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White (*Mniotilta varia*) and Golden-Cheeked Warblers
(*Setophaga crysoptera*) in the Juniper-Oak Woodlands of
Central Texas**

CHRISTOPHER C. WARREN,¹ JAMES R. OTT² AND JOSEPH A. VEECH

*Population and Conservation Biology Program, Department of Biology, Texas State University – San Marcos,
San Marcos 78666*



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ABSTRACT.—The golden-cheeked warbler (*Setophaga chrysoparia*) and the black-and-white warbler (*Mniotilta varia*) breed in the deciduous/evergreen woodlands of central Texas. The golden-cheeked warbler is endemic, while for the geographically widespread, black-and-white warbler, these woodlands represent the southwestern terminus of the breeding range. To estimate relative abundance and to compare habitat associations, we estimated occupancy, corrected for probability of detection, for both species using replicated point-count surveys of 36 survey stations at each of six sites within the Balcones Canyonlands Preserve Travis Co. TX. Model selection using an *a priori* set of candidate models suggested that the probability of detection differed among warbler species and study sites and both species were influenced by time of season, time of day, and habitat characteristics of the survey station—slope and canopy cover. Naïve occupancy estimates suggested that occupancy of black-and-white warblers was much lower than golden-cheeked warblers. However model-averaged estimates of occupancy corrected for imperfect detection suggested that occupancy of black-and-white warblers averaged across all study sites and survey stations were comparable to golden-cheeked warblers. For both black-and-white and golden-cheeked warblers occupancy was positively influenced by slope and this relationship was modulated by canopy cover. Our study provides an example of how occupancy modeling can change naïve perceptions of the relative abundance of species and be used to predict habitat associations of animals through point-count surveys while accounting for imperfect detection.

INTRODUCTION

The diverse family of passerines known as the wood-warblers (Parulidae) is widespread throughout North America. As such these species inhabit much of the spectrum of habitats the region offers. However, individual species differ greatly in range size with some being very localized and endemic and others widespread. The golden-cheeked warbler (*Setophaga chrysoparia*) is endemic to the Edward's Plateau of central Texas. Given its status as a federally listed endangered species, this species has been intensively studied and monitored throughout its range (City of Austin, 1999; Peak, 2007; Watson *et al.*, 2008; Morrison *et al.*, 2010). The Balcones Canyonland Preserve (BCP) west of Austin, Texas was established in 1996 in large part to conserve habitat for the golden-cheeked warbler (City of Austin and Travis County, 1996). The BCP consists of a series of discontinuous natural areas that represent the juniper-oak woodland habitat type characteristic of the dissected topography of the eastern edge of the Edward's Plateau (McMahan *et al.*, 2008). A variety of local and state agencies, private organizations, and individuals own and (or) manage segments of the preserve under a unified habitat conservation plan (City of Austin and Travis County, 1996).

¹ Present Address: City of Austin, Austin Water Utility, Wildland Conservation Division, Balcones Canyonlands Preserve, Austin, Texas 78738

² Corresponding author: Telephone: (512)245-2321; e-mail: Jimott@txstate.edu



FIG. 1.—Breeding ranges of black-and-white warblers (light shading) and golden-cheeked warblers (dark shading). Open square in central Texas gives approximate location of Balcones Canyonlands Preserve. Maps drawn from various published sources

As part of this management plan BCP agency partners cooperate in a long-term population-monitoring program for the golden-cheeked warbler.

Along with the golden-cheeked warbler, the black-and-white warbler (*Mniotilta varia*) is the only other species of wood warbler that commonly breeds in the juniper-oak woodlands of the BCP. During the breeding season, black-and-white warblers are typically found in closed-canopy forests in other parts of their range (James, 1971; Conner *et al.*, 1983). Affinity for this habitat likely reflects foraging strategy and resource requirements as the species is insectivorous and forages by creeping along tree trunks (Kricher, 1995). Given this reliance on mature forest habitat, the species has a breeding range (Sauer *et al.*, 2008) that includes areas of North America historically covered by extensive forests (Williams, 1989). The breeding range of the black-and-white warbler encompasses much of the Canadian boreal region, Great Lakes region, northeastern U.S.A., extends south through Appalachia to the southeastern U.S.A., and then terminates in south-central Texas (Fig. 1). Throughout much of the black-and-white warbler breeding range, broad-leaf deciduous or spruce-fir forests are the dominant vegetation type typically forming closed canopies (Vankat, 1990).

