



Special Section

The Prevailing Paradigm as a Hindrance to Conservation

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ABSTRACT We review the history of population and ecological knowledge of the golden-cheeked warbler (*Setophaga chrysoparia*). We highlight how incomplete information on distribution and abundance has led to substantial misunderstanding on species status and associated conservation goals. We discuss how once a paradigm is established, subsequent studies unconsciously fortify accepted understanding regardless of the paradigm's accuracy. For the golden-cheeked warbler, understanding of the species at the time of listing in 1990 was based on either incorrect or untested assumptions of species distribution within available habitats. Adhering to untested assumptions led to development of priorities for research and management that were well-intentioned but largely misguided. Ample information on the distribution of the warbler's habitats existed, however, which should have encouraged questions into the basis of population conditions when developing management prescriptions. Current knowledge clearly indicates that a new paradigm for the warbler is needed, that being one of a widely distributed species that is preadapted to occur within a variety of environmental conditions. © 2012 The Wildlife Society.

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A fundamental concept in ecology is that of the biological population, or a group of organisms of the same species that occur within a specific space at a particular time and are able to interbreed with each other. In conservation planning and management, understanding the structure of a population is critical (Morrison 2009:18–21) because that structure defines what management activities may or may not create beneficial conditions for the species of interest. Given the importance of the population concept to conservation actions, we are concerned that the biological population concept is one of the most frequently misunderstood, and, thus, misapplied concepts in ecology. Ambiguity in the understanding and application of the population concept likely derives from multiple definitions in the literature. Multiple definitions provide flexibility in application of the population concept to ecological research; however, it remains the responsibility of the author to justify the definition of populations for their study system (see review in Waples and Gaggiotti 2006). Scientists tend to follow popular paradigms by assigning population designations without respect to species' distribution or variation in habitat use or demographic rates across a species' range (Morrison 2012).

A scientific paradigm develops when a majority of people follow a common set of rules or norms that include 1) what was to be observed, 2) the types of questions that were to be asked, 3) how these questions were to be structured, and 4) how the results were to be interpreted (Kuhn 1996). Paradigms in the design, analysis, and interpretation of research results are perpetuated through the disinclination of peer reviewers, who often adhere to similar paradigms, to question the basic tenets from which various assumptions associated with prevailing paradigms are embedded. As such, the majority of published studies naturally confirm the paradigm, making negative or disputed results appear unsupported. Results that do not uphold a prevailing paradigm are often rejected for publication regardless of the appropriateness of the study design, analysis, and interpretation. In these situations, beliefs about the nature of systems that are false or misapplied can lead to management practices that are at best neutral or at worse harmful to the very entities we are trying to conserve (Morrison 2012).

One example of a commonly misapplied concept in population biology is that populations have a metapopulation structure, typically composed of discrete populations (subpopulations) with independent demographics but that interact through dispersal or migration (Levins 1969, Hanski and Simberloff, 1997). While the degree of demographic independence necessary for defining subpopulations is often unclear and possibly species-specific, the necessity

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for some level of population differentiation that results in local extinction and re-colonization is evident (Levins 1969, Harrison and Taylor 1997, Esler 2000). Differentiations in demography arise through geographic separation during the annual cycle wherein deterministic or stochastic events (e.g., habitat loss or fragmentation; Harrison and Taylor 1997) cause changes in population vital rates for a potentially interbreeding population. For this reason, metapopulation theory is embedded within literature on habitat fragmentation, often under the presumption that existing habitat patches represent local populations with independent within-population processes and among-population movements across an inhospitable landscape (Hanski and Simberloff, 1997). This broad application has created a prevailing paradigm in ecology and conservation biology that species with a fragmented distribution (i.e., patchily distributed), particularly those that are habitat-specialists or impacted by habitat fragmentation, often occur as multiple populations (e.g., see review in Mills 2007:211–219). However, misapplication of the metapopulation concept due to limited understanding of species-specific distributions and dynamics can distract from effective species management and conservation and lead to inaccurate assumptions regarding species viability assessments (Harrison 1994).

