

Section 6 (Texas Traditional) Report Review

Form emailed to FWS S6 coordinator (mm/dd/yyyy): 8/8/2011

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Project Title: Winter ecology, relative abundance and population monitoring of golden-cheeked warblers throughout the known and potential winter range.

Final or Interim Report? Final

Grant #: TX E-69-R

Reviewer Station: Austin ESFO

Lead station concurs with the following comments: NA (reviewer from lead station)

Interim Report (check one):

- Acceptable (no comments)
 - Needs revision prior to final report (see comments below)
 - Incomplete (see comments below)
-

Final Report (check one):

- Acceptable (no comments)
 - Needs revision (see comments below)
 - Incomplete (see comments below)
-

Comments:

FINAL REPORT

As Required by

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. TX E – 69-R

Endangered and Threatened Species Conservation

**Winter ecology, relative abundance and population monitoring of Golden-cheeked
Warblers throughout the known and potential winter range.**

Prepared by:

Dr. Oliver Komar



Carter Smith
Executive Director

Clayton Wolf
Division Director, Wildlife

4 May 2011

FINAL REPORT

STATE: Texas **GRANT NUMBER:** TX E – 69-R

GRANT TITLE: Endangered and Threatened Species Conservation

PROJECT TITLE: Winter ecology, relative abundance and population monitoring of Golden-cheeked Warblers throughout the known and potential winter range.

REPORTING PERIOD: 8/01/05 to 2/28/11

OBJECTIVE(S):

Six teams of researchers in five countries will expand knowledge of winter distribution, and quantify relative abundance, and habitat use of Golden-cheeked Warblers at known and potential wintering sites across the entire winter range, from Mexico to Nicaragua, during one winter period.

Segment Objectives:

1. Six teams of observers/researchers in each of the 5 countries (Mexico, Guatemala, Honduras, Nicaragua, El Salvador) will be assembled and coordinated on protocol.
2. Basic research protocol shall consist of:
 - a. Intensive evaluation of mixed species foraging flocks to determine density and relative abundance of Golden-cheeked Warblers.
 - b. Vegetation descriptions of each habitat patch studied, using a standardized method such as tree and shrub surveys in plots of 0.1 ha for each patch.
 - c. Field identification of sex and age classes.
 - d. Methods for selecting study sites.
 - e. Methods for mapping study sites (GIS).
3. During January 2006, and during winter 2006-2007 the teams will collect data at known and potential wintering sites for Golden-cheeked Warblers throughout the range and extent of the Central American pine-oak ecoregion.
4. During winter 2008-2009 the teams will initiate data collection at known and potential wintering sites for Golden-cheeked Warblers throughout the range and extent of the Central American pine-oak ecoregion. Site visits will last for approximately 6 days each (30 days of field work per team are planned each year).
5. Nov 2009. Five teams of observers, one for each of the 5 countries where the study will take place, will be trained for appropriate field techniques.

6. Winter 2009- 2010. The observers will all collect data following standard protocol at known and potential wintering sites for Golden-cheeked Warblers throughout the range and extent of the Central American pine-oak ecoregion as well as in Costa Rica. Site visits will last for approximately 6 days each (30 days of field work per team are planned). The protocol has been in development since 2004, and was revised in 2006 and 2007, and will be revised to include marking protocols in 2009. The revised protocol includes:
 - a. Intensive evaluation of mixed species foraging flocks to determine density and relative abundance of Golden-cheeked Warblers.
 - b. Vegetation descriptions of each habitat patch studied, using standardized methods.
 - c. Field identification of sex and age classes.
 - d. Methods for selecting study sites.
 - e. Methods for mapping study sites (GIS).
 - f. (pending) banding and marking guidelines.
7. Mar-Aug 2010. We will analyze data from this field season, combined with previous field seasons, to draw conclusions about annual changes in relative abundance, and ecological factors such as habitat use and geographic segregation of sex or age classes.
8. Sep 2010 – Feb 2011. The principal investigator will travel to present results in appropriate scientific meetings or conservation audiences. In addition, attempts at capture and banding of GCWA will be conducted on the winter grounds.

Significant Deviation:

None

Summary Of Progress:

See Attachment A.

Preliminary Findings:

See Attachment A (pdf file).

Location: Chiapas, Mexico; Honduras; Guatemala; Nicaragua; El Salvador.

Cost: available upon completion of project.

Prepared by: Craig Farquhar

Date: 4 May 2011

Approved by: 

Date: 4 May 2011



Winter ecology, relative abundance and population monitoring of Golden-cheeked Warblers (*Dendroica chrysoparia*) throughout the known and potential winter range.

FINAL REPORT, 1 MAY 2011



Foto: Golden-cheeked Warbler at La Tigra National Park, Honduras. By John van Dort.



FUNDEC/GAIA



FUNDACION DEFENSORES DE LA NATURALEZA

Winter ecology, relative abundance and population monitoring of Golden-cheeked Warblers (*Dendroica chrysoparia*) throughout the known and potential winter range.

**FINAL REPORT TO
TEXAS PARKS & WILDLIFE DEPARTMENT
(MOA E69 #172003)
1 MAY 2011**

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Abstract

This four-year study of the winter ecology of the endangered, migratory Golden-cheeked Warbler (*Dendroica chrysoparia*) was carried out across the species' entire known winter range in five countries: Mexico, Guatemala, Honduras, El Salvador, and Nicaragua. More than four hundred individual warblers were located, and 603 mixed-species foraging flocks were described from 47 sites across the Central American Pine-oak Forest Ecoregion. The results are divided into five chapters, covering winter distribution and abundance, skewed sex ratios and latitudinal sexual segregation, apparent strong population declines derived from a unique monitoring method, participation in mixed species foraging flocks, and other aspects of the winter ecology of Golden-cheeked Warblers.

In Chapter 1, we describe winter distribution, abundance, and habitat preferences for the warbler in their wintering grounds, the pine-oak forests of southern Mexico and northern Central America. Wintering warblers were found at 35 sites, including previously unknown wintering areas in southern Chiapas, El Salvador, southern Honduras and northern Nicaragua. Sites with pine forest mixed with encino-type oak trees in the mid-story were most attractive for the warblers, and mixed-species foraging flocks at such sites typically had on average one or more Golden-cheeked warblers in each flock. Overall relative abundance across the wintering range was 0.66 birds per foraging flock, and 0.30 birds per ha occupied by flocks. Abundance was twice as high where Encino oaks formed >30% of the mid-canopy cover. Male warblers were more abundant in the northern part of the winter range, whereas female types (including male and female juveniles) were more abundant in the central part of the range.

In Chapter 2, we describe skewed sex ratios and evidence for latitudinal sexual segregation in Golden-cheeked Warblers on the wintering grounds. The expected ratio of adult males to female-plumaged birds (females plus juveniles) is close to 1:2. The actual observed ratio was 1:0.7. Whereas we expected more female types, we found more male types. This skewed sex ratio was similar within foraging flocks and among birds found outside of mixed flocks. The predominance of males was much more pronounced in Guatemala and Mexico (northern part of range) than in Honduras, El Salvador, and Nicaragua (southern part of range). We also noted a strong relationship among males to elevation, with an apparent preference for elevations of 1400-2400 m.a.s.l., whereas there was no significant relationship of elevation to female abundance. The strongest evidence for latitudinal sexual segregation was the relationship of the sexes to latitude. Male abundance declined from north to south, in a linear fashion. Female-type abundance showed a peak near the northern limit of the range, and another stronger peak in the southern part of the range. The skew towards males in the sex ratio suggests either that observers were biased in seeking warblers in habitats or elevations preferred by males, or that males may have higher annual survival than females and immatures, generating an overall skew towards adult males in the population. We found no evidence of habitat segregation among the sexes, but the presence of latitudinal (and elevational) segregation suggests that females may be wintering in different areas where they have been overlooked, such as possibly oak forests of southern Central America.

Chapter 3 addresses a unique method for population monitoring of Golden-cheeked Warblers in the wintering range, based on comparing mean abundance of individuals occupying mixed-species foraging flocks at fixed locations across winters. We monitored flocks at fixed locations at 24 sites across five countries in the wintering grounds. The number of flocks monitored from one season to the next varied from 20 flocks during the first annual comparison, to 36 and 37 flocks each during the second and third annual comparisons. Mean abundance within the flocks appeared to decline each season, with a combined three-year decline of 19%. Season to season declines were not significant, except during the second annual comparison (comparing the winter of 2007-8 to 2008-9). During the first of those two winters, warblers were present in 17 of 36 flocks, but during the second, they were present in just 8 of the 36 flocks.

Declines appeared to be much stronger for females (31% annually over the three year period) than for males (8% annual decline). Many of the monitoring locations were near the periphery of the winter range, so these strong declines may not be representative across the whole range. Future monitoring can be greatly improved by increasing the number of flock locations monitored from one season to the next.

Chapter 4 addresses other aspects of winter ecology of the Golden-cheeked Warbler, such as vocalizations, use of foraging substrate, and participation in mixed-species foraging flocks. Approximately 31% of warblers, both males and female-types, vocalized with chip notes while foraging. Adult males and female types (including immatures) foraged in similar parts of trees, usually (50%) in encino-type oaks (*Quercus* spp.). The warblers are core members of mixed species flocks of insectivorous birds. Their use of the flocks was positively correlated to 16 out of 23 frequent flock members, including both migrant and resident bird species. Only two other species, the Greater Pewee (*Contopus pertinax*) and the Hermit Warbler (*Dendroica occidentalis*) presented as many or more positive correlations with other flock members.

Chapter 5 summarizes conclusions drawn from the previous chapters and future research directions for applied conservation research. We roughly estimate the wintering population to be 585,000 birds, including 405,000 males and 180,000 females, although these estimates may be based on an overestimate of available habitat. Warblers are closely associated with encino oaks, in which they forage most of the time, so conservation strategies must include the conservation of encino oaks. We recommend expanding efforts to monitor population trends, by tracking the use of mixed species foraging flocks by Golden-cheeked Warblers at fixed locations across the wintering grounds. We also highlight the need for winter banding studies, to learn more about site fidelity, survivorship, and the relationship of density in flocks to density in the landscape, and the need to continue explorations for new wintering areas, especially in southern Central America and in Oaxaca. Finally, we suggest that conservation research on Encino oaks and their ecosystem services will be useful for developing conservation strategies for Golden-cheeked Warblers.

Acknowledgments

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Field coordinators included Oscar Bolaños and Carlos Funes (El Salvador), John van Dort (Honduras), Jeff McCrary and Pablo Somarriba (Nicaragua), Byron González and Ana José Cobar (Guatemala), Efrain Castellanos and Alberto Martínez (Chiapas). Additional Field Technicians included Aura Cruz, Vanessa Dávila, Adan Flores, Javier Gómez, Serafín Gómez, Erick Hernández, Jorge Jiménez, Francisco Perla, Fabiola Rodríguez, Ana Sofía Trujillo, and Kashmir Wolf. Volunteer Field Technicians included Reynaldo Blandón, Pier-Olivier Boudreault, Jesse Fagan, Pablo Geovani Galán, Melvin López, Tomás López, Donald Mackler, John Maresh, Francisco Muñoz, Alonso Murillo, Jaime Obando, Violeta Salazar, and Iselda Vega.

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This report is a contribution of the Alliance for the Conservation of Central American Pine-oak Forests Ecoregion.

Preface

In 2003, the Alianza para la Conservación de los Bosques de Pino-Encino de Mesoamérica (APEM) was formed and immediately identified the need for coordinated monitoring of the Golden-cheeked Warbler (*Dendroica chrysoparia*), a flagship and umbrella species for conserving the critically endangered Central American pine-oak forests (Macias et al. 2004). The warbler is currently considered globally-endangered (IUCN 2010). Virtually the entire population winters in one ecoregion, Central American Pine-oak Forest. These forests are now heavily fragmented across an area of 104,000 km² from Chiapas south and east to Nicaragua, including Guatemala, Honduras, and El Salvador. Remaining forests may occupy as little as 19,509 km² and only 1,449 km² are located within protected areas (APEM 2008). Previous ecological studies of Golden-cheeked Warblers on wintering grounds have been carried out at several sites, but habitat relationships, relative abundance, and population trends across this region have not been evaluated previously.

A recent study of Golden-cheeked Warbler winter habitat requirements and interpretation of satellite imagery from the 1990s suggested that the overall population is limited by winter habitat availability, with only 6750 km² of suitable winter habitat remaining, capable of supporting 35,527 birds, only 15% of the population that those authors estimated could be supported by available breeding habitat (Rappole et al. 2003). This evaluation was based on a density estimate of 0.051 birds per hectare, derived from abundance data collected in Honduras and Guatemala (Rappole et al. 2000). The study assumed that appropriate winter habitat was restricted to areas above 1200 m above sea level (based on anecdotal reports summarized in Ladd & Gass 1999). The causes of the population limitation during winter were not determined. On the other hand, recent field surveys in Texas estimated that the breeding population included 221,000 singing males (Morrison et al. 2010), suggesting that the entire population could be over 600,000 individuals. Winter habitat limitations reported by Rappole et al. (2003), based on potentially inaccurate estimates of winter densities and/or habitat availability, require further investigation.

Another aspect of winter ecology that merits investigation is the possibility of sexual segregation on the wintering grounds. In Chiapas, Guatemala, and Honduras, male Golden-cheeked Warblers have been reported more frequently than females, leading Vidal et al. (1994) to hypothesize that the sexes may display geographic segregation on the wintering grounds. Although such segregation is known in relatively few Neotropical migratory bird species, it has been reported for two species of *Dendroica* warblers wintering in Mexico (Komar et al. 2005). Range-wide data is needed to evaluate this hypothesis, and the current study provides such data and analysis.

The purpose of the present study was to explore opportunities for monitoring of the Golden-cheeked Warbler population on its wintering grounds, and to answer a series of questions about the species' winter ecology through field studies carried out across the winter range. In particular, we evaluated questions about the winter distribution, by conducting intensive searches during four winters throughout the potential winter range. We also evaluated questions about winter density and the relationship between abundance and habitat features, such as forest type and elevation. We studied the composition of mixed-species foraging flocks used by the warblers, and collected data on sex ratios at numerous sites across the winter range. The answers to these questions should shed light on possible conservation strategies for the Golden-cheeked Warbler on its wintering grounds.

