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WINTER- VS. BREEDING-HABITAT LIMITATION FOR AN ENDANGERED AVIAN MIGRANT

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Abstract. Migratory species have critical habitat needs during both breeding and wintering portions of the life cycle. Recent advances have made it possible to use satellite imagery and computer-assisted spatial analysis technology along with fieldwork to determine estimates for these critical habitat needs for the endangered Golden-cheeked Warbler, *Dendroica chrysoparia*. Using these procedures, we estimate that the Ashe juniper–oak breeding habitat for this species covers 6430 km^2 of central Texas, USA, whereas appropriate habitat in the known winter range covers 6750 km^2 of the Middle American cordillera. When combined with information on warbler breeding and wintering ecology, these figures indicate that the amount of available winter habitat (pine–oak above 1219 m [4000′] in elevation) supports only a fraction (15%) of the population that could be supported by the amount of estimated available breeding habitat, suggesting that Golden-cheeked Warbler populations could be limited by winter habitat availability.

Key words: avian migrant; breeding habitat; Dendroica chrysoparia; *endangered species; Golden-cheeked Warbler; habitat limitation; population limitation; remote sensing; winter habitat.*

INTRODUCTION

A quarter century ago, both John Terborgh (1974) and Steven Fretwell (1972) suggested that migratory bird populations could be limited during the nonbreeding portion of the life cycle. Until recently, it has been impossible to test this idea because comparison of the potential, relative size for breeding vs. wintering populations of a migratory species requires accurate data on habitat requirements and density from both ends of the annual cycle. Such data are not available for most migratory species, but the Golden-cheeked Warbler (*Dendroica chrysoparia* is an exception (see Plate 1).

The Golden-cheeked Warbler breeds in uplands and canyons of central Texas, USA, in mature (>20 years old) Ashe juniper–oak communities (Pulich 1976, Ladd and Gass 1999). The bird's preference for this habitat evidently derives from its use of sloughing juniper bark as the principal material in nest construction, its placement of nests predominantly in juniper and oak, and its foraging focused on oak species early in the season and junipers and oaks later in the season (Ladd and Gass 1999). Although the Golden-cheeked Warbler is recorded from 41 Texas counties, Pulich considered the breeding range to include 31 counties as of 1974; by 1999, the number of counties in which breeding birds could be detected had declined to 24 (Fig. 1), despite a considerable expansion of search effort in recent years (Ladd and Gass 1999). Disappearance of the species from a significant portion of its original breeding range was cause for its placement on the U.S. Fish and Wildlife Service Endangered Species List in 1990 (U.S. Fish and Wildlife Service 1990).

Efforts also have been made to document the winter range of the species since the bird's discovery in Guatemala in 1859. Nevertheless, until the last decade, little was known about this portion of the annual cycle other than the bare outline of species' distribution, based on 12 specimens and a small number (<20) of sight records (Pulich 1976). However, recent studies have revealed not only the extent of this portion of the range (Fig. 1), but also detailed information on habitat distribution, bird density, and ecology (Rappole et al. 1999, 2000).

In this paper, we present our data on both breeding and wintering habitat availability. These data are combined with known breeding and wintering bird densities to provide the first range-wide assessment of the potential for breeding vs. wintering habitat limitation for any migratory species.

METHODS

Breeding habitat estimation

Breeding habitat assessment, derived from work by D. Diamond and C. D. True, involved analysis of Landsat thematic mapper (TM) satellite scenes, dating from 1996 to 1997, each ~180 km on a side with pixel size of 30 m, obtained from the USGS EROS Data Center and covering 29 Texas counties. Results from analyses of a 1987 scene were incorporated for an area covering ~8% of the total area analyzed, due to the lack of

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FIG. 1. Texas breeding range (blue) and Middle American wintering range (red) of the Golden-cheeked Warbler, *Dendroica chrysoparia*.

