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Winter habitat and distribution of the endangered golden-cheeked warbler (*Dendroica chrysoparia*)

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Abstract

The golden-cheeked warbler (*Dendroica chrysoparia*) is an endangered Neotropical migrant that breeds in oak (*Quercus*)/juniper (*Juniperus*) habitat of the Edwards Plateau in central Texas. Recently work has been done on the factors affecting breeding populations of this species, but little is known about winter habitat use or distribution. We used extensive field surveys in Honduras and Guatemala to obtain locational information, which was used with topographical and remote sensing data, to identify and calculate the amount of suitable habitat available, and to map the species' distribution in the region. Most individuals were found in pine–oak from 1100–2400 m ($\bar{x}$ = 1651 (± 246) m) in elevation, a habitat type that occupied 29.8% of the total land area above 914 m in the region investigated. Based on this information and existing locational data from the literature, we present a map of the winter range for the golden-cheeked warbler. Threats to the species during this period of the life cycle include logging, burning and clearing for pasture and agriculture.

INTRODUCTION

Golden-cheeked warbler (*Dendroica chrysoparia*) breeding populations currently are restricted to 18 Texas counties (Beardmore, Hatfield & Lewis, 1996:6), and the bird is listed as 'endangered' by the US Fish & Wildlife Service (Jahrsdorfer, 1990). Despite intense efforts to discover and reverse the root causes, populations actually appear to have continued to decline in the past two decades (Wahl, Diamond & Shaw, 1990). Current estimates place the total species' population at 4822–16 016 breeding pairs (Keddy-Hector & Beardmore, 1992:18).

Suggested reasons for the continued decline of the species include the following: (1) destruction of breeding habitat, (2) breeding habitat degradation caused by grazing and 'range improvement', (3) urban expansion on the breeding ground, (4) flooding of breeding habitat by dams, (5) oak wilt in breeding habitat, (6) social parasitism of nests by cowbirds, (7) fragmentation of breeding habitat (Keddy-Hector & Beardmore, 1992). However, members of this species spend less than 47% of their life cycle in Texas (earliest spring date = 2 March 1956, latest autumn date = 18 August 1962: Pulich, 1976:54, 55), passing 7 months of the year in habitats outside the USA in transit or on their wintering sites. Little is known about the migration and winter biology of the species, yet it is as vulnerable during these portions of the life cycle as during the breeding season.

At the time of the publication of the excellent monograph on the species by Pulich (1976), there were 412 specimen records for the bird, only 40 of which were collected from outside the USA (Pulich, 1976:160). Twenty-four of these were taken in Mexico. Pulich believed the Mexican birds to be transients based on the fact that all extant Mexican specimens were collected in the months of potential migratory movement: June–October and March, and there were (and are) no specimens for Mexico for the wintering months of November–January. Two specimens were taken in Matagalpa, Nicaragua on 16 and 17 September 1891, but no birds have been recorded in this country since. Thus, the extent of the specimen base for the winter range of the species is 14 individuals: seven from Guatemala and seven from Honduras (Fig. 1, Appendix I). Recent work in Chiapas, Mexico indicates that there are wintering populations of the species in highland pine-oak forest (2100–2550 m) near San Cristobal de las Casas (Braun, Braun & Terrill, 1986; Lyons, 1990, 1994; Martin, 1993; Vidal, Marcias-Caballero & Duncan, 1994). Additionally, Vannini (1991) has reported goldencheeks from south-western Guatemala. Despite these recent reports, no attempt has been made to identify and prioritize the principal winter habitats for this

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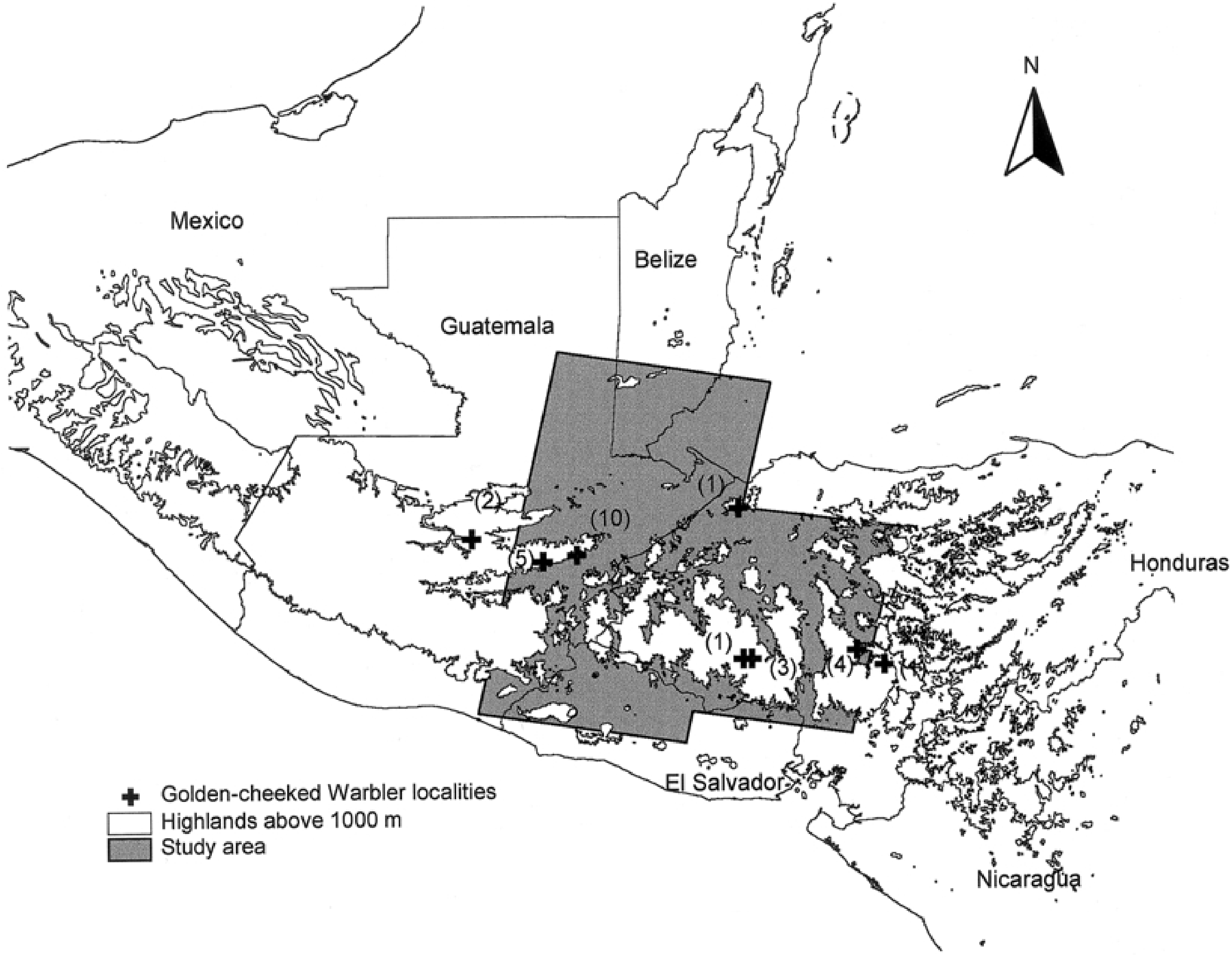

Fig. 1. Highlands (>914 m elevation) of Central America and locations for previously collected or sighted specimens of golden-cheeked warblers. The grey polygon delineates the area covered by Landsat TM imagery and used for landcover mapping in this study.

endangered and declining species, to estimate and map the extent of these habitats, or to determine what factors, if any, pose threats to the golden-cheeked warbler population during the wintering period.

Landsat Thematic Mapper (TM) imagery has been used with success in recent efforts for vegetation and landcover mapping (Lillesand & Kiefer, 1994) and for assessing deforestation rates in tropical rain forests (Sader & Joyce, 1988; Dirzo & Garcia, 1992; Skole & Tucker, 1993; Rignot, Salas & Skole, 1997). In this study, we use these techniques along with intensive field surveys to make a first step toward addressing the tropical winter distribution of the golden-cheeked warbler. Our specific objectives were as follows: (1) to obtain all available published information on specimens and sightings of the golden-cheeked warbler on its wintering grounds, (2) to select a significant portion of the species' winter range in Honduras and Guatemala for field work incorporating remote sensing (RS) and ancillary data into a geographic information system (GIS), and to conduct field investigations to identify and prioritize the principal winter habitats for the golden-cheeked warbler, (3) to obtain precise areal coverage and map the extent of these habitats, (4) to examine what factors, if any, pose threats to the golden-cheeked warbler population during the wintering period within this region, (5) to lay the groundwork for expansion of these techniques to map the preferred habitat for the species' entire winter range.