CASE STUDY: THE GOLDEN-CHEEKED WARBLER (*SETOPHAGA CHRYSOPARIA*)

Golden-cheeked warblers (*Setophaga chrysoparia*, hereafter warbler) are habitat specialists that spend the spring and summer only in central Texas, USA. Warblers use mixed woodlands of Ashe juniper (*Juniperus ashei*) and oak (*Quercus* spp.) for breeding habitat. Habitat loss and fragmentation, especially in the eastern portion of their range, prompted concerns about population declines and the federal listing of this species as endangered in 1990. For the past 20 years, research on warblers has revolved around the paradigm that they are rare and that their habitat is highly fragmented, resulting in discussions referring to the warbler existing within multiple, distinct populations. Through several examples, we show how well-intentioned and technically correct studies have perpetuated certain concepts about this species due to misapplication of spatial population structure, an inadequate understanding of species distribution, or insufficient knowledge of the species' demographics. Below we show that previous evaluations and discussions of the warbler have been driven primarily by data gathered in a few locations rather than across its breeding range. Although our examples focus on one species and the metapopulation concept as applied, the issues we raise have broad implications for designing and conducting studies and subsequently using results to craft management strategies and conservation goals (Morrison 2012).

EVOLUTION OF THE GOLDEN-CHEEKED WARBLER

The golden-cheeked warbler is considered by many to be a member of the black-throated green warbler (*S. virens*) species group, all of which are thought to share a common

ancestor similar to the black-throated green warbler. Members of the group were hypothesized by Mengel (1964) to include the golden-cheeked, black-throated gray (*S. nigrescens*), hermit (*S. occidentalis*), and Townsend's (*S. townsendi*) warblers. Mengel (1964) outlined a scenario under which a predecessor of the black-throated green warbler, which had spread across much of the northeastern and north-central portions of what is now the USA–Canadian border during early stages of the Pleistocene era, became divided into isolated locations during the advance and retreat of ice. Subsequently these isolated groups evolved into our modern species within this species group. The close relationship between members of this group is shown by the frequent hybridization in the western United States between the hermit and Townsend's warblers (Morrison and Hardy 1983, Rohwer and Wood 1998). The specific species-to-species relatedness, and timing of splitting into individual species, has been refined through genetic analyses that have led to alterations of Mengel's original hypothesis (Bermingham et al. 1992, Klicka and Zink 1997, Lovette and Bermingham 1999). Foraging behavior, nest placement, clutch size, and general behavior are also similar among members of this species group, as would be expected for birds of similar origin and morphology (e.g., Guzy and Lowther 1997, Ladd and Gass 1999, Morse and Poole 2005).

Although it did not affect relationships within the black-throated green warbler species group, the taxonomic relationships of warblers recently were modified by the American Ornithologists' Union (Chesser et al. 2011). The genus *Dendroica*, in which species in the black-throated green warbler group were classified, was subsumed into the genus *Setophaga*; *Dendroica* no longer is recognized as a distinct genus. In summary, it is clear that the golden-cheeked warbler is closely related to a number of other warblers that, collectively, are widely distributed across the United States and into Canada in a variety of habitats during the breeding season.

WARBLER HABITAT: FRAGMENTED AND DECLINING, OR EXPANSIVE AND SUSTAINING?

One of the prevailing assumptions of golden-cheeked warblers concerns the distribution of their habitat and whether current habitats are more or less fragmented than those in the past. The distribution of mixed woodlands immediately prior to the time of European settlement has been debated and may not be accurately resolved in the future (Diamond and True 2008). Historical records regarding the extent of mixed woodlands are conflicting, with some describing the historical Edwards Plateau as a mosaic of grasslands and savannahs with thick cedar brakes common in canyons and hill slopes (Smeins 1980, Smeins and Fuhlendorf 1997), whereas others describe mostly savannah or mostly scrub forest with little savannah (Ford and Van Auken 1982). Several reports have suggested or documented a decrease in mixed woodlands on the Edwards Plateau since European settlement (Pulich 1976, Wahl et al. 1990, Keddy-Hector

