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Establishing quantitative habitat targets for a 'Critically Endangered' Neotropical migrant (Golden-cheeked Warbler *Dendroica chrysoparia*) during the non-breeding season

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Summary

The Golden-cheeked Warbler *Dendroica chrysoparia* is a federally endangered Neotropical migrant that inhabits montane pine-oak forests in Mexico and northern Central America during the non-breeding season. Although it is known that Golden-cheeked Warblers are closely associated with '*encino*' oaks (evergreen or holm oak) such as *Quercus sapotifolia*, *Q. eliptica* and *Q. elongata*, which have shiny, narrow, elliptical, or oblong leaves, quantitative habitat targets are useful for effectively incorporating this information into conservation planning and forest management practices. We analysed data on wintering Golden-cheeked Warblers collected during the non-breeding season in Honduras from 1996 to 1998 to identify quantitative targets for habitat conditions for this species. Data on warbler abundance were collected using line transect surveys located in montane pine-oak forests in a stratified-random fashion. Habitat data were collected at five 0.04 ha plots on these same transects and the averaged values used as predictors of Golden-cheeked Warbler abundance. We found that Golden-cheeked Warblers were strongly associated with the basal area of *encino* oaks and density of '*roble*' oaks, such as *Q. segoviensis*, *Q. purulhana* and *Q. rugosa*, which have large, lobed leaves. Density of Golden-cheeked Warblers peaked at ≈ 5.6 m^2 ha^{-1} basal area of *encino* and ≈ 7 *roble* oaks ha^{-1}. These values can be used to identify quantitative habitat targets that can be directly incorporated into forest management practices to ensure that these activities maintain habitat conditions necessary for their use by Golden-cheeked Warblers.

Resumen

El Golden-cheeked Warbler es una especie migratoria Neotropical que habita en bosques montanos de pino y cedro en Méjico y la parte norte de Centro América durante la época de no apareamiento. Es conocido que los Golden-cheeked Warblers están fuertemente asociados con encino cedros tales como el *Quercus sapotifolia, Q. elíptica y Q. elongata,* identificados por tener hojas muy brillantes, alongadas elípticas o también oblongadas. Para definir parámetros de conservación, es importante obtener objetivos cuantificables para que efectivamente se incorpore este tipo de información en las prácticas de manejo forestal y planeamiento de su conservación. Nosotros analizamos datos en Golden-cheeked Warblers hibernando que fueron colectados durante la estación de no reproducción en Honduras entre 1996 a 1998 para identificar objetivos cuantitativos de las condiciones del ambiente aplicables a esta especie. Datos sobre la abundancia de Warblers fueron colectados utilizando encuestas con líneas transectales localizadas en regiones montanas forestales de pino y encino estratificadas en una forma aleatoria. Datos sobre el ambiente se colectaron en áreas de 0.04 hectáreas en las mismas líneas transectales y los valores promedios se usaron para predecir la abundancia de Golden-cheeked Warblers. Encontramos que los Golden-cheeded Warblers están fuertemente asociados con áreas basales de encino cedro y densidades de roble cedro tales como los *Q. segoviensis, Q. purulhana y el Q. rugosa*, los cuales todos tienen la característica de tener hojas grandes y lobulares. La densidad de los Golden-cheeked Warblers se intensificó a aproximadamente 5.6 m^2 por hectárea de área basal de encinos y aproximadamente 7 robles cedros por hectárea. Estos valores pueden ser usados para identificar ambientes objetivos que pueden ser directamente incluidos en prácticas de manejo forestal, para asegurar que estas actividades mantendrán las condiciones necesarias requeridas o usadas por los Golden-cheeked Warblers.

Introduction

The Golden-cheeked Warbler *Dendroica chrysoparia* is a 'Critically Endangered' Nearctic-Neotropical migratory bird that breeds in Texas and winters from Chiapas, Mexico, to north-west Nicaragua. Past work has indicated that wintering Golden-cheeked Warblers are associated with pine-oak forests (Vidal *et al.* 1994, Rappole *et al.* 2000, Rappole *et al.* 2003). The pine-oak forests that are inhabited by wintering Golden-cheeked Warblers are considered critically endangered due to their restricted geographic distribution and threats from expanding human activity (Perez *et al.* 2008). An understanding of the association between Golden-cheeked Warbler abundance and habitat characteristics is important for developing strategies for the conservation of this species (Perez *et al.* 2008).

