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WINTER ECOLOGY OF THE ENDANGERED GOLDEN-CHEEKED WARBLER[1]

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Abstract. We studied the ecology of the Golden-cheeked Warbler (*Dendroica chrysoparia*) during three winter seasons, 1995–1998, in Honduras, Guatemala, and Mexico. Individuals of this species occurred almost exclusively as members of mixed-species flocks, occupying sites with greater densities of encino oak and ground cover and fewer pines than random sites. Most foraging observations were recorded in mid-story, encino oak. Commonly-observed foraging maneuvers were gleaning and sally-hovering. Eighty-three percent of foraging maneuvers were directed at the outermost portions of the oak foliage. Flocks in which Golden-cheeked Warblers occurred contained an average of 20.5 individuals and 12.9 species other than Golden-cheeked Warblers. The most frequently co-occurring species were Wilson's Warbler (*Wilsonia pusilla*), Black-throated Green Warbler (*Dendroica virens*), Hermit Warbler (*D. occidentalis*), Townsend's Warbler (*D. townsendi*), and Blue-headed Vireo (*Vireo solitarius*). The ratio of males to females observed was not substantially different from 1:1, and there was little evidence of sexual differences in habitat use. Golden-cheeked Warblers appeared to be tolerant of moderate levels of logging and grazing, but understory clearing to promote grazing for cattle may pose a significant threat to winter habitat availability.

Key words: Dendroica chrysoparia, *endangered species, foraging behavior, habitat-use, Neotropical migrant, winter ecology.*

INTRODUCTION

The endangered Golden-cheeked Warbler (*Dendroica chrysoparia*) breeds in oak-juniper habitat of central Texas, arriving on territories in early March and departing by late July (Pulich 1976). This portion of the life cycle has been studied thoroughly, and the basic parameters of the species' life history during the breeding season generally are well understood (Keddy-Hector and Beardmore 1992, Beardmore et al. 1996). The same cannot be said for the nonbreeding portion of the life cycle, for which little more than anecdotal information has been available until quite recently. Only 12 specimens have been collected during what Pulich (1976) considers to be the wintering period (November–February); the northernmost specimen being from Tactic, Guatemala and the southernmost from La Esperanza, Honduras. Two specimens have been collected farther south in Matagalpa, Nicaragua, but these birds were taken in September, so whether they represent wandering migrants or winter residents is not known. No sight or specimen records have been reported from south of Honduras since these birds were taken in 1892.

According to scant information on the overwintering biology of this species, the habitat in which the Golden-cheeked Warbler is usually found is highland pine-oak (Land 1962, Monroe 1968, Pulich 1976). Within this habitat type, Golden-cheeked Warblers generally occur in mixed-species flocks (Pulich 1976, Braun et al. 1986). Although reported as a wintering bird in southern Mexico by Miller et al. (1957), Alvarez del Toro (1980), and several other authors, Pulich (1976) was unable to find evidence of wintering goldencheeks in that country. Subsequently, Braun et al. (1986), Lyons (1994), Martin (1993), and Vidal et al. (1994) have published winter sight records from Chiapas, Mexico, and

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an additional 57 records for the species in Mexico can be found in the "Fauna de Chiapas" database maintained by ECOSUR (El Colegio de la Frontera Sur, San Cristobal de las Casas, Mexico).

Of the previous studies conducted on the winter ecology of the Golden-cheeked Warbler, Thompson (1995) observed 13 birds during his survey (7 January–13 February 1995) for the U.S. Fish and Wildlife Service: 11 at four separate localities in Guatemala and 2 at separate localities in Honduras. Vidal et al. (1994), summarizing data from several sources including R. Greenberg and others, provide information on 46 independent observations of Golden-cheeked Warblers in the vicinity of San Cristobal de las Casas, Chiapas. Rappole et al. (in press), using remote sensing and field surveys, determined that Golden-cheeked Warblers were most abundant in pine-oak forest at the landscape scale, and provided a map of winter distribution for the species. Nevertheless, few data exist on ecological aspects of habitat use or reasons underlying the preferences of Golden-cheeked Warblers for pine-oak forest.