et al. 1992), while other interpretations of aerial and satellite imagery suggest that the general range and abundance of mixed woodlands has not changed much in recent history except for colonization of former grasslands (Smeins et al. 1997, Diamond and True 2008). Diamond and True (2008) modeled the distribution of woodlands and grasslands in the Hill Country (an area of approx. 2,000,000 ha and covering about two-thirds of the warbler's breeding range) and estimated that about 55% of the area was historically woodland or forest, compared with a current estimate of 57%. Woodlands were shown to have decreased in some areas, while increasing in other areas due to a variety of causes (e.g., fire suppression, urban development).

Although mixed woodlands are patchily distributed throughout Texas, all estimates of the extent of warbler habitat show widespread coverage throughout central Texas. Specific estimates of the extent of warbler habitat in Texas vary from about 120,000 ha to 1.7 million ha (see reviews in Groce et al. 2010 and Mathewson et al. 2012). Differences in habitat estimates were based, in part, on the data used to represent woodland coverage, along with the definitions adopted by various researchers to define suitable habitat. Throughout the 40-year span of research on the warbler, the debate essentially has revolved around the degree of habitat specialization, and, ultimately, thresholds for reproduction derived from various habitat metrics. Most estimates of habitat extent are based on the assumption that warbler occupancy and productivity are positively correlated with habitat patch size, interior patch size, and percent canopy cover (i.e., measurements that represent intact habitat; DeBoer and Diamond 2006). Generally these relationships hold true, but it is the assumed range (i.e., specificity) of these conditions that results in disparity of habitat estimates, incorrect identification of warbler habitat, and potential mismanagement of the warbler.

The federal listing of the warbler and the subsequent U.S. Fish and Wildlife Service (USFWS) recovery plan (USFWS 1992; see below) relied extensively upon a report released by Wahl et al. (1990). Although we now know that the majority of the conclusions from Wahl et al. (1990) were inaccurate, several assumptions originating from this work continue to define research assumptions and management directives with regard to the warbler. For example, the conclusion that two-thirds of warbler habitat occurred in "rapidly changing urban counties in the eastern Edwards Plateau" (Wahl et al. 1990:43) led to the overall belief that warbler habitat was declining and fragmenting at dramatic rates. Furthermore, statements by Wahl et al. (1990) that concerned the amount and degree of habitat fragmentation surrounding Travis County and Fort Hood Military Reservation likely contributed to subsequent studies that made assumptions concerning the suitability of woodlands between these 2 regions as habitat (USFWS 1996, Alldredge et al. 2002, Horne et al. 2011). However, recent work (Collier et al. 2012, Mathewson et al. 2012) that sampled potential habitat across the warbler's range showed that high rates of patch occupancy and density prevailed.

Specifications of warbler habitat, such as the minimum patch size or canopy cover, originated from various studies on the warbler in few locations (Wahl et al. 1990, Coldren 1998) and they failed to capture the much wider range of conditions occupied by successfully breeding warblers that we now know occurs (Butcher et al. 2010, Klassen et al. 2012). For example, management guidelines developed by Texas Parks and Wildlife Department, based primarily on information from Travis County and Fort Hood Military Reservation, indicate that the warbler prefers habitats with $\geq 50\%$ (preferably $\geq 70\%$) canopy cover (Campbell 2003). However, research in the southwestern portion of the warbler's range has demonstrated that successful breeding regularly occurs in sites with $< 35\%$ canopy cover (Klassen et al. 2012). A recent review of warbler research indicated that few generalizations could be gleaned from the current literature on population responses to habitat characteristics because of a paucity of data from a large portion of the warbler's range, namely the west and southwest (Groce et al. 2010).

