additional processing and analyses were conducted in R (76). Briefly, we followed the methods described by Kramer et al. (29) to derive nonbreeding probability density functions for each individual during the tropical dry season (i.e., January 1–February 28). This period represents the nonbreeding period when we assumed individuals were residing on nonbreeding territories and were exposed to the least environmental shading. We used FLIGHTR (77) to estimate spatially explicit likelihood surfaces (~0.5° cell size) for each transition period (i.e., sunrise, sunset) from January 1 to February 28. We used a subset of data or data from a different portion of the nonbreeding period if data were unavailable from January 1 to February 28 (due to geolocator failure or occlusion of the light sensor; Table S1). We then averaged all transition-derived likelihood surfaces for each individual to produce an average probability density function showing the most probable regions used by that individual during the nonbreeding period. We transformed individual nonbreeding likelihood surfaces into probability density functions by dividing each likelihood surface by the sum of its surface. We averaged nonbreeding probability density functions of individuals from the same breeding populations to achieve a population-level probability density function representing areas most likely used by an individual warbler from each population during the nonbreeding period.

Because that portion of the Neotropics used during the nonbreeding period by *Vermivora* warblers extends primarily from west to east, we used longitude as a proxy for individual nonbreeding site location in our calculations and estimations of overlap. Longitude is more accurate than latitude in geolocator analyses and can be useful for determining movement and location (78), especially in terrestrial organisms that are constrained to land during the period of interest but travel through regions that are bounded to the north and south by expansive water (e.g., Central America). To estimate nonbreeding site longitude, we extracted the longitude of the highest probability cell in the probability density function for each individual. We averaged the nonbreeding probability density functions for warblers for which we collected 2 y of data ($n = 6$) so that those individuals did not bias estimates of average nonbreeding distribution of populations.

Statistical Analysis. We evaluated differences between the nonbreeding distributions of populations using linear regression and one-way ANOVA and post hoc Tukey honest significance difference tests in R unless otherwise noted. Results of all tests were considered significant at $\alpha = 0.05$. We investigated the level of migratory connectivity in populations of *Vermivora*

warblers based on BCRs for which annual population-level sampling is conducted and reported by the Breeding Bird Survey (44). Golden-winged warbler populations are largely contained within two BCRs: Boreal Hardwood Transition BCR (S12; i.e., Great Lakes population) and Appalachian Mountains BCR (S28; i.e., Appalachian Mountains population). Blue-winged warblers are more widespread, but our study sites fell primarily in three BCRs: Prairie Hardwood Transition BCR (S23), Central Hardwoods BCR (S24), and Appalachian Mountains BCR (S28). For both blue-winged warblers and golden-winged warblers, we split the Appalachian Mountains BCR into northern and southern halves (separated at ~39° N) to investigate potential differences in the nonbreeding distributions of these groups of *Vermivora*. For golden-winged warblers, we also split the Great Lakes population (BCR 12) into eastern and western portions (~85° W) for the same purpose.

Predicting Other Species with Nonbreeding Population Structure. We used range data from BirdLife International (45) to visually inspect the nonbreeding distributions of Nearctic-Neotropical migrant songbird species. We identified species that occurred in both Central America and South America during the nonbreeding period, as observed in golden-winged warblers (Table S2). We then visually inspected breeding period trend maps from the Breeding Bird Survey (44) and identified species that showed structured, regional variation in population trends. Finally, we visually inspected the survey-wide population trends for those species and noted their general population trends from 1966 to 1990 and 1991 to 2015. From 1966 to ~1985, the range-wide population trend of golden-winged warblers declined as a result of the loss of individuals from the Appalachian Mountains breeding population. Following that decline, the range-wide population trend stabilized between 1985 and 1990. If other species had strong migratory connectivity similar to that which we observed in golden-winged warblers (i.e., isolated breeding populations occurring separately in Central America and South America during the nonbreeding period), one might expect to see a similar trend over the same period if limiting factors (e.g., deforestation, fragmentation; Fig. 4) were also affecting other Nearctic-Neotropical migrant populations. For example, yellow-throated vireos (*Vireo flavifrons*) are broadly dispersed throughout eastern North America during the breeding period and occur in both Central America and northern South America during the nonbreeding period. Eastern populations of yellow-throated vireos tend

to be declining more than western populations. However, survey-wide trends of yellow-throated vireos revealed a stationary trend from 1966 to 1985, switching to increasing population trends from 1986 to 2010 (44). This suggests that the factors limiting yellow-throated vireos are different from those limiting golden-winged warblers; therefore, we predict that it is unlikely that yellow-throated vireos have similar nonbreeding population distribution and migratory connectivity as golden-winged warblers.