METHODS

Study area

We chose to focus our work on the central and western highlands of Honduras and the eastern highlands of Guatemala, an area which covers approximately 84 237 km^2, and includes 24 of the 28 previously-documented localities for golden-cheeked warbler specimens and sightings in Honduras and Guatemala (Fig. 1, Appendix I). For field surveys and habitat mapping, we used three satellite images, each depicting an area roughly 180 km square, covering most of the highlands in this region (Fig. 1). Forest in the highlands of our study area is dominated by pine, pine-oak, broadleaf and cloud forest (Monroe, 1968). Other major habitat types in the highlands are pasture, agricultural fields (e.g. sun coffee, beans, corn), tree crops (e.g. bananas, shade coffee, citrus) and various early successional stages of forest re-growth.

Field studies

We gathered data on golden-cheeked warbler occurrence and habitat use during two field seasons in Honduras (1 December 1995–1 February 1996; 10 January–15 February 1997) and one field season in Guatemala (10 January–26 February 1998). We also visited San Cristobal de las Casas in the Mexican State of Chiapas (26 February–3 March 1998). Because of the large extent of the region to be surveyed, the evident scarcity of our focal species, and the fact that most previously-published winter records for the species were recorded in pine-oak woodlands above 1000 m (Appendix I), we restricted our surveys mostly to this habitat type (935 out of 1363 observer-hours (o-hs), where 1 o-h = one skilled observer searching for golden-cheeked warblers for 1 h); 174 o-hs were spent in broadleaf forest (cloud forest, rain forest, second growth); 168 o-hs in pine forests with skimpy oak mid- and understory; 9 o-hs in mixed pine and roble (broadleaved) oak; and 77 o-hs in various agricultural and scrub habitats. These observer-hour figures are estimates based on field notes to provide a sense of the amount of time spent surveying major habitat types in the region. We used topographic maps, digital elevation information (*Digital charts of the world*, ESRI, 1993), aerial photographs, satellite imagery and personal contacts to identify forested areas above 1000 m for field surveys.

At survey points, observers walked through forested habitats searching visually for individual golden-cheeked warblers (vocalizations by the species are infrequent), and listening for vocal members of the mixed-species flocks frequented by goldencheeks. Examples of these vocal species include greater pewee (*Contopus pertinax*), dusky-capped flycatcher (*Myiarchus tuberculifer*) and slate-throated redstart (*Myioborus miniatus*). When a flock was located, the observer stayed with it until either a goldencheek had been sighted or the observer determined that no goldencheek accompanied the flock. Average time required to determine presence/absence of a goldencheek in a mixed-species flock was about 2 h. It is likely that we failed to discover the presence of goldencheeks in some flocks in which they did, in fact, occur. However, we believe that this was a rare occurrence because of the distinctive foraging behaviour and microhabitat use characteristics of the species (Rappole, King & Barrow, in press). For the same reason, we feel that our ability to detect goldencheeks was not biased by differences in habitat type, flock size, or flock movement rate.

Once a goldencheek was observed, the tree in which the bird was first sighted was marked using flagging, and a precise geographical location and altitude of the sighting was determined using a global positioning system (GPS). Where possible, this position was later corrected using base-station data. Positions for which we lacked base-station corrections were calculated based on an average of 100 points. We believe that each sighting represented a separate individual because sightings were far enough apart (generally >300 m) that, given the observed speed of goldencheek movements in flocks, double-counting of the same individual was highly unlikely.

Vegetation data were recorded at each point where a goldencheek was first sighted for most Honduras birds using 0.04-ha plots centred on the tree in which the bird was first sighted (James & Shugart, 1970). Parameters recorded for each plot were as follows: canopy height, number and size (diameter at breast height (dbh)) of trees by species, shrub density, canopy cover and ground cover. In addition, these same vegetation parameters were sampled on plots located at a random direction and distance (50–500 m) from points at which goldencheeks were sighted. The random direction and distance were obtained by entering a random numbers table using the first (direction) and second (distance) three digits of the position's map coordinates to enter the table. Because the data were not normally distributed, the Wilcoxon 2-sample test (normal approximation with continuity correction of 0.5) was used to compare data from the plots on which goldencheeks were observed using randomly-located plots. To reduce Type I error in our analysis of differences among sites, the significance levels were determined using the Bonferroni adjustment: with an *a priori* alpha level of 0.1 and seven statistical tests, only alpha levels ≤ 0.015 were considered significant. The distribution of each variable was evaluated for normality using the Shapiro–Wilk test (SAS Institute, 1989).

Mapping of forest habitats

We mapped highland forest types in Central America using two sets of multispectral Landsat TM 5 images obtained from the United States Geological Service, Earth Resources Observation Satellite (USGS EROS) data centre. The first set consisted of an image that covered the central and western highlands of Honduras (recorded 27 July 1994). The second set consisted of two images that covered the eastern highlands of Guatemala (recorded 17 March 1996) combined into a single image by the USGS EROS data centre. Our main concern in the selection of images was to minimize cloud coverage – a common problem that obstructs the production of landcover maps in humid and tropical regions (Rignot *et al*., 1997). Images were purchased after being geometrically corrected, projected on to a universal transverse mercator (UTM) projection grid, and resampled using a nearest neighbour algorithm by the image provider. Spatial resolution, the size of the picture elements (pixels), was 29 m × 29 m.

For our habitat mapping, we were interested in an accurate delineation of actual and potential habitat for goldencheeks. Because data collected by previous studies showed that goldencheeks are restricted to high elevation areas on the wintering grounds (Pulich, 1976), we excluded all areas below 914 m (3000 feet) elevation from our images, using elevation data from the *Digital charts of the world* (DCW) data set (ESRI, 1993). The total area above 914 m on our three images was 24 734 km^2, or about 29 % of the total area covered by the satellite images. This approach allowed us to concentrate on differentiating forest habitats in the highlands. Our hierarchical classification system focused on broad landcover categories with special emphasis on forest types (Table 1). Cloud forest was included with other types of broadleaf forest in a single category because variation in spectral values caused by topographic effects made the differentiation between these types difficult.

Table 1. Classification system used in remote sensing analyses of Landsat TM images

Level I	Level II
Forest	Broadleaf forest
	Pine-oak forest
	Pine forest
	Early-successional forest
	Savanna
Shrubland	Dry scrub
Non-forest	Pasture
	Agriculture
	Developed/bare

The images were classified separately using unsupervised classification techniques (ERDAS, 1997). We employed the ISODATA clustering algorithms on bands 3, 4 and 5 of the Landsat TM images to produce 60 spectral clusters in the initial classification (ERDAS, 1997). Each of the 60 clusters was assigned to a landcover category of level I in the classification system (Table 1). Assignment was based on the investigators' knowledge of the vegetation in the study region, ground-truth information collected at random points during the field seasons of 1996/97 and 1997/98, and aerial photography. To improve our differentiation of forest types, we used the initial classification to determine all areas that were forested in the original multispectral satellite images. We reclassified the spectral data for bands 3,4 and 5 for these forested areas into 60 spectral clusters. Each of the final 60 clusters was assigned to one of the five level II forest classes. Similar procedures were used to separate pastures from other agricultural landcover (e.g. crops and ploughed fields). After the images had been classified, we combined them into a single landcover map (ERDAS, 1997). To remove pixel variation representing noise in the landcover map, we applied a majority filter within a moving window, 7 × 7 pixels in size (ERDAS, 1997).

During field visits in 1996, 1997 and 1998, we collected ground-truth information at 442 reference points to evaluate the accuracy of our final landcover map. Each reference point was assigned to a landcover class according to our classification scheme (Table 1). We used a GPS, corrected with base-station data wherever possible, to determine location for all reference points. Assessment of the accuracy of our landcover map was based on the percentage of reference points in all landcover categories that were correctly classified. We also calculated an error matrix with user's and producer's accuracies for all forest types. User's accuracies are the percentage of pixels in a landcover category that belonged to that category during ground-truthing. Producer's accuracies are the percentage of reference points in a landcover category that belonged to the same landcover category on the map.