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Chapter 1

Winter distribution, abundance, and habitat of Golden-cheeked Warblers (*Dendroica chrysoparia*) in pine-oak forests of Mexico and Central America

Introduction

The Golden-cheeked Warbler (*Dendroica chrysoparia*) has been a focus of conservation interest and research since the species was first recognized as an endangered species in 1991. As with many species of Neotropical migratory birds, the warbler has been studied far more on the temperate breeding grounds than on the wintering grounds. Nevertheless, the wintering area is subject to numerous threats and pressures, and could be the source for population limitation (Rappole et al. 2003). The winter range was previously thought to include principally the central highlands of Chiapas, Guatemala, and Honduras (Rappole et al. 2003). However, recent observations suggest the range may be broader, potentially including coastal highlands stretching from southwestern Chiapas to central El Salvador and northwestern Nicaragua (various observers *vide* O. Komar and C. Macias, unpublished data; Morales et al. 2008).

Previous ecological studies of the warbler on its wintering grounds were carried out in small portions of the winter range (Vidal et al. 1994, Rappole et al. 1999), raising questions about the applicability of the results to the entire winter range. The previous studies established that the warblers frequently joined mixed-species foraging flocks of insectivorous birds, such as flycatchers, vireos, and warblers. They also indicated that Golden-cheeked Warblers showed a marked preference for encino-type oaks (*Quercus* spp. with relatively narrow leaves) as a foraging substrate, and were most abundant between 1200 and 2400 m above sea level.

The present study aimed to extend ecological studies of habitat use and relative abundance of Golden-cheeked Warblers to additional areas across the entire winter range. Virtually all reports of wintering birds come from within the Central American Pine-oak Forests Ecoregion (Ladd & Gass 1999). This region extends from western Chiapas (southern Mexico, east of the Isthmus of Tehuantepec) south and east to the highlands of northern Nicaragua and eastern Honduras.

Study area and methods

The study was carried out at 47 sites in the Central American Pine-oak Forests Ecoregion (Table 1). These forests are now heavily fragmented across an area of 104,000 km² from Chiapas south and east to Nicaragua, including Guatemala, Honduras, and El Salvador. Remaining forests may occupy as little as 19,509 km² and only 1,449 km² are located within protected areas (APEM 2008).

Each winter from November 2006 to February 2010, five or six separate teams of two to three (rarely four) observers studied Golden-cheeked Warblers in mixed species foraging flocks across the Central American Pine-oak Forests Ecoregion. Each team worked at five (sometimes more or less) habitat patches (sites) within one country. Within a patch site, they collected data during five mornings, by seeking and then following foraging flocks of insectivorous birds as long as possible up to 4 h (or up to 12:00 h, whichever came first). Searches for flocks began at 06:00 h. Data was only used from flocks studied for at least 1.5 h. If observers lost track of a flock, they spent the rest of the morning attempting to relocate it, and if successful, took up

Table 1. Study sites and numbers of flocks where Golden-cheeked Warblers were studied during four winter seasons.

Country	Site	2006-07	2007-08	2008-09	2009-10	Lat & long degrees		Elev. masl	Individuals documented in flocks
Mexico	Arcotetes	5	7	5	5	16.722	-92.601	2295	20
Mexico	Coapilla	3	5	5	4	17.155	-93.245	1812	18
Mexico	Corazón del Valle*		1			16.406	-93.977	865	0
Mexico	Huitepec	1	5	5	5	16.75	-92.684	2415	4
Mexico	Independencia		3			15.872	-92.903	1398	0
Mexico	La Granada	3	5	5		16.534	-92.44	1919	12
Mexico	Montebello	2	5		3	16.124	-91.728	1500	13
Mexico	Moxiquil	2	5	6	5	16.759	-92.634	2310	23
Mexico	Tres Picos*		7	6		16.201	-93.626	1357	13
Mexico	Monte Sinaí				5	16.641	-94.019	1386	2
Mexico	Buenos Aires				5	15.593	-92.509	1351	2
Guatemala	Cerro Alux*	5	5	5	5	14.618	-90.643	2127	3
Guatemala	Chimusinique*	5	5	5		15.277	-91.518	2027	2
Guatemala	San Jerónimo	4	5	5	4	15.07	-90.19	1579	19
Guatemala	San Lorenzo Mármol	4	5	4	5	15.086	-89.674	1733	16
Guatemala	Tecpán*		5			14.761	-91.018	2657	0
Guatemala	Las Granadillas			4	5	14.934	-89.42	1210	7
Guatemala	San Pedro Pinula				5	14.726	-89.796	1192	1
Guatemala	San Pedro Soloma			5		15.635	-91.481	2359	1
Guatemala	Quezaltepeque			5		14.583	-89.412	2288	0
Guatemala	Chichicastenango			5		14.973	-91.112	2000	0
Guatemala	San Cristóbal Alta Verapaz			5		15.364	-90.468	1379	2
Guatemala	Cubulco			5		15.055	-90.634	1383	6
Guatemala	Morazán			5		15.001	-90.11	1739	2
Honduras	Cusuco	5	5	5	5	15.495	-88.203	1431	7
Honduras	La Botija*	6	5	4	5	13.345	-86.787	1369	7
Honduras	La Esperanza	6	5	5	5	14.288	-88.134	1693	21
Honduras	La Muralla	4				15.083	-86.739	1374	4
Honduras	La Tigra	6	7	4	5	14.193	-87.137	1500	32
Honduras	San Francisco Soroguara	4	6			14.319	-87.401	1454	2
Honduras	Uyuca*	2	6	9	5	14.034	-87.084	1594	42
El Salvador	El Manzano*	5	5	5	5	14.23	-89.021	1530	13
El Salvador	La Montañona*	5	5	5	5	14.134	-88.913	1395	5
El Salvador	Parque Nacional Montecristo	5	5	5	5	14.433	-89.413	1742	21
El Salvador	Perquín*	5	5	5	5	13.958	-88.11	1246	0
El Salvador	Candelaria de la Frontera*				4	14.14	-89.64	969	0
El Salvador	Volcan Chinchontepec*	5	5			13.602	-88.835	1536	0
Nicaragua	Isla de Upá*		6			12.98	-85.727	840	0
Nicaragua	Loma Fria*	7	6	5	6	13.741	-86.544	1228	12
Nicaragua	Miraflor*	6	6		5	13.225	-86.325	1364	2
Nicaragua	Mozonte-San Fernando	1	6	5	5	13.704	-86.388	1008	3

Country	Site	2006-07	2007-08	2008-09	2009-10	Lat & long degrees		Elev. masl	Individuals documented in flocks
Nicaragua	San Rafael-Jaguar		6			13.216	-86.075	1201	0
Nicaragua	Tepesomoto-Patasta*	6	6	5	6	13.362	-86.629	1365	3
Nicaragua	Tisey*	5	6	5	6	12.966	-86.371	1374	17
Nicaragua	Yali*		6			13.257	-86.159	1176	0
Nicaragua	Yúcul			5	5	12.911	-85.771	1017	2
Nicaragua	San José de Cusmapa				5	13.293	-86.654	1407	0
Total number sites		27	33	31	29				
Total number flocks		117	175	157	143				

*Sites where Golden-cheeked Warbler has not been previously documented.

observation again (without counting the minutes that the flock was lost as observation time). Each foraging flock was studied just one morning. Thus each of the five sites generated data for five separate foraging flocks each winter. Some flock locations were revisited in subsequent years, such that the 603 total reports of flock data were generated from 573 independent locations. Locations were never repeated in the same year, and the few (5%) that were repeated were assumed to generate independent data across years.

The protocol instructed observers to work within forests containing at least 5 km² (500 ha) of continuous habitat; although in several sites (in particular, in Nicaragua) such extensive patches were not located by observers, and they studied flocks in smaller patches of forest. Each flock was located at least 500 m from any other. Observers occasionally studied flocks that were closer in space on subsequent days, when they were confident that they represented different flocks, for instance when locations were separated by extensive fields or other unsuitable habitat.

A flock was defined as a group of at least 10 individuals of at least three species. The observers noted each individual in the flock according to the time it was first observed. Golden-cheeked Warbler (GCWA) observations were noted along with probable sex and age, and species of tree at first sighting. Elevations, species composition, and area used by the flock were noted.

Statistical tests were carried out using Minitab software. For simple and multiple linear and polynomial regression analysis, the response variables (counts of birds) were square-root transformed. For stepwise multiple regression analysis, we selected alpha = 0.15 as the criterion to enter or remove a variable from the models. Only one predictor was highly correlated ($r > 0.75$) to another and was not considered for multiple regression models (maximum tree height was selected for analysis instead of average tree height, $r = 0.845$). We regressed GCWA abundance in flocks (only sites with confirmed GCWA presence were included) against 28 predictor variables, including 18 habitat variables and 10 other variables. The habitat variables included canopy percent cover total, canopy pine (*Pinus* spp.) cover, canopy encino-oak (thin-leaved *Quercus* spp.) cover, canopy roble-oak (broad-leaved *Quercus* spp.) cover, canopy cypress (*Cupressus lusitanicus*) cover, canopy sweetgum (*Liquidambar styraciflua*) cover, canopy other broadleaf cover, canopy maximum height, midlevel total cover (2–10 m), midlevel pine cover, midlevel encino-oak cover, midlevel roble-oak cover, midlevel cypress cover, midlevel sweetgum cover, midlevel other broadleaf cover, epiphytes density (1= 0–10 per tree, 2=10–20 per tree, 3=>20 per tree), and ground cover (<2 m). The non-habitat variables included latitude, longitude, date, elevation, effort (minutes of observation of flocks),

temperature, cloud cover, wind (Beaufort scale), flock size (abundance of flock members), and flock species richness (not including GCWA).

Results

We documented presence of GCWA in flocks at 35 of the 47 study sites, including at least 10 sites where GCWA has not been reported previously (Table 1). We made first documentation at one site in Mexico (Tres Picos); at one site in Guatemala (Cerro Alux); at two sites in Honduras (La Botija, Uyuca); and at two sites in El Salvador (El Manzano, La Montañona). In Nicaragua, wintering was noted in at least four previously undocumented sites (Loma Fría; Mirafior; Tepesomoto-Patasta; Tisey), and an additional observation was made at another previously undocumented site (Peñas Blancas, 13.2416°N, -85.6836°E, 1480 masl).

GCWA abundance varied considerably by site, but many sites across the range showed relatively high abundance (>1 bird per flock) in appropriate habitat (Fig. 1). Average values for the entire study area were 0.66 birds per flock, and 0.30 birds per ha occupied by the flock. The sites with above-average abundance or population density are shown in Table 2. The mean population density over all sites with non-zero population densities was determined at a variety of habitat conditions, varying from 0.30 to 0.74 GCWA per ha (Table 3).

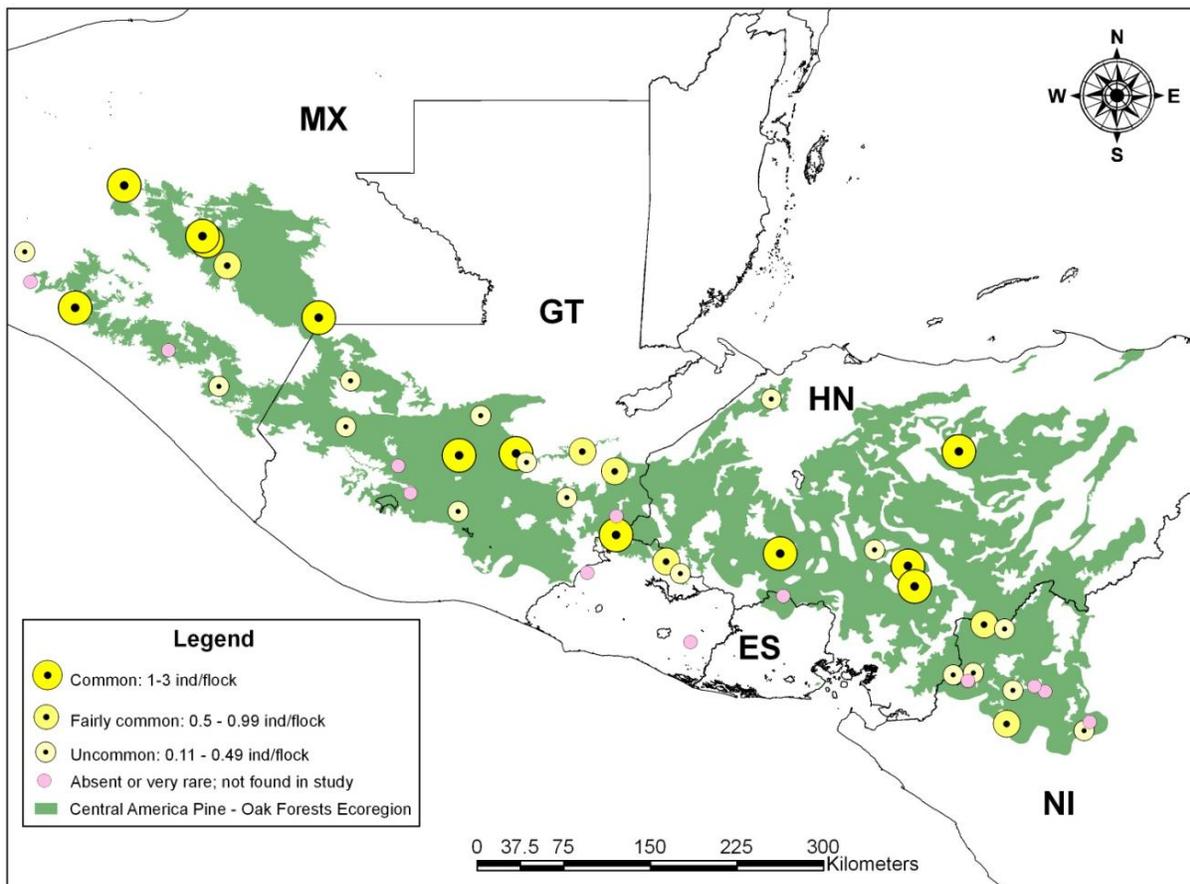


Figure 1. Map of the Central American Pine-oak Forests Ecoregion, showing the relative abundance of Golden-cheeked Warbler at each study site.

Table 2. Sites with above average GCWA abundance (>0.66 per flock).

Country	Site	Abundance (ind/flock)	Pop. Density (ind/ha)
Mexico	Arcotetes	1.12	0.31
	Coapilla	1.06	0.33
	La Granada	0.92	0.30
	Montebello	1.30	0.40
	Moxviquil	1.28	0.41
	Tres Picos	1.00	0.69
Guatemala	San Jerónimo	1.06	0.50
	San Lorenzo Mármol	0.89	0.45
	Las Granadillas	0.78	0.43
	Cubulco	1.20	1.20
Honduras	La Esperanza	1.00	0.26
	La Muralla	1.00	0.44
	La Tigra	1.45	0.68
	Uyuca	1.91	0.83
El Salvador	Montecristo	1.05	0.69
Nicaragua	Tisey	0.77	0.61

Table 3. GCWA population density under different habitat conditions.