available cloud-free images for more recent dates. Six counties, with a combined estimate of ~29 000 ha of possible Golden-cheeked Warbler habitat, were not included in this study. Classification procedures included: (1) georectification and georeferencing of all four scenes, (2) scenes merged (mosaiced) to form a single image, (3) performance of an unsupervised classification using reflectance bands 1–6 (Isodata module, ERDAS Imagine software) to assign all pixels into 60 spectral clusters, and (4) assignment of land cover values to each of the 60 spectral clusters. Land cover was characterized as forest, woodland, savanna, grassland, urban, and water. Extent of the mature Ashe juniper–oak community identified as Golden-cheeked Warbler breeding habitat ("forest") was calculated following geographic information system procedures using ArcInfo software (ESRI, Redlands, California, USA).

Breeding density estimation

Estimates of territorial male density in appropriate habitat from across the species' breeding range vary from 0 to 0.58 adult males/ha (Pulich 1976, Ladd 1985, Wahl et al. 1990, Keddy-Hector 1992, Jettj et al. 1998). For our purposes, we use the figure of 0.188 ± 0.000536 males/ha (mean ± 1 SE; n = 167 males and females) for a population from Ft. Hood in Bell and Coryell counties, Texas, studied intensively since 1992 (Jettj et al. 1998). Our reasons for selecting this value for average potential breeding density are as follows: (1) the Fort Hood data are derived from an intensive, long-term study covering a significant portion of the bird's breeding range (>1% of the total breeding population, according to Keddy-Hector 1992); (2) the data represent an average over a large area that incorporates a wide range of apparent habitat quality (as reflected by breeding male density); (3) the Ft. Hood data are those that were used as the basis for breeding population estimates in the Population Habitat Viability Assessment (PHVA) performed by a panel of experts on the bird convened by the U.S. Fish and Wildlife Service in August 1995 (Beardmore et al. 1996).

Winter habitat estimation

For 38.8% of the known winter range (Fig. 1; see Ladd and Gass 1999), we identified pine–oak habitat using Landsat TM imagery, with a spatial resolution of 30 m (900 m^2 per pixel), and extensive ground-truth data (442 site visits) following procedures similar to those just described for breeding habitat estimation. Pine–oak habitat outside the area covered by the satellite imagery (61.2% of the range) was identified using a land cover database produced by the USGS EROS Data Center, the University of Nebraska–Lincoln, and the Joint Research Centre of the European Commission (Brown et al. 1999, Loveland et al. 1999). This effort generated a global land cover characteristics database of 1-km resolution using Advanced Very High Resolution Radiometer data from April 1992 to March 1993. A seasonal land cover map was derived from the original land cover map using ancillary data, from which we used the class defined as "pine–oak" for our calculations.

Winter density estimation

Density of wintering Golden-cheeked Warblers was measured by walking transects. Transects averaged 1 km in length and, where possible, were located in a stratified-random manner by choosing a random number distance 0–100 m as a starting point within a randomly selected 1-km^2 block located on or near a point of ready access. Thus, transects often followed small roads or paths, although the canopy was nearly always closed overhead, so the effect on bird distributions was probably minimal. Observers walked slowly (~1.5 km/h) along transects scanning vegetation and listening for vocal members of the mixed-species foraging flocks, of which wintering Golden-cheeked Warblers are almost always members. Only two of 157 birds observed during our study were found foraging alone, away from any evidence of a mixed-species flock. The distance and angle to the nearest flock member was measured using a compass and measuring tape. We added 25 m, our conservative estimate of the radius of mixed-species flocks, to the distance value, and we used the program DISTANCE to calculate the density of flocks occupied by Golden-cheeked Warblers (Buckland et al. 1993).

RESULTS

Breeding habitat, densities, and carrying capacity

The amount of Golden-cheeked Warbler breeding habitat was assessed using a combination of remote-sensing thematic mapper (TM) Landsat satellite data and limited on-site verification ("ground truthing").