We initiated this study to quantify habitat parameters associated with wintering Golden-cheeked Warblers as well as to provide further information on other aspects of their winter ecology, including: (1) participation in mixed-species flocks, (2) vocalizations, (3) intra- and inter-specific interactions, (4) sex-ratios, (5) habitat segregation by sex, and (6) foraging behavior.

METHODS

STUDY AREA

Field work was conducted over three winter seasons (1 December 1995–1 February 1996; 10 January–15 February 1997; 10 January–3 March 1998) primarily in the central and western highlands of Honduras and the eastern highlands of Guatemala, an area which covers 84,237 km^2, and includes 24 of the 28 previously-documented localities for Golden-cheeked Warbler specimens and sightings in Honduras and Guatemala. We concentrated our field efforts in pine-oak habitat above 1,000 m elevation because there are no published winter records for the species from below this elevation, and previous research indicated wintering Golden-cheeked Warblers are restricted largely to habitat between 1,300 and 2,400 m (Rappole et al., in press). Other major habitat types in the highlands are pine forest, broadleaf forest (including cloud forest), pasture, agricultural fields (sun coffee, beans, corn), tree crops (bananas, shade coffee, citrus), and various early successional stages of forest regrowth.

FIELD STUDIES

Golden-cheeked Warblers were located by walking transects through forested habitats, often along roads or paths, searching visually for individual Golden-cheeked Warblers and listening for vocal members of the mixed-species flocks frequented by Golden-cheeked Warblers, such as the Greater Pewee (*Contopus pertinax*), Dusky-capped Flycatcher (*Myiarchus tuberculifer*), and Painted Redstart (*Myioborus pictus*). During the 1995–1996 and 1996–1997 field seasons, Golden-cheeked Warblers also were sampled using measured, 1-km transects. These transects were sampled by walking slowly (< 1 km hr^{-1}), and watching and listening for goldencheeks or their associates.

When a flock was located, the observer stayed with it until either a Golden-cheeked Warbler had been sighted or the observer determined that it was unlikely that a Golden-cheeked Warbler accompanied the flock. Average time required to determine presence/absence of a Golden-cheeked Warbler in a mixed-species flock was about 1.5 hr, although it ranged up to 4 hr, depending on flock size and habitat conditions.

Golden-cheeked Warblers are sympatric on the wintering grounds with other species of *Dendroica* warblers that are similar in appearance: Black-throated Green Warbler (*D. virens*), Townsend's Warbler (*D. townsendi*), and Hermit Warbler (*D. occidentalis*). We were aware of the potential for misidentifying one of these species as a Golden-cheeked Warbler, especially some plumage variants of the Black-throated Green Warbler. All birds classified as Golden-cheeked Warblers had a sharp black or gray eyeline against a bright yellow cheek in combination with a jet black or streaked back, and a complete lack of yellow on the underparts. Golden-cheeked Warblers are polymorphic in terms of sexual variation in plumage coloration, as evidenced by the range of plumages shown by specimens of known sex in the collection of the National Museum of Natural History, Washington, D.C. One specimen we examined was a fe-

male according to the label, yet had the black throat, cap, and back considered typical of males (Ridgway 1902). Most adult females have a gray or white throat and olive cap and back. Such variation is not uncommon among sexually "dimorphic" passerines (Rappole 1988). In addition, there is at least some variation in plumage within a given sex that may be age-related, with immatures appearing somewhat lighter in plumage coloration than adults of the corresponding sex (Pulich 1976). For this reason, and because we do not know the range of variation nor the percentages of occurrence of the different plumages by sex and age, we refer to the Golden-cheeked Warblers in this paper as having male-type plumage or female-type plumage.

Each Golden-cheeked Warbler sighted was carefully examined for leg bands that were attached on the breeding ground, and a simple description of its plumage was recorded for categorization as "probable male" (dark plumage) or "probable female" (lighter plumage). These categorizations are used to calculate winter sex ratio of our sample along with habitat use by sex. In addition to taking notes on Golden-cheeked Warblers present in flocks, we recorded each species observed in the flock, along with an estimate of the number of individuals for each species.