To determine habitat preference for the golden-cheeked warbler on a landscape scale and to test whether this preference differs from what would be expected by chance alone, we determined the landcover type that was most common in a 9 × 9 pixel window centred on each goldencheek locality. We used a random number generator to create 1000 random points on our landcover map located above 1100 m, and determined the most common landcover type in a 9 × 9 pixel window for the random points. To establish whether or not the percentage of goldencheek localities that were in pine-oak dominated landscapes differed from the percentage of random points in the same habitat type, we used a Chi-square test.

RESULTS

Observations of the golden-cheeked warbler in Honduras

A total of 148 golden-cheeked warbler sightings were recorded over the course of this study during 1363 o-hs in five habitat types (Table 2). We believe that each sighting represents a separate individual for the reasons described in the Methods, above. These birds were found at 126 distinct sites, where a 'distinct site' is defined as a site located a minimum of 200 m from any previous sighting (Appendix II), an interval defined on the basis of our estimate of the probable amount of distance separating individual mixed-species flocks. On 15 occasions, more than one goldencheek was recorded in the same mixed-species flock. Most of the sites were found in regional localities, where a 'regional locality' is defined as a geographical location containing one or more golden-cheeked warbler localities within a radius of 10 km (Appendix II). This number was chosen to reflect the fact that most sightings for the species occurred in regional habitat clumps covering several square kilometers.

Habitat use

As reported by previous workers in Honduras and elsewhere (Monroe, 1968; Pulich, 1976; Thompson, 1995), we found that golden-cheeked warblers frequented pine-oak habitat above 1100 m in elevation (Table 2, Appendix II). Golden-cheeked warblers were non-randomly distributed among habitat types ($\chi^2 = 30.70$, d.f. = 4, $P < 0.001$), and were significantly more

Table 2. Search effort for golden-cheeked warblers (GCW) by habitat

Habitat	Observer hours	GCW Observed	GCW Expected	χ^2	d.f.
Pine–encino	935	115	86.2	9.60[a]	1
Pine–roble	9	0	0.8	0.83	1
Pine	168	5	15.5	7.09[a]	1
Broad-leaved forest	174	5	16.1	7.63[a]	1
Agriculture/scrub	77	1	7.1	5.26[a]	1
Total	1363	126[c]	126.0	30.70	

[a]$P<0.01$
[b]$P<0.05$
[c]Number of distinct localities at which golden-cheeked warblers were actually observed during this study.

abundant in pine-oak forest than expected (Table 2). In contrast, the birds were less abundant in pine forest, broad-leaved forest and agricultural and scrub habitats than expected (Table 2). The mean elevation at which birds were found in this study was 1651 (± 246) m. The lowest elevation at which we located a goldencheek was 1100 m near Gualaco in Olancho State, however goldencheeks were significantly less abundant below 1300 m than expected by chance (χ^2 = 5.16, d.f. = 1, P < 0.016). The highest elevation at which we found the bird was 2400 m, just outside the town of Guayjiquiro in south-western Honduras. The highest elevation at which a goldencheek has been previously recorded is 2550 m (Vidal *et al*., 1994).

Vegetation data were collected at 91 plots centred on trees in which goldencheeks were observed and at 184 randomly-located plots (Table 3). The dominant pine species at both goldencheek 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 (e.g. *Q. sapotifolia, Q. eliptica, Q. elongata, Q. cortesii*), species with shiny narrow, elliptical, or oblong leaves, and (2) 'roble' oaks (*Q. segoviensis, Q. purulhana, Q. rugosa*), species with large, lobed leaves. Note that, despite the fact that the random points were located basically within the same habitat type as points where the bird was discovered, they differed significantly in the number of pines (random points had nearly double the number of pines as sighting points) and in the number of encino oaks (sighting points had nearly double the number of encinos as random points: Table 3).

For a sample of 46 goldencheeks, 44 (96%) were first recorded in one of the encino species, despite the fact that only 37% of trees on goldencheek vegetation plots were encino, a proportion significantly greater than expected by chance (χ^2 = 35.5, d.f. = 1, P < 0.001). For the other members of this sample, one individual was first sighted in roble (*Q. segoviensis*), and one in *Clethra macrophylla*, a narrow-leaved tree somewhat similar in basic morphology to encino oaks. Other common, broad-leaved tree species in the habitat frequented by goldencheeks included *Liquidambar styraciflua*, *Myrica cerifera, Oreopanax* spp. and *Olmediella betschleriana*; common understory species included *Cuphea* spp., *Calliandra houstoniana*, *Heterocentron subtriplineriums* and *Stevia* spp. Encino oaks were significantly more frequent on sites where goldencheeks were recorded while pines were significantly less frequent on these sites than on the random sites (Table 3). This habitat is 'humid lower montane oak pine forest' as described by Holdridge (1962) and House (1996).

Landcover mapping

We produced a landcover map using unsupervised classification of Landsat TM imagery (Fig. 2). Pine-oak forest was the most important landcover category followed closely by pine forest and early-successional forest (Table 4). We used extensive ground-truthing, and found that we were able to distinguish forested from non-forested areas with an accuracy of 89%. Our accuracy in identifying pine-oak forest (i.e. habitat in which *both* pine and oak occur as dominant tree species in the canopy) from all other landcover types was 84%. Overall accuracy for all landcover types is 72% (Table 5). User's and producer's accuracies indicate that our landcover map is accurate in delineating broadleaf and pine-oak forest categories. Pine forest is often confused with pine-oak forest and has low producer's accuracies. This result can be explained by the variation in spectral reflectance that is caused by the extreme topography of the study region. However, pine forest is rarely classified into the early-successional or non-forest categories, which means

Table 3. Comparison of vegetation attributes between 'observed' (O, n = 91) and 'random' (R, n = 184) sites for golden-cheeked warbler

Variable	Site	$\bar{x} \pm SE$	Z^a	P
Pine trees per site (> 3 cm dbh)	O	8.5 ± 0.9	–3.25	0.001
	R	16.4 ± 1.6		
Encino trees per site (> 3 cm dbh)	O	11.1 ± 1.1	3.77	<0.001022
	R	6.2 ± 1.6		
Woody stems per site (≤ 3 cm dbh)	O	181 ± 20.3	2.45	0.014
	R	179 ± 24.0		
% vegetation cover (ground)	O	42.0 ± 2.5	4.46	<0.001
	R	40.9 ± 3.3		
% vegetation cover canopy (> 10 m)	O	67.7 ± 2.2	–2.07	0.038
	R	61.8 ± 3.6		

[a]Wilcoxon 2-sample test (normal approximation with continuity correction of 0.5).
dbh, diameter at breast height.

