CHAPTER FOURTEEN

Research on Golden-winged Warblers*

RECENT PROGRESS AND CURRENT NEEDS

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Abstract. Considerable advances have been made in knowledge about Golden-winged Warblers (*Vermivora chrysoptera*) in the past decade. Recent employment of molecular analysis, stable-isotope analysis, telemetry-based monitoring of survival and behavior, and spatially explicit modeling techniques have added to, and revised, an already broad base of published knowledge. Here, we synthesize findings primarily from recent peer-reviewed literature on Golden-winged Warblers, from this volume and elsewhere, and we identify some of the substantial remaining research needs. We have organized this synthesis by stages of the Golden-winged Warbler annual cycle. First, we discuss the relatively well-studied breeding-grounds ecology including nesting and post-fledging ecology and hybridization with closely related Blue-winged Warblers (*Vermivora cyanoptera*). Second, we discuss the much-less-studied, non-breeding-grounds ecology, including the first empirical studies of non-breeding-grounds cover-type associations and spatial and social behavioral ecology. Third, we address migratory connectivity and migration ecology, for which little is known and research has only just begun. Last, we close with cautious optimism that current knowledge is adequate to inform initial conservation and management plans for Golden-winged Warblers, and with a sobering acknowledgement of the quantity of research still needed.

Key Words: annual cycle, breeding ecology, hybridization, migration, nonbreeding ecology, *Vermivora cyanoptera*.

BREEDING-GROUNDS ECOLOGY

Nesting-Habitat Associations and Nesting Ecology

The nesting ecology of Golden-winged Warblers has been the focus of most research on the species prior to this volume of Studies in Avian Biology (Ficken and Ficken 1968, Klaus and Buehler 2001, Martin et al. 2007, Vallender et al. 2007a, Confer et al. 2010) and within this volume (Chapters 7 and 9, this volume). Across their breeding distribution, Golden-winged Warblers are typically associated

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with landscapes dominated by forest in later seral stages (hereafter, later successional forest) with openings of shrub–sapling and herbaceous vegetation that can be shrub-dominated uplands or wetlands or very young forest (hereafter, shrublands or early successional areas). However, beyond this broad-stroke description of the breeding landscape structure, results reported here and elsewhere suggest there is no one-size-fits-all breeding habitat description at the stand-level scale (Chapter 9, this volume) or the territory or nest-site scale (Confer et al. 2003, Bulluck and Buehler 2008, Aldinger and Wood 2014; Chapter 7, this volume) that is consistently associated with nesting habitat selection and nest success of Golden-winged Warblers.

Perhaps not surprising, considering the tremendous variation in plant communities across the breeding distribution of Golden-winged Warblers, the relative importance of small-scale vegetation characteristics such as percent ground cover by certain species or vegetation types to nesting habitat selection and nest success is not generalizable among regions or even among sites within a region (Chapter 7, this volume). Studies incorporating data from many sites primarily in the Appalachian Mountains region support the results of previous single-site studies (Confer et al. 2003, 2010; Bulluck and Buehler 2008; Kubel and Yahner 2008; Roth et al. 2014), indicating fine-scale vegetation associations of nesting Golden-winged Warblers are mostly site-specific. Furthermore, spatially explicit models of full-season productivity, or young raised to independence from adult care, indicate that a single management action can affect productivity differently depending on the cover-type composition of the surrounding landscape (Chapter 10, this volume). Therefore, it is unlikely there is any single stand-level management action, such as increasing area of shrubland, that generally increases Golden-winged Warbler productivity, at least in the western Great Lakes region. In fact, Chapter 10 (this volume) demonstrated that in some areas that already host highly productive populations, reducing the area of later successional forest can have a net negative impact on population productivity, even if breeding density increases. As frustrating as it might be that there is no evidence for a single management prescription that can be applied broadly to benefit breeding Golden-winged Warblers, the knowledge that management and conservation plans must be flexible and locally informed is an equally important research outcome.

Postfledging Survival and Habitat Associations

For two decades, a growing body of literature has demonstrated that postfledging survival and habitat associations are critical components of breeding-grounds ecology in migratory songbirds (Anders et al. 1997, Streby and Andersen 2011). Several species that nest in later successional forest use early successional areas during the postfledging period (Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007, Streby et al. 2011) and in some species, a mid-season switch in cover-type associations can benefit body condition (Stoleson 2013) and fledgling survival (Streby and Andersen 2013a, Vitz and Rodewald 2013). To our knowledge, recent postfledging research on Golden-winged Warblers represents the first report of the opposite pattern, in which a species most commonly associated with nesting in early successional areas selects later successional forest for raising young (Streby et al. 2014a, 2015a; Chapters 8 through 10, this volume).