Studies of wintering Golden-cheeked Warblers have shown that warblers forage preferentially on the leaves of oaks such as *Quercus sapotifolia*, *Q. eliptica* and *Q. elongata*, which have shiny, narrow, elliptical, or oblong leaves, and are collectively referred to as '*encino*' oaks in our Honduran study areas (Rappole *et al.* 1999). In contrast, Golden-cheeked Warblers forage less than expected in '*roble*' oaks such as *Q. segoviensis*, *Q. purulhana* and *Q. rugosa*, which have large, lobed leaves. Data collected on transect counts from 1996 to 1998 indicated that points where Golden-cheeked Warblers were detected had more *encino* oaks than corresponding random locations (Rappole *et al.* 1999). Findings such as these have led to the identification of *encino* as a "critical habitat feature" (sensu Villard and Jonsson 2009a) for non-breeding wintering Golden-cheeked Warbler habitat (Perez *et al.* 2008).

Although the identification of critical habitat features is valuable for making coarse-filter assessments, modelling variation in abundance over a range of habitat conditions yields information useful for the development of quantitative targets for conservation (Guenette and Villard 2005). Quantitative targets are important in the context of sustainable forest management for defining desired future conditions needed to support specific biodiversity values (Villard and Jonsson 2009b). In the case of the Golden-cheeked Warbler, managers are aware that *encino* oaks represent a critical habitat feature; however forestry operations are carried out under management plans that prescribe desired future conditions, and in the absence of quantitative targets for the retention of *encino* oaks for Golden-cheeked Warblers, the success and defensibility of forestry operations in terms of meeting their statutory obligations to conserve endangered species is in doubt. In this study, we analyse abundance of Golden-cheeked Warblers in relation to habitat conditions to aid in the identification of quantitative habitat targets for the management of non-breeding Golden-cheeked Warblers.

Methods

To establish quantitative habitat targets for Golden-cheeked Warblers, we used data collected by Rappole *et al.* (2003) from a 30,000 km^2 region in the central and western highlands of Honduras. Golden-cheeked Warblers were surveyed on 44 transects located throughout this region in potential Golden-cheeked Warbler habitat, which consists of montane pine-oak forest > 1,000 m above sea level (Rappole *et al.* 2000). The area surveyed was 74.8% forested, with the remainder consisting of savannah, scrubland and agricultural and developed land (Rappole *et al.* 2000). Transects averaged 1 km in length and, where possible, were located in a stratified-random manner by choosing a random distance 0–100 m as a starting point within a randomly selected 1-km^2 block located on or near a point of ready access (Rappole *et al.* 2003). Fifteen transects were surveyed in 1996, 25 in 1997, and 4 in 1998. Transects were surveyed by walking slowly ($\approx$ 1 km h^{-1}) and watching and listening for Golden-cheeked Warblers or vocal members of mixed-species flocks with which they associate. 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. Afterwards, observers measured the distance from the point on the transect from which the flock was located to the point where the first bird in the flock was detected, as well as the angle between the transect and the point where the first bird in the flock was detected in degrees. The average radius of flocks in the study area, 25 m, was added to the distance measurement for analyses (Rappole *et al.* 2003).