Conditions	N	Birds per hectare ± SE
All sites with GCWA in flocks	351	0.30 ± 0.05
All sites with GCWA in flocks, >6 m average midlevel height, >20% encino midlevel	200	0.46 ± 0.06
All sites with GCWA in flocks, >6 m average midlevel height, >30% encino midlevel	119	0.58 ± 0.08
All sites with GCWA in flocks, >6 m average midlevel height, >30% encino midlevel, >10% encino canopy	95	0.74 ± 0.09

Observed GCWA abundance in flocks depended on the effort invested in flock observation (Fig. 2). Of 176 GCWA observed in flocks during the first two winters of the study, first detection of 50 birds (28%) occurred after at least 90 minutes of flock observation. Ninety-four percent of the observed GCWA (165 birds) were detected by 3.5 h of flock monitoring. GCWA abundance (birds per flock) correlated with effort (minutes) according to the equation: $GCWA = 0.0185 + 0.00379 \cdot \text{effort}$ (DF = 136, $R^2 = 3.8\%$, $P = 0.022$).

GCWA abundance varied with latitude ($R^2 = 3.9\%$, $F_{1,528} = 22.28$, $P = 0.000$) and slightly with longitude ($R^2 = 1.3\%$, $F_{1,529} = 8.15$, $P = 0.004$). Abundance was higher northward and westward. These trends were reflected in the relative abundance by country (Fig. 3), but the trends were weak and potentially due to observer bias. Warbler abundance was much more strongly related to altitude. We studied flocks from 705 to 2975 masl (mean $1577 \pm SD 408$ masl; $N=581$), and observed GCWA from 902 masl to 2492 masl (mean $1659 \pm SD 350$ masl, $N=241$ flocks with GCWA present). GCWA abundance in flocks was concentrated in elevations from 1400 masl to 2400 masl (Fig. 4). A quadratic regression equation with elevation as the predictor variable explained 6.0% of the variance in abundance of GCWA in foraging flocks. Differences in elevational distribution by sex (and age) class are presented in the next chapter.

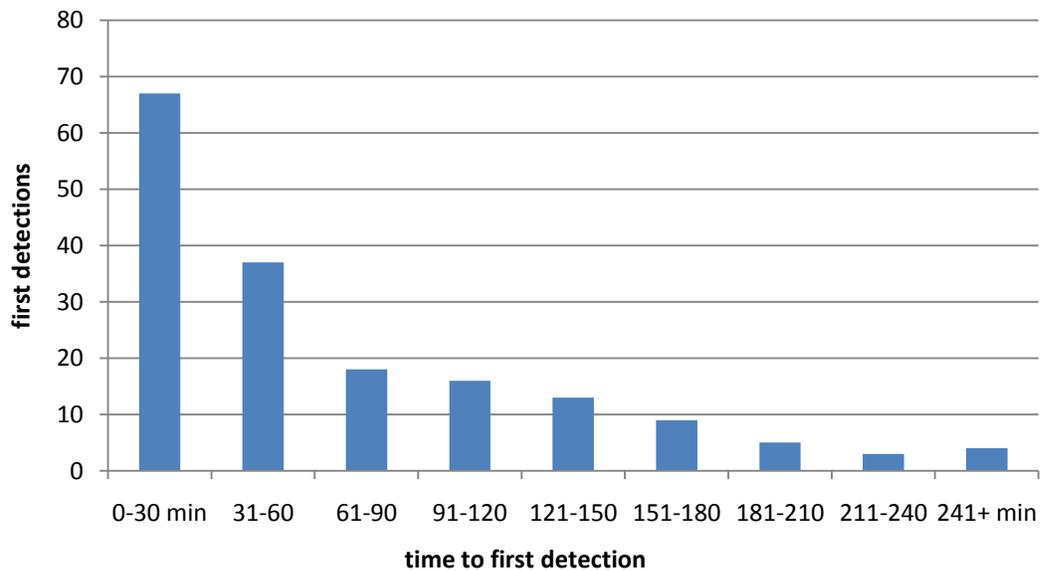


Figure 2. Time of flock monitoring to first detection of GCWA (minutes).

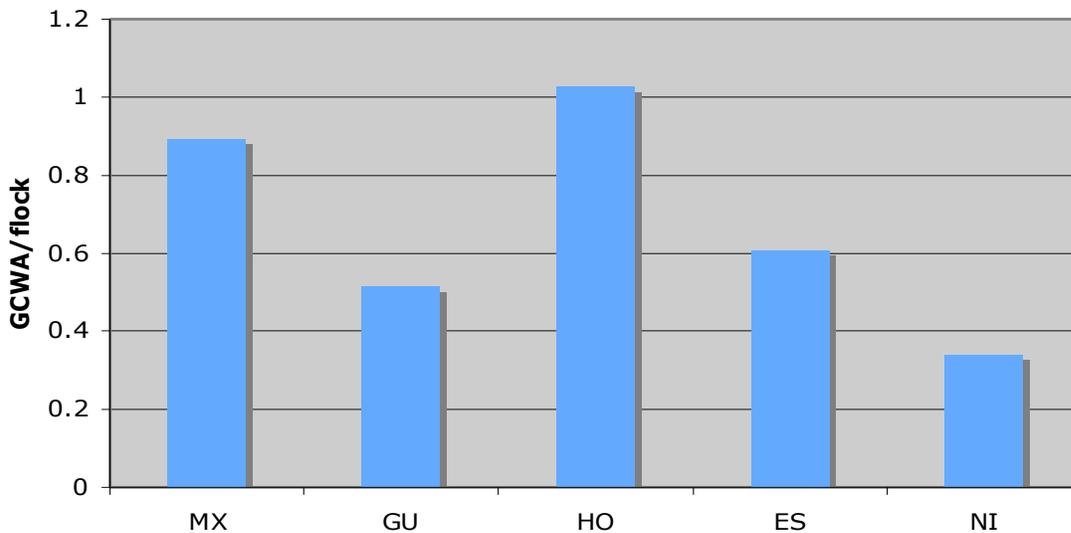


Figure 3. Variation of abundance of GCWA in 528 flocks, by country (sites without GCWA present were not included).

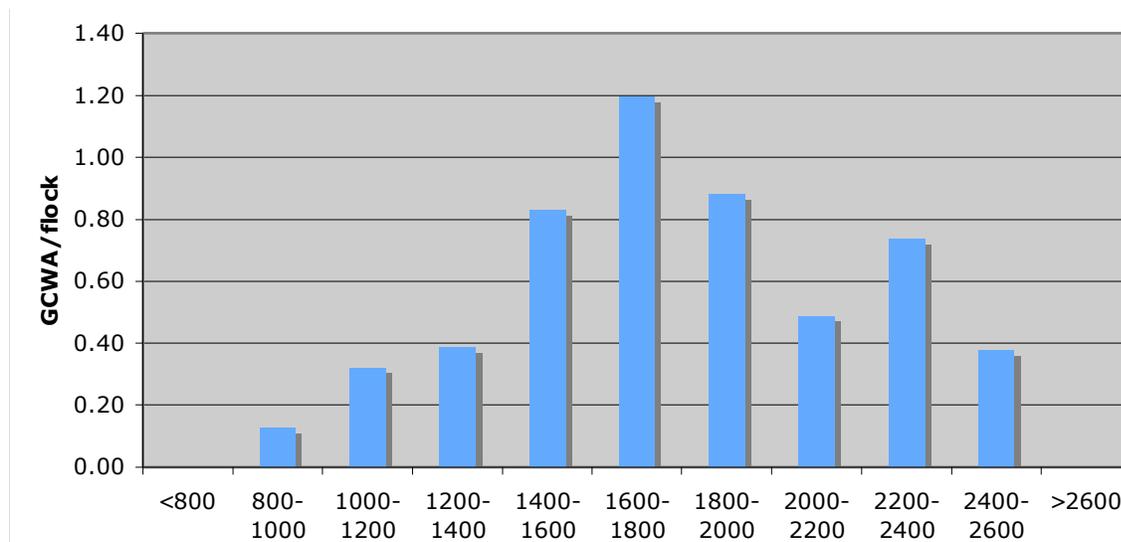


Figure 4. GCWA abundance in 528 flocks by elevation (sites without GCWA present were not included).

Thirteen of 20 habitat parameters differed significantly between flocks with and without GCWA (Table 4). The highest levels of significance were found in total midlevel cover, midlevel encino cover, canopy encino cover, and canopy tree height (maximum and average). GCWA abundance in flocks also demonstrated a rising trend with increasing midlevel plus canopy encino (Fig. 5). Such a trend was not evident for pine cover, “roble” oak cover, cypress cover, or broadleaf (non-oak) cover. Stepwise multiple regression of GCWA abundance in flocks on 18 habitat variables created a model that explained 26% of the variance in abundance, although only 15.6% of the variance was explained by habitat factors. The most important habitat predictor was midlevel encino cover, which explained 13% of GCWA abundance, and the second most important predictor variable was canopy maximum tree height, which explained only 1.5% (Table 5). A minor parameter in the model was canopy sweetgum cover, which was negatively correlated with GCWA abundance.

Non-habitat parameters that were significant predictor variables included species richness of the flocks, which explained 3.8% of GCWA abundance, ambient temperature (1.5% of GCWA abundance), latitude and longitude (combined, 4.3% of GCWA abundance), and date (negatively correlated, 0.1% of GCWA abundance) (Table 5). Minor declines throughout each season, due to natural mortality, are expected.

Data for the tree where GCWA were first sighted also supported the hypothesis that encino oaks either increase abundance or are preferred by GCWA. Approximately half the GCWA were first sighted in encino, whereas no other type of trees were used by more than 15% of individual GCWA (Fig. 6). This apparent preference was shared by all sex and age classes of GCWA.

Table 4. Habitat characteristics of flocks with and without GCWA, and linear regression results for individual factors as predictors of GCWA abundance (birds per flock).

Parameter	GCWA present		GCWA absent		T-test	Simple regression (DF = 509)			
	N	Mean ± SE	N	Mean ± SE	Significance of difference ¹	R ²	F	P	Model
Canopy cover %	243	64.39 ± 1.34	284	58.95 ± 1.35	**	0.012	7.21	0.008	linear
Canopy pine	243	30.15 ± 1.48	284	26.69 ± 1.55		0.026	7.92	0.000	quadratic
Canopy encino	243	18.59 ± 1.20	284	11.58 ± 1.89	***	0.061	17.57	0.000	quadratic
Canopy roble	243	10.29 ± 1.01	284	13.55 ± 1.36	*	0.014	8.03	0.005	linear
Canopy sweetgum	243	1.94 ± 0.28	284	1.73 ± 9.35		0.016	3.7	0.012	cubic
Canopy cypress	243	0.42 ± 0.18	284	0.90 ± 0.28		0.002	2.23	0.136	linear
Canopy broadleaf	243	2.99 ± 0.50	284	4.53 ± 5.56	**	0.005	3.48	0.063	linear
Canopy max tree height, m	243	26.31 ± 0.49	283	23.39 ± 9.53	***	0.057	16.47	0.000	quadratic
Epiphytes	243	0.51 ± 0.05	284	0.34 ± 8.64	**	0.014	8.27	0.004	linear
Midlevel cover %	242	54.05 ± 1.53	282	46.64 ± 1.42	***	0.020	11.39	0.001	linear
Midlevel pine	242	8.14 ± 0.80	282	10.66 ± 3.93	*	0.008	5.02	0.025	linear
Midlevel encino	242	21.87 ± 1.23	282	10.91 ± 1.82	***	0.119	69.96	0.000	linear
Midlevel roble	242	10.93 ± 0.96	282	12.89 ± 1.03		0.005	3.51	0.062	linear
Midlevel sweetgum	242	2.05 ± 0.44	282	0.69 ± 1.25	**	0.023	5.08	0.002	cubic
Midlevel cypress	242	0.45 ± 0.16	282	0.68 ± 1.24		0.000	1.21	0.271	linear
Midlevel broadleaf	242	11.03 ± 1.08	282	11.39 ± 1.48		0.000	0.00	0.946	linear
Midlevel max tree height, m	242	9.46 ± 0.07	281	9.19 ± 5.79	*	0.016	9.39	0.002	linear
Midlevel avg. tree height, m	242	6.40 ± 0.10	281	6.29 ± 3.16		0.001	1.70	0.193	linear
Understory cover %	243	67.34 ± 1.73	284	60.01 ± 1.92	**	0.012	6.97	0.009	linear

¹Significance of differences was determined by 2-tailed t-test: *=P<0.05; **=P<0.01; ***=P<0.005. Only sites with GCWA present in flocks were analyzed.

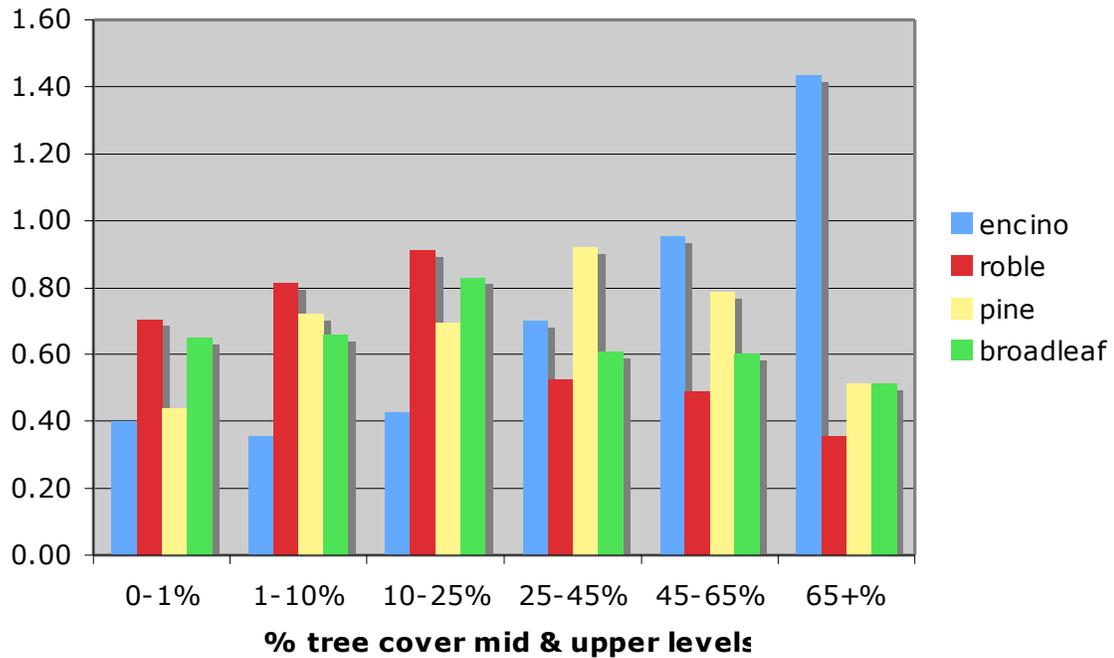


Figure 5. GCWA abundance in 528 flocks according to combined midstory and canopy cover by tree type.