The woodlands on the eastern edge of the Edward's Plateau are relatively open consisting primarily of juniper and oak scrub with small trees (<12 m height) that rarely produce extensive areas of closed-canopy forests (>95% canopy cover) (Russell and Fowler, 2002; McMahan *et al.*, 2008). Instead, canopy cover is typically 60–90% with some small areas having <20% cover. Steep ridges and gullies define the topography on the eastern edge of the Edward's Plateau, such that the slope and aspect of the terrain can vary substantially within areas much smaller than a square kilometer. Therefore, at the southwestern edge of

the breeding range, black-and-white warblers encounter a “forest” habitat type that is both structurally and compositionally very different from northern and eastern forests. The golden-cheeked warbler’s affinity for the closed-canopy woodlands of the region is well established (Pulich, 1976; Kroll, 1980; Magness *et al.*, 2006). In contrast, little is known regarding the habitat affinities of the black-and-white warbler in central Texas and to date no studies have examined the abundance of this species in this region as function of habitat. In this study we compared the habitat affinities of the two species by examining patterns of occurrence as a function of habitat characteristics. The comparison is interesting given that black-and-white warblers are ground-nesters with a very extensive breeding range, whereas golden-cheeked warblers are canopy-nesters with a very limited breeding range (Fig. 1). These fundamental biological differences could lead to differences in habitat affinities.

The long term monitoring program for the golden-cheeked warbler within the BCP provided the opportunity to simultaneously assess patterns of occurrence and habitat affinities of these two warbler species. Thus, we conducted point count surveys and estimated occupancy of golden-cheeked and black-and-white warblers on six study sites distributed throughout the BCP. We then asked what was the relative occupancy of the two species, and how does variation in occupancy relate to variation in habitat? To address these questions, we developed occupancy models that incorporated habitat variables as covariates that may affect probability of detection and/or occupancy. We investigated percent canopy cover, degree of slope, and aspect as these variables describe aspects of the physiognomy of the BCP with the potential to influence vegetation structure and composition (Buechner, 1944; Van Auken *et al.*, 1981; Russell and Fowler, 1999).

METHODS

SURVEY SITES AND STUDY DESIGN

A primary mandate of the BCP is to manage the land to support populations of golden-cheeked warblers. Therefore, golden-cheeked warblers were known to exist within the preserve prior to our study and many parts of the preserve are considered beneficial habitat for the species. However, black-and-white warblers had not been surveyed in the preserve prior to our study. The City of Austin’s Wildland Conservation Division had previously established 40.5 ha survey sites for long-term monitoring of golden-cheeked warblers through a territory mapping approach (City of Austin, 1999). We selected six of these sites for this comparative study. The six sites were between 1–10 km apart from the next closest site. The density of golden-cheeked warblers varied among the six study sites in 2009 from 2.5–18 territorial males per 40.5 ha (City of Austin, 2009).

In 2008, a 113 ha grid was established at each of the six sites as part of an on-going study of methods for monitoring the golden-cheeked warbler (Hunt *et al.*, 2012). Each grid subsumed the 40.5 ha plots and consisted of 36 survey stations spaced 200 m apart in a 6 × 6 array. The spacing of stations at 200 m was based on the typical golden-cheeked warbler territory size (Pulich, 1976; Watson *et al.*, 2008; Warren unpublished data) and was intended to decrease the likelihood that a given golden-cheeked warbler male would be detected at more than one station during a given sampling occasion. At each site, we conducted single-day surveys repeated for four sampling occasions (separated by at least five days) between 20 Mar. and 11 Apr. 2009. Surveys were initiated 2 w after the typical first arrival date of golden-cheeked warblers (City of Austin, 2009) and the survey interval corresponded to the peak singing activity of golden-cheeked warblers in this area (Warren, 2011). A single observer surveyed each site for the four sampling occasions. Each point count station was surveyed for 5 min during which the presence of both black-and-white and golden-cheeked warblers was