PLATE 1. Male-plumaged Golden-cheeked Warbler (*Dendroica chrysoparia*) foraging in encino (*Quercus virginiana*). Photograph courtesy fo M. Lockwood and VIREO (Academy of Natural Sciences, Philadelphia).

These procedures were used to identify and quantify the Ashe juniper–oak communities characteristic of the species' breeding habitat. Patches of habitat <5 ha in size were excluded from the totals. Warblers are known to use patches < 5 ha, and readily use smaller blocks of the Ashe juniper–oak plant community located in the vicinity of larger blocks, as dictated by the very nature of their habitat, which is often found along winding, steep-walled canyons (Benson 1990). However, studies have documented that small patches can be isolated, degraded, and underutilized, especially in urban and residential zones, and mean reproductive success is often reduced (Benson 1990, Engels and Sexton 1994, Beardmore et al. 1996). Therefore, we chose the 5-ha value as a conservative estimate for minimum patch occupancy size, following the recommendation contained in the U.S. Fish and Wildlife Service's (USFWS) 1995 PHVA for the species (Beardmore et al. 1996). Using these data, the total area of Ashe juniper–oak woodlands breeding habitat for Golden-cheeked Warblers in patches ≥5 ha was estimated to be 643 454 ha (Fig. 2).

To compute average density of total adult birds (male and female) in breeding habitat, we calculated the density for adult females by multiplying the figure for average male density by the percentage of mated males (89%) and adding this to the average number of adult males (0.188), for a total of 0.355 ± 0.00101 adult

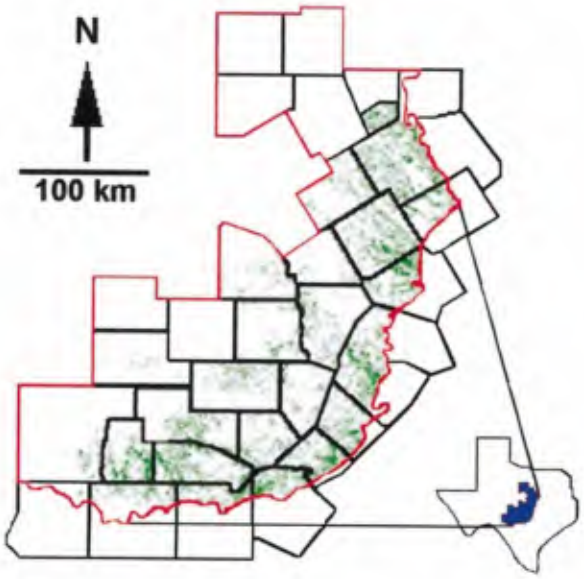

FIG. 2. Distribution of Ashe juniper–oak, breeding habitat (green) for the Golden-cheeked Warbler, in Texas. The southern and eastern portions of the species' range (red line) extend to the edge of the Edwards Plateau or Lampasas Cut-Plain, abrupt natural borders where plant communities change markedly. Western and northern portions of the range are not easily defined by a natural boundary, so we show its extent to the county boundaries in this region for all counties with a specimen record.

birds/ha (mean ± 1 SE). The 95% confidence interval for this estimate was calculated as $0.355 \pm t_{0.05(2),\nu}\, s_x = 0.00199$, or 0.353–0.357 birds/ha (where t is student's t, ν is the degrees of freedom and s_x is the standard error of the mean). We do not imply that all suitable habitat actually supports this density of birds, only that it potentially could support at least this number if the population were not limited by other factors.

The potential size of the adult breeding population that could be supported by Texas habitat was calculated by multiplying the amount of available breeding habitat, using total area of Ashe juniper–oak woodlands in patches ≥5 ha (643 454 ha), by a density of 0.355 adult Golden-cheeked Warblers for an estimated potential breeding population size of 228 426 birds. Using the upper and lower 95% CIs for our breeding density estimate yielded a 95% CI for the estimated potential breeding population of 227 142–229 710 birds.