Table 5. Stepwise multivariate regression of GCWA abundance in flocks on 28 predictor variables generated an 8-variable model (N=493; R²=25.9%; Mallows' Cp=10.5).

Predictor variable	T	P	Variance attributed to variable, %
Midlevel encino cover	8.85	0.000	13.01%
Flock species richness	4.46	0.000	3.80%
Canopy maximum tree height	3.90	0.000	1.48%
Average ambient temperature	4.35	0.000	1.47%
Latitude	6.05	0.000	1.32%
Longitude	4.94	0.000	3.03%
Canopy sweetgum cover	-2.71	0.007	1.11%
Date	-2.35	0.019	0.08%

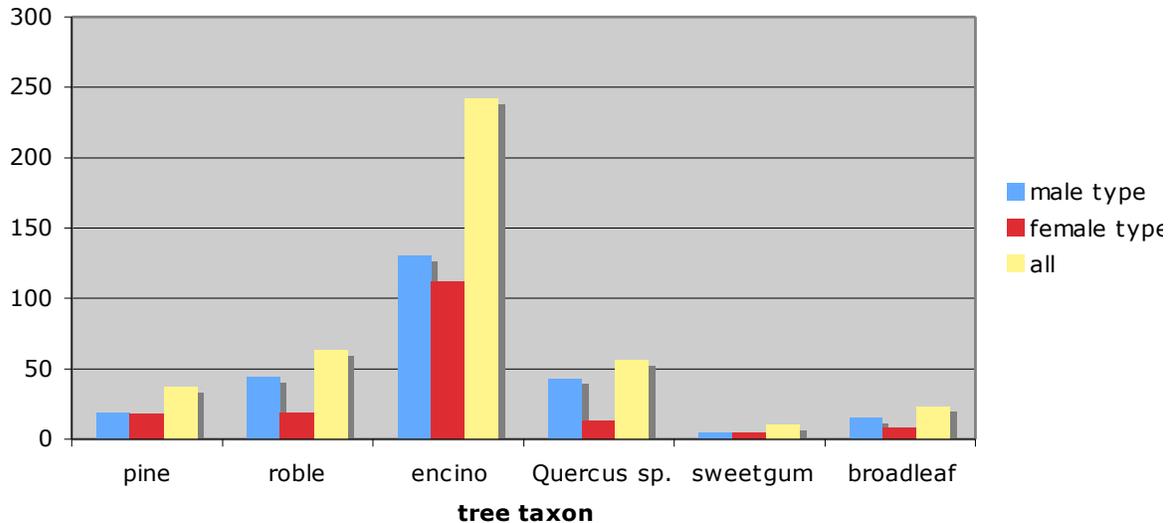


Figure 6. Taxon of tree in which GCWA was first observed (N=431).

Discussion

Winter distribution

The new wintering sites discovered in southern Chiapas, central El Salvador, southern Honduras and northern Nicaragua were all predicted by a maps of potential habitat for the warbler (Rappole et al. 2000, APEM 2008). All sites with above-average GCWA abundance and population density were in typical pine-encino oak habitat. The sites in El Salvador fall within the area predicted as prime winter habitat (6750 km²) by Rappole et al. (2003). The type specimen was collected in Nicaragua over 100 years ago, although the species then went unreported from the country until recently (Morales et al. 2008). The long gap in Nicaragua records was probably due to lack of effort or reporting from the appropriate habitat. The Nicaraguan wintering population was simultaneously confirmed during the 2006–7 winter season by an independent research group (King et al. 2009).

Approximately nine winter records of Golden-cheeked Warbler from southern Central America (Costa Rican and Panamanian highlands; various observers cited in Jones 2005, Jones and Komar 2006, Jones and Komar 2008) suggest that the species' wintering range may include oak forests and similar habitats in southern Central America. However, these extralimital birds may only be vagrants and not represent a regular wintering population. All of these records are recent, having been registered almost annually since 2000. The presence of almost annual vagrants in Costa Rica could suggest that the overall population may have recently increased, or it could reflect increased birdwatching activity and increased local capacity for bird identification. These new records correspond to the initiation of a Central American column in the bird distribution journal *North American Birds*, where all of the records have been published. Could the species' presence before 2000 in southern Central America have been overlooked or underreported? Efforts to confirm a potential Costa Rican (and Panamanian) wintering population may be worthwhile, and if carried out, should also determine the sex ratio for that population.

GCWA was observed in flocks as low as 902 masl, lower than previously recorded in its wintering range (Ladd & Gass 1999, Rappole et al. 2000). The mean elevation of GCWA in flocks, 1683 ± 355 masl, coincided with the results of Rappole et al. (2000), given as 1651 ± 246 masl. Our highest bird, 2471 masl, did not exceed the highest recorded observation on wintering grounds (Vidal et al. 1994). Although males had marked preference for elevations from 1400–2400 masl, this tendency was less evident in females and immatures, suggesting that males may demonstrate greater specificity in selecting wintering locations than females.

Habitat preferences

Rappole et al. (1999) compared the habitat characteristics between areas containing GCWA and random sites and found significant differences for pine basal area (lower where GCWA were found), encino oak basal area, and ground cover (both higher where GCWA were found). They did not find significant differences for stem density, canopy cover, average tree height, or ground slope. We used different methods, but our regression analysis supported Rappole et al.'s results with positive relationships for GCWA presence with encino cover at both canopy and midlevel, and ground cover. We also found positive highly significant ($P < 0.002$) relationships between GCWA abundance and canopy pine cover, canopy height, midlevel canopy cover, and midlevel sweetgum cover.

Our stepwise multivariate regression of GCWA abundance found midlevel Encino cover to be the most important predictor variable. These results fortify and extend Rappole and colleagues' (1999) earlier results that encino oaks are of great importance to GCWA habitat, and extend the results to emphasize the role of encino oaks and other species at midlevel. Our results also confirm the observation of Rappole et al. (1999) that encino oaks, with "shiny, narrow, elliptical or oblong leaves" were preferred over the roble oaks "with large, lobed leaves".

Winter abundance

We expected our two measures of winter abundance, density and birds per foraging flock, to be highest in the center of the wintering range, or potentially at the northern extreme of the range, closest to the breeding grounds. The latter trend was apparent among males, but not among females and immatures. Our results suggest the center of abundance (median latitude) for males is at 15.038°N , 78 km northward of the median latitude for females and immatures. (14.334°N). To put in perspective, the latitudinal depth of the known wintering range is 455 km. Thus, male abundance is centered 17% further north than female abundance.

We used a different method than earlier researchers to estimate density. Rappole et al. (2000) used strip transects to find flocks with GCWA, then counted all birds in the flocks during up to 1.5 h of effort. We tracked individuals and their associated foraging flocks 1.5–4 hours during the morning in order to estimate the area occupied by each flock. By obtaining geographic areas occupied by flocks, we were able to estimate a GCWA population density of 0.30 ± 0.05 birds ha^{-1} , approximately six times higher than an earlier estimate (0.05 ± 0.04 birds ha^{-1}) based on the above-mentioned strip transects (Rappole et al. 2003). Our estimate assumes that most GCWA utilize foraging flocks on a daily basis, that the flocks occupy similar areas each day, and that areas with similar habitat are likely to be visited daily by a foraging flock covering similar areas per day. More research on flock dynamics is needed to confirm these assumptions.

As did Rappole's field team, we attempted to determine how many GCWA occupied each foraging flock, and used the mean number of birds per flock as an alternate measure of relative abundance. Rappole et al. (1999) reported that they followed flocks for a maximum of 1.5 h, and that once they confirmed that a flock contained the warbler, they moved on to search for another flock. Our data suggest that they ceased observations before detecting approximately 20% of

warbler individuals present. During trial runs of flock observations, we noted that new individual birds (of various species) were frequently detected right up to the 1.5 h mark, and even up to 4 h after beginning to follow a flock. We trained field staff to follow each flock for 4 h and required flocks to be observed for a minimum of 1.5 h (some flocks either dissipated or were lost before the full 4 h of observation were possible). In practice, field staff observed flocks for an average of 200.6 min (3.34 h). The mean time that flocks were observed varied among years 1–4 as follows: 183.7 min, 213.6 min, 198.3 min, and 202.0 min, respectively.

Our higher abundance estimates, with respect to Rappole et al. (2000), may reflect in part the increased observation time, rather than a true increase, and in part a difference in methods. Although the selection of our flocks was arbitrary (and often included flocks with no GCWA present), nonetheless we only calculated density where flocks were observed. Rappole et al.'s transect method included in their density calculations areas where no flocks were observed. Until more information can be obtained about flock formation across time and space, we suggest that our density estimates be considered a relative abundance measure and not a measure of true density.

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Chapter 2

Skewed sex ratios and evidence for latitudinal sexual segregation in Golden-cheeked Warblers (*Dendroica chrysoparia*) wintering in Mexico and Central America

Introduction

An important aspect of the ecology of migratory birds is the relative winter distribution of sex and age classes. In some species, males and females have evolved different ecological niches during the non-breeding season, occupying wintering areas in different habitats or latitudes (Ketterson & Nolan 1983, Cristol et al. 1999). These differences may lead to different annual survival rates between sexes which could influence conservation strategies for threatened species (Komar et al. 2005). This issue is especially important for the Golden-cheeked Warbler (*Dendroica chrysoparia*), a globally threatened species (IUCN 2010) for which little information about sex ratios has been collected on the breeding grounds (Jetté et al. 1998) or elsewhere.

The Golden-cheeked Warbler winters almost exclusively in the pine-oak forests of southern Mexico (Chiapas) and northern Central America (Ladd & Gass 1999). Vidal et al. (1994) noted consistently high proportions of male Golden-cheeked Warblers observed in Chiapas near the northern limits of wintering, and proposed that male and females may segregate on the wintering grounds, although they had no data from other parts of the range. Although this phenomenon is well documented in short-distance, temperate migratory species, it is much less documented in long-distance Nearctic-Neotropical migratory species, and only in two species of the large parulid genus *Dendroica* (Komar et al. 2005). During the last decade, reports of Golden-cheeked Warblers south of the known wintering range in Costa Rica and Panama indicated that female types (potentially including immature males) outnumbered adult males 7:1 (reports published in Jones 2005, Jones & Komar 2006, Jones & Komar 2008). These reports, although poorly documented, would seem to support the hypothesis of latitudinal sexual segregation for Golden-cheeked Warblers.

Here we evaluate a data set of more than 400 independent observations of Golden-cheeked Warblers from across the winter range, from southern Mexico to northern Nicaragua. We test the data for differences in male versus female abundance, and examine if sex ratios are influenced by latitude. Because of difficulties in separating some sex and age classes in the field, we combined all immatures into the female class, such that the expected ratios of male types to female types should not be 1:1 (assuming equal survival of males and females after birth), but rather should be approximately 1:2, or even as skewed as 1:3, depending on annual productivity. If each adult female generated one surviving immature on average per year, then the expected ratio of adult males to female types (adult females plus immatures) would be 1:2. In this case, adult males should comprise 33% of all wintering birds. This assumption seems reasonable based on reports of 2.2 juveniles produced annually per successful male, combined with a 55% nest success rate (Ladd & Gass 1999), and combined further with an unknown mortality rate for young birds migrating to wintering grounds.

The plumage of young males wears into a near-alternate plumage before the return to breeding grounds, and thus some young males may be identified in the field as adult males during the latter part of the wintering season. The exact timing of the transition of some immature-plumaged males to apparent adult males is unknown, although reported roughly as “March”

(Pyle 1997). If a quarter of the young males observed during the winter are mistaken for adult males, then the expected proportion of putative adult males would increase only to 37.5% of all wintering birds. This proportion may vary depending on annual productivity and on the timing of winter observations. If annual productivity is higher than one young per female, then the proportion of putative adult males would decline, because of larger numbers of young birds in the population. If productivity is lower, or if female mortality on the nest is unusually high, the proportion of adult males observed in winter should increase.

Study area and methods

Golden-cheeked Warblers were observed and classified to sex (adult males, and a female-type class that includes adult females and all immatures) at 35 sites in pine-oak forests from western Chiapas to northwestern Nicaragua, encompassing the principal wintering grounds for Golden-cheeked Warbler (Ladd & Gass 1999). These sites were distributed in Mexico (9 sites), Guatemala (10 sites), Honduras (7 sites), El Salvador (3 sites), and Nicaragua (6 sites). Sites ranged in elevation from 902 masl to 2471 masl, although most of the sites were within the range of 1400–2200 masl. Most sites were forests containing at least 5 km² (500 ha) of continuous habitat; although several sites (in particular, in Nicaragua) were smaller patches of forest.

Several teams of observers were trained to identify *Dendroica* warblers, separating sex and age classes as much as possible, through field workshops prior to each field season. They collected data on sex ratios during the mid-winter, 15 November to 15 February, when warblers were assumed to occupy wintering habitat, rather than be actively migrating. The study was repeated during four consecutive winters, beginning in November 2006 and ending in February 2010. Observers found warblers by searching through large forest patches (generally >500 ha) for mixed species foraging flocks of insectivorous birds, and then screening all the birds in each flock (a process that took up to 4 h in the morning). Golden-cheeked Warblers were also identified to sex when individuals were found outside of foraging flocks.

To maintain independence, each foraging flock was studied just one morning, and was located at least 500 m from any other flocks studied during the same winter season. Observers occasionally studied flocks that were closer in space, when they were confident that they represented different flocks. Most specific flock locations were visited just once, however 63 flock locations were repeated (the reported central coordinates of the flock foraging area being within 250 m of the original location) across one or more years.

Statistical tests were carried out using Minitab software. Hypothesis tests were considered significant when $\alpha < 0.05$. For regression analysis, the response variables (counts of birds) were square-root transformed. We compared frequencies with which Golden-cheeked Warblers were encountered as single individuals, pairs, or larger groups within flocks to a Poisson distribution using a Chi-square test.