Data Accessibility

Data used for this study are freely and publicly available [data conservation provided by the Data Repository for the University of Minnesota (<https://conservancy.umn.edu/handle/11299/193202>)]. All other data used in this study were retrieved from publicly accessible databases.

ACKNOWLEDGMENTS. We thank M. Barber, M. Barnes, J. Bell, J. Chancey, L. Coe-Starr, C. Colley, E. Davis, J. Dodson, K. Eckert, R. Eckstein, R. Fenty, C. Fiss, M. Gallagher, B. Gray, A. Grupenhoff, C. Henderson, L. Hendrixson, N. Henke, E. Hess, L. Hoehn, J. Kawlewski, B. Keinath, J. Koberdahl, L. Loegering, S. McLaughlin, S. Midthune, L. Mielke, D. Miles, M. Morin, N. Moy, J. Nelson, A. Pesano, S. Prevost, J. Reubensam, M. Schilling, N. Seeger, L. Schofield, A. Tomcho, S. Wallace, J. Warmbold, J. Wessels, A. Worm, B. Yliniemi, and others for assistance in the field. We are especially grateful to N. Hill, K. Maley, D. McNeil, R. Pagel, P. Rodrigues, K. Stein, and C. Ziegler for their commitment to the project, and to W. Ford, W. Bringer, A. Hewitt, D. King, J. Larkin, and H. Saloka for providing logistical support. We thank D. Toews and two anonymous reviewers for comments improving earlier drafts of this manuscript. These data were collected during a project funded by the US Fish and Wildlife Service and the US Geological Survey through Research Work Order 98 at the US Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, and by the National Science Foundation through Postdoctoral Research Fellowship 1202729 (to H.M.S.). Additional funding was provided by the Virginia Department of Game and Inland Fisheries and the Grace Jones Richardson Trust. None of our funders had any influence on the content of the submitted or published manuscript, and only the US Geological Survey required approval of the final manuscript prior to publication as required in their Fundamental Sciences Practices protocols. Use of trade names does not imply endorsement by the US Geological Survey or any other institutions affiliated with this study.

- Sherry TW, Holmes RT (1996) Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77:36–48.
- Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: Unraveling migratory connectivity. *Trends Ecol Evol* 17:76–83.
- Faaborg J, et al. (2010) Conserving migratory land birds in the New World: Do we know enough? *Ecol Appl* 20:398–418.
- Wilkes C (1845) *Narrative of the United States Exploring Expedition During the Years 1838, 1839, 1840, 1841 and 1842* (C Sherman, Philadelphia), Vol 5.
- Maury MF (1851) *The Winds and Currents of the Sea* (National Observatory, Washington, DC).
- Lincoln FC (1921) The history and purposes of bird banding. *Auk* 38:217–218.
- Hanson HC, Smith RH (1950) Canada geese of the Mississippi flyway with special reference to an Illinois flock. *Bull Ill Nat Hist Surv* 25:67–210.
- Dawbin WH (1956) The migrations of humpback whales which pass the New Zealand coast. *Trans R Soc NZ* 84:147–196.
- Mandel JT, Bildstein KL, Bohrer G, Winkler DW (2008) Movement ecology of migration in turkey vultures. *Proc Natl Acad Sci USA* 105:19102–19107.
- Holland RA, Wikelski M, Wilcove DS (2006) How and why do insects migrate? *Science* 313:794–796.
- Stutchbury BJM, et al. (2009) Tracking long-distance songbird migration by using geolocators. *Science* 323:896.
- Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* 120:314–326.
- Hewson CM, Thorup K, Pearce-Higgins JW, Atkinson PW (2016) Population decline is linked to migration route in the common cuckoo. *Nat Commun* 7:12296.
- Prop J, Black JM, Shimmings P (2003) Travel schedules to the high Arctic: Barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103:403–414.
- Hebblewhite M, Merrill EH (2007) Multiscale wolf predation risk for elk: Does migration reduce risk? *Oecologia* 152:377–387.
- Deppe JL, et al. (2015) Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proc Natl Acad Sci USA* 112:E6331–E6338.
- Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71:296–308.
- Taylor CM, Stutchbury BJM (2016) Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. *Ecol Appl* 26:424–437.
- Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- Fraser KC, et al. (2012) Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proc Biol Sci* 297:4901–4906.
- Stanley CQ, et al. (2015) Connectivity of wood thrush breeding, wintering, and migration sites based on range-wide tracking. *Conserv Biol* 29:164–174.
- Hallworth MT, Sillett TS, Van Wilgenburg SL, Hobson KA, Marra PP (2015) Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. *Ecol Appl* 25:336–347.
- Toews DPL (2017) Habitat suitability and the constraints of migration in New World warblers. *J Avian Biol* 48:1614–1623.
- Burgio KR, Carlson CJ, Tingley MW (2017) Lazarus ecology: Recovering the distribution and migratory patterns of the extinct Carolina parakeet. *Ecol Evol* 7:5467–5475.
- Winger BM, Barker FK, Ree RH (2014) Temperate origins of long-distance seasonal migration in New World songbirds. *Proc Natl Acad Sci USA* 111:12115–12120.
- Richardson DE, et al. (2016) Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*). *Proc Natl Acad Sci USA* 113:3299–3304.
- Sawyer H, Kauffman MJ, Nielson RM, Horne JS (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecol Appl* 19:2016–2025.
- Iwamura T, et al. (2013) Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proc Biol Sci* 280:20130325.
- Kramer GR, et al. (2017) Nonbreeding isolation and population-specific migration patterns among three populations of golden-winged warblers. *Condor Ornith Appl* 119:108–121.
- Wolfson D, Fieberg J, Lawrence JS, Cooper TR, Andersen DE (2017) Range overlap between Mid-Continent and Eastern sandhill cranes revealed by GPS-tracking. *Wildl Soc Bull* 41:489–498.
- Finch T, Butler SJ, Franco AMA, Cresswell W (2017) Low migratory connectivity is common in long-distance migrant birds. *J Anim Ecol* 86:662–673.
- Hahn S, Amrhein V, Zehntindjiev P, Liechti F (2013) Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. *Oecologia* 173:1217–1225.
- Finch T, et al. (2015) A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. *Divers Distrib* 21:1051–1062.
- Hobson KA, et al. (2015) A continent-wide migratory divide in North American breeding barn swallows (*Hirundo rustica*). *PLoS One* 10:e0129340.
- Ouwehand J, et al. (2016) Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *J Avian Biol* 47:69–83.
- Toews DPL, et al. (2016) Plumage genes and little else distinguish the genomes of hybridizing warblers. *Curr Biol* 26:2313–2318.