recorded when singing males were detected. The grids were located in rugged terrain; having the same observer survey the same site each occasion allowed for the observer to become familiar with station locations and this facilitated data collection. Surveys began at sunrise (~0700 hours CST) and were completed by 1300–1500 h. The time required to traverse the rugged terrain prevented randomization of visitation order for the survey stations. Thus the order in which survey stations 1–36 were surveyed at each study site was reversed for each successive visit to reduce time of day bias for survey stations at the beginning and ends of survey grids. Typically 24–26 point-count stations were surveyed by 1100 h CST. Time of survey was standardized relative to sunrise and was included as a covariate in estimating detection probability.

HABITAT VARIABLES

We quantified canopy cover, slope, and aspect within a circle of 100 m radius centered on each of the 216 survey stations. This dimension was selected to match the estimated maximum detection radius at survey stations (Hunt *et al.*, 2012) and to provide independent habitat estimates among the stations. The area encompassed by circles was also comparable to estimates of the mean breeding territory size that have been reported for black-and-white (Kricher, 1995) and golden-cheeked warblers (Pulich, 1976; Warren unpublished data). We obtained data (*i.e.*, GIS files) on canopy cover from the National Land Cover Database 2001 (NLCD) and data on slope and aspect from the National Elevation Database. The “percent forest canopy” layer of the NLCD provides estimates of percent canopy cover at a 30 m spatial resolution (*i.e.*, within 30×30 m pixels). We used the Zonal Statistics tool within the Spatial Analyst package in ArcMap 10.1 (ESRI, 2012) to estimate average percent canopy cover over the approximate 30 pixels contained within the 100 m radius circle at each survey station. Our estimates of canopy cover represent a reasonable approximation to land cover at the time of our surveys (2009) as the sites studied are characterized by mid- to late-successional forest and no major changes to land cover have taken place within the preserve previous to our study (City of Austin, 2009).

We also used the Spatial Analyst package to obtain estimates of slope and aspect per survey station. We first converted a 1/9 arc-second resolution elevation map using the Slope tool and then used the Zonal Statistics tool to estimate average degree slope within the 100 m radius circle around each survey station. To estimate aspect per survey station we created an aspect layer using the Aspect tool, partitioned aspect into three categories; (1) flat, (2) $0\text{--}90^\circ$ (NE) + $315\text{--}360^\circ$ (NNW), and (3) $90\text{--}315^\circ$ (S), and then calculated aspect as the proportion of cells ($n \approx 338$) within the radius of each survey station classified as category 2 (*i.e.*, mesic).

ESTIMATION OF DETECTION PROBABILITY AND OCCUPANCY

We designed the study (*i.e.*, repeated visits to each site) to use occupancy modeling (MacKenzie *et al.*, 2002; MacKenzie, 2006) to estimate the effect of environmental variables (percent canopy cover, slope, and aspect) on habitat use by both warbler species. Repeated visits to the same survey stations allowed us to estimate a detection probability (*i.e.*, the probability of detecting a species given that it is present) and estimate occupancy or the probability that the species actually occurred at the survey station adjusted for probability of detection (MacKenzie *et al.*, 2002). Estimation of occupancy in this way can greatly improve studies of resource or habitat use because locations where the species was not detected are not automatically assumed to represent an absence but rather are assigned a probability that the species was present but not detected (MacKenzie, 2006). The proportion of survey stations estimated to be occupied then serves as an estimate of the proportion of the study