Results

Fifty-nine percent of all Golden-cheeked Warblers (GCWA) found on the wintering grounds were classified as adult males. This proportion varied among years, with adult males forming as few as 54% of all birds in year 2, and as many as 65% of all birds in year 4 (Table 1). This represents a ratio of 1 male: 0.69 female types. Adult males were almost twice as common, with respect to females, as was expected. Although the proportions of adult males were higher than

expected throughout the study area, male:female ratios were highest in Mexico and especially Guatemala, where nearly three adult males were reported for every female type (Fig. 1). We tested whether our method of seeking birds in flocks was biased toward males. We compared the sex ratio for birds found in flocks (201 male types, 151 female types) to birds encountered outside flocks (14 male types, 8 female types). Although the second sample was small, the proportions were similar and not significantly different ($X^2 = 0.362$, $DF = 1$, $P = 0.548$). We also considered whether males were more detectable by our field observers than females, which could explain apparently biased sex ratios in some countries. However, the variation among observer teams was no greater than the variation within observer teams from one year to another, nor were there any apparent trends that suggested that observer teams improved their abilities to identify non-males over time.

Table 1. Sex and age of GCWA by year of study as reported by field staff.

	All years		Year 1		Year 2		Year 3		Year 4	
	Birds	%	Birds	%	Birds	%	Birds	%	Birds	%
Adult male	253	59	50	60	73	54	65	58	65	65
Adult female	98	23	28	34	25	19	25	22	20	20
Imm male	34	8	0	0	20	15	9	8	5	5
Imm female	26	6	5	6	16	12	1	1	4	4
unknown	19	4	0	0	0	0	13	11	6	6
total	430	100	83	100	134	100	113	100	100	100

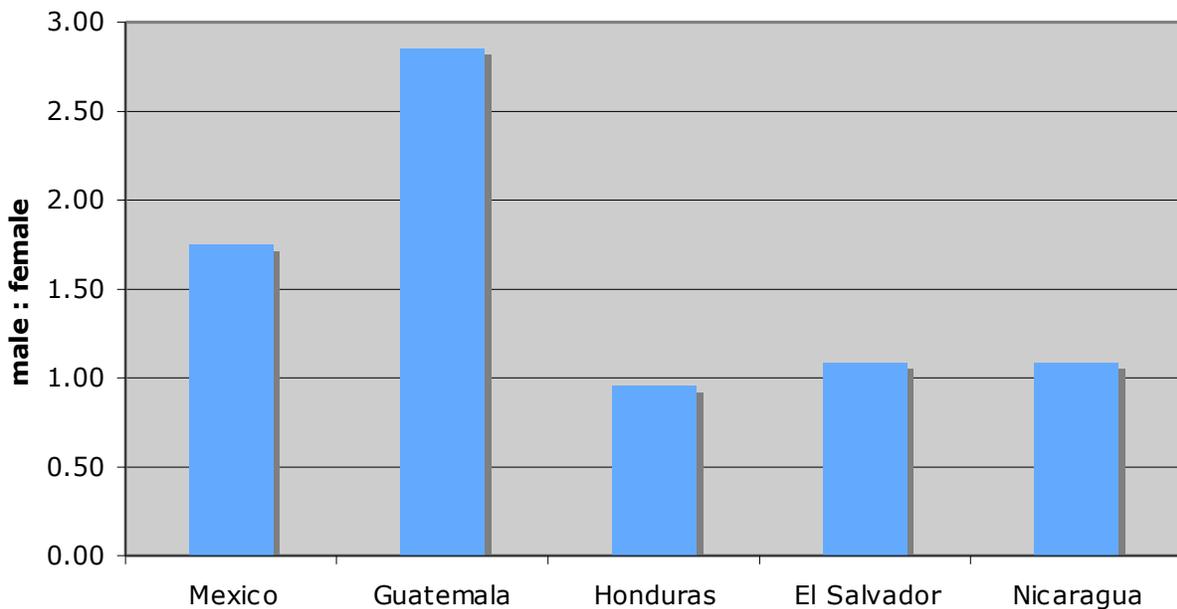


Figure 1. Adult male type to female type ratio by country, all years (N=440).

Males were distributed non-randomly in flocks, with fewer males accompanied by other males, than expected by random distribution ($N=244$, $\chi^2=18.77$, $P=0.000$) (Fig. 2), whereas females were distributed randomly ($N=244$, $\chi^2=2.31$, $P=0.130$) (Fig. 3). The distribution of females in flocks that also contained males, however, was closer to non-random, with slightly more single females with males than expected and fewer flocks with more than one female ($N=91$, $\chi^2=2.84$, $P=0.092$) (Fig. 4).

Adult male GCWA displayed a much stronger relationship to elevation than female types, with highest abundance between 1400 and 2400 masl; female types were more uniformly distributed than males, between 900 and 2500 masl (Fig. 5). The quadratic regression equations for GCWA abundance regressed against elevation explained 8.2% of the variation in abundance of adult males, vs. only 0.5% of the variation in abundance of female types. The relationship for males to elevation was highly significant, with $P < 0.0005$, whereas the relationship for females was not significant ($P = 0.097$, $F_{2,524} = 2.34$).

Adult male GCWA showed a northward tendency, with highest abundance in flocks above 16°N , whereas this tendency was less evident for female types (Fig. 6). The relationship for males was linear and highly significant; the regression equation explained 5.0% of the variance in male abundance ($F_{1,529} = 29.04$, $P < 0.000$). The relationship for females was best represented by a polynomial regression equation that explained 2.2% of the variance in female abundance ($F_{3,527} = 5.05$, $P = 0.002$). The fitted curve shows peaks in female-type abundance at 17°N and around 14°N (these two peaks could conceivably reflect the fact that the female-type class includes young males as well as females).

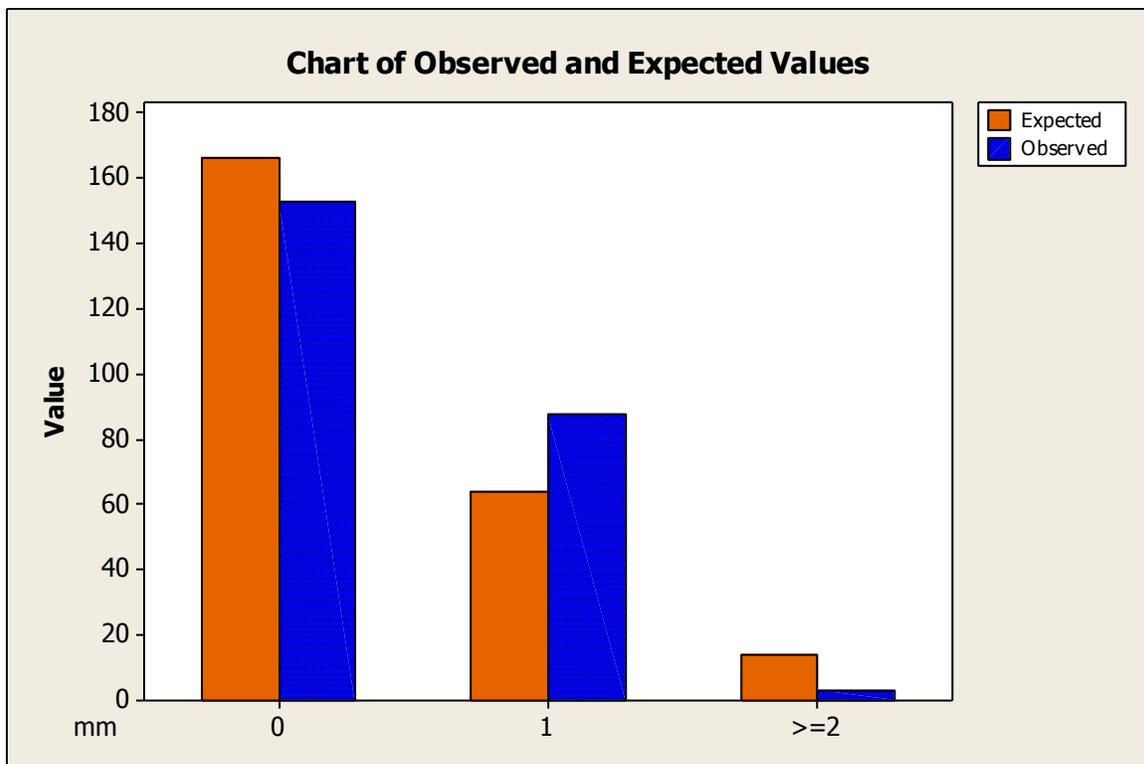


Figure 2. Distribution of adult male GCWA in flocks compared to Poisson (random) distribution (N=244).

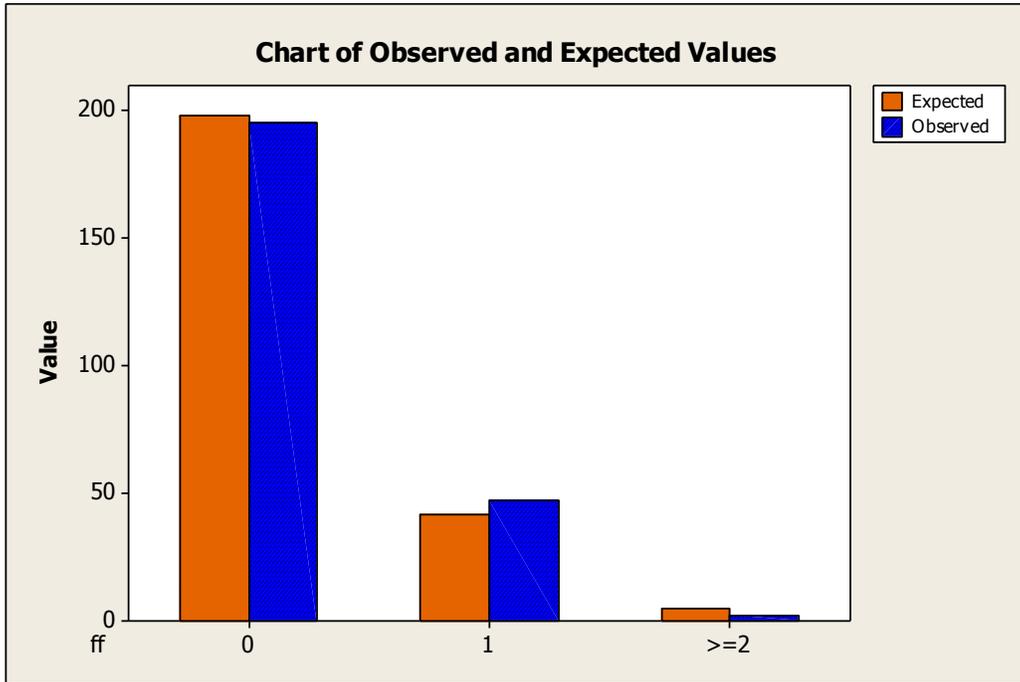


Figure 3. Distribution of adult female GCWA in flocks compared to Poisson (random) distribution (N=244)

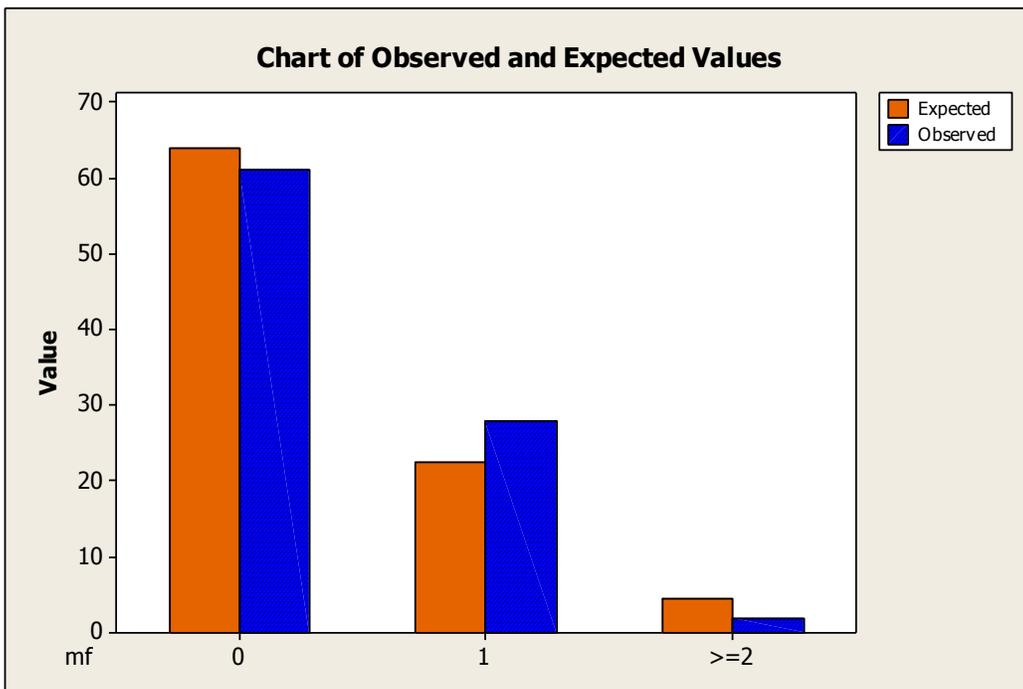


Figure 4. Distribution of adult female GCWA in flocks containing one or more male compared to Poisson (random) distribution (N=244).

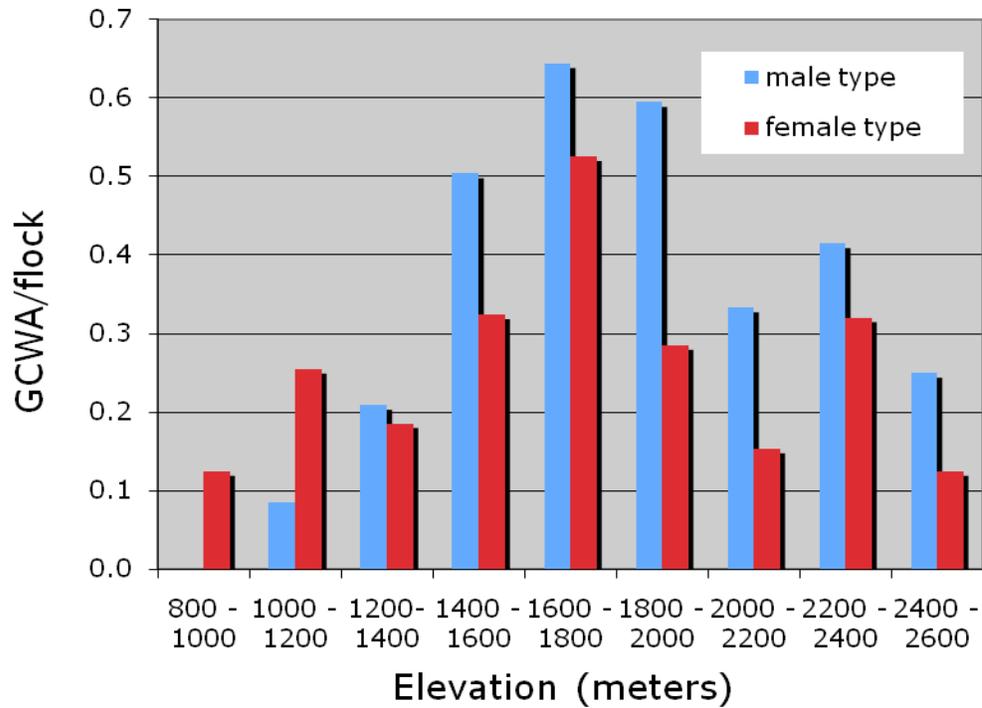


Figure 5. GCWA abundance in flocks by sex, elevation.