Winter habitat, densities, and carrying capacity

We established the following criteria to define the Golden-cheeked Warbler's winter habitat in space and time.

Winter period.—We define "winter period" as October–February. Golden-cheeked Warblers disappear from their breeding grounds by late July and, although data are few, the fall migratory period is presumed to extend from then until at least mid-October (Ladd and Gass 1999). Spring migration must begin by late February, because males arrive on territory in mid- to late March (Ladd and Gass 1999). Records for birds outside Texas that do not occur within this period are considered to be probable transients, including the two specimens from Nicaragua taken in mid-September of 1890 (Pulich 1976).

Preferred plant communities in winter.—Recent observations and censuses have documented that the principal plant community in which the Golden-cheeked Warbler occurs during winter is pine–oak forest above 1219 m (4000 feet) elevation (Pulich 1976, Rappole et al. 1999, 2000). Characteristics of this habitat that appear to be most significant for the warbler are an abundance of oak species with shiny narrow, elliptical, or oblong leaves (e.g., *Quercus sapotifolia*, *Q. eliptica*, *Q. elongata*, *Q. cortesii*) mixed with a pine overstory; >94% of foraging attempts observed occurred in these tree species, and basal area of these oaks was significantly higher on sites occupied by warblers than on unoccupied sites (Rappole et al. 1999).

Region.—We define the outline of the winter range (Fig. 1) as extending from central Chiapas, Mexico, southeast along a relatively narrow band of the Middle American cordillera to southern Honduras (Tegucigalpa), matching rather closely the extent of "Humid Lower Montane Oak Pine Forest" as defined by Holdridge (1962).

All of our calculations, discussions, and comparisons are based on these definitions of Golden-cheeked Warbler winter distribution. Two of 157 birds were found outside mixed-species flocks and 87% of flocks containing Golden-cheeked Warblers contained a single individual of the species, a number significantly higher than expected by chance compared with a Poisson distribution ($\chi^2_1 = 7.6$, $P < 0.001$), whereas significantly fewer flocks contained two ($\chi^2_1 = 8.3$, $P = 0.004$) or three ($\chi^2_1 = 4.5$, $P < 0.04$) Golden-cheeked Warblers. We found only three of 157 individuals at elevations lower than 1219 m, and only two individuals in a habitat other than pine–oak, vastly fewer than expected by chance when the number of birds found was standardized for search effort (Rappole et al. 1999). Furthermore, despite the numerous studies of the distribution of Neotropical birds conducted by generations of field biologists, there are no credible reports for Golden-cheeked Warblers from outside our proposed geographic distributional boundaries during the winter period (Pulich 1976, Rappole et al. 1999, 2000).

Estimates of winter habitat availability for Golden-cheeked Warblers, as defined by the stated parameters, were made using a combination of remote-sensing data from two sources (Fig. 3).

Our fieldwork, in addition to that of others, documented that winter distribution of Golden-cheeked Warblers was restricted mainly to highland, mixed-species flocks, normally with one individual per flock. Thus, density within the wintering range was calculated based on 50 transect counts focused on locating mixed-species flocks in pine–oak habitat above 1219 m elevation from 20 December 1995 to 10 February 1997.

We calculated the carrying capacity of winter habitat by multiplying the amount of suitable winter habitat (defined as pine–oak above 1219 m from within the species' known range) by the density of wintering Golden-cheeked Warblers, based on our transect data. We detected 47 Golden-cheeked Warblers on the transect counts. We calculated that there were 0.048 ± 0.034 flocks/ha (mean ± 1 SE) containing Golden-cheeked Warblers, which when multiplied by 1.07, the average number of Golden-cheeked Warblers per occupied flock, yielded a density of 0.051 ± 0.036 Golden-cheeked Warblers/ha (mean ± 1 SE). The 95% CI for this estimate was calculated as $0.051 \pm t_{0.05(2),\nu}\, s_x = 0.0724$, or −0.021 to 0.123 birds/ha. We use this number as a maximum density estimate based on our field observations indicating that Golden-cheeked Warbler intraspecific interactions limit the number of conspecific individuals participating in any given flock, a phenomenon observed in several other species as well (Rappole 1995:44). We found that there were 675 005 ha of pine–oak habitat above 1219 m (see Fig. 3) by combining results of our Landsat data analysis (362 010 ha) with the USGS coverage (312 995 ha). Based on the estimates of the amount of wintering habitat available and the amount of wintering habitat required per bird, we calculated that there is enough wintering habitat to support 34 425 birds. Using the upper and lower