37. Bennett RE, et al. (2017) Extreme genetic similarity does not predict non-breeding distribution of two closely related warblers. *J Field Ornithol* 88:156–158.
38. Vallender R, Friesen VL, Robertson RJ (2007) Paternity and performance of golden-winged warbler (*Vermivora chrysoptera*) and golden-winged X blue-winged warbler (*V. pinus*) hybrids at the leading edge of a hybrid zone. *Behav Ecol Sociobiol* 61: 1797–1807.
39. Vallender R, Robertson RJ, Friesen VL, Lovette IJ (2007) Complex hybridization dynamics between golden-winged and blue-winged warblers (*Vermivora chrysoptera* and *Vermivora pinus*) revealed by AFLP, microsatellite, intron and mtDNA markers. *Mol Ecol* 16:2017–2029.
40. Neville KJ, Vallender R, Robertson RJ (2008) Nestling sex ratio of golden-winged warblers *Vermivora chrysoptera* in an introgressed population. *J Avian Biol* 39: 599–604.
41. Rosenberg KV, et al. (2016) Dynamic distributions and population declines of golden-winged warblers. *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*, eds Streby HM, Andersen DE, Buehler DA (CRC, Boca Raton, FL), pp 3–28.
42. Streby HM, et al. (2016) Research on golden-winged warblers: Recent progress and current needs. *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*, eds Streby HM, Andersen DE, Buehler DA (CRC, Boca Raton, FL), pp 217–227.
43. Pardieck KL, Ziolkowski DJ, Jr, Lutmerding M, Campbell K, Hudson MAR (2016) North American Breeding Bird Survey Dataset 1966–2016 (US Geological Survey, Patuxent Wildlife Research Center, Laurel, MD). Version 2016.0. Available at <https://www.pwrc.usgs.gov/bbs/results/>. Accessed August 1, 2016.
44. Sauer JR, et al. (2017) *The North American Breeding Bird Survey, Results and Analysis 1966–2015* (US Geological Survey Patuxent Wildlife Research Center, Laurel, MD). Version 2.07.2017.
45. BirdLife International and Handbook of the Birds of the World (2016) Bird species distribution maps of the world. Version 6.0. Available at datazone.birdlife.org/species/requestdis. Accessed June 30, 2017.
46. Hobson KA, et al. (2016) Golden-winged warbler migratory connectivity derived from stable isotopes. *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*, eds Streby HM, Andersen DE, Buehler DA (CRC, Boca Raton, FL), pp 193–203.
47. Fuller RA (2016) Animal migration: Dispersion explains declines. *Nature* 531:451–452.
48. Gilroy JJ, Gill JA, Butchart SHM, Jones VR, Franco AMA (2016) Migratory diversity predicts population declines in birds. *Ecol Lett* 19:308–317.
49. Hansen MC, Stehman SV, Potapov PV (2010) Quantification of global gross forest cover loss. *Proc Natl Acad Sci USA* 107:8650–8655.
50. Negret PJ, Allan J, Braczkowski A, Maron M, Watson JEM (2017) Need for conservation planning in postconflict Colombia. *Conserv Biol* 31:499–500.
51. Runge CA, et al. (2015) Protected areas and global conservation of migratory birds. *Science* 350:1255–1258.
52. Dávalos LM, et al. (2011) Forests and drugs: Coca-driven deforestation in tropical biodiversity hotspots. *Environ Sci Technol* 45:1219–1227.
53. Goldewijk KK, Beusen A, Janssen P (2010) Long term dynamic modeling of global population and build-up area in a spatially explicit way, HYDE 3.1. *Holocene* 20: 565–573.
54. Goldewijk KK, Beusen A, van Drecht G, de Vos M (2011) The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Glob Ecol Biogeogr* 20:73–86.