Habitat variables were measured on 0.04 ha plots centered at the point at which a Golden-cheeked Warbler was first sighted (James and Shugart 1970). The following vegetation parameters were measured: canopy height, number and size (dbh) of trees by species, shrub density, canopy cover, and ground cover. These parameters also were sampled at five randomly-located points along each transect. We collected leaf, flower, and fruit samples from trees and shrubs on our plots for taxonomic identification. These identifications were made by botanists Paul House of the University of Honduras in Honduras and César Castañeda of Defensores de la Naturaleza in Guatemala.

Foraging behavior of Golden-cheeked Warblers was sampled by observing focal individuals, and recording the first foraging maneuver observed. Only one foraging maneuver per species per flock was recorded to maximize independence among observations (Hejl et al. 1990). Foraging behaviors were classified following Remsen and Robinson (1990), and included glean, reach, sally, sally-hover, hang, reach-down, and flutter-chase. We also recorded the approximate height of each foraging maneuver and the substrate on which the bird was foraging, including plant species, as well as whether the bird was foraging in the inner or outer half of the plant.

STATISTICAL ANALYSES

Habitat variables were averaged for each transect, tested for normality using Shapiro-Wilk tests, and log- or arcsine-transformed where necessary to improve normality and equality of variances. The frequency with which Golden-cheeked Warblers were encountered as single individuals, pairs, and trios within the same flock was compared with a Poisson distribution using a Chi-square test. Vegetation variables at sites where Golden-cheeked Warblers were found versus random plots were compared using two-sample *t*-tests and discriminant analysis. In addition, we compared the vegetation characteristics of sites occupied by male versus female Golden-cheeked Warblers. Statistical tests were considered significant at $P \leq 0.05$, and were corrected using the Bonferroni correction in the case of multiple tests (Sokal and Rohlf 1995). The values reported in the results section are means ± SE.

RESULTS

One-hundred and fifty-seven Golden-cheeked Warblers were encountered during the course of the study, 155 of these as members of 134 mixed-species flocks (39.9% of total flocks observed). Of 131 flocks containing Golden-cheeked Warblers for which we have flock-size data, flocks averaged 20.5 ± 1.8 individuals of 12.9 ± 1.1 other species. The most common associates are listed in Table 1. Significantly more flocks (117; 87%) contained one Golden-cheeked Warbler, when compared with a Poisson distribution than expected by chance ($\chi^2_1 = 7.6$, $P < 0.001$), whereas significantly fewer flocks (13) contained two ($\chi^2_1 = 8.3$, $P = 0.004$) or three Golden-cheeked Warblers (4) than expected by chance ($\chi^2_1 = 4.5$, $P < 0.04$). Two Golden-cheeked Warblers were observed as solitary individuals, separate from any apparent flock. One of the solitary birds was encountered in pine/oak habitat on 3 December 1995 at 06:30, possibly prior to the hour when flocks first coalesce in the morning. The second bird was encountered in pine-oak habitat on 7 January 1996

TABLE 1. Bird species occurring in 131 flocks in which Golden-cheeked Warblers were located, ranked in order of decreasing frequency of occurrence. Only species sighted in ≥25% of flocks are included.

Species	Frequency (%)	Number of individuals (mean ± SE)
Wilson's Warbler	82.7	1.18 ± 0.08
Black-throated Green Warbler	82.0	2.13 ± 0.19
Hermit Warbler	78.9	2.19 ± 0.20
Blue-headed Vireo	71.4	0.89 ± 0.08
Townsend's Warbler	69.2	1.15 ± 0.09
Olive Warbler (*Peucedramus taeniatus*)	63.9	0.86 ± 0.07
Painted Redstart (*Myioborus pictus*)	63.2	0.76 ± 0.07
Crescent-chested Warbler (*Vermivora superciliosa*)	61.7	0.99 ± 0.10
Slate-throated Redstart (*Myioborus miniatus*)	60.9	0.76 ± 0.06
Black-and-white Warbler (*Mniotilta varia*)	60.9	0.65 ± 0.05
Grace's Warbler (*Dendroica gracia*)	54.9	0.64 ± 0.06
Greater Pewee (*Contopus pertinax*)	50.4	0.52 ± 0.05
Brown Creeper (*Certhia americana*)	35.3	0.36 ± 0.05
Streak-headed Woodcreeper (*Lepidocolaptes affinis*)	33.8	0.41 ± 0.06
Tufted Flycatcher (*Mitrephanes phaeocercus*)	30.8	0.37 ± 0.06
Dusky-capped Flycatcher (*Myiarchus tuberculifer*)	29.3	0.32 ± 0.05
Hammond's Flycatcher (*Empidonax hammondii*)	26.3	0.24 ± 0.04
Acorn Woodpecker (*Melanerpes formicivorus*)	25.6	0.41 ± 0.09