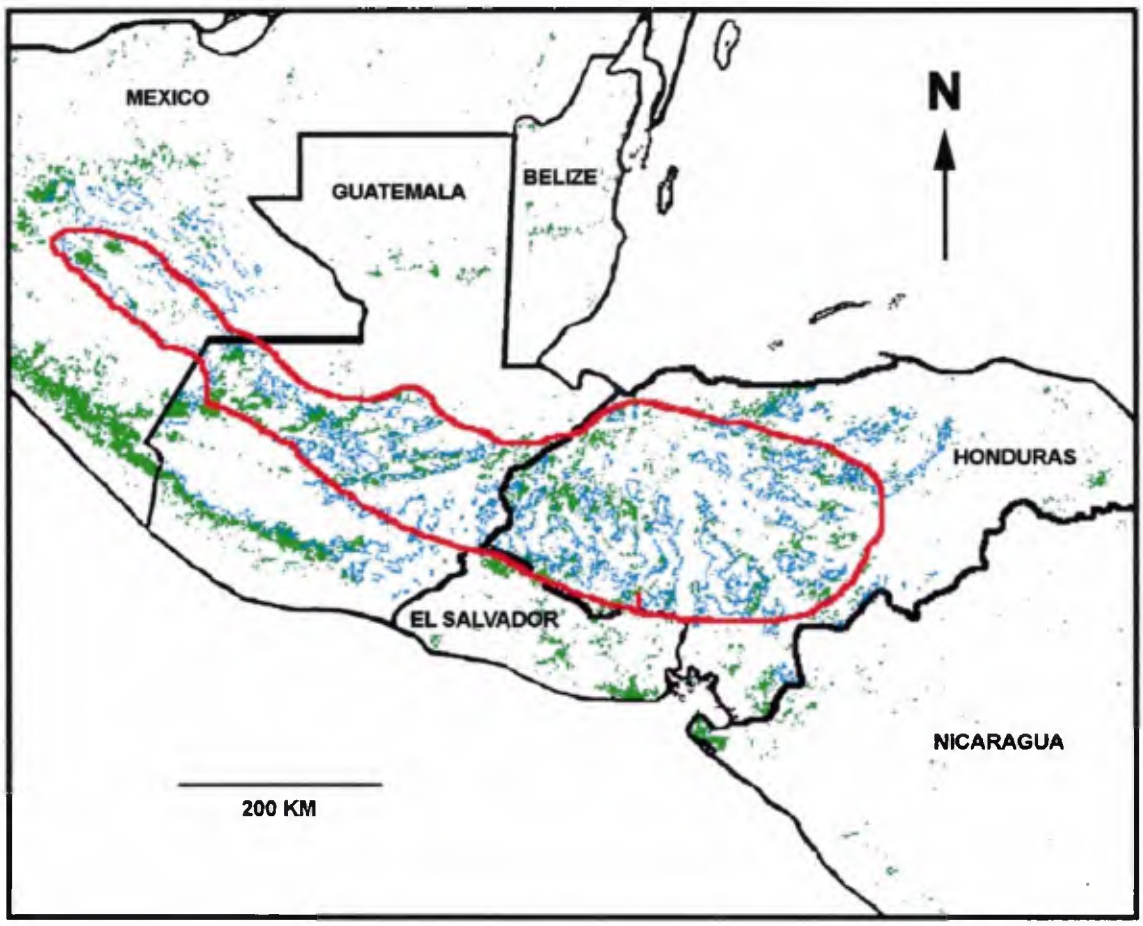

FIG. 3. Distribution of Middle American highland pine–oak (green), wintering habitat for the Golden-cheeked Warbler. The known winter range for the species is outlined with a red line. Blue lines indicate the 4000-foot (1219.2-m) contour line.