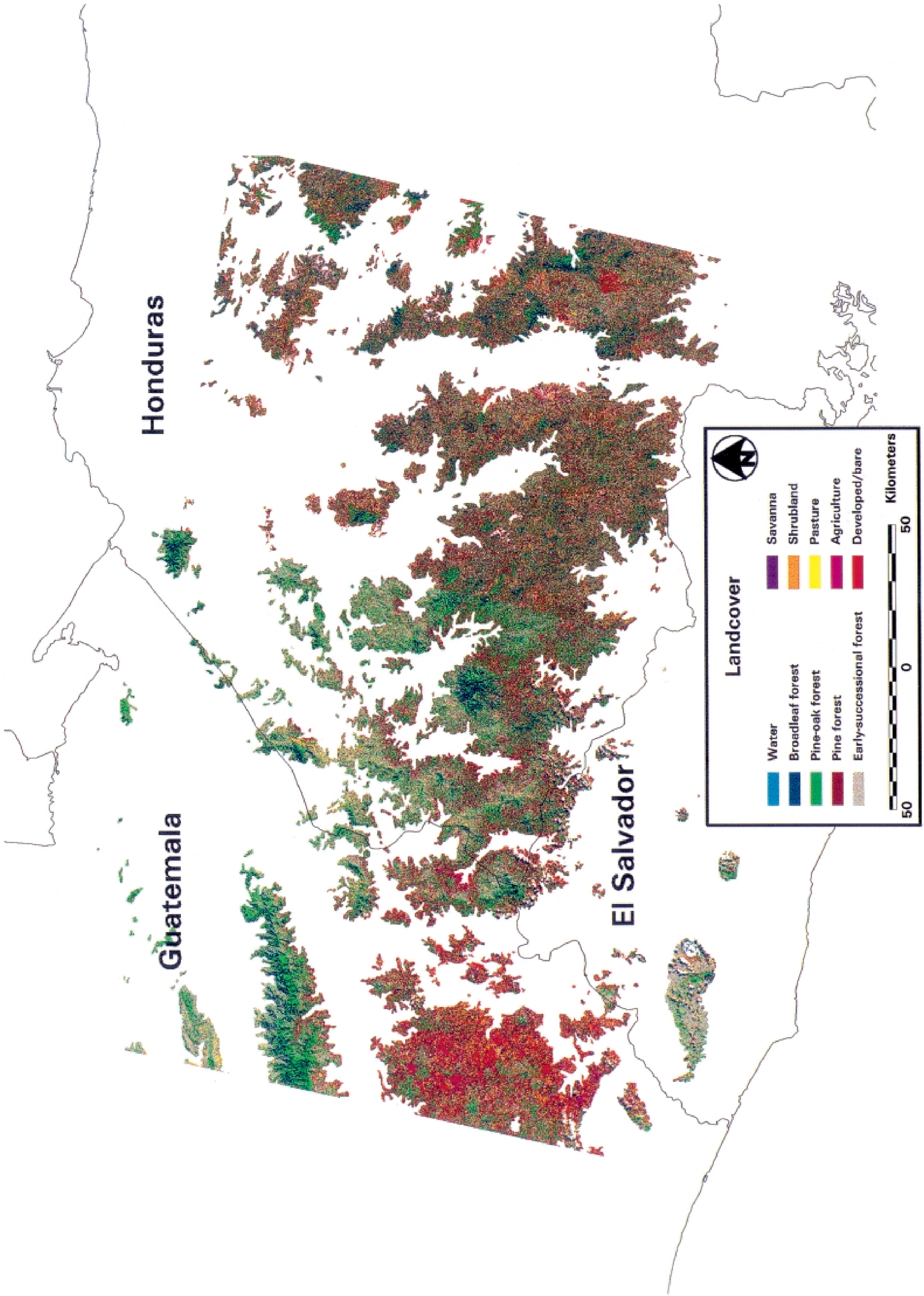

Fig. 2. Landcover map delineating all landcover categories above 914 m elevation.

Table 4. Landcover above 1000 m elevation within the study region as determined from remote sensing analyses using Landsat TM images

Landcover category	Area (km^2)	Total percentage
Broadleaf forest	1935	7.8
Pine-oak forest	7370	29.8
Pine forest	5182	21.0
Early-successional forest	4016	16.2
Savanna	1635	6.6
Scrubland	1171	4.7
Pasture	1531	6.2
Agriculture	709	2.9
Developed/bare	1185	4.8
Total	**24734**	**100.0**

that the area covered by pine forest is probably underestimated and some of these habitat types are inflating the values for pine-oak forest. Early-successional forest is frequently confused with agricultural areas mainly because sun-coffee, banana plantations and similar crops cannot be distinguished accurately from early-successional forests using spectral reflectance data alone. On the landscape scale, goldencheeks were found significantly more often in areas dominated by pine-oak than would be expected by chance alone ($\chi^2 = 22.75$, d.f. = 1, $P < 0.001$).

DISCUSSION

Winter habitat use

The principal winter habitat in which we found golden-cheeked warblers was open pine-oak (Table 2, Fig. 3) in which the dominant canopy tree species was *Pinus oocarpa,* although several other species of pine occurred with varying frequency. The principal mid-story tree species was one or more of a group of elliptical-leaved oak species known collectively as 'encino' oaks (e.g. *Quercus eliptica*, *Q. sapotifolia, Q. elongata, Q. cortesii*). Presence or absence of oaks with broad, toothed, rough leaves ('roble' oaks e.g. *Q. segoviensis*) did not appear to affect warbler use, nor did any particular aspect of the understory, which was quite variable depending on slope, aspect and human land use patterns in the area. On south facing slopes in areas that were ungrazed and unburned, the understory was often extraordinarily dense, with heavy growths of bracken fern (*Pteridium*) and other shrub species to a height of 2–3 m. On burned or grazed areas, the understory could be quite sparse.

Golden-cheeked warblers were scarce or absent in areas where pines formed a nearly closed canopy and encino oaks were sparse, e.g. the eastern Honduran State of Olancho. We observed only five birds during roughly 120 o-hs of work in this region. Vegetation analyses were performed on 25 plots in this area, and these sites were found to have significantly fewer encino oaks per plot (0.76) than either the sites on which goldencheeks were observed (11.06) or random plots (6.19) from elsewhere in Honduras.

Vidal *et al*. (1994) reported 47 observations of golden-cheeked warblers (probably representing 33 individuals) from the San Cristobal de las Casas region of Mexico in the following habitats: pine-oak, 18 (38%); oak, 9 (19%); pine, 6 (13%); cloud forest, 3 (7%); early-successional, 1 (2%); 'mixed' (a combination of pieces of three or more of the previously-mentioned habitats), 10 (21%). We did not find evidence for this breadth of habitat use during our field work in San Cristobal or elsewhere within the species' winter range. The three birds recorded during our surveys in San Cristobal were all in pine-oak. In fact, although we spent time in other habitats in Mexico, Guatemala and Honduras, we found few birds in habitats other than pine-oak. Despite the presence of mixed-species flocks and encino-type oaks (e.g. *Q. cortesii*) in cloud forest, we located only five goldencheeks during roughly 174 o-hs of search in highland broadleaf habitats. Therefore, we conclude that this habitat is of minor importance for the species. Similarly, we also found goldencheeks to be rare in agricultural and scrub habitats.

One explanation for the breadth of habitat use found by Vidal *et al*. (1994), as opposed to the highly-selective pattern seen in our study, could be that nearly half their sample is based on birds that are possible transients (i.e., 42% of their observations were made in August, September, March and April) with the less rigid habitat requirements characteristic of birds in transit. Further studies, preferably including banded birds, will be needed to clarify this point.

Winter distribution of the golden-cheeked warbler

In Fig. 4, we provide a map of the winter range of the golden-cheeked warbler in Middle America. This map

Table 5. Matrix of classification errors for forest categories mapped using Landsat TM imagery

Landcover category on ground	Landcover category on map						
	Broadleaf	Pine-oak	Pine	Early-successional	Other	Total	User's accuracy (%)
Broadleaf	52	9	9	5	4	79	65.8
Pine-oak	10	167	19	6	13	215	77.7
Pine	3	5	16	2	–	26	61.5
Early-successional	1	4	5	34	–	44	77.3
Other	2	3	2	21	50	78	64.1
Total	68	188	51	68	67	442	–
Producer's accuracy (%)	76.5	88.8	31.4	50	83.3	–	72.2

Diagonal elements give the number of correctly classified pixels.