at 10:30. Both solitary birds had female type plumage.

Of 148 birds for which we recorded plumage, 76 were male-plumaged birds, i.e., with black crown, back, and throat, whereas 70 were female-plumaged birds, with dark olive crown and back, and with gray or white throat. However, there was a considerable range of variation within each of these broad categories. Of the 17 flocks with more than one Golden-cheeked Warbler, 2 had only male types, 1 had only female types, and the remainder had both male and female types.

Golden-cheeked Warblers were heard to vocalize on three occasions: 19 October 1995, 5 December 1995, and 25 January 1997. In each instance, the vocalization was a rapid series of "tsih" notes. The October 1995 observation was made by JHR of a male-plumaged bird in a mixed-species foraging flock that included two other Golden-cheeked Warblers in the El Cantoral region of Honduras. The other two observations were made by DK, the first at 10:58 at El Cantoral, and the second at 09:30 at Zambrano, Honduras. In both cases, they were female-plumaged birds, and the only Golden-cheeked Warblers present in the flock. We observed 11 aggressive interactions between birds over the course of our study. Of these, three involved goldencheeks: (1) a goldencheek was chased by a White-eared Hummingbird (*Hylocharis xantusi*), (2) a male-plumaged goldencheek chased a female-plumaged goldencheek, and (3) a goldencheek attacked a Black-throated Green Warbler.

HABITAT USE

Habitat variables were measured at 44 Golden-cheeked Warbler locations and at random locations on 42 transects. The dominant pine species at both Golden-cheeked Warbler and randomly-located sites in habitats frequented by Golden-cheeked Warblers in Honduras was ocote (*Pinus oocarpa*), although other pine species were predominant in some localities, mainly pinabete (*P. maximinoi*). The dominant broad-leaved trees were oaks (*Quercus*) of several species. These oaks were divided into two groups based on leaf morphology: (1) "encino" oaks (*Q. sapotifolia, Q. eliptica, Q. elongata, Q. cortesii*) with shiny narrow, elliptical, or oblong leaves, and (2) "roble" oaks (*Q. segoviensis, Q. purulhana, Q. rugosa*) with large, lobed leaves. Pine and encino oak species comprised > 60% of the total number of trees and > 80% of the basal area of trees on our study sites. The next most abundant group of tree species in Golden-cheeked Warbler habitat, roble oaks, comprised only 7% of the number of stems and 7% of the basal area on our study plots. Such small amounts precluded meaningful analysis of trees other than pine and encino oak. Therefore, we restricted our analys-

TABLE 2. Habitat variables compared between 44 plots at which Golden-cheeked Warblers were observed (GCW) and on 42 random plots (Random) on transects. Only *P*-values < 0.006, the Bonferroni corrected *P*-value, are considered statistically significant.

	GCW (mean ± SE)	Random (mean ± SE)	*P*
l_n (No. pines)	8.3 ± 1.1	11.7 ± 1.3	0.02
l_n (Basal area pines) (m^2 ha^{-1})	8.8 ± 1.1	14.7 ± 1.3	<0.001
l_n (N encino oaks)	10.6 ± 1.4	6.4 ± 0.9	0.04
l_n (Basal area encino oaks) (m^2 ha^{-1})	7.5 ± 1.2	2.5 ± 0.4	<0.001
l_n (Stem density) (stems m^{-2})	141.3 ± 14.2	138.8 ± 12.6	0.32
Percent ground cover	40.0 ± 3.4	28.5 ± 2.0	0.005
Percent canopy cover	74.0 ± 2.5	70.6 ± 2.3	0.38
Average tree height (m)	22.9 ± 0.7	23.4 ± 0.6	0.62
Percent slope	19.1 ± 1.4	20.4 ± 1.1	0.48