In the western Great Lakes region, Golden-winged Warblers choose later successional forest over shrublands for raising recently fledged young (Streby et al. 2014a; Chapter 8, this volume). Parents of both sexes raise fledglings in later successional forest, but adult females lead fledglings hundreds of meters away from natal stands before young are independent from adult care (Chapter 10, this volume). In addition, fledglings choose later successional forest over all other cover types after independence from adult care (Streby et al. 2015a). Postfledging research is currently underway in populations within the Appalachian Mountains region (J. A. Lehman, unpubl. data), and those studies could provide at least a partial explanation for the substantial differences in population growth between regions with similar fledgling production from nests and apparently similar adult annual survival. Indeed, pilot research in Tennessee suggests that fledgling survival there might be low (J. A. Lehman, unpubl. data).

Limitations of Current Breeding-Grounds Knowledge

A tremendous amount of research has focused on breeding Golden-winged Warblers in the past few decades and that research has provided considerable new insights. However, many important gaps remain in our understanding of the breeding-grounds ecology of Golden-winged Warblers. For example, attempts to relate food availability to foraging habitat selection (Chapter 6, this volume) are complicated by limited available data on the diet of Golden-winged Warblers (Streby et al. 2014b). The published and anecdotal descriptions of diet in Golden-winged Warblers (summarized in Confer et al. 2011, Streby et al. 2014b) suggest their diet may be too specialized for food availability to be sampled with standard methods. Leaf-roller caterpillars (*Archips* spp.) constitute 89% of the diet of nestling and fledgling Golden-winged Warblers in Minnesota and Manitoba (Streby et al. 2014b), but initial attempts to develop efficient prey sampling methods indicated the required sampling effort might be a prohibitive challenge (B. Vernasco, unpubl. data). Regardless, recent evidence suggests patterns of differential arthropod abundance and distribution among shrub and tree species influence territory placement by Golden-winged Warblers in central Pennsylvania (Chapter 6, this volume). Quantifying diet across the entire distribution and throughout the breeding season, and developing methods for sampling prey abundance and phenology, is necessary precursors for future work regarding potential range shifts, predator–prey mismatches, and inter- and intraspecific resource competition.

Many remaining gaps in knowledge of the breeding ecology of Golden-winged Warblers are related to the question of transferability or the geographic range of inference from observations made at only one or a few locations. For example, are the radiotelemetry-based observations that song territories are considerably larger than those based on spot mapping (Streby et al. 2012), that breeding adults forage in later successional forest (Streby et al. 2012; Chapter 5, this volume), and that a considerable proportion of females nest in later successional forest adjacent to early successional stands (Streby et al. 2014a; Chapter 10, this volume) consistent in other portions of the breeding distribution? How widespread is the problem of misidentifying nest fates based on traditional monitoring methods (Streby and Andersen 2013b), and what impact does that bias have on local and regional productivity estimates? What are the factors underlying female mate choice, as song variation (Harper et al. 2010) and plumage phenotype of social mates (Vallender et al. 2007a) do not appear to be important? Are the positive relationships between residual tree retention after forest harvest and breeding-male density and pairing success observed in Wisconsin (Roth et al. 2014) also present in the Appalachian region where breeding densities are relatively low, or in areas of Minnesota where pairing success is near 100%? Do patterns of postfledging cover-type selection observed in the western Great Lakes region (Chapter 8, this volume) hold true in the rest of the Golden-winged Warbler breeding distribution? If not, what are the cover types and habitat characteristics associated with high fledgling survival in populations outside the western Great Lakes region?

The vast majority of research on breeding Golden-winged Warblers has focused on the nesting season in the Appalachian population segment, which is declining and represents ~5% of the global breeding population (Chapter 1, this volume). Current breeding-distribution-wide conservation plans are based on published and unpublished data of which nearly all represent the Appalachian Mountains region (A. M. Roth et al., unpubl. plan), and little data represent the other 95% of the global breeding population of Golden-winged Warblers. The precipitous decline of the Appalachian population segment necessitates intensive monitoring and research designed to identify the causes of the decline and develop strategies and plans to reverse it. However, there is an inherent risk of bias when deriving most of the knowledge about a species from small and declining populations, especially if that knowledge is intended to inform management and conservation for the species as a whole. Until recently, relatively little research had focused on Golden-winged Warblers in the western Great Lakes region where a majority of the species breeds (Streby et al. 2012, Roth et al. 2014; Chapters 9 and 10, this volume). More information is needed on breeding-grounds ecology in this core, with respect to population density, of the Golden-winged Warbler breeding distribution, where population numbers are relatively stable (Chapter 1, this volume), or apparently recently populated and increasing, such as parts of Manitoba (Sauer et al. 2012). Currently, the only information available about postfledging ecology of Golden-winged Warblers is from the western Great Lakes region. Considering the importance of fledgling survival to full-season productivity and population growth of songbirds (Anders et al. 1997, Faaborg et al. 2010a, Streby and

Andersen 2011), and of Golden-winged Warblers in particular (Streby et al. 2014a; Chapter 8, this volume), research on postfledging ecology is a pressing need in the Appalachian Mountains breeding-distribution segment.