Rappole *et al.* (2003) measured habitat characteristics on five randomly located 0.04-ha plots on each transect (James and Shugart 1970). These plots were situated by proceeding to points 100, 300, 500, 700 and 900 m along each transect, and from these points, choosing a direction right or left from the transect with a coin toss and selecting the plot location at a random distance 12–100 m from the transect selected with a random number table. Four 11.3-m transects were established radiating from the center of each plot in the cardinal directions. Canopy and herb cover were measured at five points along each transect (20 of each per plot) with a sighting tube, and canopy and herb cover were calculated as the proportion of the 20 points at which canopy and herb cover were sighted at crosshairs fitted to the distal end of the sighting tube (James and Shugart 1970). The diameter of all trees on the plots was measured at breast height, and the number of trees of each species and size class (small 1–9 cm, medium > 9–27 cm, and large > 27 cm) within 11.3 m of the centre point was recorded. Habitat variables were averaged for each transect and the averages used in the analyses as possible predictors of Golden-cheeked Warbler abundance.

These data were originally used to calculate population density of wintering Golden-cheeked Warblers (Rappole *et al.* 2003) using the program DISTANCE (Buckland *et al.* 2001), and also to identify habitat variables that were associated with Golden-cheeked Warbler presence (Rappole *et al.* 1999, 2000). These researchers were unable to directly relate warbler density to habitat characteristics because DISTANCE estimates the effect of habitat covariates on detectability, not abundance. A recently developed technique, however, allows for modelling of both density and detection probability simultaneously (Royle *et al.* 2004). This model is based on specifying the distance-sampling likelihood at each sample unit in terms of abundance with a regression model parameterised in terms of habitat covariates. Maximum-likelihood estimation of detection and density parameters is based on the integrated likelihood. We applied this methodology to the data collected by Rappole *et al.* (2003) with the program R (version 2.9.0, R Development Core Team 2009) and the package "unmarked" (version 2.9-0; Fiske and Chandler 2011).

Independent variables included basal area and density of trees (all sizes combined as well as separately by size class) for tree species comprising > 5% of the average basal area, which included pines (mostly *Pinus oocarpa* and *P. maximinoi*), *encino* oaks and *roble* oaks. These species comprised 93% of the tree basal area. Other variables included percentage tree canopy cover and percentage ground cover. Variables were log or arcsine transformed as appropriate to improve normality, examined for correlation with other predictor variables, and analysed individually as predictors of Golden-cheeked Warbler abundance. Variables that performed better (i.e. lower AIC_c values) than the intercept only model were retained and included additively in multivariate models. The appropriate abundance model (Poisson versus negative binomial) and detection function (uniform, hazard, half-normal, exponential) was chosen based upon AIC_c values (Buckland *et al.* 2001). We examined univariate scatterplots of all habitat variables and fitted non-linear curves (quadratic and sigmoid) where higher order relationships were indicated. Observer was not included as a covariate in the detectability term because the same observer (DK) conducted all of the surveys at these sites. A total of 18 models were run. Models were ranked using AIC_c values. Those that performed better than the intercept only model are presented, and those with AIC_c values within 2 units of the highest ranked model were considered to be supported. We encountered substantial model-selection uncertainty and used model averaging to incorporate this uncertainty into parameter estimates (Burnham and Anderson 2002). Goodness of fit was evaluated using the parametric bootstrap procedure based on a chi-squared fit statistic (Royle *et al.* 2004).

Results

During the course of the study we detected 31 Golden-cheeked Warblers on 20 of the 44 transects surveyed. Three individuals were detected on two transects, two individuals on seven transects, and a single individual was sighted on 11 transects. Four models of Golden-cheeked Warbler abundance as a function of habitat variables had ΔAIC_c values of ≤ 2, and were considered to be supported (Table 1). Because the model weights were distributed relatively evenly among these four models, model averaging was used to incorporate model selection uncertainty into the parameter estimates. The two most supported models had weights that indicated the probability of their being the best model was $>$ twice that of the two other supported models. These two most supported models both included linear and quadratic terms for *encino* basal area, and the top model included a linear and quadratic term for *roble* density as well. The top model indicated that the density of Golden-cheeked Warblers increased with *encino* basal area to ≈ 5.6 m^2 ha^{-1} and with *roble* density to ≈ 7 trees ha^{-1}, and then decreased thereafter (Figure 1). Bootstrap estimates for 95% confidence intervals of these estimates for *encino* basal area and *roble* density were 3.9–6.8 m^2 ha^{-1} and 2.5–20 trees ha^{-1}, respectively. The other supported models included a single term indicating a linear increase of Golden-cheeked Warbler abundance with increasing density of small (1–9 cm dbh) *encino* oaks and density of all *encino* size classes combined, respectively. Parametric bootstrap procedures indicated no evidence of over-dispersion for the top-ranked model ($P = 0.66$) and examination of the model residuals did not indicate the presence of outliers or points with very strong leverage. Neither first order, quadratic nor sigmoid relationships with any other habitat variables (e.g. density of *encino*, basal area of *roble*, density or basal area of pine, canopy or