95% CIs for our winter density estimate yields a 95% CI for the estimated potential wintering population of −14 467 to 83 317 birds. If we include an additional 3.2% for birds occurring at elevations below 1219 m or in habitats other than pine–oak, the wintering population estimate becomes 35 527 individuals.

DISCUSSION

All previous summary studies of the conservation status of the Golden-cheeked Warbler have concluded that principal threats to the species' long-term survival center on preservation of high-quality breeding habitat, based on obvious changes in the Ashe juniper–oak community caused by clearing and grazing, and documented disappearance of the bird from large parts of its former breeding range (Pulich 1976, Wahl et al. 1990, Beardmore et al. 1996, Ladd and Gass 1999). Principal reasons suggested for this decline in extent of the breeding distribution are habitat destruction and fragmentation (Ladd and Gass 1999).

Habitat destruction obviously could cause local extirpation of the species, an explanation that applies to the absence of the bird from Dallas County, where the last remaining Ashe juniper–oak has been cleared and where birds no longer can be found (Pulich 1976). However, Ashe juniper–oak communities still persist as altered (second-growth or grazed), but apparently suitable, nesting habitat over much of the species' former range (Benson 1990), including areas from which recent surveys have failed to document the species (Wahl et al. 1990, Beardmore et al. 1996). Absence from apparently suitable habitat has been explained as the result of habitat fragmentation in which occupancy by breeding birds is reduced or eliminated from patches <50 ha (Wahl et al. 1990, Beardmore et al. 1996, Ladd and Gass 1999). Mechanisms suggested as causes for reducing numbers of breeding warblers on patches <50 ha include: (1) decreased likelihood that males will be able to attract females; (2) decreased likelihood of successful dispersal by offspring; and (3) decreased re-

productive success due to increased probability of predation by Blue Jays (*Cyanocitta cristata*) and other predators, as well as social parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Keddy-Hector 2000). Benson (1990), however, found no evidence to indicate that patch size had an effect on warbler occupancy of breeding habitat, based on surveys for singing birds on 300 randomly selected sites varying in size from <1 ha to >250 ha. In fact, he found singing birds on patches as small as 0.66 ha. Furthermore, although several studies have shown negative effects on reproductive success for birds breeding in small (<5-ha) patches or urban sites, evidently as the result of increased predation, none has shown an effect of patch size per se on occupancy (Engels and Sexton 1994, Mass-Burleigh 1998). Thus, although we understand how possible exposure to increased rates of predation or parasitism could explain why Golden-cheeked Warblers would choose one site over another, we question whether these explanations provide adequate reasons for the absence of the species from apparently suitable habitat if breeding habitat were, in fact, limiting. Reproductive success on sites of even apparently low quality is still on the order of 40–60% per season (Mass-Burleigh 1998).

Evidence for wintering-ground population limitation

Our calculations, based on GIS and remote-sensing technology in combination with intensive ground surveys, indicate that the amount of winter habitat is sufficient to support a population of Golden-cheeked Warblers ~15% (35 527 birds) the size of what the measured amount of breeding habitat should be able to support (228 426 birds).