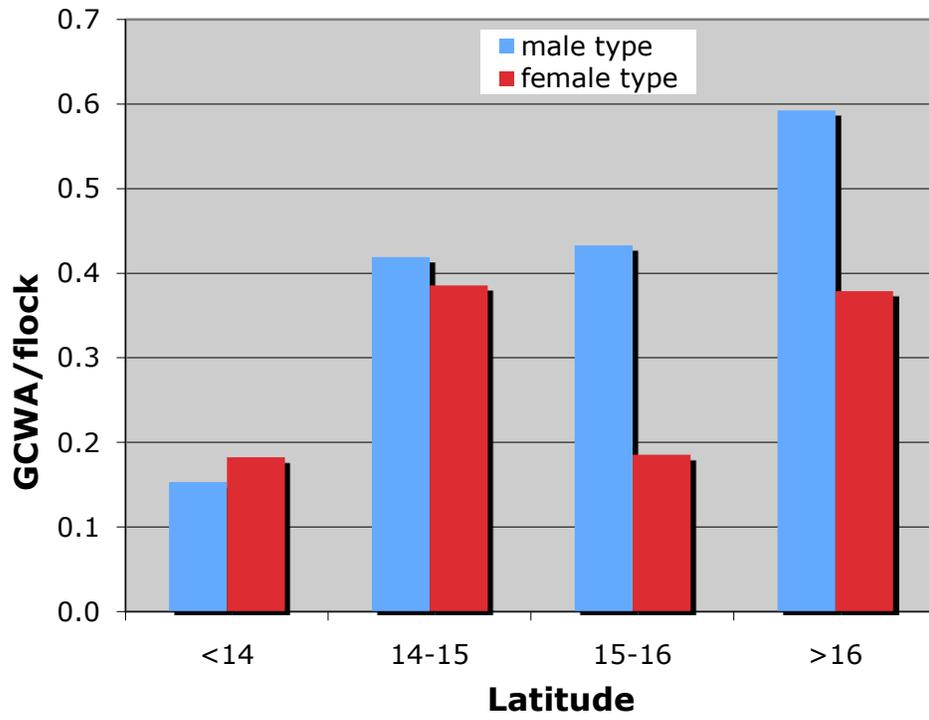


Figure 6. GCWA abundance in flocks by sex, latitude.

Discussion

For the first time, data from the central and southern regions of the Golden-cheeked Warbler's winter range are available to test Vidal et al.'s (1994) hypothesis suggesting that sexes segregate on the wintering grounds, with males dominating in the northern extremes of the range. Our results confirmed Vidal et al.'s (1994) observations of more males than female types in Chiapas, and supported the hypothesis that adult males preferred northern parts of the winter range. Male abundance appeared to decline steadily from north to south. On the other hand, females had a peak in abundance in Honduras, in the southern portion of the winter range. We conclude that Golden-cheeked Warblers demonstrate latitudinal sexual segregation on the wintering grounds. The geographic center for male abundance in the winter range was shifted to the north of the geographic center for female abundance, by 78 km, representing 17% of the latitudinal width of the winter range (details given in Chapter 1 discussion).

A secondary peak of abundance for the female class at the northern extreme of the range does not fit the pattern suggested by latitudinal segregation, but suggests a new hypothesis that requires testing: perhaps young males (part of the female-type morphoclass) are concentrated in the northern part of the winter range. That could explain the abundance pattern observed for female types.

In addition, our results suggest that adult males also prefer higher elevations than females and immature. One possible explanation for this apparent pattern is pine-oak forests occurring at higher elevations, preferred by males, are more prevalent in the northern parts of the winter range (Mexico and Guatemala). The marked elevation preference of males was not reflected in females and immatures, suggesting that females and immatures may have considerably more potential habitat than previously recognized. More field exploration, especially in oak forests of Costa Rica and Panama, is required to evaluate this question. The overall bias of males throughout the winter range, with male abundance much higher than expected with respect to female abundance, could be explained in part by an observer bias related to elevation, since most field sites were within the elevational range preferred by males. Observers may have inadvertently avoided working at sites outside of the elevational range preferred by males, thereby missing many females.

Our finding of higher proportions of males (56%) in the wintering population throughout the winter was very different from the expected proportion of 37%. One possible explanation for more adult males being recorded throughout the known wintering grounds could be that some females and/or immatures are wintering farther south in southern Central America. It is indeed possible that many individuals could winter in Costa Rica or Panama undetected by the local ornithological community (or visiting avian ecotourists). The warblers were overlooked for many decades in other parts of their range, now recognized as regular wintering areas, such as in Nicaragua, northern El Salvador and southern Chiapas. Females and immatures closely resemble the more widespread Black-throated Green Warbler (*Dendroica virens*), and untrained observers could easily confuse the two species.

Another possible explanation for the higher proportion of males than expected is habitat segregation among sexes, especially if field observers were searching for the warblers in a habitat preferred by males. We considered this possibility and analyzed data on use of foraging substrate (type of tree species and location in the foraging tree), but we could not find any evidence for differential habitat use (methods and results reported in Chapter 1).

While we hope that the lower proportion of females (and immatures) in the population may be due to observer bias, or yet undiscovered wintering areas for females, the lower abundance of female types may also be real. Reduced abundance of females could be caused by lower survival of adult females than males, perhaps due to greater predation risk while incubating eggs or caring for young. Lower abundance of the female types could also be explained by low productivity or high mortality of young, since juveniles are classed during winter as female types. Demographic data reported from breeding grounds indicated that minimum survival estimates of males were much higher than comparable estimates for females (Ladd & Gass 1999).

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Chapter 3

A unique method for population monitoring of Golden-cheeked Warblers (*Dendroica chrysoparia*) throughout the known winter range in Central American pine-oak forests

Introduction

Much uncertainty exists about the direction of population trends for Golden-cheeked Warbler (*Dendroica chrysoparia*) in the species' breeding range, which is limited to central Texas, USA. For example, the North American Breeding Bird Survey does not have data for Golden-cheeked Warbler. Restricted access to private property throughout the breeding range has impeded progress in population research in Texas. Given the endangered status of the warbler (IUCN 2010), the protection provided by the Endangered Species Act in the United States, and conservation efforts by a variety of public and private institutions in Texas, range-wide population monitoring is needed to determine the effects of these conservation efforts and the need for additional efforts.

The only monitoring data currently available, from Fort Hood, Texas, suggests that the breeding population at that site doubled between 1991 and 2002 (Jetté et al. 1998, R. Peak, The Nature Conservancy, unpublished data). However, that data may not reflect populations at many other sites that have less intensive conservation activities. Although few studies have attempted to document actual population trends, two recent population estimates have been published. Rich et al. (2004) proposed that the global population was only 22,000 individuals. More recently, Morrison et al. (2010) achieved a geographically broad breeding survey that predicted the existence of more than 220,000 territorial (singing) males throughout the Texas breeding grounds. This much higher population estimate (which can be extrapolated to represent a population of more than 500,000 individuals of both sexes and including young birds) could be due in part to recent increases in population, or could be due only to differences in methods for achieving the estimate.

On the wintering grounds in the Central American Pine-Oak Forests Ecoregion, biologists have access to many important patches of pine-oak forests throughout the warbler's winter range. In 2006, we began a range-wide monitoring study for the warbler during winter. Monitoring in winter provides not only an important opportunity for evaluating the species' overall population status, but also could potentially provide insights into differences in population pressures between breeding and wintering grounds. We developed a unique method for winter monitoring of a passerine bird, based on comparing mean abundance of individuals occupying mixed-species foraging flocks of insectivorous birds at fixed locations across winters.

Study area and methods

The study was carried out at 24 sites in the Central American Pine-oak Forests Ecoregion (Fig. 1), the principal wintering ground for Golden-cheeked Warbler (Ladd & Gass 1999). Observers were instructed to study avian foraging flocks within forests containing at least 5 km² (500 ha) of continuous pine-oak, pine (*Pinus* spp.) or oak (*Quercus* spp.) habitat; although in several sites

(in particular, in Nicaragua) such extensive patches were not located by workers, and they studied flocks in smaller patches of forest.

A protocol was developed that was followed by five separate teams of two to four observers each winter for four years, from 15 November 2006 to 15 February 2010. In some years, six teams participated. Each team worked at five (sometimes more or less) sites within one country each year, although data from sites that were not repeated from one year to another are excluded from this analysis. Within a site, observers collected data during five mornings, beginning at 06:00 h, by seeking and then following mixed species foraging flocks of insectivorous birds as long as possible up to 4 h (or up to 12:00, whichever came first). Data was only used from flocks studied for at least 1.5 h. If observers lost track of a flock, they spent the rest of the morning attempting to relocate it, and if successful, took up observation again (without counting lost time). Each foraging flock was studied just one morning during a season.

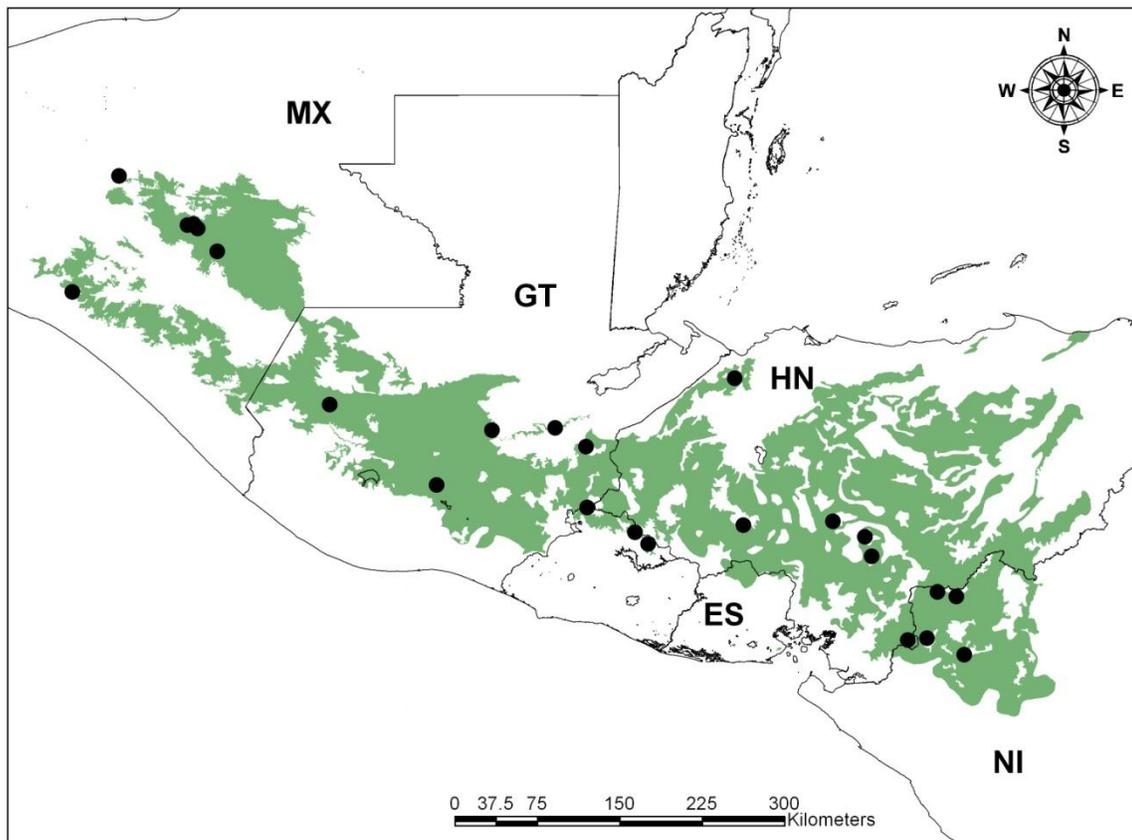


Figure 1. Golden-cheeked Warbler monitoring sites (black dots) within the Central American Pine-oak Forests Ecoregion (green shading).

A flock was defined as a group of at least 10 individuals of at least three species of insectivorous birds. Five (occasionally more or less) flocks were monitored in each forest each year, each flock being located at least 500 m from any other. Observers occasionally studied flocks that were closer in space, when they were confident that they represented different flocks. The observers noted each individual in the flock according to the time it was first observed, and every individual was identified to sex and age when those classifications were possible based on field observations. Because of potential difficulties distinguishing immature Golden-cheeked Warblers from adult females in the field, data was analyzed for just two sex/age classes: adult males, and female morphotypes, which included adult females and all immatures. We considered as insignificant the possibility that a very small proportion of adult females may closely resemble adult males in the field.

Table 1. Twenty-four study sites where 63 flocks were monitored across years for abundance of Golden-cheeked Warblers.

Country	Site	Lat & long degrees		Elev. masl	Specific flock locations repeated at least once
Mexico	Arcotetes	16.722	-92.601	2295	1
Mexico	Coapilla	17.155	-93.245	1812	1
Mexico	Huitepec	16.75	-92.684	2415	2
Mexico	La Granada	16.534	-92.44	1919	1
Mexico	Moxviquil	16.759	-92.634	2310	4
Mexico	Tres Picos	16.201	-93.626	1357	2
Guatemala	Cerro Alux	14.618	-90.643	2127	4
Guatemala	Chimusinique	15.277	-91.518	2027	4
Guatemala	San Jerónimo	15.07	-90.19	1579	2
Guatemala	San Lorenzo Mármol	15.086	-89.674	1733	2
Guatemala	Las Granadillas	14.934	-89.42	1210	3
Honduras	Cusuco	15.495	-88.203	1431	1
Honduras	La Botija	13.345	-86.787	1369	1
Honduras	La Esperanza	14.288	-88.134	1693	1
Honduras	La Tigra	14.193	-87.137	1500	1
Honduras	San Francisco Soroguara	14.319	-87.401	1454	2
Honduras	Uyuca	14.034	-87.084	1594	2
El Salvador	El Manzano	14.23	-89.021	1530	5
El Salvador	La Montañona	14.134	-88.913	1395	6
El Salvador	Parque Nacional Montecristo	14.433	-89.413	1742	3
Nicaragua	Loma Fría	13.741	-86.544	1228	6
Nicaragua	Mozonte-San Fernando	13.704	-86.388	1008	4
Nicaragua	Tepesomoto-Patasta	13.362	-86.629	1365	4
Nicaragua	Tisey	12.966	-86.371	1374	1

For evaluating annual trends, we considered the mean number of Golden-cheeked Warblers occupying the flocks, at 63 specific flock locations within 24 study sites (Table 1). The number of

flock locations varied each year: in the first annual comparison, 20 flock locations were repeated; in the second annual comparison, 36 flock locations were repeated, and in the third annual comparison, 37 flock locations were repeated. The flock location was assumed to be the same location across years if GPS coordinates taken in subsequent visits were 250 m or less from the original location. Because the flock locations were repeated across years, we expect that individual Golden-cheeked Warblers present in different years in a single flock location may be the same individual (unless clearly of different sexes). Winter site fidelity is not yet documented for Golden-cheeked Warbler but is likely, considering that closely-related *Dendroica* warblers, such as *D. townsendi* and *D. virens*, are faithful to wintering sites across years (Thurber & Villeda 1980, Morse 1993).