One of the paradigms concerning warbler habitat, which is inherently incorporated into assumptions of population structure, is that the habitat is fragmented to such a degree to create isolation within the species' distribution (Lindsay et al. 2008, Athrey et al. 2011). This perception has been repeatedly reinforced in the warbler literature and management directives, regardless of the evidence contradictory to early assumptions. As noted by Klassen et al. (2012), we should not be surprised that warblers can regularly occupy and successfully breed in a wide range of conditions because the environment in which they evolved would have been constantly changing due to longer term changes in climate and shorter term changes in fire, drought, and other natural conditions. What we formerly considered "marginal" habitats (i.e., 35% cover) was based on an incomplete—although not incorrect *per se*—understanding of warbler ecology.

WARBLER POPULATION ECOLOGY: NOBLE INTENT, INACCURATE ASSUMPTIONS

In ecology, we often find that concepts about how animals may be distributed in time and space are assumed valid based on limited data from localized studies using unplanned sampling designs (Elith et al. 2006). As reviewed by Morrison (2012), most studies of animal ecology fail to properly discuss, let alone define, properties of the population(s) under study. The ramifications of such a failure can have substantial negative impacts to the gaining of reliable knowledge and subsequent management prescriptions. In the case of the golden-cheeked warbler, misunderstandings concerning the distribution of warbler habitat have promoted the perception that habitat is fragmented across the breeding range. However, as we discussed above, most of these habitat delineations were based on limited data regarding suitable warbler habitat. This paradigm that warblers exist in fragmented, sparsely distributed habitat has limited the strength of inferences made by a variety of authors on population dynamics, trajectory, and sustainability.

Soon after the warbler was listed as endangered, USFWS developed a recovery plan listing specific goals and objectives leading to species protection and possible delisting (USFWS 1992). In the plan, USFWS delineated 8 recovery regions across the warbler's breeding range and one of the criteria for delisting was to protect sufficient breeding habitat "to ensure the continued existence of at least one viable, self-sustaining population in each of eight regions . . ." (USFWS 1992:iv). Furthermore, they stressed that, "fundamental to the recovery strategy is the creation of a system of protected populations scattered over the present breeding distribution" (USFWS 1992:38). As described below, subsequent population viability analyses (PVAs) assumed warblers were divided into multiple populations as a way to address the recovery plan's request of determining "the population sizes and arrangements necessary to attain and maintain viability" in each recovery region (USFWS 1992:38). We believe that the notion that golden-cheeked warbler occurs in multiple populations originated from the language within this recovery plan. The intention of USFWS was to designate specific units within which to manage the warbler across the range, yet the concept of several separate populations was adopted and perpetuated in subsequent research endeavors.

U.S. Fish and Wildlife Service (1996) conducted a simulation exercise to evaluate the long-term viability of golden-cheeked warblers and to identify potential demographic parameters where additional information was needed. The approach assumed isolation of warbler subpopulations (hence, no between sub-population dispersal) and the resulting population viability estimates were at the recovery region level as per requirements in the recovery plan. This was the first suggestion within the literature that golden-cheeked warblers exhibit "metapopulation" structure, and in fact the report recommends that a spatially explicit PVA be developed that models dispersal between habitat patches, thus suggesting that future works should consider metapopulation structure and focus on dispersal studies (e.g., emphasize banding of birds).

Allredge et al. (2002) and Allredge et al. (2004) built on the USFWS (1996) model and conducted a PVA for the warbler wherein they assumed that "the fragmented landscape of publicly managed golden-cheeked warbler breeding habitat creates a potential metapopulation dynamic" (Allredge et al. 2002:2). That is, they hypothesized a metapopulation structure based on the availability of public lands within their study area. Although the authors acknowledged that the model assumed a metapopulation structure and was limited in terms of demographic data (e.g., dispersal), the concept that warblers are organized in multiple populations, and thus that the metapopulation theory applies to this species, took hold in the warbler literature (Lindsay et al. 2008, Athrey et al. 2011, Horne et al. 2011).