55. Meiyappan P, Jain AK (2012) Three distinct global estimates of historical land-cover change and land-use conversions for over 200 years. *Front Earth Sci* 6:122–139.
56. Chandler RB, et al. (2016) Conservation implications of golden-winged warbler social and foraging behaviors during the nonbreeding season. *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*, eds Streby HM, Andersen DE, Buehler DA (CRC, Boca Raton, FL), pp 175–192.
57. Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* 80:4–18.
58. Legagneux P, Fast PLF, Gauthier G, Bêty J (2012) Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. *Proc Biol Sci* 279:876–883.
59. Loss SR, Will T, Loss SA, Marra PP (2014) Bird-building collisions in the United States: Estimates of annual mortality and species vulnerability. *Condor Ornith Appl* 116:8–23.
60. Parkes KC (1951) The genetics of the golden-winged X blue-winged warbler complex. *Wilson Bull* 63:5–15.
61. Delmore KE, Irwin DE (2014) Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol Lett* 17:1211–1218.
62. Lundberg M, et al. (2017) Genetic differences between willow warbler migratory phenotypes are few and cluster in large haplotype blocks. *Evol Lett* 1:155–168.
63. Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM (2015) A call for full annual cycle research in animal ecology. *Biol Lett* 11:201500552.
64. Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. *Trends Ecol Evol* 17:474–480.
65. Vansteelant WMG, Kekkonen J, Byholm P (2017) Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. *Proc Biol Sci* 284:20170387.
66. Gill RE, et al. (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? *Proc Biol Sci* 276:447–457.
67. Streby HM, et al. (2015) Tornadoic storm avoidance behavior in breeding songbirds. *Curr Biol* 25:98–102.
68. Egevang C, et al. (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc Natl Acad Sci USA* 107:2078–2081.
69. McKinnon EA, Artuso C, Love OP (2017) The mystery of the missing warbler. *Ecology* 98:1970–1972.
70. Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
71. Aldinger KR, et al. (2015) Variables associated with nest survival of golden-winged warblers (*Vermivora chrysoptera*) among vegetation communities commonly used for nesting. *Avian Conserv Ecol* 10:6.
72. Rappole JH, Tipton AR (1991) New harness design for attachment of radio transmitters to small passerines. *J Field Ornithol* 62:335–337.
73. Peterson SM, et al. (2015) Geolocators on golden-winged warblers do not affect migratory ecology. *Condor Ornith Appl* 117:256–261.
74. Streby HM, et al. (2015) Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. *Condor Ornith Appl* 117: 249–255.
75. Bulluck L, Buehler D, Vallender R, Robertson RJ (2013) Demographic comparison of golden-winged warbler (*Vermivora chrysoptera*) populations in northern and southern extremes of their breeding range. *Wilson J Ornithol* 125:479–490.
76. R Core Team (2016) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna). Available at <https://www.R-project.org/>. Accessed June 30, 2016.
77. Rakhimberdiev E, Saveliev A, Piersma T, Karagicheva J (2017) FLIGHTR: An R package for reconstructing animal paths from solar geolocation loggers. *Methods Ecol Evol* 8: 1482–1487.
78. Rakhimberdiev E, et al. (2016) Comparing inferences of solar geolocation data against high-precision GPS data: Annual movements of a double-tagged black-tailed godwit. *J Avian Biol* 47:589–596.