Table 1. Model selection results of relationship between Golden-cheeked Warbler density and habitat variables from 44 l-km transects in 1996, 1997, and 1998 in montane pine forests throughout western and central Honduras. Models that performed better than the intercept only model are presented.

Model[1]	Intercept	EBA	EBA^2	RD	RD^2	ED small	ED	RBA	ED^2	EBA small	K	AIC_c	ΔAIC_c	w_i	R^2
EBA^2+RD^2	−2.99	0.61	−0.64	−0.17	0.76						6	183.6	0.00	0.21	0.43
EBA^2	−2.81	0.68	−0.60								4	183.8	0.18	0.19	0.36
ED small	−3.29					0.39					3	184.8	1.23	0.11	0.31
ED	−3.28						0.38				3	185.1	1.53	0.10	0.30
RD^2	−3.39			−0.19	0.79						4	185.7	2.06	0.08	0.33
RBA	−3.26							−0.54			3	186.55	2.93	0.05	0.28
EBA small	−2.98									0.31	3	186.62	3.00	0.05	0.28
ED^2	−3.16						0.52		−0.14		4	187.07	3.45	0.04	0.31
Intercept	−3.21										2	187.58	3.97	0.03	0.22

[1]EBA = basal area of *encino* oaks (m^2 ha^{-1}); RD = density (trees ha^{-1}) *roble* oaks; ED small = density of *encino* oaks 1–9 cm dbh; ED = density of *encino* oaks; RBA = basal area of *roble* oaks, EBA small = basal area *encino* oaks 1–9 cm dbh.

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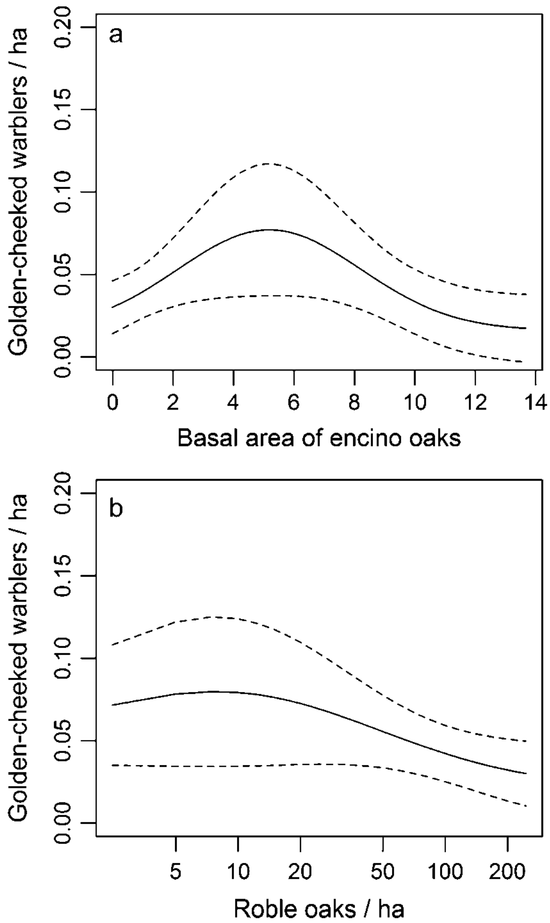

Figure 1. Relationship between density of Golden-cheeked Warblers and basal area (m^2 ha^{-1}) of (a) *encino* oaks and (b) density of *roble* oaks (trees ha^{-1}) from data collected on 44 transects in Honduras, Guatemala and Chiapas, Mexico 1996–1998. Response curves represent model-averaged estimates and standard errors.

ground cover) were included in supported models (ΔAIC_c values of ≤ 2). There was no support for basal area or density of small, medium or large pines or *roble* oaks or medium or large *Encino* oaks. Average values for habitat parameters with standard errors are in Table 2.