Subsequently, Horne et al. (2011) analyzed potential changes in population viability of the warbler due to changes in the distribution and characteristics of habitat patches. They made the same assumption as Allredge et al. (2004), in that warblers were structured as a metapopulation. Although we are not criticizing the analytical approach used

by Horne et al. (2011), their inferences hinge on inappropriate assumptions regarding the biological population concept and suffer from a lack of knowledge about both the species and system under study. For example, in discussing the breeding distribution of the warbler, Horne et al. commented that, despite a large number of birds that occur on Fort Hood, "a viable population . . . is not guaranteed" (Horne et al. 2011:2479). This assumes that birds occurring within the jurisdiction of Fort Hood must form a "viable population," which by definition assumes that a biological population exists and is largely isolated from other such populations. There are, however, a large number of woodland patches occupied by the warbler beyond the borders of Fort Hood and throughout the ecoregion (Butcher et al. 2010; Collier et al. 2010, 2012). In addition, as noted above, although mixed woodlands are not contiguous in the area, woodland patches are not separated or isolated by large distances throughout most of the breeding range (Collier et al. 2012). This lack of physical separation violates a fundamental assumption of the metapopulation concept (Hanski and Simberloff, 1997), especially when considering that the species is a long-distance migrant (see below).

Regardless of the distribution patterns exhibited by warbler habitat patches, the critical process for determining population structure, and that which a metapopulation designation depends on, is movement patterns (Levins 1969, Hanski and Simberloff, 1997). For non-migratory species, the concept of habitat corridors and connectivity is logical, in that an individual might require specific habitat in order to move from one point to another. However, it has been long acknowledged that detecting population structure in migratory birds is challenging unless there is discrete geographic separation within the species at some point during their annual cycle (Esler 2000). For example, a metapopulation structure might exist if migratory birds winter on separate islands or different latitudes such that local factors create differentiation in vital rates. For golden-cheeked warblers, little is known about their wintering distribution and studies on the breeding ground acknowledge the lack of information available on movement patterns, such as natal and breeding site dispersal or emigration among habitat patches (see review in Groce et al. 2010). Regardless, limited dispersal distances would not be expected to compromise the viability of a species inhabiting a widely distributed vegetation type. However, this has not hindered several authors from making unsupported statements that golden-cheeked warblers have limited dispersal ability in order to support their research assumptions, as in recent PVA assessments (USFWS 1996; Allredge et al. 2002, 2004; Horne et al. 2011) and the conservation genetics literature (Lindsay et al. 2008). Additionally, without relying on the assumption that breeding dispersal is zero, there is no evidence from genetic studies that warblers should be separated into multiple populations (Lindsay et al. 2008, Athrey et al. 2011). For example, Athrey et al. (2011) stated that the genetic differentiation observed in their study is "expected when habitat becomes fragmented and remnant populations become isolated on patches of preserved habitat—the current situation with *S. chrysoparia*" (Athrey

et al. 2011:1351). However, there is no evidence in the scientific literature that any part of the warbler population is currently isolated, which is not surprising because few studies on migratory birds have supported a metapopulation structure based on genetics information (Veit et al. 2005, Mayer et al. 2009). As reviewed by Haig et al. (2011), migratory species tend to show low levels of genetic structure because their ability to fly makes them good dispersers. These dispersal abilities usually minimize genetic differentiation within such species. Further, habitat fragmentation has not been found to have much detectable effect on genetic structure in most recent avian studies (Haig et al. 2011).

Although Collier et al. (2012) and Mathewson et al. (2012) represented the first range-wide assessments of the distribution and abundance of the warbler, there were earlier papers that should have alerted scientists that the paradigm about golden-cheeked warblers being rare and fragmented was likely incorrect. As summarized by Mathewson et al. (2012; table 1), estimates of potential carrying capacity have ranged as high as 228,426 individuals in earlier studies. Thus, we can see how the history of studies on the warbler, as reviewed above, show that a prevailing paradigm can lead to recommendations for further research based on inappropriate assumptions. Unfortunately, this practice is widespread in ecology and can substantially retard the pace at which new information is gathered and new ideas become acceptable to the scientific community (Morrison 2012).