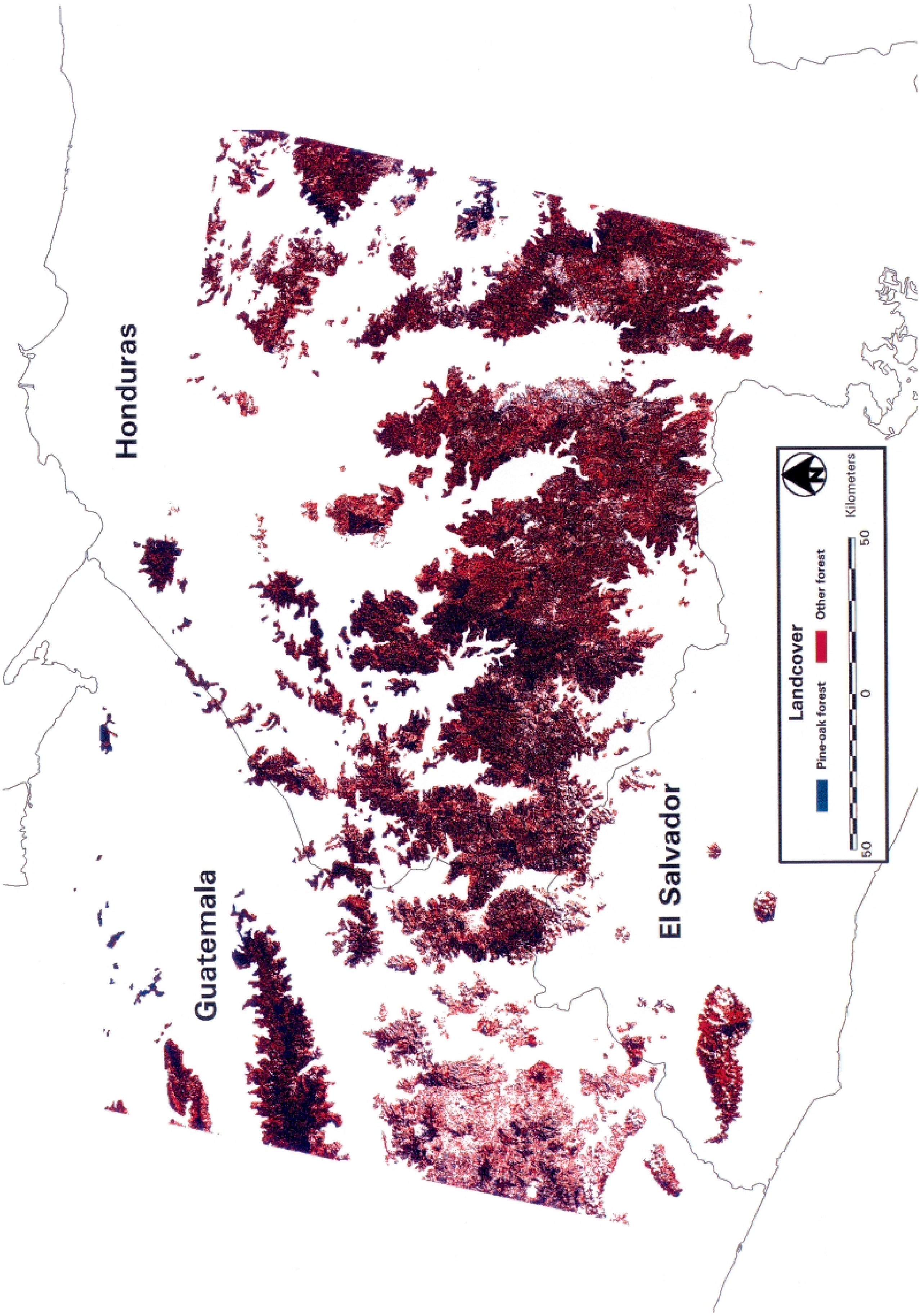

Fig. 3. Pine-oak versus other forest habitats above 914 m in the study region.

should be considered as a working hypothesis because not all parts of the range have been investigated. Below, we discuss what is known about the winter range on a country-by-country basis.

Guatemala

Prior to the present study, more records of wintering (October–February) golden-cheeked warblers had been recorded in Guatemala than in any other country. However, almost all of the sightings and specimens came from the southern slopes of a single mountain range, the Sierra de las Minas (Land, 1962; Pulich, 1976; Thompson, 1995). Our field surveys in Guatemala produced similar results. Although we searched extensively for the bird at highland sites away from the Sierra de las Minas, we found few localities for the species outside the Sierra de Las Minas region in Guatemala. A partial explanation is that there is little pine-oak habitat left in highlands south of the Sierra, where climatic conditions appear to be otherwise suitable for pine-oak. In areas west and north of the Sierra, conditions appeared to be either too dry or too wet to support 'humid lower montane oak pine forest' habitat. East of the Sierra is mostly lowlands.

Honduras

Honduras appears to be the heart of the winter range for the golden-cheeked warbler, on the basis of our field work, as well as previous work reported by Monroe (1968) and Thompson (1995). We found several regional localities where the species occurred in Honduras, areas where significant patches of pine-oak habitat remained, and in which flocks frequented by goldencheeks were common. Most of these areas were located in a belt roughly 100 km in width, stretching east to Tegucigalpa and west to the El Salvadoran and Guatemalan borders. This belt conforms closely with that defined by Holdridge for the distribution of 'humid lower montane oak pine forest' (Holdridge, 1962; House, 1996), the habitat type in which we found the bird most commonly. We did find five birds east of Tegucigalpa near Gualaco and La Union in Olancho State. However, the species was scarce, and the habitat sparse in encino oaks. We also found one bird in the wet pine-oak forest near San Pedro Sula in north-western Honduras, as did Thompson (1995). We consider this area to be a low density portion of the winter range for the species because we were unable to locate other individuals despite surveys over several days.

El Salvador

El Salvador has not been included in previous published descriptions of the winter range for the golden-cheeked warbler, but on the basis of our field work in regions bordering this country in Honduras, it seems probable that the few areas of pine-oak habitat that remain along the Salvadoran border with Honduras support small numbers of goldencheeks. These habitats are continuous with similar habitats in Honduras where we were able to find the bird (e.g. Sabanitas, Honduras).

Mexico

Vidal *et al*. (1994) summarize information on probable wintering (October–February) golden-cheeked warblers in Chiapas, raising questions regarding possible recent changes in the species' distribution. Their work confirms earlier reports of winter records for this species in the region (Braun *et al*., 1986; Martin, 1993; Lyons, 1994). Furthermore, there are 57 additional sight records for the species contained in the 'Fauna de Chiapas' database, and our party observed three birds during a visit to Mexico in February–March of 1998. Most of these records come from within a radius of 20 km of the city of San Cristobal de las Casas, Chiapas. Nevertheless, the distance between San Cristobal and the nearest confirmed Guatemalan records (Tactic) is 300 km, and a significant portion of this area is above 1000 m in elevation. At present, this area has not been surveyed adequately for goldencheeks, and we do not know whether the San Cristobal birds are a disjunct wintering population or part of a continuous winter range following the spine of the Sierra Madre.

Pulich (1976) examined available data on golden-cheeked warblers in Mexico, and found no reliable winter records for the bird. Furthermore, he and Allan Phillips visited reported Mexican winter localities for the species from 26 December 1960–4 January 1961, collecting any individuals that were questionable in terms of identification. They were unable to find any goldencheeks in this region, the same region from which Vidal *et al*. (1994) and others now report the bird. The fact that there were no winter sight or specimen records for the golden-cheeked warbler in Chiapas prior to 1978, and that there have been several sight records recorded for this period since is an interesting point. The implication in Vidal *et al*. (1994) is that Pulich, Phillips and other ornithologists visiting the highlands of Chiapas during the century of active ornithological work in the region that took place prior to 1978 simply missed the bird. However, there is an alternative explanation, namely that Chiapas was not previously part of the normal winter range for the species. Rappole and McDonald (1994) have proposed that species of migrants whose populations are limited on the wintering ground should have the following characteristics:

1. Marginal winter habitat should be occupied due to intense competition for optimal winter habitat.
2. Apparently suitable but marginal breeding habitat should be abandoned due to lack of competition for optimal breeding sites.

Based on these predictions, if golden-cheeked warblers have become limited by winter habitat availability in the past four decades, we would expect individuals of the species to have expanded their use of marginal