Discussion

The identification of critical habitat features through comparisons of habitat conditions between occupied and unoccupied sites is thought to aid in conservation efforts by providing general criteria for discriminating between suitable and unsuitable habitat for the purpose of habitat inventory or assessments, but there are concerns that this information falls short of that required for integrating biodiversity values into management plans in montane pine-oak forests because forest conditions and species responses are not necessarily dichotomous (Guenette and Villard 2005). Previous analyses of these data indicated that Golden-cheeked Warblers were detected more

Table 2. Mean (SE) values for habitat variables from 44 1-km transects surveyed for Golden-cheeked Warblers in 1996, 1997 and 1998 in montane pine forests throughout western and central Honduras.

Basal area *encino* oaks [a]	3.60 (0.52)
Basal area small *encino* oaks	1.15 (0.17)
Basal area medium *encino* oaks	1.61 (0.32)
Basal area large *encino* oaks	0.80 (0.28)
Density *encino* oaks [b]	164.0 (22.4)
Density small *encino* oaks	150.8 (20.9)
Density area medium *encino* oaks	12.1 (2.24)
Density area large *encino* oaks	1.22 (0.39)
Basal area *roble* oaks	1.67 (0.58)
Density *roble* oaks	50.0 (10.3)
Basal area pines	20.9 (1.73)
Density pines	296.0 (30.4)
Canopy cover (%)	0.70 (0.14)
Herbaceous cover (%)	0.29 (0.12)

[a.] $m^2\ ha^{-1}$
[b.] trees ha^{-1}

often in pine-oak forest (Rappole *et al.* 2000), and at points that had greater basal area of *encino* oak than corresponding random points (Rappole *et al.* 1999), results which have also been reported from studies in Mexico (Vidal *et al.* 1994) and Nicaragua (King *et al.* 2009). Habitats with at least as much basal area as these published values measured at occupied sites are probably suitable, and habitats with no *encino* oaks are clearly unsuitable. However, by treating habitat suitability as a discrete function, conservationists run the risk of mischaracterising the response of species to habitat conditions with potentially important consequences (Guenette and Villard 2005).

Our analyses of Golden-cheeked Warbler density along a continuous habitat gradient better reflect the actual response of this species to habitat conditions, and permit the establishment of quantitative conservation targets that will enable the accurate identification of suitable habitat to inform conservation efforts. The montane pine-oak forests preferred by the Golden-cheeked Warbler also have substantial commercial and subsistence value (pines primarily for building supplies and oaks for fuel), and much of the region within the winter range of the Golden-cheeked Warbler is lacking in economic activity that could be supplied by the sustainable management of montane pine-oak forests (Perez *et al.* 2008). An important aspect of the development of this resource is ensuring the maintenance of biodiversity, and because it is an endangered species and a montane pine-oak obligate, the conservation of the Golden-cheeked Warbler clearly should be a component of this conservation effort. Since the retention of all *encino* oaks could interfere with the cultivation of pines and the use of oaks as fuel, conservation of this species will require the identification of minimum values for habitat conditions below which this species will be scarce or absent. Our analyses indicate that Golden-cheeked Warbler abundance does not increase at values above $\approx 5.6\ m^2\ ha^{-1}$ of *encino*. Since some of the stands we studied contained as much as $29\ m^2\ ha^{-1}$ encino basal area, managers could prescribe the harvest of a considerable amount of *encino* and still provide suitable habitat for Golden-cheeked Warblers.