CONCLUSIONS

It is evident that the golden-cheeked warbler is widely distributed throughout its breeding range (Collier et al. 2012), is breeding successfully in a variety of habitat conditions (Butcher et al. 2010, Klassen et al. 2012, see also Campomizzi et al., this section), and is more abundant than previous estimates have indicated (Mathewson et al. 2012). Within those areas with the longest record of research, the warbler has been shown to occur at a roughly stable abundance and shows a level of breeding success expected for similar species (Groce et al. 2010). Additionally, there is scant evidence that habitat or other resources are limited outside of the Texas breeding range. We are not implying that there are no potential threats that could negatively impact the warbler's distribution and abundance; however, given current estimates of habitat and abundance, their situation may not be as dire as it was originally assumed.

Evidence from recent statewide surveys of the warbler, when combined with the genetic evidence showing no discernible subpopulations, indicate that the warbler exists as a single population across its breeding range. Rather than forcing a metapopulation structure on the species through maintaining a viable population in each recovery region, we suggest that the warbler can be maintained across the current breeding range given that reasonable steps are in place for maintaining landscape coverage of mixed woodlands in a variety of ages, sizes, and conditions. For example, maintaining patches of mixed woodland across the landscape, and encouraging retention of larger patches, would serve as the foundation for a conservation plan that involved both public

and private land managers. Although the absolute amount of woodland available for warbler occupancy has declined during the past approximately 20 years (Groce et al. 2010), most of that loss has been concentrated around expanding urban centers (e.g., Austin, San Antonio). A conservation plan that ensures maintenance of an adequate distribution of habitat across the breeding range is feasible given the large amount of potential habitat available to the species, and the apparent fact that not all suitable habitat is currently occupied (e.g., results of conspecific attraction studies; Farrell et al. 2012).

A paradigm is generally defined as a set of assumptions, concepts, and values that constitutes a way of viewing reality for the group of people that shares them, including in an intellectual discipline. A paradigm is difficult to change because it gains strength and inertia as more and more people come to accept it. It is not enough to make assumptions on the structure of a population; rather, conducting rigorous science requires that assumptions be thoroughly explored and the likelihood that the assumption actually applies needs to be conducted (i.e., due diligence). The paradigm that the golden-cheeked warbler is a rare and fragmented species is based on information now 2 decades old. More recent and thorough information indicates that a new perspective of the warbler is needed, that being one of a widely distributed and abundant species that is adapted to occupy a number of environmental conditions.

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LITERATURE CITED

- Allredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True. 2002. Population viability analysis of the golden-cheeked warbler. Final report for Grant no. 1448-2018 1-00-J605, submitted to U.S. Fish and Wildlife Service, Region 2, Albuquerque, New Mexico, USA.
- Allredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True. 2004. Golden-cheeked warbler (*Dendroica chrysoparia*) in Texas: Importance of dispersal toward persistence in a metapopulation. Pages 372–383 in H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management: case studies. Oxford University Press, New York, New York, USA.
- Athrey, G., D. Lindsay, R. Lance, and P. Leberg. 2011. Crumbling diversity: comparison of historical archived and contemporary natural populations indicate reduced genetic diversity and increasing genetic differentiation in the golden-cheeked warbler. *Conservation Genetics* 12:1345–1355.
- Bermingham, E., S. Rohwer, S. Freeman, and C. Wood. 1992. Vicariance biogeography in the Pleistocene and speciation in American wood warblers: a test of Mangel's model. *Proceedings of the National Academy of Sciences of the United States of America* 89:6624–6628.