Rapidly Changing Knowledge of Breeding-Grounds Cover-Type Associations

In a special section of The Wildlife Society Bulletin summarizing research on Golden-cheeked Warblers (*Setophaga chrysoparia*), Morrison et al. (2012) made a unique and valuable contribution that also rings true with Golden-winged Warblers. Morrison et al. (2012) described how a prevailing paradigm can hinder progress in current research and conservation. In Golden-cheeked Warblers, a limited and biased understanding of the distribution, habitat associations, and status of the species led to research unconsciously designed to perpetuate the prevailing paradigm, which reduced the efficacy of conservation efforts (Morrison et al. 2012). Similar biased paradigm perpetuation is evident in Golden-winged Warbler breeding-grounds research. Golden-winged Warblers are commonly described as an early successional shrubland specialist throughout the published literature (Confer and Knapp 1981, Confer et al. 2011). The current paradigm acknowledges that early successional stands or patches must be within a later successional forested matrix to host breeding Golden-winged Warblers, and a positive association between Golden-winged Warblers and primarily forested landscapes has been demonstrated (Thogmartin 2010). However, the degree to which later successional forest is used by Golden-winged Warblers throughout the breeding season is only starting to be appreciated.

The early successional specialist paradigm is so entrenched in Golden-winged Warbler research that early successional or open shrubby areas are commonly described as "study sites" bounded by the edges of later successional forest (Ficken and Ficken 1968; Confer et al. 2011; Roth et al. 2014; Chapter 7, this volume). Early successional areas are certainly a critical component of breeding habitat, and Golden-winged Warblers are usually not observed breeding in landscapes that lack at least some forest openings. However, recent research published in this volume and elsewhere demonstrates that later successional forest is used throughout the breeding season for nesting, foraging, and raising young. Adult Golden-winged Warblers usually include later successional forest in territories and home ranges (Streby et al. 2012; Chapter 5, this volume), especially later in the day when territorial defense subsides (Streby et al. 2012). The use of later successional forest by territorial males goes undetected when forest edges are assumed to be study-site boundaries (Streby et al. 2012). In addition, tracking radio-marked females to nest sites reveals that some females nest in later successional forest ≤100 m away from early successional areas (Streby et al. 2014a; Chapter 9, this volume). It is not possible to locate nests in areas not searched in traditional nest-finding protocols, and the prevailing paradigm results in study designs that only consider early successional shrublands, which can result in a biased distribution of nest sites and a biased estimate of nest success (S. M. Peterson, unpubl. data). Golden-winged Warbler nests in later successional forest can be found during standard nest-finding methods if search areas are expanded to include later successional forest (H. M. Streby, unpubl. data).

It remains to be seen if the nesting and postfledging use of later successional forest by Golden-winged Warblers in the western Great Lakes region is also common in the Appalachian breeding-distribution segment. However, the recent observations that Golden-winged Warblers use at least some later successional forest during the nesting season in two areas in the central Appalachians (Chapter 5, this volume), and a radiomarked adult male that traveled into forest with fledglings in West Virginia (Chapter 5, this volume), suggest the early successional specialist description is likely inappropriate across the breeding distribution. A more appropriate categorization for Golden-winged Warblers might be diverse-forest obligate or dynamic-forest specialist. Incorporating full-season habitat associations in breeding-grounds management and conservation planning will be crucial to the success of conservation plans for Golden-winged Warblers and likely other forest-associated songbirds.

Hybridization of Golden-winged Warbler × Blue-winged Warbler

Hybridization between Golden-winged and Blue-winged Warblers (*Vermivora cyanoptera*) is thought to be one of the principal drivers behind widespread population declines in Golden-winged

Warblers. Indeed, a typical pattern of replacement of the Golden-winged Warbler phenotype by the Blue-winged Warbler phenotype has been documented in several regions throughout the breeding distribution, and replacement tends to occur within 50 years of contact between the two species. The hybridization system has interested researchers for many years (Gill and Murray 1972; Gill 1980, 1987) but has only been quantitatively examined since the application of genetic markers in several studies since the late 1990s (Gill 1997; Shapiro et al. 2004; Dabrowski et al. 2005; Vallender et al. 2007a,b, 2009). There is variation across the breeding distribution—perhaps dependent on the length of time that the two species have been in contact with one another in a given region—with a well-established pattern of bidirectional gene flow between Blue-winged Warblers and Golden-winged Warblers. To date, patterns in gene flow have been established using genetic markers derived from the mitochondrial genome, as attempts to quantify hybridization using markers from the nuclear genome have been largely uninformative (Vallender et al. 2007b). The lack of data from the nuclear genome is the most significant challenge to elucidating the true impact of hybridization on Golden-winged Warblers and to enabling researchers to make predictions about the future of this species pair.