Ladd and Gass (1999), citing data from Wahl et al. (1990), estimate Golden-cheeked Warbler breeding population size to be between 4822 and 16 016 pairs (9644–32 032 adult males and females). The PHVA for the species reported average breeding success (fecundity) to be 0.75 males produced for each second-year (SY) breeding male and 1.08 males produced for each after-second-year (ASY) male, or a little less than two individuals produced pair per (Beardmore et al. 1996). These figures show that young birds add nearly 100% to the population by the close of the breeding season, for a total population size of 19 288–64 064 individuals at the time of southward migration. Thus our estimated winter population size of 35 527 birds fits well with available breeding population estimates (Ladd and Gass 1999). The discrepancy between our findings and those of breeding-ground workers does not concern population size, but rather which phase of the life cycle is limiting as regards habitat availability. Our surveys documented that suitable winter habitat appeared to be occupied. However, based on breeding population size estimates, average known density of breeding birds per hectare, and the amount of apparently suitable breeding habitat, there appear to be fewer birds breeding than available breeding habitat can support. Some factor seems to be holding the Golden-cheeked Warbler breeding population well below capacity, based on available habitat. We propose that available winter habitat could be that factor.

Winter limitation of Golden-cheeked Warbler population size is based on several assumptions, the validity of which remains to be tested. The most critical of these are the estimates of maximum density for breeding and wintering areas. These result in the counterintuitive finding that although breeding and wintering habitat are roughly equivalent in amount (at ~650 000 ha), the wintering ground may be much more restrictive due to potentially large differences in carrying capacity during these different phases of the life cycle (0.188 pairs/ha on the breeding ground vs. 0.051 individuals/ha on the wintering ground). These assumptions are founded on the following observations: (1) average breeding density in a large, intensively studied population is 0.188 pairs/ha; (2) extensive areas of apparently suitable breeding habitat are unoccupied for reasons that are not evident; (3) nearly all suitable winter habitat surveyed by us appeared to contain Golden-cheeked Warblers in mixed-species flocks, with an average of 1.07 individuals per flock; and (4) participation in flocks appeared to be restricted by intraspecific competition. Based on these data and observations, we hypothesize that the reason warblers are absent from apparently suitable breeding habitat, as reported in the PHVA (Beardmore et al. 1996), is that there is more breeding habitat than there are birds to fill it (Rappole and McDonald 1994). A similar situation has been reported for the endangered Kirtland's Warbler (*Dendroica kirtlandii*), in which vast areas of apparently suitable breeding habitat are unoccupied, presumably because of the extremely limited distribution of its preferred winter habitat, Caribbean pine savanna (Haney et al. 1998).

Our data raise the possibility of a wintering-ground habitat limitation hypothesis for Golden-cheeked Warblers. The species spends more than half of the year (August–February) away from its Texas breeding grounds (Pulich 1976, Jettj et al. 1998, Ladd and Gass 1999). The species has distinctive habitat requirements during this period, as well as apparently obligate association with mixed-species flocks (Pulich 1976, Rappole et al. 1999, 2000, King and Rappole 2000); of 157 Golden-cheeked Warblers encountered during the course of our study, 155 were in mixed-species flocks. Furthermore, only flocks having a particular species composition appear to be suitable (Rappole et al. 1999). Finally, members of the species appear to be strongly territorial toward conspecifics; the vast majority (87%) of flocks with Golden-cheeked Warblers contained a single individual of the species. This information indicates that high-quality winter habitat is limited and that intraspecific behavioral interaction probably limits flock participation to a single Golden-cheeked Warbler, under most circumstances. Thus, although the winter-

ing range is geographically broad (Fig. 1), distribution of highland pine–oak habitat and occurrence of suitable mixed-species flocks within this habitat are restricted (King and Rappole 2000).

Limitations of the data

In addition to the assumptions already discussed, we have made two key assumptions in our comparison of breeding vs. wintering potential population sizes for the Golden-cheeked Warbler. First, we have assumed that all Ashe juniper–oak habitat ≥5 ha in size and occurring within the known breeding range of the species could be used to support breeding populations if there enough birds were available. We base this assumption on two kinds of data: (1) the large number of detailed accounts describing the critical aspects of warbler breeding habitat as a mixture of mature Ashe juniper and oak (Pulich 1976, Wahl et al. 1990, Keddy-Hector 1992, Engels and Sexton 1994, Beardmore et al. 1996, Jettj et al. 1998, Ladd and Gass 1999, Keddy-Hector 2000); and (2) the fact that breeding records for the species are scattered throughout the range (Pulich 1976, Wahl et al. 1990, Beardmore et al. 1996, Ladd and Gass 1999).