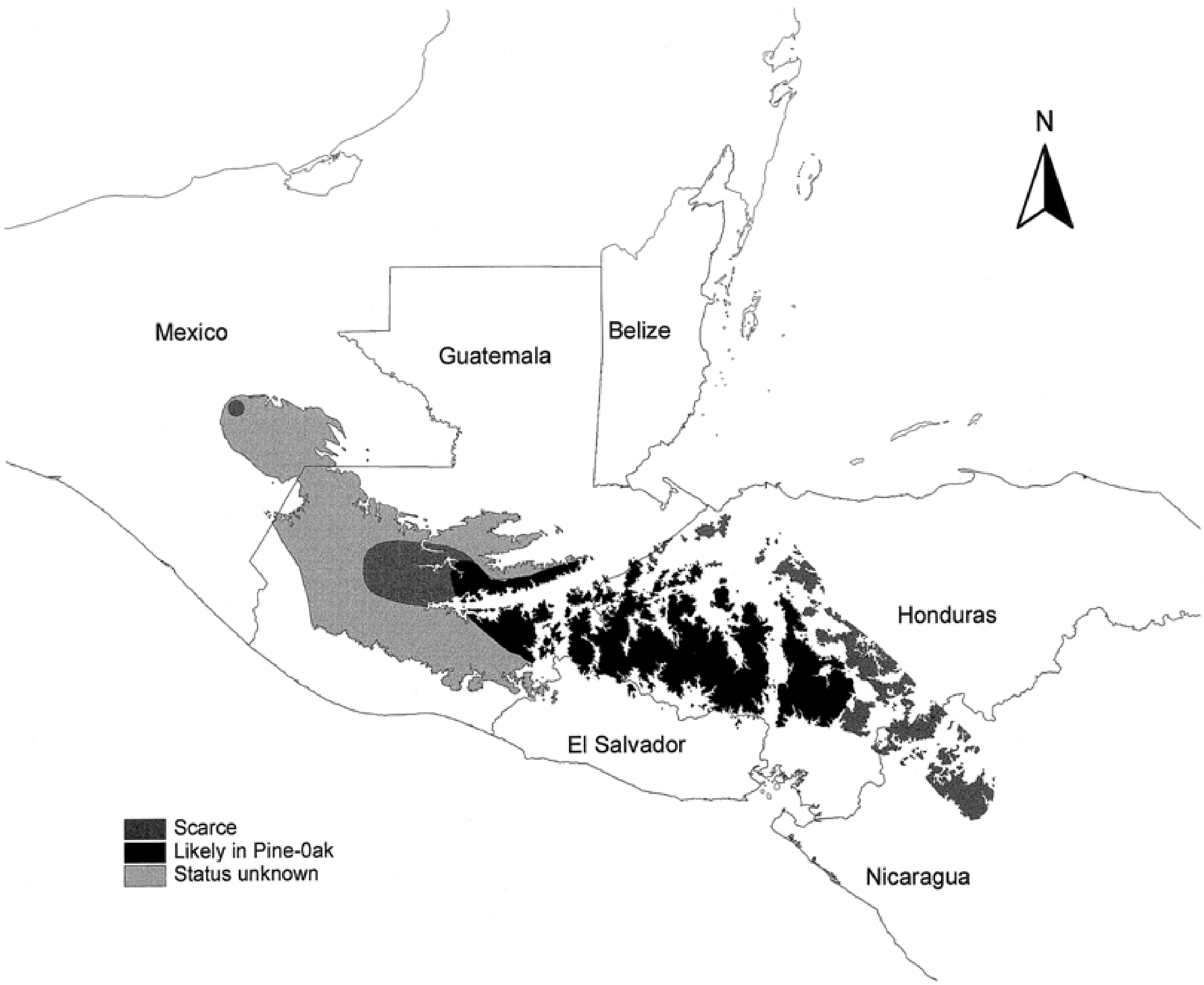

Fig. 4. Map of the winter range of the golden-cheeked warbler in Middle America. 'Likely' is defined as a > 50% probability of locating one or more individuals/10 hours of field survey in appropriate habitat. 'Scarce' is defined as <50% probability of locating one individual/10 hours of field survey in appropriate habitat.

winter habitats, and, perhaps, the species' winter range, which could explain its appearance as a wintering species in the highlands of Chiapas. A criticism of this explanation might be that it is more logical for birds in search of suitable, but marginal, habitat to expand into neighbouring pine, scrub and broadleaf habitats than to expand their actual range. Such use of marginal winter habitats may, in fact, be what Vidal *et al*. (1994) observed in their study. A second possibility is that it appears from our data that there are two critical factors determining the presence of golden-cheeked warblers in a particular winter habitat: encino oaks and mixed species flocks (Rappole, King *et al*., in press). At sites where either of these factors is missing, the bird is not likely to be present.

If golden-cheeked warblers are limited by the availability of suitable winter habitat, this situation could explain why it is that there are areas of apparently suitable breeding habitat in Texas that are not occupied by breeding pairs (Beardmore *et al*., 1996:7).

Nicaragua

The south-eastern end of the winter range has always been considered to be northern Nicaragua, based on the two specimens taken in September, 1890 near Matagalpa. We have spent significant time (120 o-hs) in the field in the south-eastern portion of the range in Honduras, and although we were able to find a few goldencheeks (five birds) in pine-dominated habitat with oak understory, the density was far lower than what was found further west. We have not been as far east and south as Nicaragua, but it seems likely that this region, like that of eastern Honduras, is in the low-density portion of the winter range for the species.

Breeding versus wintering ground control of golden-cheeked warbler populations

Past studies of the golden-cheeked warbler have concluded that populations were threatened by factors occurring on the breeding ground (Keddy-Hector & Beardmore, 1992; Beardmore *et al*., 1996), where indeed, there have been significant changes. However, it appears that the principal winter habitat is more restricted in distribution than had heretofore been understood. The current winter range of the golden-cheeked warbler extends from San Cristobal de las Casas in southern Mexico to (possibly) Matagalpa in Nicaragua; a distance of over 800 km. This long distance, including parts of four countries, should seemingly provide a sufficient amount of winter habitat for the relatively low number of birds that make up the world population of the golden-cheeked warbler. However, four factors appear to limit the bird's distribution within this vast area: (1) it is restricted to highlands above 1100 m, (2) it is found principally in pine-oak forest with extensive encino oak mid-story, (3) it is restricted to a relatively narrow latitudinal zone (dictated by a combination of climate and elevation that determine habitat), (4) it occurs principally in mixed-species foraging flocks (Braun *et al*., 1986; Vidal *et al*., 1994; Thompson, 1995; J. H. Rappole & D. I. King, pers. obs). Using a combination of intensive field sampling and remote sensing, we have been able to identify and map the principal habitat, and we calculate that the total amount is about 7370 km^2. This total seems as though it should be sufficient to support the 10 000–20 000 birds estimated to comprise the breeding population. However, consider that only a small percentage, less than one-third of the random vegetation plots taken *within* pine-oak habitat, possessed encino oak, pine, ground cover and canopy cover distributions comparable to sites at which the bird was found. Pine-oak habitat above 1100 m can be considered as a minimal requirement for the bird. Specific distribution of these vegetation parameters appears to be the critical determinant of the species' presence or absence, and only a limited, and as yet undetermined, amount of available pine-oak evidently meets these criteria. Threats to Middle American pine-oak habitat are similar to those confronting other forested habitats in the region: logging, burning and clearing for agriculture, pasture and silviculture. As this study shows, there are few significant stands of this habitat remaining in Middle America, and fewer still that can support wintering populations of golden-cheeked warblers.

CONCLUSIONS

1. Golden-cheeked warbler winter habitat can be accurately identified using a combination of satellite imagery, topographic data, warbler sightings and vegetation information gathered in the field.
2. The amount and quality of remaining golden-cheeked warbler winter habitat is less than the 800-km length of the winter range would indicate. Warbler winter distribution appears to be restricted to a relatively small number of localities in Honduras, Guatemala, Mexico and, perhaps, El Salvador. Most records for the species fall within a latitudinal gradient of less than 100 km from north to south, and 95.6% of records fall within an elevational range of 1300m to 2400m.
3. Warbler populations may be limited by the availability of high quality pine-oak winter habitat located in appropriate elevational and latitudinal range.

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Appendix I. Locality data collected prior to this study for known sight and specimen records of the golden-cheeked warbler during the winter period (November–February) outside Mexico

Date	Latitude/Longitude		Locality	Elevation (m)
4 Nov 1859[a]	15°15'N	90°25'W	Tactic, Guatemala	1370
4 Nov 1859[a]	15°15'N	90°25'W	Tactic, Guatemala	1370
7 Dec 1931[a]	14°21'N	87°17'W	El Cantoral, Honduras	1700
10 Feb 1935[a]	14°21'N	87°17'W	El Cantoral, Honduras	1700
28 Nov 1936[a]	14°21'N	87°17'W	El Cantoral, Honduras	1700
9 Dec 1936[a]	14°21'N	87°17'W	El Cantoral, Honduras	1700
5 Dec 1958[a]	15°02'N	89°50'W	Usumatlan, Guatemala	1800
15 Dec 1958[a]	15°03'N	89°51'W	Usumatlan, Guatemala	1800
22 Dec 1958[a]	15°03'N	89°51'W	Usumatlan, Guatemala	2560
22 Jan 1963[a]	14°17'N	88°07'W	La Esperanza, Honduras	1800
23 Jan 1963[a]	14°17'N,	88°07'W	La Esperanza, Honduras	1800
24 Jan 1963[a]	14°17'N,	88°07'W	La Esperanza, Honduras	1800
8 Jan 1995[b]	15°06'N,	89°40'W	San Lorenzo, Guatemala	1880
8 Jan 1995[b]	15°05N,	89°40'W	San Lorenzo, Guatemala	1860
8 Jan 1995[b]	15°05'N,	89°40'W	San Lorenzo, Guatemala	1860
8 Jan 1995[b]	15°06'N,	89°40'W	San Lorenzo, Guatemala	2010
9 Jan 1995[b]	15°05'N,	89°41'W	San Lorenzo, Guatemala	1785
10 Jan 1995[b]	15°05'N,	89°39'W	San Lorenzo, Guatemala	1575
11 Jan 1995[b]	15°06'N,	89°40'W	San Lorenzo, Guatemala	2000
14 Jan 1995[b]	15°08'N,	89°31'W	Jones, Guatemala	1400
15 Jan 1995[b]	15°06'N,	89°36'W	Jones, Guatemala	1425
22 Jan 1995[b]	15°'15'N,	90°25'W	Tactic, Guatemala	1860
22 Jan 1995[b]	15°15'N,	90°25'W	Tactic, Guatemala	1860
1 Feb 1995[b]	14°17'N,	88°11'W	La Esperanza, Honduras	1815
12 Feb 1995[b]	15°29'N,	88°13'W	Cusuco, Honduras	1630

[a]Pulich, 1976. Records in bold type are specimens.
[b]Thompson, 1995.