es to these two taxa. Golden-cheeked Warblers occupied sites that had significantly higher basal area of encino oaks and ground-cover and significantly lower basal area of pines than random areas (Table 2). No other habitat variable differed significantly between sites occupied by Golden-cheeked Warblers and unoccupied sites (Table 2). Similarly, discriminant analysis indicated that the vegetation characteristics at sites occupied by Golden-cheeked Warblers differed significantly from unoccupied sites (Wilk's-Lambda $F_{9,74} = 5.6$, $P < 0.001$). The resulting discriminant function correctly classified 70.4% of occupied sites and 90.4% of unoccupied sites. Examination of the discriminant loadings indicated that Golden-cheeked Warblers were significantly negatively associated with the abundance and basal area of pines, and significantly positively associated with the abundance and basal area of encino oaks and with percent ground cover, consistent with the results of the univariate comparisons.

MICRO-HABITAT USE BY SEX

Male-plumaged and female-plumaged Golden-cheeked Warblers overlapped substantially in habitat use. Male-plumaged birds used sites with fewer pines and taller trees than female-plumaged individuals. These differences were not significantly different at the Bonferroni corrected *P*-value of 0.006. Similarly, discriminant analysis indicated that the habitat at sites occupied by males did not differ significantly from sites occupied by females (Wilk's-Lambda $F_{9,63} = 1.7$, $P = 0.15$).

FORAGING BEHAVIOR

We observed 33 independent foraging maneuvers. Golden-cheeked Warblers foraged primarily in encino oaks (94%), a proportion much larger than expected based on the proportion of encino at sites occupied by Golden-cheeked Warblers (42%) ($\chi^2_1 = 20.2$, $P < 0.001$). They also were observed foraging in pine (4%) and roble oak (4%). Ninety-six percent of foraging maneuvers were directed at leaves. Golden-cheeked Warblers foraged principally on the outer half of the tree (93%) at an average height of 9.18 ± 1.06 m, mainly by sally-hovering (30%), gleaning (24%), and reaching (18%). Other foraging maneuvers used included flutter-chasing (9%), sallying (9%), reaching-down (6%), and hanging (3%).

DISCUSSION

We found Golden-cheeked Warblers wintering primarily in pine-oak habitat above 1,300 m. Even in those instances where Golden-cheeked Warblers were found in habitat that could not be characterized as pine-oak, as in cases where pine occupied the entire canopy, encino oaks constituted a significant portion of the mid- or understory. Other investigators also have reported that Golden-cheeked Warblers were found mainly in pine-oak habitat (Monroe 1968, Thompson 1995). An exception is the report by Vidal et al. (1994), in which wintering Golden-cheeked Warblers were widely distributed among habitat types in Chiapas. However, Vidal et al. (1994) made this assertion based on a relatively modest sample size (16 birds encountered on transects, and only one transect per habitat) that may have included migrating as well as wintering individuals. Migrating individuals often exhibit greater habitat breadth than wintering individuals (Rappole 1995).

Other reports of wintering Golden-cheeked

Warbler foraging behavior are consistent with our findings that Golden-cheeked Warblers prefer encino oaks to other available substrates (Johnson et. al. 1988, Thompson 1995), and forage primarily by sally-hovering and gleaning (Vidal et al. 1994, Thompson 1995). The strong tendency of Golden-cheeked Warblers to forage in encino oaks probably explains our observation that sites occupied by Golden-cheeked Warblers had significantly higher basal area of encino than random points. The occurrence of higher amounts of ground-cover at sites occupied by Golden-cheeked Warblers may reflect the absence of extensive burning and grazing, which can reduce the amount of encino oaks in which they forage.