site occupied which can then be used to make inference about temporal or spatial changes in occupancy when studies are replicated across time or space (Hunt *et al.*, 2012). As well the station-specific estimate of occupancy can be interpreted as the probability that a particular survey station is occupied. In the terminology of MacKenzie *et al.* (2002) we assessed occupancy using single-season occupancy models as we had one “sampling season” (approximately a 4 w period in Mar. and Apr. 2009) with four sampling “occasions” during the season. Presence/absence data (series of 0 s and 1 s) were recorded at each of the 36 stations at a site. We used the “Analysis: single season—Custom” model-fitting option in program PRESENCE 4.4 (Available at <http://www.mbrpwr.usgs.gov/software/doc/presence/presence.html>) to estimate detection probability and occupancy of both black-and-white and golden-cheeked warblers from a dataset representing all six study sites.

We first modeled the effects of covariates that influenced detection probability (P) for each warbler species. Occupancy was modeled as constant $\psi(\cdot)$ as this first step in model selection examined only covariates that influenced detection. Many passerine species vocalize most often in the morning (Amrhein *et al.*, 2004; Liu and Kroodsma, 2007; Avey *et al.*, 2008), thus “time of observation at a survey station” was examined as a covariate on detection probability. Male passerines sometimes sing less toward the end of the breeding season (Amrhein *et al.*, 2004; Avey *et al.*, 2008). Therefore, we included “season” (coded as weeks 1–4) as a discrete covariate to account for the possibility that males of both species may not be detectable to the same extent from week to week. We used “study site” (coded as a dummy variable) as a covariate to represent potential effects of study site on the probability of detection. Previous analysis by Hunt *et al.* (2012) indicated that the probability of detecting golden-cheeked warblers differed among the study sites and was influenced by time of season and time of day. Hunt *et al.* (2012) found two equally competitive models for detection [$\psi(\cdot)$ P(site, season, time linear) and $\psi(\cdot)$ P(site, season, time quadratic)], thus we included these models (and a null model) in our set of candidate models for detection of golden-cheeked warblers and black-and white warblers. Additionally we investigated as possible covariates of detection, canopy cover and slope, and thus included these covariates in a spectrum of candidate models both with and without the covariates modeled by Hunt *et al.* (2012).

The next step in model selection (Bailey *et al.*, 2004) was to select an occupancy model(s) to estimate occupancy of each warbler species. Canopy cover, slope, and aspect of the terrain at each station were investigated as habitat covariates likely to influence the spatial distribution of these species. Slope and aspect are important in determining deciduous forest composition in central Texas as mixed woodlands of deciduous and evergreen canopy trees are most extensive on slopes (Buechner, 1944; Russell and Fowler, 1999) and mesic (NNE facing) slopes tend to have higher woody plant species richness and greater density (Van Auken *et al.*, 1981). The candidate set of models considered site as a covariate and habitat variables both singly and in combination. We also included all two-way interactions between habitat variables in the fullest model. For all models, we used the logistic equation to represent the effect of covariates on both detection probability and occupancy (MacKenzie, 2006). Given that detection is a binary process (a species is either detected or not) as is occupancy (a species is either present at a station or not), it is appropriate to model the effects of the covariates using the logistic equation. We used the Akaike Information Criterion (Akaike, 1973) corrected for small sample size (AIC_c) to compare models (Sugiura, 1978). Model-averaged estimates of parameters (regression coefficients for covariates and their unconditional SE 's) are presented and represent weighted estimates based on all models considered; *i.e.*, the “candidate set” (Burnham and Anderson, 2002). Unconditional standard errors incorporate model selection variance (Burnham and

TABLE 1.—Summary statistics of habitat characteristics and naïve detection of black-and-white (BAWW) and golden-cheeked (GCWA) warblers at six study sites within the BCP. Canopy cover (%), Slope (°) and Aspect (%) represent means (\pm SD) of the 36 survey stations at each site. Naïve occupancy = the percent of stations where warblers were observed ≥ 1 survey. Total detections = \sum detections across survey stations and surveys. Site abbreviations: EL = Emma Long, IV = Ivanhoe, SE = St. Edwards, FR = Forest Ridge, BO = Bohls, and JT = Double J&T