We estimated the expected proportion of adult males to female morphotypes, as follows. The female morphotype class includes adult females as well as most juvenile males and juvenile females. Demographic data summarized by Ladd and Gass (1999) suggest that each successful male produces an average of 2.2 juveniles, and that nest success may only be 55%. We estimate therefore that each female (or nest) produces on average 1.2 juveniles. An unknown proportion of juveniles perish before arriving at wintering grounds. For simplicity, we estimate the annual productivity to be one juvenile per adult female. If we also assume (1) equal sex ratio at birth, (2) equal mortality rate by sex, then we would expect to find 2 female morphotypes for every 1 adult male. However, feather wear in young males during the winter may possibly render some immature males very similar to adult males; therefore we conservatively estimate that one quarter of the immature males (one eighth of all immatures) are identified in the field as adult males. As a result, we expect to find 1.875 female types per every 1.125 male types (a ratio of 1.67:1 female types to male types).

Statistical tests comparing the observed proportions to the expected proportions, from one year to the next, were carried out using Minitab software. Tests were considered significant when $P < 0.05$.

Results

Relative abundance for Golden-cheeked Warblers (males and females combined) appeared to decline three years in a row, with a mean decline of 19% over the full period (Table 2). Means of abundance counts were not significantly different from year to year, but the overall decline over the four years of observation was marginally significant when the probabilities for the annual hypothesis tests were combined ($P = 0.03$). The mean abundance in 2009 showed a near significant decline compared to 2008 with a two-tailed t-test ($P = 0.07$). This decline was supported by a chi-square test of presence and absence of GCWA in the flocks in the two winters ($X^2 = 4.963$, $DF = 1$, $P = 0.026$); of the flocks studied at fixed locations in both 2008 and 2009, Golden-cheeked Warblers were present in 17 flocks in 2008 but just 8 flocks in 2009. We considered changes for just males and just females, and noted stronger apparent declines for females (31%) than for males (8%).

Table 2: Annual monitoring results for Golden-cheeked Warblers on the wintering grounds.

	Annual change in abundance (birds/flock)			Mean
	2007 vs. 2008	2008 vs. 2009	2009 vs. 2010	
Change in males abundance	0	-0.11	0.03	-0.03
Change in female abundance	-0.05	-0.11	-0.14	-0.10
Change in abundance (males + females)	-0.05	-0.22	-0.11	-0.13
Males + females per flock in first year	0.75	0.58	0.70	0.68
% change, both sexes combined	-7%	-38%	-15%	-19%
P (from t-test)	0.772	0.073	0.524	0.03 ^a
N (flocks)	20	36	37	–
Males per flock in first year	0.40	0.31	0.38	0.36
Females per flock in first year	0.35	0.28	0.32	0.32
% change for males	0%	-36%	7%	-8%
% change for females	-14%	-40%	-42%	-31%

^aThe combined probability (P) value of 0.03 is not a mean, but rather a product of the three P values generated each year.

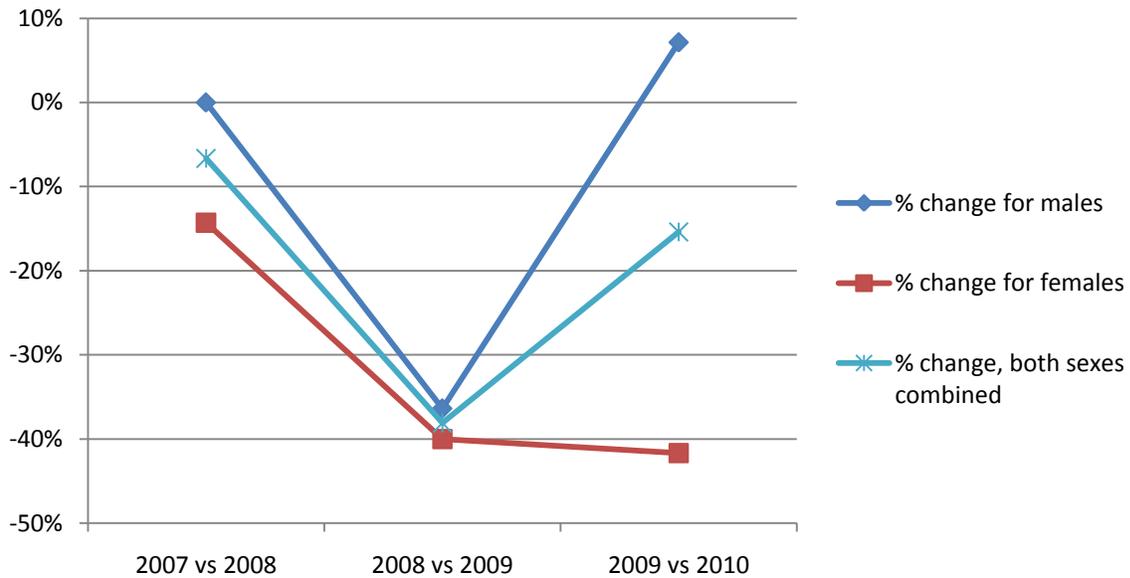


Figure 1. Proportional annual declines in Golden-cheeked Warbler abundance detected on wintering grounds.

Discussion

The number of flock locations repeated in subsequent years varied from year to year. Only 20 flock locations from the first season were repeated during the second season. The sample of flock locations in the second season repeated in the third season was nearly twice as large. These repeated locations formed part of a broader study of winter ecology and habitat use, in which close to 150 flock locations were studied each season, but most of the locations were not repeated in subsequent years (and some were at exploratory sites where presence of Golden-cheeked Warbler was never confirmed). Future monitoring can be greatly improved by increasing the number of repeated flock locations from one season to the next.

Our larger data set, based on all flock locations and not just the repeated locations, also suggested that Golden-cheeked Warbler abundance declined (except for the first annual comparison), but we identified several observer biases associated with the data, that we felt may have been hiding true declines. For example, as field teams searched for new sites to study Golden-cheeked Warblers, and simultaneously gained experience, they probably selected sites with better habitat that were more likely to have higher abundances of Golden-cheeked Warblers. By using fixed flock locations, this problem was eliminated, although we also reduced our sample size considerably.

We were surprised that the data suggested such high annual declines (19% annual decline average, with nearly 40% decline in one year). We suggest that such a high decline may not apply to the entire range. Many of the sites used for monitoring were located near the edges of the birds' range. For example, 18 of the 73 monitoring locations were near the southern edge in Nicaragua, 15 near the northern edge in Mexico, and 15 along the southwest edge in El Salvador. Only 26 monitoring locations were in the core range of Guatemala and Honduras. Species declines are likely to be sharper at the peripheries of a range than within the core (Hardie & Hutchings 2010).

We recommend that future monitoring include a larger sample of repeated flock locations. We suggest a set of 150 locations (five locations at each of 30 sites), with half near the periphery of the range, and half in the core of the range. All monitoring locations should be in optimal habitat, where the presence of the species has already been documented.

The large difference in population trend between males and females (or juveniles) in 2010 was noteworthy. While we cannot exclude random variation for this pattern (because of our small sample sizes), future monitoring should consider the possibility that annual survival differs by sex and/or age in some years. Females could experience higher mortality in some years due to higher predation on nesting grounds, or perhaps because of occupying peripheral habitat. Juveniles may experience higher mortality than adults from climate-induced food shortages or inclement weather during the fall migration.

Our preliminary findings of apparent declines across the winter range, during three consecutive years, suggest that the Golden-cheeked Warbler may continue to be losing ground, and should continue to be considered threatened or endangered. The pine-oak forest habitat where the warbler winters is poorly protected, and encino-type oaks used by the birds for foraging are often targeted for harvesting by rural farming families searching for firewood or charcoal (APEM 2008). The Golden-cheeked Warbler is also more sensitive to elevation than most migratory bird species, with a marked preference for the elevational range 1400–2400 masl (Rappole et al. 1999, this report). The population may experience further pressure on the wintering grounds if

global warming causes predicted ecological changes, such as upward migration of ecosystems, that may reduce the availability of the warbler's prime wintering habitat.

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Chapter 4

Notes on winter ecology of Golden-cheeked Warblers (*Dendroica chrysoparia*), including vocalizations, foraging substrate, and participation in mixed-species foraging flocks in Central American pine-oak habitat

Introduction

The endangered Golden-cheeked Warbler (*Dendroica chrysoparia*) has been extensively studied on its Texas breeding grounds, but much less so on Central American wintering grounds. Distribution in winter is thought to be restricted to the Central American Pine-oak Forests Ecoregion (Ladd & Gass 1999). A study carried out during the 1990s in Honduras and Guatemala established much of what is known about Golden-cheeked Warbler winter ecology (Rappole et al. 1999). That study documented warbler participation in mixed-species foraging flocks, and presented the relative abundance of 15 insectivorous species that were associated with the same flocks in which Golden-cheeked Warblers foraged. That study also reported that Golden-cheeked Warblers did not vocalize on the wintering grounds. Here we expand on the results reported by Rappole et al. (1999), by documenting species associations in a larger number of foraging flocks, covering a broader geographical area. We also quantify observations of Golden-cheeked Warblers vocalizing during winter.

Study Area and Methods

Golden-cheeked Warblers were observed at 35 sites on their principal wintering grounds in the Central American Pine-oak Forests Ecoregion (Fig. 1). As part of a broader study of the distribution, abundance, and demography of Golden-cheeked Warbler (Komar et al., this report), teams of two to four observers studied 603 mixed-species foraging flocks of insectivorous birds each winter for four years, following a standardized protocol, and locating 440 individual Golden-cheeked Warblers. Each morning, the observers began walking through the forest in search of flocks at 06:00 or shortly thereafter. Once encountering a flock, they followed it as long as possible up to 4 h (or up to 12:00 h, whichever came first). Golden-cheeked Warbler (GCWA) observations were noted along with apparent sex and age, and location in the tree at first sighting. On successive mornings, the teams studied flocks in different parts of the forest, aiming to leave at least 500 m of space between flock study locations, in order to avoid studying individual flock members more than once. However, 63 flocks were at locations repeated (within 250 m) from a previous year.

All field work was carried out after 15 November and before 28 February, in order to avoid influence of migratory movements on flock composition. A flock was defined as a group of at least 10 individuals of at least three species. The observers noted each individual in the flock according to the time it was first observed.

The counts of each species in each flock were assembled into a matrix. Species that were present in less than 15% of flocks were considered marginal participants of the flock community, and were removed for the analysis of flock associations. For the remaining species, we generated a correlation matrix using Minitab software. We classified species pairs with significantly positive correlations ($P < 0.01$) as associated species. We considered the species with the most associations among all possible pairs to be core flock members.

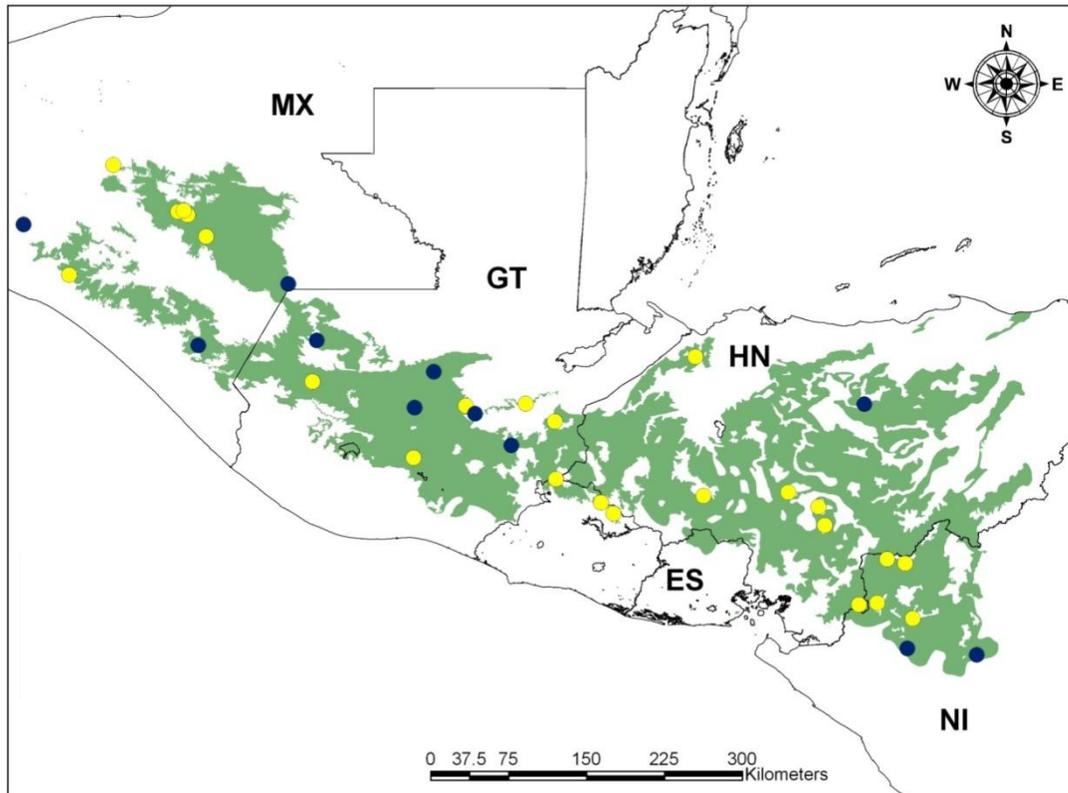


Figure 1. Golden-cheeked Warbler study sites within the Central American Pine-oak Forests Ecoregion (green shading). Blue dots indicate sites studied in one year; yellow dots indicate sites studied in multiple years.