The question of why Golden-cheeked Warblers prefer foraging in encino oaks is unanswerable without sampling of available prey. We presume that foraging movements, microhabitat structure, and prey base provide the principal defining dimensions for the species' foraging niche. Golden-cheeked Warblers have a stereotypical manner of foraging in which they glean and flutter along the outer portions of an encino oak, generally working on the foliage at the very tips of the branches. Encino oaks have a different structure from roble oak species and pines in that encino leaves, at the level at which Golden-cheeked Warblers forage, stick out above the horizontal plane, whereas the leaves of these other common tree taxa droop. Vegetation structure may be important in determining what substrates are and are not suitable for foraging (Parrish 1995), and the distinctive structure of encino oaks in combination with the foraging behavior of the Golden-cheeked Warbler may restrict this species to forest including a large component of encino oaks. Laboratory experiments involving captive individuals and manipulations of foliage structure could be helpful in elucidating the relationship between Golden-cheeked Warblers and their foraging substrate (Morton et al. 1993, Parrish 1995).

It is clear from Ridgway (1902), Chapman (1907), Oberholser (1974), and Pulich (1976) that most female Golden-cheeked Warblers (> 80%) are lighter in color and show less contrast than most males. The modest differences in terms of habitat use found in this study by birds with male-type plumage as opposed to those with female-type plumage do not lend significant support to the existence of sexual-habitat segregation in Golden-cheeked Warblers as has been observed in some other wintering warblers (Rappole and Warner 1980, Lopez-Ornat and Greenberg 1990, Parrish and Sherry 1994). Twelve of the 17 flocks (71%) in which more than one Golden-cheeked Warbler was known to occur contained birds of both male- and female-type plumage. Similarly, 7 of 13 flocks (54%) with more than one Golden-cheeked Warbler observed by Vidal et al. (1994) had birds of both plumage types.

We found that wintering Golden-cheeked Warblers were almost always encountered as single individuals in mixed-species flocks. Although this species generally occurs in the company of other species during the winter period, the percentage of solitary birds reported by others is far higher than the 1% we found. For example, Vidal et al. (1994) reported that 10% of 36 birds were not members of mixed-species flocks. A partial explanation for this difference may be that they include records from as early as 5 August and as late as 13 April. Thus, their sample may include a number of birds in transit. However, Thompson (1995) reported that 31% (4 of 13) of the birds he observed were solitary. His records were taken from 7 January–13 February 1995, and are unlikely to have included transients.

We found only a single Golden-cheeked Warbler in 87% of the flocks we encountered, a phenomenon reported by Braun et al. (1986) and Thompson (1995) as well. In contrast, Vidal et al. (1994) reported that 52% of goldencheeks they observed were in flocks containing more than one individual, whereas Johnson et al. (1988) reported 5–7 goldencheeks in one flock on 18 March 1987, and Kroll (1980) found 12 goldencheeks in the same flock on 20 March 1975. Given that the birds arrive on the breeding grounds as early as 2 March (Pulich 1976), it is possible that these observations represent migratory individuals, which may also explain the greater proportion of multiple goldencheeks per flock reported by Vidal et al. (1994).

The lack of vocalization and overt intraspecific interaction between Golden-cheeked Warblers observed in this study (only one brief chase) is typical of other species of birds that occur normally as solitary individuals in mixed-species flocks. Single Black-and-white Warblers (*Mniotilta varia*) and Worm-eating Warblers (*Helmitheros vermivorus*) are common in

mixed-species flocks in southern Veracruz rainforest (Rappole and Morton 1985). Intraspecific interactions between members of these species are rare, and the birds are generally silent (Rappole and Warner 1980). There are two possible explanations for the fact that a single Golden-cheeked Warbler occurs in most flocks. The first is that significant interaction probably does take place to exclude conspecifics from intruding into an individual's "flock space" at some time during the year, probably immediately after arrival on the wintering grounds as Skutch (in Bent 1953) reported for Black-and-white Warblers arriving in Guatemala in September. An alternative explanation is that winter population sizes are lower than available winter habitat will allow, i.e., more Golden-cheeked Warblers would occur in flocks if there were more birds. We believe that the first explanation is correct, and that the number of individuals per flock for Golden-cheeked Warblers is a result of intraspecific competition for limited resources. We base our conclusion on two lines of reasoning. First, if prey availability were not a limiting factor, then the best flock associates for Golden-cheeked Warblers would be other Golden-cheeked Warblers. Conspecifics make the best potential sentinels for predators for each other by sharing the same susceptibility to predators and using the same foraging areas within the environment (foraging height, substrate, prey). Thus, if intraspecific competition for limited resources were not a factor, we should observe some flocks with several Golden-cheeked Warblers, and others with none, rather than what we actually found, which was many flocks with a single individual. Second, common species also occur as single individuals in flocks (e.g., Black-and-white Warbler), indicating that the social structure is likely a matter of individual choice rather than a stochastic function based on total number of individuals and total amount of habitat.