Site	Canopy	Slope	Aspect	BAWW		GCWA	
				Naïve occup.	Total detections	Naïve occup.	Total detections
EL	83.3 \pm 10.8	6.0 \pm 3.4	17.2 \pm 24.2	19.4	7	100	142
IV	85.0 \pm 5.8	9.9 \pm 4.2	41.0 \pm 34.8	47.2	25	97.2	135
SE	81.3 \pm 8.1	9.7 \pm 4.0	57.5 \pm 23.4	44.4	26	94.4	137
FR	84.1 \pm 5.6	11.5 \pm 3.2	34.1 \pm 34.0	44.4	24	86.1	97
BO	69.0 \pm 13.1	12.9 \pm 5.3	50.5 \pm 27.4	47.2	26	47.2	33
JT	60.4 \pm 23.3	6.7 \pm 3.0	31.6 \pm 35.8	0.06	2	38.9	24
				\bar{x} = 34.7	\sum = 110	\bar{x} = 77.31	\sum = 568

Anderson, 2002). Habitat covariates were standardized as $(x_i - \bar{x})/\sigma_x$ prior to analysis. To estimate occupancy (adjusted for imperfect detection) we used the model-averaged parameter estimates to predict occupancy per survey station and then averaged predicted occupancy across the 36 stations per study site. To predict occupancy as a function (logistic equation) of the observed range of habitat covariates across the 216 survey stations we used the model-averaged parameter estimates for each habitat covariate while holding the other habitat covariates constant at their minimum, mean, and maximum value. Goodness of fit was assessed for the global (fullest) occupancy model for each species and no evidence of over-dispersion of the presence-absence data was present. Means throughout are presented as $\bar{x} \pm SE$ unless otherwise indicated.

RESULTS

Canopy cover, slope, and aspect (proportion of each detection radius classified as mesic) varied substantially within and among the six study sites distributed throughout the BCP (Table 1). At the site level, combinations of relatively high canopy cover, slope, or aspect appear in combination with relatively low averages for the other habitat characteristics. Across all 216 survey stations only weak and/or non-significant correlations were present between the habitat characteristics: slope \times canopy cover $r = 0.22$, $P < 0.001$; slope \times aspect $r = 0.15$, $P < 0.03$; canopy \times aspect $r = 0.11$, $P > 0.1$. None of the survey points had a combination of high slope and low canopy cover. These sources of variation were important for testing our hypotheses; that is, within all study sites, there was environmental variation that individual birds could presumably respond to when establishing breeding territories.

Across the six study sites, total detections of black-and-white and golden-cheeked warblers were 110 and 568, respectively. Total detections of warblers varied substantially among study sites (Table 1). At all study sites we detected more golden-cheeked than black-and-white warbler individuals, typically by a wide margin. Naïve occupancy (percent of survey stations where each species was detected) ranged from 6–47% and 39–100% across study sites for black-and-white and golden-cheeked warblers respectively and was greatest for golden-cheeked warblers at all but one study site (Table 1). Across all sites and stations naïve occupancy of black-and-white warblers (34.7%) was less than that of golden-cheeked warblers (77.3%).

TABLE 2.—Summary of model selection showing covariates influencing the probability of detecting (A) black-and-white and (B) golden-cheeked warblers at six study sites in the BCP, TX. Parameters estimated were occupancy (ψ) and probability of detection (p). Covariates of detection: site, season, time of day linear (time) and time of day quadratic (time^2), canopy, slope, and no influence of a covariate (.). Selected models are indicated in bold. Model selection statistics shown are ΔAIC_c values corrected for small sample size (ΔAIC_c), weight (w), number of parameters (k), and twice the log likelihood (-2LL). A total of 216 detection stations were surveyed on each of four sampling occasions