The most immediate short-term research need with respect to hybridization between Golden-winged and Blue-winged Warblers is the development of informative genetic markers from the nuclear genome for each species. Once available, genetic markers can be applied to the large number of samples already collected from across the breeding distributions of both species. As detailed in the chapter on hybridization of these species (Chapter 4, this volume), next-generation sequencing likely provides the most promise in this regard. A second short-term need is a better understanding of the ecology of Blue-winged Warblers and the impact of hybridization on allopatric populations of this poorly studied species, and a better understanding of the mate-choice dynamics within this hybrid complex (Vallender et al. 2007a, Hartman et al. 2012). Over the long term, the continued application of genetic techniques using markers derived from both the mitochondrial and nuclear genomes to better reveal patterns and extent of hybridization between Golden-winged Warblers and Blue-winged Warblers will inform conservation plans for both species. Some have suggested that Golden-winged Warblers may become very rare or even extinct by 2080 (Gill 1980). Continuing to document the progression and impact of hybridization is paramount for determining where genetically pure populations of Golden-winged Warblers remain and for applying appropriate on-the-ground conservation measures.

Chapter 3 (this volume) reported that landscape-scale settlement patterns of Golden-winged Warblers in the Appalachian Mountains region are positively associated with increasing percent forest and high elevations, and negatively correlated with increasing agriculture and human development, whereas Blue-winged Warblers showed the opposite relationship with these covariates. In fact, Blue-winged Warblers were positively associated with agriculture. The findings may be important to better understanding the land-use patterns that are driving spatial interactions between Golden-winged and Blue-winged Warblers and in describing potential distribution shifts for both species. More work, however, is needed to understand how landscape-scale changes in distribution and abundance of cover types used by Golden-winged Warblers are related to population trends in both species and if these changes have a role in mediating hybridization.

Breeding-Grounds Research Needs

In addition to the needs discussed above about broad inference from local studies, research is needed on habitat characteristics associated with Golden-winged Warbler breeding density and population productivity throughout the western Great Lakes region, especially in northern Minnesota where populations are dense and highly productive, and in south-central Canada where the breeding distribution is expanding northward. In the Appalachian Mountains region, research is needed to determine the efficacy of current conservation and management actions intended to benefit Golden-winged Warblers, and to identify additional forested landscapes or landscapes that could be converted to forest where management efforts will have the greatest impact. Research on habitat associations and survival during the postfledging period is an immediate need in the Appalachian Mountains region; results from that research will be important for adapting management actions already underway and plans to be implemented in the near future.

Future Research on Golden-winged Warblers and Blue-winged Warblers

Over at least the past two decades, *Vermivora* conservation attention and action has primarily been driven by the decline and vulnerability of Golden-winged Warblers. Hybridization with Blue-winged Warblers has been viewed primarily as a threat to the continued persistence of Golden-winged Warblers, and as such the research agenda has largely focused on Golden-winged Warblers. We are not aware of any research that has focused on Blue-winged Warblers in the core of their breeding distribution where Golden-winged Warblers are rare or absent. In addition, no studies have considered the *Vermivora* complex as an adaptive evolutionary system in its own right. However, given their propensity to hybridize whenever sympatric, attempts to unravel individual life histories for Golden-winged and Blue-winged Warblers in isolation are unlikely to be successful.

Several studies have examined the genetics of hybridization between Golden-winged and Blue-winged Warblers with the goal of understanding the impact and implications of their intermixing (Gill 1997; Shapiro et al. 2004; Dabrowski et al. 2005; Vallender et al. 2007b, 2009). However, most genetic sampling to date has been done either in the zone of breeding distribution overlap between Golden-winged and Blue-winged Warblers or in regions where phenotypic Golden-winged Warblers are more common (Vallender et al. 2009). Our understanding of the genetic and ecological effects of hybridization and introgression on Golden-winged Warblers is growing, but far less is known about the impact on Blue-winged Warbler populations. Moreover, basic information is lacking about breeding, mate choice, wintering-ground ecology, migration, and many other aspects of Blue-winged Warbler ecology. It has therefore been recommended that general research be conducted on life history characteristics of Blue-winged Warblers, particularly in the distribution of phenotypically "pure" Blue-winged Warblers (Chapter 4, this volume). Such work could include behavioral and genetic analyses of mate choice in allopatry and sympatry with Golden-winged Warblers and hybrids, realized reproductive success, and blood-parasite load (Hartman et al. 2012; Vallender et al. 2007a,b, 2012). An important first step will be additional genetic sampling and purity analyses of Blue-winged Warblers, especially from regions where they have been poorly sampled to date, such as Missouri and both peninsulas of Michigan.