Appendix II. Locality data collected during this study for wintering golden-cheeked warblers in Honduras and Guatemala.

Date	Latitude/Longitude[a]		Locality[b]	Elevation (m)[c]
2 Dec 95	14°19.44'N,	87°18.21'W	El Cantoral, Honduras	1600
2 Dec 95	14°19.44'N,	87°18.21'W	El Cantoral, Honduras	1600
2 Dec 95	14°19.44'N,	87°18.21'W	El Cantoral, Honduras	1600
2 Dec 95	14°19.40'N,	87°18.32'W	El Cantoral, Honduras	1600
3 Dec 95	14°19.39'N,	87°18.53'W	El Cantoral, Honduras	1400
3 Dec 95	14°19.29'N,	87°18.20'W	El Cantoral, Honduras	?
5 Dec 95	14°19.62'N,	87°18.28'W	El Cantoral, Honduras	1700
5 Dec 95	14°19.62'N,	87°18.28'W	El Cantoral, Honduras	1700
5 Dec 95	14°19.53'N,	87°18.35'W	El Cantoral, Honduras	?
5 Dec 95	14°19.24'N,	87°18.35'W	El Cantoral, Honduras	?
6 Dec 95	14°19.44'N,	87°16.94'W	El Cantoral, Honduras	1200
6 Dec 95	14°19.48'N,	87°16.94'W	El Cantoral, Honduras	1400
6 Dec 95	14°19.51'N,	87°17.48'W	El Cantoral, Honduras	1500
6 Dec 95	14°19.53'N,	87°17.74'W	El Cantoral, Honduras	1700
7 Dec 95	14°19.42'N,	87°17.72'W	El Cantoral, Honduras	1400
7 Dec 95	14°19.40'N,	87°17.33'W	El Cantoral, Honduras	1400
7 Dec 95	14°19.40'N,	87°17.33'W	El Cantoral, Honduras	1400
7 Dec 95	14°19.40'N,	87°17.33'W	El Cantoral, Honduras	1400
7 Dec 95	14°19.80'N,	87°17.72'W	El Cantoral, Honduras	1400
9 Dec 95	14°15.90'N,	88°08.13'W	La Esperanza, Honduras	1800
9 Dec 95	14°15.96'N,	88°08.16'W	La Esperanza, Honduras	1900
9 Dec 95	14°16.29'N,	88°07.54'W	La Esperanza, Honduras	1700
10 Dec 95	14°16.30'N,	88°07.56'W	La Esperanza, Honduras	1600
12 Dec 95	15°29.42'N,	88°13.16'W	Cusuco, Honduras	1700
14 Dec 95	14°08.77'N,	87°49.26'W	Guayjiquiro, Honduras	2000
14 Dec 95	14°08.61'N,	87°50.61'W	Guayjiquiro, Honduras	2400
15 Dec 95	14°04.84'N,	87°26.72'W	Lepaterique, Honduras	1800
15 Dec 95	14°04.71'N,	87°27.01'W	Lepaterique, Honduras	1900
15 Dec 95	14°05.30'N,	87°26.78'W	Lepaterique, Honduras	1800
15 Dec 95	14°05.01'N,	87°26.82'W	Lepaterique, Honduras	2000
15 Dec 95	14°04.55'N,	87°26.78'W	Lepaterique, Honduras	1800
17 Dec 95	14°04.67'N,	87°25.77'W	Lepaterique, Honduras	1700
17 Dec 95	14°04.67'N,	87°25.77'W	Lepaterique, Honduras	1700
17 Dec 95	14°04.67'N,	87°25.77'W	Lepaterique, Honduras	1700
18 Dec 95	14°05.07'N,	87°26.06'W	Lepaterique, Honduras	1700
18 Dec 95	14°05.07'N,	87°26.06'W	Lepaterique, Honduras	1700
18 Dec 95	14°05.00'N,	87°25.96'W	Lepaterique, Honduras	1900

Appendix II. continued.