- Butcher, J. A., M. L. Morrison, D. Ransom, Jr., R. D. Slack, and N. Wilkins. 2010. Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *Journal of Wildlife Management* 74:133–139.
- Campbell, L. 2003. Endangered and threatened animals of Texas: their life history and management. Texas Parks and Wildlife Department, Austin, USA.
- Chesser, R. T., R. C. Banks, F. K. Barker, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasussen, J. V. Remsen, Jr., J. D. Rising, D. F. Stotz, and K. Winker. 2011. Fifty-second supplement to the American Ornithologists' Union check-list of North American birds. *Auk* 128: 600–613.
- Coldren, C. L. 1998. The effects of habitat fragmentation on the golden-cheeked warbler. Dissertation, Texas A&M University, College Station, USA.
- Collier, B. A., J. E. Groce, M. L. Morrison, J. C. Newnam, A. J. Campomizzi, S. L. Farrell, H. A. Mathewson, R. T. Snelgrove, R. J. Carroll, and R. N. Wilkins. 2012. Predicted patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Diversity and Distributions* 18:158–167.
- Collier, B. A., M. L. Morrison, S. L. Farrell, A. J. Campomizzi, J. A. Butcher, K. B. Hays, D. I. MacKenzie, and R. N. Wilkins. 2010. Monitoring endangered species occupying private lands: case study using the golden-cheeked warbler. *Journal of Wildlife Management* 74:140–147.
- DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence–absence of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). *Southwestern Naturalist* 51:181–190.
- Diamond, D. D., and C. D. True. 2008. Distribution of *Juniperus* woodlands in central Texas in relation to general abiotic site type. Pages 48–57 in O. W. V. Auken, editor. *Western North American Juniperus communities: a dynamic vegetation type*. Springer Science + Business Media, New York, New York, USA.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachette-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Esler, D. 2000. Applying metapopulation theory to conservation of migratory birds. *Conservation Biology* 14:366–372.
- Farrell, S. L., M. L. Morrison, A. J. Campomizzi, R. N. Wilkins. 2012. Conspecific cues and breeding habitat selection in an endangered woodland warbler. *Journal of Animal Ecology*.
- Ford, A. L., and O. W. Van Auken. 1982. The distribution of woody species in the Guadalupe River floodplain forest on the Edwards Plateau of Texas. *Southwestern Naturalist* 27:383–392.
- Groce, J. E., H. A. Mathewson, M. L. Morrison, and N. Wilkins. 2010. Scientific evaluation for the 5-year status review of the golden-cheeked warbler. Prepared for the U.S. Fish and Wildlife Service by the Institute of Renewable Natural Resources, Texas A&M University, College Station, USA.
- Guzy, M. J., and P. E. Lowther. 1997. Black-throated gray warbler (*Setophaga nigrescens*). Account 319 in A. Poole, editor. *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/bna/species/319>, DOI: 10.2173/bna.319
- Haig, S. M., W. M. Bronaugh, R. S. Crowhurst, J. D'Elia, C. A. Eagles-Smith, C. W. Epps, B. Knaus, M. P. Miller, M. L. Moses, S. Oyler-McCance, W. D. Robinson, and B. Sidlauskas. 2011. Genetic applications in avian conservation. *Auk* 128:205–229.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific, London, England, United Kingdom.
- Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Horne, J. S., K. M. Strickler, and M. Alldredge. 2011. Quantifying the importance of patch-specific changes in habitat to metapopulation viability of an endangered songbird. *Ecological Applications* 21:2478–2486.
- Keddy-Hector, D. P., T. L. Cook, and R. C. Maggio. 1992. Remote sensing and GIS of golden-cheeked warbler breeding habitat and vegetation types in the Balcones Canyonlands. Texas Parks and Wildlife Department Performance Report, Austin, USA.
- Klassen, J. A., M. L. Morrison, H. A. Mathewson, G. G. Rosenthal, and R. N. Wilkins. 2012. Canopy characteristics affecting avian reproductive success: the golden-cheeked warbler. *Wildlife Society Bulletin* 36:54–60.
- Klicka, J., and R. M. Zink. 1997. The importance of recent ice ages in speciation: a failed paradigm. *Science* 277:1666–1669.