NONBREEDING ECOLOGY

Key Findings and Knowledge Gaps

Until recently, little was known about the status, distribution, or ecology of Golden-winged Warblers on their nonbreeding grounds, and much of what has been observed is reported in the gray literature (Chavarría and Duriaux 2009, Chandler 2013). Chapters 1, 2, and 11 (this volume) are among the first peer-reviewed publications focused on Golden-winged Warblers during the nonbreeding period. We know from the work reported herein that wintering Golden-winged Warblers are concentrated in the highlands and Caribbean slopes from Guatemala and Belize to northwestern Nicaragua, at middle elevations of both Caribbean and Pacific slopes in Costa Rica and western Panama, and in an arc of the northern Andes from central Colombia to northern Venezuela. Little is known about patterns of habitat use across the full nonbreeding distribution (Chapter 2, this volume), but abundance appears to be greatest in mid-elevation primary and secondary forest (Bennett 2013, Chandler 2013). Golden-winged Warblers on the nonbreeding grounds select microhabitat features associated with intermediate forest disturbance, likely due to their use of hanging dead leaves as foraging substrates (Chandler and King 2011). Golden-winged Warbler use of agricultural cover types, such as shade coffee, appears to be contingent on adjacency of those cover types to intact primary or secondary forest (Chavarría and Duriaux 2009, Chandler 2010).

In Costa Rica and Nicaragua, Golden-winged Warblers maintain larger nonbreeding territories and home ranges, and may have larger area requirements than other Neotropical migrants. They display a high propensity to join mixed-species flocks where they forage by probing dead-leaf clusters and epiphytes (Chapter 11, this volume). A high degree of sociality may have important conservation implications. For example, territoriality and group size can clearly affect population density, which is a primary determinant of carrying capacity, and dependence upon mixed-species flocks may be a liability because forest fragmentation can disrupt cohesion within mixed-species flocks (Rappole and Morton 1985, Stouffer and Bierregaard 1995).

Non-Breeding-Grounds Research Needs

The first, and primary, hurdle in non-breeding-grounds research is gaining a better understanding of Golden-winged Warbler nonbreeding distribution. Even more so than on the breeding grounds, knowledge of non-breeding-grounds ecology in Golden-winged Warblers is limited geographically, with the published research coming from a few sites in the northwestern region of the nonbreeding distribution. Analyses of distribution-wide survey data yielded a coarse-scale indication of Golden-winged Warbler nonbreeding distribution and general cover-type associations (Chandler 2013); however, sampling intensity was modest relative to the area covered and was not evenly dispersed across the nonbreeding distribution. Therefore, a primary wintering-ecology research need is additional surveys in poorly sampled portions of the distribution, such as Belize, and in a greater range of land-use and cover-type associations.

Knowledge of the regions and cover types occupied by Golden-winged Warblers on the nonbreeding grounds is important to their conservation; however, despotic interactions among conspecifics may cause individuals to be forced into marginal sites where survival or other elements of overwinter performance can be compromised. The relationship between land use and cover-type-specific survival and body condition in Golden-winged Warblers is poorly understood. Therefore, broad-scale surveys of geographic and cover-type distribution should be followed up with detailed studies of demographic parameters. Last, replication of previous studies on space requirements and behavioral ecology should be undertaken in unstudied areas of the nonbreeding distribution. Better knowledge of the nonbreeding distribution, variation in cover-type associations, behavioral ecology throughout that distribution, and cover-type-specific survival will facilitate additional needed studies on correlations between nonbreeding habitat associations and subsequent survival and reproductive success, migratory connectivity between wintering and breeding locations, and winter-range shifts owing to climate change or other factors. A better understanding of resource selection and demography would permit the identification of the factors that limit population growth during the annual cycle, which can enable conservationists to target resources most efficiently and effectively.