Model	ΔAIC_c	w	K	-2LL
A. BAWW				
ψ (.) p (site, season, time^2, canopy, slope)	0.00	0.950	11	561.31
ψ (.) p (site, season, time^2 , slope)	6.57	0.036	10	570.10
ψ (.) p (site, season, time, slope)	8.92	0.011	10	572.45
ψ (.) p (site, season, time^2 , canopy)	11.66	0.003	10	575.19
ψ (.) p (site, season, time, canopy)	15.74	<0.001	10	579.27
ψ (.) p (site, season, time, canopy, slope)	21.33	<0.001	11	565.30
ψ (.) p (site, season, time^2)	22.41	<0.001	9	588.14
ψ (.) p (site, season, time)	24.12	<0.001	9	589.85
ψ (.) p (.)	55.99	<0.001	2	636.19
B. GCWA				
ψ (.) p (site, season, time, canopy, slope)	0.00	0.713	11	970.17
ψ (.) p (site, season, time^2, canopy, slope)	1.89	0.277	11	972.06
ψ (.) p (site, season, time, canopy)	9.74	0.005	10	982.13
ψ (.) p (site, season, time^2 , canopy)	11.58	0.002	10	983.97
ψ (.) p (site, season, time, slope)	12.22	0.002	10	984.61
ψ (.) p (site, season, time^2 , slope)	13.77	0.001	10	986.16
ψ (.) p (site, season, time)	29.93	<0.001	9	1004.52
ψ (.) p (site, season, time^2)	31.13	<0.001	9	1005.72
ψ (.) p (.)	121.63	<0.001	2	1111.04

For black-and-white warblers model selection indicated a single competitive detection model that included the study design covariates, site, season, and time^2 and the habitat covariates, canopy and slope (Table 2A). These results indicate that the probability of detecting a black-and-white warbler differed among sites and was further influenced by the time of the season when the survey was conducted, the time after sunrise that the station was surveyed, and physiognomic attributes of survey stations. Based on the selected model, the estimated mean probability of detection for black-and-white warblers across all 216 stations and the four sampling occasions was 0.15 ± 0.04 . Detection probabilities for black-and-white warblers among study sites ranged from 0.02 ± 0.01 to 0.22 ± 0.06 .

For golden-cheeked warblers, model selection indicated two equally competitive detection models (Table 2B). Both models included the covariates site, season, canopy, and slope and differed only in including either the covariate time or time^2 . These results indicate that detection of the golden-cheeked warbler is influenced by the same study design and habitat covariates that were found to be important in detection of black-and-white warblers. The mean estimated probability of detection for golden-cheeked warblers across both models was $0.49 (\pm 0.05)$. Therefore, golden-cheeked warblers were more readily detected than were black-and-white warblers. Among study sites, average detection probabilities for golden-cheeked warblers ranged from 0.16 ± 0.04 to 0.69 ± 0.06 . Because

TABLE 3.—Summary of model selection showing covariates influencing the occupancy of (A) black-and-white and (B) golden-cheeked warblers at six study sites in the BCP, TX. Occupancy (ψ) was modeled for each species using covariates of detection selected in Table 2. Covariates of occupancy were site, canopy (C), slope (S), aspect (A) and interactions between habitat covariates. Selected models are indicated in bold. Model statistics and headings follow Table 2

Model	ΔAIC_c	<i>W</i>	<i>k</i>	-2LL
A. BAWW				
ψ (slope) p (site, season, time ² , canopy, slope) ^a	0.00	0.253	11	562.78
ψ (.)	0.33	0.215	11	547.42
ψ (canopy, slope, aspect)	0.35	0.213	13	558.62
ψ (site, canopy)	0.45	0.202	17	549.43
ψ (site, slope)	2.79	0.063	17	551.77
ψ (site, canopy, slope, aspect)	3.62	0.041	19	547.82
ψ (site, canopy, slope, aspect, C × S, S × A, C × A)	7.39	0.007	22	544.15
ψ (site)	7.79	0.005	16	559.13
ψ (aspect)	10.89	0.001	11	573.67
ψ (canopy)	11.86	0.001	11	574.64
ψ (site, aspect)	— ^c			
B. GCWA				
ψ (site, slope) p (site, season, time, canopy, slope) ^b	0.00	0.374	17	955.98
ψ (.)	0.39	0.307	11	970.17
ψ (site)	1.85	0.148	16	960.19
ψ (site, canopy)	3.44	0.067	17	959.42
ψ (site, aspect)	3.82	0.055	17	959.80
ψ (site, canopy, slope, aspect)	4.07	0.049	19	955.26
ψ (canopy)	142.40	<0.001	11	1112.18
ψ (aspect)	143.75	<0.001	11	1113.53
ψ (slope)	143.87	<0.001	11	1113.65
ψ (canopy, slope, aspect)	146.80	<0.001	13	1112.07
ψ (site, canopy, slope, aspect, S × A, S × C, C × A)	— ^c			