Our finding that the abundance of Golden-cheeked Warblers was closely associated with *encino* oaks can be explained by their foraging behaviour. Rappole *et al.* (1999) reported that most (94%) foraging manoeuvres by Golden-cheeked Warblers at these sites were directed at *encinos*. It is not clear why Golden-cheeked Warbler abundance declined beyond basal areas $> 5.6\ m^2\ ha^{-1}$ of *encino*. Models of Golden-cheeked Warbler abundance that included a sigmoid relationship for *encino* received far less support ($\Delta AIC_c = 11.6$) compared to the quadratic relationship ($\Delta AIC_c = 3.76$), indicating the shape of the curve is not an artefact of fitting a quadratic relationship. Similarly, an *ad hoc* model including *encino* basal area as a covariate of detectability had a higher AIC_c value than the top-ranked model

($\Delta AIC_c = 2.55$) and was thus not supported, indicating declines in abundance with increased *encino* basal area did not reflect a decrease in detectability. Rather it appears that Golden-cheeked Warblers actually are most abundant in stands with intermediate levels of *encino* oak basal area. Chandler and King (2011) reported that non-breeding Golden-winged Warblers *Vermivora chrysoptera* were most abundant at intermediate levels of canopy closure, and suggested that increased light penetration resulted in increased food resources. Perhaps a similar mechanism is responsible for the association of Golden-cheeked Warblers with intermediate levels of *encino* basal area.

Golden-cheeked Warblers were seldom observed foraging in *roble* oaks in our study (Rappole *et al.* 1999), so there is no clear explanation for their positive relationship up to ≈ 7 *robles* ha^{-1}. Although supported, the model including both *encino* basal area and *roble* density had nearly the same model weight as the model including *encino* only, indicating *roble* actually added little extra explanatory power to the model. Furthermore, *roble* density ranged up to 235 trees ha^{-1}, so the relationship between Golden-cheeked Warbler density and *roble* density was negative over nearly the entire range of *roble* density.

We did not find any significant relationship between Golden-cheeked Warblers and pines, which generally dominated the stands where we worked. Golden-cheeked Warblers seldom forage in pines (Rappole *et al.* 1999), however nearly all Golden-cheeked Warblers we encountered (99%) were associated with mixed-species flocks, and many of these flock associates, such as Hermit Warblers *Dendroica occidentalis* and Olive Warblers *Peucedramus taeniatus*, are closely associated with pines (King and Rappole 2000). King *et al.* (2009) found that generally Golden-cheeked Warbler habitat selection in Nicaragua was similar to that in the core of their range, however a small number of Golden-cheeked Warblers in their study were encountered at sites with *encinos* but no pines. The lack of association between Golden-cheeked Warblers and pines suggests that Golden-cheeked Warblers are relatively flexible with respect to their habitat requirements as long as the sites are forested and contain ≈ 5.6 m^2 ha^{-1} of *encino* basal area.

Landscape composition is considered important in influencing habitat quality of breeding Golden-cheeked Warblers (Magness *et al.* 2006, Peak 2007), but it is not clear whether non-breeding Golden-cheeked Warblers are affected by landscape composition. Although the high elevation areas within our study area were extensively forested and thus probably above the threshold levels for fragmentation effects to be manifested, the relatively unfragmented condition of our study sites is not representative of other portions of the species range, such as south-eastern Guatemala (Rappole *et al.* 2000, Perez *et al.* 2008) or Nicaragua (King *et al.* 2009). Thus we advise caution in extending our results to less forested parts of this species' range.

Recently managers have turned to integrating wildlife values into management plans in Mesoamerican montane pine-oak forests, and because these forests are occupied by endangered Golden-cheeked Warblers, the quantitative habitat targets we have generated for this species will be an important component of these efforts (Perez *et al.* 2008). Although focal-species analyses are an important component of biodiversity conservation efforts (Villard and Jonsson 2009b), species-specific efforts lack generality and should be complemented by coarse-filter modelling exercises to encompass the habitat needs of more species (Lindenmayer *et al.* 2006, Lindell *et al.* 2011). Because its endangered status makes monitoring a priority, investigations of the extent to which Golden-cheeked Warblers could indicate habitat quality for other sensitive species would be valuable.

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