MIGRATORY CONNECTIVITY AND MIGRATION ROUTES

Key Findings and Knowledge Gaps

The most difficult challenge for informing full life-cycle conservation plans for small migratory songbirds is connecting geographically distinct areas in the absence of adequate tools to track individual birds (e.g., GPS tags). Chapter 12 (this volume) used stable-isotope analysis to take a first step in understanding migratory connectivity across Golden-winged Warbler breeding and nonbreeding distributions and made reasonable speculation about likely migration routes. The authors used stable isotopes in tissues generated on the breeding grounds and collected on the nonbreeding grounds to create a coarse, but informative map linking Golden-winged Warblers from the Appalachian population segment to more southern wintering grounds, and Golden-winged Warblers from the Great Lakes breeding-distribution segment generally to more northwestern wintering grounds. It is possible that Chapter 12 (this volume) has provided an explanation, aside from insufficient non-breeding-ground sampling effort, for why thousands of Golden-winged Warblers banded on the breeding grounds have yielded no recaptures on the nonbreeding grounds. The majority of breeding-grounds research that involved banding was in the Appalachian breeding-distribution segment and the majority of non-breeding-grounds research was in northwestern Central America, which are likely two, largely unconnected populations.

Migratory Connectivity and Migration Research Needs

Establishing fine-resolution, distribution-wide migratory connectivity is a research challenge in Golden-winged Warblers and in many other migratory species (Hobson 2003; Faaborg et al. 2010a,b). Building upon the framework established by Chapter 12 (this volume) is necessary to allow conservation efforts to target individual populations on their breeding and wintering grounds and along their migration routes. Until recently, the only feasible step toward that goal was to increase the geographic coverage of non-breeding-grounds sampling locations and to increase the number of birds sampled across the nonbreeding distribution to improve accuracy of stable-isotope-based connectivity maps (Chapter 12, this volume). However, light-level geolocators have now been carried by Golden-winged Warblers with no deleterious effects (Peterson et al. 2015; Streby et al. 2015b,c) and preliminary results suggest geolocator tags will considerably improve knowledge of Golden-winged Warbler migratory connectivity in the next few years (H. M. Streby, unpubl. data).

The only information available about Golden-winged Warbler migration routes is speculation in this volume based on coarse migratory connectivity (Chapter 12, this volume) and incidental reports from eBird (www.ebird.org) or banding stations (Chapter 1, this volume). Chapters 1 and 12 (this volume) referenced eBird records, which suggest that Golden-winged Warblers use a trans-Gulf of Mexico migration pathway during spring and fall migrations. However, eBird observations of Golden-winged Warblers during migration are sparse (<0.5% of checklists) and the distribution of detections is likely biased by highly nonrepresentative spatial sampling of perceived migration hotspots such as the Gulf of Mexico Coast of North America. Current research using light-level geolocation has provided promising preliminary data about Golden-winged Warbler migration routes and stopover locations and duration (H. M. Streby, unpubl. data). Questions about when and where Golden-winged Warblers rest and refuel during migration, and about their diet, habitat associations, and survival along migration routes, and about how these factors affect their ability to reproduce, remain urgent research needs.

CONCLUSIONS

A common limiting factor in conservation of migratory birds is a lack of adequate knowledge from all stages of the annual cycle to inform full life-cycle models and identify conservation priorities for individual populations (Faaborg et al. 2010a). Despite the recent increase in knowledge about Golden-winged Warblers, their ecology during most of the annual cycle, especially during spring and fall migration, has not been studied thoroughly enough to inform such models. Migratory connectivity and cover-type-specific survival on the wintering grounds are likely the most urgent problems to address with respect to full life-cycle research in Golden-winged Warblers. Until individual populations can be studied throughout their annual cycle, and factors most limiting growth for a population of interest can be identified, conservation plans will be limited to focusing on the apparent needs of different populations during different times of the year.

While acknowledging that many substantial research gaps remain and that some previously held truths about Golden-winged Warblers are being revised, the current information must be translated into conservation and management actions within areas of appropriate geographic inference sooner rather than later. Otherwise, we risk current knowledge being useful only for describing eventual extinction events (Lindenmayer et al. 2013), especially for the Appalachian breeding-distribution segment if long-term trends continue. Forest management efforts designed to benefit Golden-winged Warblers and other disturbance-dependent species are underway in many areas across the Golden-winged Warbler breeding distribution, and some progress is being made in reversing deforestation in areas of their nonbreeding distribution (Chapter 2, this volume). New research is needed not only to address remaining information gaps, but also to study the effects of conservation and management actions and to inform the adaptive nature of long-term management plans. Our volume of Studies in Avian Biology provides a solid foundation on which future research in Golden-winged Warblers can be built, but the recent acceleration in knowledge about Golden-winged Warblers indicates above all else that there is still much to be learned.

LITERATURE CITED

Aldinger, K. R., and P. B. Wood. 2014. Reproductive success and habitat characteristics of Golden-winged Warblers in high-elevation pasturelands. Wilson Journal of Ornithology 127:279–287.