- Kuhn, T. 1996. *The structure of scientific revolutions*. Third edition. University of Chicago Press, Chicago, Illinois, USA.
- Ladd, C., and L. Gass. 1999. Golden-cheeked warbler (*Dendroica chrysoparia*). Account 420 in A. Poole, editor. *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/bna/species/420>, DOI: 10.2173/bna.420
- Levins, R. 1969. *Evolution in changing environments*. Princeton University Press, New Jersey, USA.
- Lindsay, D. L., K. R. Barr, R. F. Lance, S. A. Tweddle, T. J. Hayden, and P. L. Leberg. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). *Molecular Ecology* 17:2122–2133.
- Lovette, I. J., and E. Bermingham. 1999. Explosive speciation in the New World *Dendroica* warblers. *Proceedings of the Royal Society of London B* 266:1629–1636.
- Mathewson, H. A., J. E. Groce, T. M. McFarland, M. L. Morrison, J. C. Newnam, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins. 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas. *Journal of Wildlife Management* 76: DOI: 10.1002/jwmg.352
- Mayer, C., K. Schiegg, and G. Pasinelli. 2009. Patchy population structure in a short-distance migrant: evidence from genetic and demographic data. *Molecular Ecology* 18:2353–2364.
- Mengel, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). *Living Bird* 3:9–43.
- Mills, L. S. 2007. *Conservation of wildlife populations: demography, genetics, and management*. Blackwell, Oxford, England, United Kingdom.
- Morrison, M. L. 2009. *Restoring wildlife: ecological concepts and practical applications*. Island Press, Washington, D.C., USA.
- Morrison, M. L. 2012. The habitat sampling and analysis paradigm has limited value in animal conservation: a prequel. *Journal of Wildlife Management* 76:438–450.
- Morrison, M. L., and J. W. Hardy. 1983. Hybridization between the hermit and Townsend's warblers. *Murrelet* 64:65–72.
- Morse, D. H., and A. F. Poole. 2005. Black-throated green warbler (*Setophaga virens*). Account 55 in A. Poole, editor. *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/bna/species/055>, DOI: 10.2173/bna.55
- Pulich, W. M. 1976. *The golden-cheeked warbler: a bioecological study*. Texas Parks and Wildlife Department, Austin, USA.
- Rohwer, S., and C. Wood. 1998. Three hybrid zones between hermit and Townsend's warblers in Washington and Oregon. *Auk* 115:284–310.
- Smeins, F. E. 1980. Natural role of fire on the Edwards Plateau. Pages 4–16 in L. D. White, editor. *Prescribed burning of the Edwards Plateau of Texas*. Texas Agricultural Extension Service, College Station, USA.
- Smeins, F. E., and S. D. Fuhlendorf. 1997. Biology and ecology of ashe (blueberry) juniper. Chapter 3 Pages 33–47 in C. A. Taylor, editor. 1997 Juniper Symposium. Texas Agricultural Experiment Station Technical Report, San Angelo, USA.
- Smeins, F., S. Fuhlendorf, and C. Taylor, Jr., 1997. Environmental and land use changes: a long-term perspective. Chapter 1 Pages 3–21 in C. A. Taylor, editor. 1997 Juniper Symposium Proceedings. Texas Agricultural Experiment Station Technical Report, San Angelo, USA.
- U.S. Fish and Wildlife Service [USFWS]. 1992. Golden-cheeked warbler (*Dendroica chrysoparia*) recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- U.S. Fish and Wildlife Service [USFWS]. 1996. Golden-cheeked warbler population and habitat viability assessment report. Compiled and edited by

- Carol Beardmore, Jeff Hatfield, and Jim Lewis in conjunction with workshop participants. Report of an August 21–24, 1995 workshop arranged by the U.S. Fish and Wildlife Service in partial fulfillment of U.S. National Biological Service Grant No. 80333-1423, Austin, Texas, USA.
- Veit, M. L., R. J. Robertson, P. B. Hamel, and V. L. Friesen. 2005. Population genetic structure and dispersal across a fragmented landscape in cerulean warblers (*Dendroica cerulea*). *Conservation Genetics* 6:159–174.
- Wahl, R., D. D. Diamond, and D. Shaw. 1990. The golden-cheeked warbler: a status review. Report submitted to Ecological Services. U.S. Fish and Wildlife Service, Fort Worth, Texas, USA.
- Waples, R. S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology* 15:1419–1439.

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