Vidal et al. (1994) reported a sex ratio in their sample significantly skewed towards birds in male-type plumage (36 male, 15 female). We observed a ratio in plumage type not significantly different from 1:1 (76 male, 70 female). Their explanation for the severe skew observed in the Mexican sample is that, "The true sex ratio . . . may be masked by the fact that male Golden-cheeked Warblers are more easily distinguished from the sibling species than are females. Thus, female Golden-cheeked Warblers seen imperfectly might have gone unrecorded." Another possible explanation is that suggested by Fretwell (1972), Gauthreaux (1982), and others, namely that males of migratory species tend to winter at the northern extremity of their winter range. So far as is known, San Cristobal de las Casas, at latitude 16°44′, is the northernmost locality where the birds regularly occur in winter.

The five most abundant flock associates for goldencheeks that we observed were, in descending order of frequency of occurrence, Wilson's Warbler, Black-throated Green Warbler, Hermit Warbler, Blue-headed Vireo, and Townsend's Warbler; the same five species were observed to be the most common associates by Thompson (1995). Vidal et al. (1994) found Townsend's Warblers, Hermit Warblers, Red-faced Warblers, Blue-headed Vireos, and Crescent-chested Warblers to be the most common associates. Differences between our list and that of Vidal et al. may be due to the considerable latitudinal difference between our study sites and theirs. The list of associates reported by Kroll (1980) was similar to ours, as was that provided by Monroe (pers. comm. in Pulich 1976), although the latter included Black-and-white and Yellow-rumped Warblers. Black-and-white Warblers ranked 11th in abundance in our sample, but they occurred in 60% of the flocks we observed and thus were relatively common in terms of frequency of co-occurrence with Golden-cheeked Warblers. We observed Yellow-rumped Warblers in fewer than 10 flocks in which we observed Golden-cheeked Warblers, although, when we did encounter them, they were often in large numbers, and this may account for Monroe's assertion that they were common associates of Golden-cheeked Warblers.

CONCLUSIONS

The Golden-cheeked Warbler has remarkably restricted social, habitat, and foraging requirements on its wintering grounds in Honduras, Guatemala, and southern Mexico. Individuals occur as single individuals in mixed-species foraging flocks in pine-oak habitat above 1,300 m in elevation. These unique ecological requirements make the species vulnerable to habitat loss at any point during its life cycle, on migration and during the winter, as well as during the breeding season. Although Golden-cheeked

Warblers appear to be tolerant of moderate levels of timber-cutting or grazing, our results suggest that clear-cutting or any practice reducing the amount of oak in the mid or understory, such as overgrazing or the widespread practice of clearing the understory by burning to promote grass growth for cattle grazing, can be expected to reduce the suitability of the habitat for wintering Golden-cheeked Warblers. Furthermore, the nearly obligate association with mixed-species foraging flocks exhibited by Golden-cheeked Warblers suggests that they would be adversely affected by forest fragmentation, because this practice reduces the suitability of the remaining habitat for mixed-species flocks (Rappole and Morton 1985).

The winter range of the Golden-cheeked Warbler extends from Chiapas, Mexico to central Honduras, a distance of nearly 800 km, and, therefore, at first look, winter habitat appears to be less restricted than the present extent of occupied breeding habitat, which currently is found in only 18 counties in Texas. However, our results indicate that Golden-cheeked Warblers are restricted in winter to sites with significant amounts of encino oak, a habitat that is much more limited than the broad geographic distribution of wintering Golden-cheeked Warblers might suggest.

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