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III. 1997. Juvenile survival in a population of migrant birds. Conservation Biology 11:698–707.

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115:349–358.

Bennett, R. E. 2013. Habitat associations of the Golden-winged Warbler in Honduras. M.S. thesis, Michigan Technological University, Houghton, MI.

Bulluck, L. P., and D. A. Buehler. 2008. Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. Auk 125:551–559.

Chandler, R. B. 2010. Avian ecology and conservation in tropical agricultural landscapes with emphasis on *Vermivora chrysoptera*. Ph.D. thesis, University of Massachusetts, Amherst, MA.

Chandler, R. B. 2013. Analysis of Golden-winged Warbler winter survey data. Report prepared for the Cornell Lab of Ornithology, Ithaca, NY.

Chandler, R. B., and D. I. King. 2011. Habitat quality and habitat selection of Golden-winged Warblers in Costa Rica: an application of hierarchical models for open populations. Journal of Avian Ecology 48:1037–1048.

Chavarría, L., and G. Duriaux. [online]. 2009. Informe preliminar del primer censo de *Vermivora chrysoptera*: realizado en Marzo 2009 en la zona norcentral de Nicaragua. <http://www.bio-nica.info/Biblioteca/Chavarria2009FinalGWWA.pdf> (19 April 2014).

Confer, J. L., K. W. Barnes, and E. C. Alvey. 2010. Golden- and Blue-winged Warblers: distribution, nesting success, and genetic differences in two habitats. Wilson Journal of Ornithology 122:273–278.

Confer, J. L., P. Hartman, and A. Roth. 2011. Golden-winged Warbler (*Vermivora chrystoptera*). *In* A. Poole (editor), The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY.

Confer, J. L., and K. Knapp. 1981. Golden-winged Warblers and Blue-winged Warblers: the relative success of a habitat specialist and a generalist. Auk 98:108–114.

Confer, J. L., J. L. Larkin, and P. E. Allen. 2003. Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. Auk 120:138–144.

Dabrowski, A., R. Fraser, J. L. Confer, and I. J. Lovette. 2005. Geographic variability in mitochondrial introgression among hybridizing populations of Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*). Conservation Genetics 6:843–853.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010a. Conserving migratory land birds in the New World: do we know enough? Ecological Applications 20:398–418.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010b. Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80:3–48.

Ficken, M. S., and R. W. Ficken. 1968. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. Wilson Bulletin 80:442–451.

Gill, F. B. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged Warblers. Auk 97:1–18.

Gill, F. B. 1987. Allozymes and genetic similarity of Blue-winged and Golden-winged Warblers. Auk 104:444–449.

Gill, F. B. 1997. Local cytonuclear extinction of the Golden-winged Warbler. Evolution 51:519–525.

Gill, F. B., and B. G. Murray. 1972. Discrimination behavior and hybridization of the Blue-winged and Golden-winged Warblers. Evolution 26:282–293.

Harper, S. L., R. Vallender, and R. J. Robertson. 2010. Male song variation and mate choice in the Golden-winged Warbler. Condor 112:105–114.

Hartman, P. J., D. P. Wetzel, P. H. Crowley, and D. F. Westneat. 2012. The impact of extra-pair mating behavior on hybridization and genetic introgression. Theoretical Ecology 5:219–229.

Hobson, K. A. 2003. Making migratory connections with stable isotopes. Pp. 379–391 *in* P. Berthold, E. Gwinner, and E. Sonnenschein (editors), Avian migration. Springer-Verlag, Berlin, Germany.

Klaus, N. A., and D. A. Buehler. 2001. Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. Wilson Bulletin 113:297–301.

Kubel, J. E., and R. H. Yahner. 2008. Quality of anthropogenic habitats for Golden-winged Warblers in central Pennsylvania. Wilson Journal of Ornithology 120:801–812.

Lindenmayer, D. B., M. P. Piggot, and B. A. Wintle. 2013. Counting the books while the library burns: why conservation monitoring programs need a plan for action. Frontiers in Ecology and the Environment 11:549–555.

Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. Forest Ecology and Management 183:127–135.

Martin, K. J., R. S. Lutz, and M. Worland. 2007. Golden-winged Warbler habitat use and abundance in northern Wisconsin. Wilson Journal of Ornithology 119:523–532.

Morrison, M. L., B. A. Collier, H. A. Mathewson, J. E. Groce, and R. N. Wilkins. 2012. The prevailing paradigm as a hindrance to conservation. Wildlife Society Bulletin 36:408–414.

Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. Condor 102:738–747.

Peterson, S. M., G. R. Kramer, H. M. Streby, J. A. Lehman, D. A. Buehler, and D. E. Andersen. 2015. Geolocators on Golden-winged Warblers do not affect migratory ecology. Condor 117:256–261.