The second important assumption is that the USGS data are adequate for Golden-cheeked Warbler winter habitat assessment. Our analysis of pine–oak habitat from within the area covered by the TM scenes (southeastern Guatemala and western Honduras) is 84% accurate, based on data gathered from 442 reference points (Rappole et al. 2000). However, the USGS data set was created primarily for large-scale applications, necessarily sacrificing some accuracy and precision at the individual pixel level. The probability is that the USGS data underestimate the extent of pine–oak because of the much larger area represented by the USGS pixels (1 km on a side [100 ha] for the USGS data, as opposed to 30 m on a side [0.09 ha] for the TM scenes). This difference in resolution means that small patches of pine–oak habitat (<50 ha) are likely to be misclassified into other habitat categories. We attempted to assess the implications of this finding by plotting known Golden-cheeked Warbler locations on the USGS land cover map. Next to the expected pine–oak class, the largest number of locations fell within "evergreen needleleaf forest," which covers 25% of the region and could reasonably be assumed (based on geographic and spectral relatedness) to contain some pine–oak habitat as well. Including this entire pine class in the assessment for the region outside the area covered by the TM scenes adds 440 648 ha of possible Golden-cheeked Warbler habitat, and increases the estimated winter carrying capacity to 56 674 birds, higher than the estimate using only USGS pine–oak, but still significantly below the estimated size supportable on the breeding grounds. Additionally, there are few published records of the bird from the regions outside of the area covered by the TM imagery, and we encountered significantly fewer birds per unit of observer effort ($\chi^2_1 = 22.9$, $P < 0.001$) in these areas (eastern Honduras, western Guatemala, and Chiapas). Thus, we are confident that the conclusions regarding the relative influence of breeding- and wintering-ground habitat limitation are not critically affected by restrictions of the data.

Conclusions

The amount of information available on the breeding portion of the life cycle (March–August) for the Golden-cheeked Warbler is extensive, whereas that available for the nonbreeding portion is minimal. Of 145 works cited in a recent bibliography for the species, <16% related to the nonbreeding portion of the life cycle, and most of these were individual distributional records (Sexton et al. 1995). Similarly, of 412 specimens collected, 370 were taken on the Texas breeding grounds (Pulich 1976). Symptomatic of the lack of nonbreeding season information is the fact that the locations of major portions of the species' winter range were subject to debate until quite recently (Pulich 1976, Rappole et al. 1999).

Our findings indicate that lack of winter habitat could limit population size for the Golden-cheeked Warbler. We hope that this information will stimulate efforts to study the importance of tropical highland pine–oak, a habitat that is under significant pressure as vast areas of Middle America are cleared for coffee, timber, pasture, and other commercial land use (Rappole et al. 2000). In fact, highland Middle American pine–oak forest was given a conservation status of "endangered" in a recent World Bank report (Dinerstein et al. 1995).

It is certainly not our intent to minimize the importance of breeding habitat for the bird. Clearly, high-quality breeding habitat that is protected against clearing for pasture or development is critical for the species' long-term survival, a fact that has been pointed out repeatedly (Pulich 1976, Keddy-Hector 1992, Engels and Sexton 1994, Beardmore et al. 1996, Ladd and Gass 1999, Keddy-Hector 2000). We merely wish to redress the current imbalance that exists, whereby nearly all of the focus for study of the species is placed on its breeding biology and habitat needs. Work needs to be done to understand the Golden-cheeked Warbler and similar species during other portions of the life cycle as well (Fretwell 1972, Terborgh 1974, Haney et al. 1998).

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