Results

We found Golden-cheeked Warblers to be frequent members of mixed species insectivorous foraging flocks during the winter, along with 23 other species (Table 1). Eleven species are migrants visiting Central America from North American breeding grounds, while 13 species are permanent residents. Golden-cheeked Warblers were encountered in 39% of all flocks studied within pine-oak forest habitat. In terms of species associations, Golden-cheeked Warbler was positively correlated with 16 of the 23 species recorded in the flocks, and can be considered a core flock member. Only the Greater Pewee (*Contopus pertinax*), a locally resident species, was positively associated with more species (Table 2).

Male and non-male GCWA used foraging trees in a similar fashion (Table 3). On average, GCWA were found 10.09 m high in trees. The overall tree height averaged 12.93 m, such that the birds foraged on average about 20% below the tree top, and 80% above the ground. The birds foraged on average 2.45 m from the trunk, and 0.91 m from the outer edge of the tree canopy. Maximum width of trees used for foraging was 6.43 m, such that on average, birds foraged 29% in from the tree edge towards the trunk. None of the differences in these

measurements between males and female-type birds were significant. The comparison that appeared most different was the proportional distance from the edge of the foliage, in which males averaged 31% from the edge and females 26%; however, the means were not significantly different ($T = -1.51$, $P = 0.131$, $DF = 367$). Approximately 50% of the foraging trees where GCWA were first observed were narrow-leaved encino-type oaks (*Quercus* spp.); more information about trees is given in Chapter 1 above. Approximately 31% of Golden-cheeked Warblers vocalized with chips while foraging (Table 4). The percentage of birds to vocalize did not vary by sex (2-sample Fisher's Exact test: female types vs. adult males $P=0.755$).

Table 1. Relative abundance and frequency of migrant and resident insectivorous bird species in 603 mixed foraging flocks of Central American pine-oak forests, in order by frequency.

Species	Frequency (%)	Number of individuals (Mean \pm SE)
Wilson's Warbler (<i>Wilsonia pusilla</i>)*	82.3	1.86 \pm 0.06
Blue-headed Vireo (<i>Vireo solitarius</i>)*	78.0	1.41 \pm 0.05
Black-and-white Warbler (<i>Mniotilta varia</i>)*	77.5	1.37 \pm 0.05
Black-throated Green Warbler (<i>Dendroica virens</i>)*	74.8	2.67 \pm 0.11
Townsend's Warbler (<i>Dendroica townsendi</i>)*	72.4	2.69 \pm 0.13
Greater Pewee (<i>Contopus pertinax</i>)	59.4	0.89 \pm 0.04
Hermit Warbler (<i>Dendroica occidentalis</i>)*	58.8	1.95 \pm 0.13
Slate-throated Redstart (<i>Myioborus miniatus</i>)	40.1	0.64 \pm 0.04
Crescent-chested Warbler (<i>Oreothlypis superciliosa</i>)	39.4	0.80 \pm 0.06
Golden-cheeked Warbler (<i>Dendroica chrysoparia</i>)*	39.1	0.58 \pm 0.04
Grace's Warbler (<i>Dendroica graciae</i>)	38.1	0.67 \pm 0.04
Olive Warbler (<i>Peucedramus taeniatus</i>)	36.9	0.58 \pm 0.04
Tennessee Warbler (<i>Oreothlypis peregrina</i>)*	36.4	1.16 \pm 0.09
Dusky-capped Flycatcher (<i>Myiarchus tuberculifer</i>)	33.9	0.45 \pm 0.03
Painted Redstart (<i>Myioborus pictus</i>)	32.8	0.50 \pm 0.03
Hepatic Tanager (<i>Piranga flava</i>)	29.0	0.46 \pm 0.03
Spot-crowned Woodcreeper (<i>Lepidocolaptes affinis</i>)	22.2	0.33 \pm 0.03
Rufous-browed Peppershrike (<i>Cyclarhis gujanensis</i>)	21.9	0.26 \pm 0.02
Yellow-throated Warbler (<i>Dendroica dominica</i>)*	18.2	0.29 \pm 0.03
Hutton's Vireo (<i>Vireo huttoni</i>)	17.4	0.37 \pm 0.04
Tufted Flycatcher (<i>Mitrephanes phaeocercus</i>)	16.6	0.25 \pm 0.03
Western Tanager (<i>Piranga ludoviciana</i>)*	16.4	0.29 \pm 0.04
Brown Creeper (<i>Certhia americana</i>)	15.6	0.24 \pm 0.02
Red-faced Warbler (<i>Cardellina rubrifrons</i>)*	15.2	0.20 \pm 0.02

*Migratory bird species visiting Central America in non-breeding season.

Table 2. Summary of a species correlation matrix for presence and absence of 24 insectivorous birds in mixed species foraging flocks of Central American pine-oak forest (taxonomic order).

Species	Positive correlations	No correlation	Negative correlations
Spot-crowned Woodcreeper (<i>Lepidocolaptes affinis</i>)	13	6	4
Tufted Flycatcher (<i>Mitrephanes phaeocercus</i>)	12	7	4
Greater Pewee (<i>Contopus pertinax</i>)	20	2	1
Dusky-capped Flycatcher (<i>Myiarchus tuberculifer</i>)	9	12	2
Blue-headed Vireo (<i>Vireo solitarius</i>)	14	7	2
Hutton's Vireo (<i>Vireo huttoni</i>)	11	4	8
Rufous-browed Peppershrike (<i>Cyclarhis gujanensis</i>)	9	9	5
Brown Creeper (<i>Certhia americana</i>)	10	10	3
Olive Warbler (<i>Peucedramus taeniatus</i>)	15	4	4
Tennessee Warbler (<i>Oreothlypis peregrina</i>)	4	9	10
Crescent-chested Warbler (<i>Oreothlypis superciliosa</i>)	13	2	8
Golden-cheeked Warbler (<i>Dendroica chrysoparia</i>)	16	5	2
Black-throated Green Warbler (<i>Dendroica virens</i>)	13	6	4
Townsend's Warbler (<i>Dendroica townsendi</i>)	15	6	2
Hermit Warbler (<i>Dendroica occidentalis</i>)	16	6	1
Yellow-throated Warbler (<i>Dendroica dominica</i>)	7	7	9
Grace's Warbler (<i>Dendroica graciae</i>)	6	11	6
Black-and-white Warbler (<i>Mniotilta varia</i>)	12	11	0
Wilson's Warbler (<i>Wilsonia pusilla</i>)	13	9	1
Red-faced Warbler (<i>Cardellina rubrifrons</i>)	12	6	5
Painted Redstart (<i>Myioborus pictus</i>)	9	12	2
Slate-throated Redstart (<i>Myioborus miniatus</i>)	14	5	4
Hepatic Tanager (<i>Piranga flava</i>)	5	12	6
Western Tanager (<i>Piranga ludoviciana</i>)	1	19	3

Discussion

The similar use of foraging substrate suggests that male and female Golden-cheeked Warblers use the winter habitat in similar fashion. Rappole et al. (1999) also reported no differences in microhabitat use by males and females in winter. Although the warbler appears to have developed latitudinal and elevational sexual segregation (Chapter 2), there is no evidence for habitat segregation.

The use of mixed-species foraging flocks of insectivorous birds during winter is characteristic of Golden-cheeked Warbler. Not only were warblers frequent members of such flocks, but they met the criteria for a core species, being positively correlated to most of the other frequent flock member species. The descriptions of flock membership are generally similar to the descriptions provided by Rappole et al. (1999), who provided descriptions of 134 flocks that contained Golden-cheeked Warblers. Like Rappole et al. (1999), we found Golden-cheeked Warblers occupying 39% of all flocks studied. However, Rappole et al. did not present data for the 60% of flocks that did not contain Golden-cheeked Warbler. In this sense, we presented data that more generally describes mixed-species flock composition for insectivorous birds across the ecoregion. We also included flocks from throughout the ecoregion, rather than just Honduras and eastern Guatemala.

Table 3. Position of Golden-cheeked Warblers in foraging trees where first observed.

Variable	Category	Sample Size (N)	Mean ± SE
tree height, m	male	249	13.00 ± 0.42
	female	175	12.83 ± 0.50
	all	424	12.93 ± 0.32
max tree width, m	male	246	6.39 ± 0.26
	female	174	6.49 ± 0.35
	all	420	6.43 ± 0.21
bird height, m	male	249	10.15 ± 0.35
	female	175	10.01 ± 0.41
	all	424	10.09 ± 0.27
bird distance from trunk, m	male	216	2.51 ± 0.17
	female	158	2.37 ± 0.18
	all	374	2.45 ± 0.12
bird distance from edge, m	male	211	0.99 ± 0.10
	female	154	0.81 ± 0.10
	all	365	0.91 ± 0.07
% of height of tree	male	248	78.32 ± 1.16
	female	174	79.12 ± 1.28
	all	422	78.65 ± 0.86
% of distance from outer edge	male	213	30.79 ± 2.16
	female	156	25.72 ± 2.57
	all	369	28.64 ± 1.66

Table 4. Vocalizations of Golden-cheeked Warblers on wintering grounds.

Vocalization type	Total	Adult male	Female-type	%
None	304	173	131	69
Chip	136	75	61	31
Song	0	0	0	0
<i>Sum</i>	<i>440</i>	<i>248</i>	<i>192</i>	<i>100</i>

Since Rappole et al. (2000) reported that only three of the 148 GCWA that they observed in Honduras and Guatemala vocalized, and only with “tsih” notes, we were surprised to observe several birds during our first winter season vocalizing with a variety of chip notes. For the second season, we carefully noted when birds under observation chipped or sang. Although not all observers described the chip notes, some observers noted several different classes of chip notes given, including “tseet” and a soft or hard “chip”, sometimes sounding only every minute or so and sometimes sounding 5–10 times in 15 seconds. The lower proportion of silent birds observed in our study, 69%, was highly significantly different from Rappole’s proportion of 98% (Poisson $Z=3.57$, $P<0.0005$). We suggest that Rappole et al.’s (1999) earlier report of winter silence was an observer error, and probably due to the shorter period of flock observation employed. Rappole et al. (2000) reported that observers abandoned the flock almost as soon as the presence of one Golden-cheeked Warbler was confirmed. Thus Rappole’s field team spent relatively little time observing individual warblers, whereas our team followed individual warblers and their flocks often for several hours each morning.

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Chapter 5

Conclusions, population estimates, and future research directions

There is much uncertainty about the overall population of the Golden-cheeked Warbler. Based on breeding density at Fort Hood and remote sensing of the breeding habitat, the *potential* breeding population was estimated to be approximately 228,000 adult birds (Rappole et al. 2003). This estimate did not take into account limiting factors, such as non-availability of appropriate nest sites, or high rates of nest parasitism or nest predation in areas that lack extensive conservation measures. The same authors (Rappole et al. 2003) estimated that the winter population was 35,500 individuals, but the upper limit of the 95% confidence interval was 83,000. Based on these data, those authors suggested that factors on the wintering grounds are limiting the species' population. Rich et al. (2004) published an even lower estimate of 22,000 individuals. Then in 2010, Morrison et al. (2010) carried out a wide-spread breeding survey that suggested that territorial males numbered over 220,000 individuals, in which case extrapolation for females and immatures could put the population well over 500,000.

Our results suggest that density on the wintering grounds averages 0.3 birds per ha and may surpass 1 bird per ha in appropriate conditions, such as when the forest contains at least 30% encino cover at midlevel. If we combine our rough density estimate of 0.3 birds per ha with the estimate of 1,950,000 ha of available habitat (APEM 2008), then an overall population estimate based on winter data would be 585,000 birds. Based on the sex ratio that we found, we can break that estimate down as 345,000 adult males, 60,000 young males, 120,000 adult females, and 60,000 young females. We suspect that the available habitat is considerably less than the figure given, so these are likely overestimates of the warbler population. However, better estimates of the overall population can now be developed based on the density estimates we provide here, by combining with information from recent satellite imagery to determine the quantity of adequate habitat available for the warblers.

We found alarming evidence of severe declines in the population of Golden-cheeked Warblers during the study. Females appeared to be declining much faster than males, which may explain why males are more common than expected throughout the wintering range. If female survival is lower than male survival, the limiting factor for the population may likely be predation on the breeding grounds. Nonetheless, conservation strategies are needed on the wintering grounds, where much of the natural habitat remaining is suboptimal because of low densities of encino-oaks. Midlevel encinos are the most important element of GCWA habitat in winter. Management of pine-oak lands should incorporate conservation of mid-level encino oak as a priority.

We recommend five lines of additional research. (1) Geographic analysis of the region using the indicators developed by habitat type and elevation, in order to estimate the overall population of GCWA. Lower elevations, and forests with lower encino content, which may have lower GCWA carrying capacities, nonetheless may be important wintering regions for females and immatures. A map of sex-specific habitat available will permit more accurate estimates of limiting factors for the population in winter.

(2) The monitoring effort should be expanded, to document range-wide population trends. The population trends are important conservation indicators for the species as well as, potentially, indicators of climate change.

(3) Search for wintering habitat used mostly by females or immature. A target area for investigation are the montane oak forests of Costa Rica and perhaps Panama. Additional areas may be found in lower elevations of the pine-oak ecoregion (below 1400 masl), and in similar pine-oak ecoregions west of the Isthmus of Tehuantepec, for example in Oaxaca, México.

(4) Banding on the wintering grounds will be important for advancing ecological studies of the Golden-cheeked Warbler. During the present study, field technicians were able to examine the legs of 90% of all Golden-cheeked Warblers identified. Of the 384 individuals examined, none carried plastic or aluminum bands or any other markings applied by researchers from other studies. Banding is essential for learning about site fidelity, survivorship, and the relationship of density in flocks to density in the landscape. By following uniquely marked birds in flocks, it should become clear if birds form similar flocks daily, and if the flocks occupy similar areas each day.

(5) Finally, we suggest that conservation research on Encino oaks and their ecosystem services will be useful for developing conservation strategies for Golden-cheeked Warblers.

In summary, we demonstrated that the winter distribution is broader than previously recognized, and wintering density is probably higher than previous estimates. Nonetheless, habitat preferences are fairly strict, and the warbler is clearly an encino-oak specialist, and found within a fairly narrow elevational range, such that it occupies only a portion of the Central American Pine-oak Forests Ecoregion. Although overall relative abundance is consistent across the winter range in appropriate habitat. males are more abundant at northern latitudes and higher elevations. Conservation priorities across the winter range should focus on the conservation of encino-oaks.

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