Rappole, J. H., and E. S. Morton. 1985. Effects of habitat alteration on a tropical avian forest community. Ornithological Monographs 36:1013–1021.

Roth, A. M., D. J. Flaspohler, and C. R. Webster. 2014. Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (*Vermivora chrysoptera*). Forest Ecology and Management 321:61–70.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2012. The North American Breeding Bird Survey, results and analysis 1966–2011, version 07.03.2013. USGS Patuxent Wildlife Research Center, Laurel, MD.

Shapiro, L. H., R. A. Canterbury, D. M. Stover, and R. C. Fleischer. 2004. Reciprocal introgression between Golden-winged Warblers (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*) in eastern North America. Auk 121:1019–1030.

Stouffer, P. C., and R. O. Bierregaard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76:2429–2445.

Stoleson, S. H. 2013. Condition varies with habitat choice in postbreeding forest birds. Auk 130:417–428.

Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2:78.

Streby, H. M., and D. E. Andersen. 2013a. Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed-coniferous forests. Forest Ecology and Management 287:9–16.

Streby, H. M., and D. E. Andersen. 2013b. Testing common assumptions in studies of songbird nest success. Ibis 155:327–337.

Streby, H. M., G. R. Kramer, S. M. Peterson, J. A. Lehman, D. A. Buehler, and D. E. Andersen. 2015c. Tornadic storm avoidance behavior in breeding songbirds. Current Biology 25:98–102.

Streby, H. M., J. P. Loegering, and D. E. Andersen. 2012. Spot mapping underestimates song-territory size and use of mature forest by breeding Golden-winged Warblers in Minnesota, USA. Wildlife Society Bulletin 36:40–46.

Streby, H. M., T. L. McAllister, G. R. Kramer, S. M. Peterson, J. A. Lehman, and D. E. Andersen. 2015b. Minimizing marker mass and handling time when attaching radio transmitters and geolocators to small songbirds. Condor 117:249–255.

Streby, H. M., S. M. Peterson, G. R. Kramer, and D. E. Andersen. 2015a. Post-independence fledgling ecology in a migratory songbird: implications for breeding-grounds conservation. Animal Conservation 18:228–235.

Streby, H. M., S. M. Peterson, J. A. Lehman, G. R. Kramer, B. J. Vernasco, and D. E. Andersen. 2014b. Do digestive contents confound body mass as a measure of relative condition in nestling songbirds? Wildlife Society Bulletin 38:305–310.

Streby, H. M., S. M. Peterson, T. L. McAllister, and D. E. Andersen. 2011. Use of early-successional managed northern forest by mature-forest species during the post-fledging period. Condor 113:817–824.

Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen. 2014a. Retirement investment theory explains patterns in songbird nest-site choice. Proceedings of the Royal Society of London B 281:20131834.

Thogmartin, W. E. 2010. Modeling and mapping Golden-winged Warbler abundance to improve regional conservation strategies. Avian Conservation and Ecology 5:12.

Vallender, R., R. D. Bull, L. L. Moulton, and R. J. Robertson. 2012. Blood parasite infection and heterozygosity in pure and genetic-hybrid Golden-winged Warblers (*Vermivora chrysoptera*) across Canada. Auk 129:716–724.

Vallender, R., V. L. Friesen, and R. J. Robertson. 2007a. Paternity and performance of Golden-winged Warblers (*Vermivora chrysoptera*) and Golden-winged × Blue-winged Warbler (*V. pinus*) hybrids at the leading edge of a hybrid zone. Behavioral Ecology and Sociobiology 61:1797–1807.

Vallender, R., R. J. Robertson, V. L. Friesen, and I. J. Lovette. 2007b. Complex hybridization dynamics between Golden-winged and Blue-winged

Warblers (*Vermivora chrysoptera* and *V. pinus*) revealed by AFLP, microsatellite, intron and mtDNA markers. Molecular Ecology 16:2017–2029.

Vallender, R., S. Van Wilgenburg, L. Bulluck, A. Roth, R. Canterbury, J. Larkin, R. M. Fowlds, and I. J. Lovette. 2009. Extensive rangewide mitochondrial introgression indicates substantial cryptic hybridization in the Golden-winged Warbler. Avian Conservation and Ecology 4:4.

Vitz, A. C., and A. D. Rodewald. 2007. Vegetative and fruit resources as determinants of habitat use by mature forest birds during the postbreeding period. Auk 124:494–507.

Vitz, A. C., and A. D. Rodewald. 2013. Behavioral and demographic consequences of access to early-successional habitat in juvenile Ovenbirds (*Seiurus aurocapilla*): an experimental approach. Auk 130:21–29.