Date	Latitude/Longitude[a]		Locality[b]	Elevation (m)[c]
18 Dec 95	14°05.00'N,	87°25.96'W	Lepaterique, Honduras	1900
18 Dec 95	14°04.80'N,	87°25.88'W	Lepaterique, Honduras	1700
21 Dec 95	14°18.98'N,	87°17.32'W	El Cantoral, Honduras	1400
21 Dec 95	14°18.98'N,	87°17.32'W	El Cantoral, Honduras	1400
21 Dec 95	14°18.95'N,	87°17.17'W	El Cantoral, Honduras	1500
22 Dec 95	14°19.30'N,	87°18.34'W	El Cantoral, Honduras	1700
22 Dec 95	14°19.12'N,	87°18.09'W	El Cantoral, Honduras	1600
22 Dec 95	14°19.19'N,	87°17.40'W	El Cantoral, Honduras	1500
26 Dec 95	14°07.00'N,	87°23.69'W	Lepaterique, Honduras	1800
26 Dec 95	14°06.81'N,	87°24.26'W	Lepaterique, Honduras	1800
26 Dec 95	14°06.91'N,	87°23.94'W	Lepaterique, Honduras	1600
26 Dec 95	14°06.60'N,	87°24.12'W	Lepaterique, Honduras	1600
27 Dec 95	14°04.50'N,	87°25.00'W	Lepaterique, Honduras	1800
28 Dec 95	14°04.43'N,	87°25.92'W	Lepaterique, Honduras	1700
28 Dec 95	14°04.54'N,	87°25.92'W	Lepaterique, Honduras	1800
28 Dec 95	14°04.93'N,	87°26.78'W	Lepaterique, Honduras	1800
28 Dec 95	14°05.48'N,	87°28.43'W	La Esperanza, Honduras	1600
29 Dec 95	14°17.68'N,	88°11.94'W	La Esperanza, Honduras	1700
29 Dec 95	14°17.58'N,	88°11.78'W	La Esperanza, Honduras	1700
29 Dec 95	14°17.58'N,	88°11.78'W	La Esperanza, Honduras	1700
29 Dec 95	14°17.18'N,	88°11.47'W	La Esperanza, Honduras	1700
29 Dec 95	14°17.98'N,	88°11.07'W	La Esperanza, Honduras	1700
30 Dec 95	14°15.84'N,	88°11.65'W	La Esperanza, Honduras	1700
30 Dec 95	14°16.16'N,	88°12.30'W	La Esperanza, Honduras	1700
31 Dec 95	14°16.98'N,	88°12.05'W	La Esperanza, Honduras	1800
31 Dec 95	14°16.96'N,	88°12.52'W	La Esperanza, Honduras	2000
31 Dec 95	14°16.96'N,	88°12.52'W	La Esperanza, Honduras	2000
31 Dec 95	14°17.02'N,	88°12.16'W	La Esperanza, Honduras	1800
3 Jan 96	14°05.57'N,	87°28.41'W	Lepaterique, Honduras	1600
3 Jan 96	14°05.78'N,	87°28.39'W	Lepaterique, Honduras	1700
3 Jan 96	14°04.24'N,	87°25.97'W	Lepaterique, Honduras	1800
5 Jan 96	14°58.51'N,	86°00.49'W	Gualaco, Honduras	1100
6 Jan 96	14°58.56'N,	86°00.23'W	Gualaco, Honduras	1300
7 Jan 96	14°58.26'N,	86°01.51'W	Gualaco, Honduras	1400
7 Jan 96	14°58.05'N,	86°01.52'W	Gualaco, Honduras	1400
13 Jan 96	14°18.23'N,	88°11.18'W	La Esperanza, Honduras	1600
14 Jan 96	14°16.90'N,	88°10.13'W	La Esperanza, Honduras	1900
14 Jan 96	14°16.90'N,	88°10.13'W	La Esperanza, Honduras	1900
14 Jan 96	14°16'N,	88°10'W[d]	La Esperanza, Honduras	1700
18 Jan 96	14°18.65'N,	87°17.92'W	El Cantoral, Honduras	1300
18 Jan 96	14°18.43'N,	87°18.23'W	El Cantoral, Honduras	1400
18 Jan 96	14°18.80'N,	87°18.32'W	El Cantoral, Honduras	1400
27 Jan 96	15°06.97'N,	86°47.44'W	La Union, Honduras	1300
14 Jan 97	14°05.27'N,	87°23.72'W	El Escabadero, Honduras	1600
15 Jan 97	14°01.06'N,	88°05.45'W	Loma Isla, Honduras	1700
20 Jan 97	14°25' N,	87°18'W[d]	Vallecillos, Honduras	1500
24 Jan 97	14°48.13'N,	87°50.21'W	San José de los Planes, Honduras	1300
25 Jan 97	14°14.77'N,	87°29.16'W	Cerro El Cojón, Honduras	1700
25 Jan 97	14°14.77'N,	87°29.16'W	Cerro El Cojón, Honduras	1700
25 Jan 97	14°14.77'N,	87°29.16'W	Cerro El Cojón, Honduras	1700
25 Jan 97	14°14.77'N,	87°29.16'W	Cerro El Cojón, Honduras	1700
25 Jan 97	14°14.20'N,	87°28.99'W	Quebrada Honda, Honduras	1600
30 Jan 97	14°13.78'N,	87°29.39'W	Quebrada Honda, Honduras	1600
30 Jan 97	14°13.92'N,	87°29.42'W	Quebrada Honda, Honduras	1700
30 Jan 97	14°14.22'N,	87°29.14'W	Quebrada Honda,, Honduras	1700
1 Feb 97	14°03.65'N,	87°07.31'W	Cerro Triquilapa, Honduras	1700
1 Feb 97	14°03.78'N,	87°07.54'W	Cerro Triquilapa, Honduras	1700
1 Feb 97	14°04.81'N,	87°06.03'W	El Eden, Honduras	1400
1 Feb 97	14°04.78'N,	87°06.43'W	El Eden, Honduras	1500
2 Feb 97	14°12.22'N,	87°03.42'W	Valle de Angeles, Honduras	1500
2 Feb 97	14°09.52'N,	87°00.52'W	Valle de Angeles, Honduras	1600
6 Feb 97	14°36.59'N,	88°26.05'W	Cerro El Cantil, Honduras	1400
6 Feb 97	14°36.59'N,	88°26.05'W	Cerro El Cantil, Honduras	1400
6 Feb 97	14°36.66'N,	88°25.06'W	Cerro El Cantil, Honduras	1500
6 Feb 97	14°36.64'N,	88°24.93'W	Cerro El Cantil, Honduras	1500
7 Feb 97	14°24.04'N,	88°22.05'W	Los Lesquines, Honduras	1600
7 Feb 97	14°02.66'N,	88°04.79'W	Sabinitas, Honduras	1700
9 Feb 97	14°18.99'N,	87°47.18'W	Las Moras, Honduras	1700
9 Feb 97	14°26.73'N,	87°47.01'W	Las Moras, Honduras	1800
9 Feb 97	14°19.69'N,	87°46.72'W	Las Moras, Honduras	2000
10 Feb 97	14°26.67'N,	87°32.96'W	Cerro Volcan, Honduras	1600
15 Jan 98	15°04.32'N,	89°56.94'W	Albores, Guatemala	2100

Appendix II. continued.

Date	Latitude/Longitude[a]		Locality[b]	Elevation (m)[c]
15 Jan 98	15°04.30’N,	89°57.05’W	Albores, Guatemala	2200
16 Jan 98	15°02.67’N,	89°57.06’W	Albores, Guatemala	1300
16 Jan 98	15°02.66’N,	89°58.05’W	Albores, Guatemala	1500
17 Jan 98	15°03.88’N,	89°40.56’W	San Lorenzo, Guatemala	1400
17 Jan 98	15°04.16’N,	89°40.66’W	San Lorenzo, Guatemala	1600
17 Jan 98	15°03.75’N,	89°40.72’W	San Lorenzo, Guatemala	1300
17 Jan 98	15°03.98’N,	89°40.76’W	San Lorenzo, Guatemala	1400
17 Jan 98	15°04.06’N,	89°40.98’W	San Lorenzo, Guatemala	1500
17 Jan 98	15°04.05’N,	89°41.32’W	San Lorenzo, Guatemala	1600
17 Jan 98	15°04.38’N,	89°41.39’W	San Lorenzo, Guatemala	1600
17 Jan 98	15°04.29’N,	89°41.50’W	San Lorenzo, Guatemala	1500
19 Jan 98	15°05.14’N,	89°39.55’W	San Lorenzo, Guatemala	1800
18 Jan 98	15°05.38’N,	89°39.64’W	San Lorenzo, Guatemala	1700
18 Jan 98	15°05.72’N,	89°39.43’W	San Lorenzo, Guatemala	1600
18 Jan 98	15°05.72’N,	89°39.43’W	San Lorenzo, Guatemala	1600
18 Jan 98	15°05.99’N,	89°39.24’W	San Lorenzo, Guatemala	1700
18 Jan 98	15°05.99’N,	89°39.24’W	San Lorenzo, Guatemala	1700
18 Jan 98	15°06.21’N,	89°39.14’W	San Lorenzo, Guatemala	1800
18 Jan 98	15°06.21’N,	89°39.14’W	San Lorenzo, Guatemala	1800
19 Jan 98	15°03.80’N,	89°40.86’W	San Lorenzo, Guatemala	1300
19 Jan 98	15°03.90’N,	89°40.93’W	San Lorenzo, Guatemala	1300
24 Jan 98	15°04.47’N,	89°48.94’W	Cemiento, Guatemala	1900
24 Jan 98	15°04.11’N,	89°48.90’W	Cemiento, Guatemala	2100
24 Jan 98	15°04.25’N,	89°49.28’W	Cemiento, Guatemala	2200
24 Jan 98	15°03.91’N,	89°49.16’W	Cemiento, Guatemala	2200
24 Jan 98	15°03.21’N,	89°49.11’W	Cemiento, Guatemala	1700
24 Jan 98	15°03.21’N,	89°49.11’W	Cemiento, Guatemala	1700
24 Jan 98	15°03.32’N,	89°49.36’W	Cemiento, Guatemala	1600
1 Feb 98	14°45.92’N,	89°55.60’W	Matazano, Guatemala	1700
2 Feb 98	14°44.14’N,	89°58.97’W	Portrero Carrillo, Guatemala	1700
4 Feb 98	14°22.57’N,	90°06.66’W	Lago Ayarza, Guatemala	1900
5 Feb 98	14°21.55’N,	90°05.30’W	Lago Ayarza, Guatemala	1500
8 Feb 98	14°29.05’N,	89°25.22’W	Finca San Jose, Guatemala	1400
8 Feb 98	14°29.21’N,	89°25.41’W	Finca San Jose, Guatemala	1400
11 Feb 98	14°14.35’N,	88°32.09’W	Erandique, Honduras	2200
11 Feb 98	14°20.13’N,	88°28.20’W	Erandique, Honduras	1400
11 Feb 98	14°33.62’N,	88°39.21’W	Erandique, Honduras	1700
13 Feb 98	14°27.96’N,	89°07.42’W	Aldea El Volcan, Honduras	1700
14 Feb 98	14°22.78’N,	88°50.29’W	Aldea Planes, Honduras	1700
14 Feb 98	14°23.02’N,	88°50.08’W	Aldea Planes, Honduras	2100
15 Feb 98	14°34.22’N,	88°44.39’W	Aldea Petatillo, Honduras	1700
19 Feb 98	15°21.76’N,	90°49.45’W	Aldea Rincon, Guatemala	2000

[a]Rounded to the nearest 0.01 minute (18.4 m).
[b]Nearest named town or geographical feature from topographic map.
[c]Rounded to the nearest 100 m.
[d]Data are approximate due to equipment failure.