^a Detection covariates used for all models of BAWW occupancy

^b Detection covariates used for all models of GCWA occupancy

—^c Model did not reach numerical convergence

two detection models were equally competitive we subsequently ran all candidate occupancy models for golden-cheeked warblers using both detection models. However, choice of time linear or time² in the detection models did not affect the outcome of model selection, significantly alter Akaike importance weights for parameters, or alter parameter estimates. Thus for golden-cheeked warblers we report only results and parameter estimates based on the top ranked detection model.

For both warbler species 11 occupancy models comprised the candidate set (Table 3). For the black-and-white warbler six models received some support ($\Delta AIC_c \leq 4$; Table 3A). These models represent the confidence set (*i.e.*, models receiving $\geq 10\%$ of the weight of the top model). For the golden-cheeked warbler five models had $\Delta AIC_c \leq 4$ and together with the sixth ranked model represent the confidence set (Table 3B). For both species the null model was among the selected models likely due to the strong detection models. However, all the models in each confidence set had relatively low weights emphasizing that no one model had substantially better support than the others. There was no support for models that included interactions among habitat variables in either species.

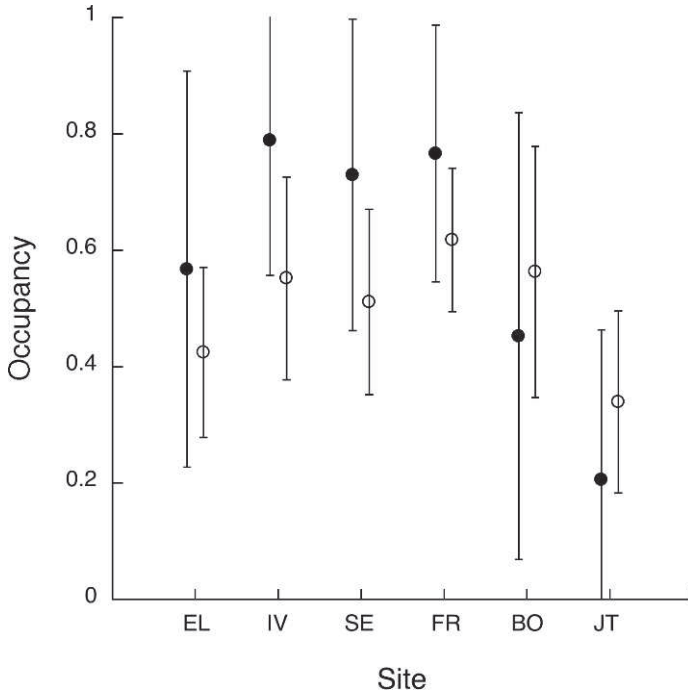


FIG. 2.—Estimated occupancy of black-and-white warblers (closed symbol) and golden-cheeked warblers (open symbol) adjusted for imperfect detection during the 2009 breeding season at six BCP study sites: Study sites are identified as in Table 1. Error bars represent ± 1 SD

Model averaging across all candidate models showed that estimated occupancy for black-and-white warblers across all sites and stations was 0.59 ± 0.36 (SD) and ranged among sites from 0.21 ± 0.26 (SD) to 0.79 ± 0.23 (SD) (Fig. 2). For golden-cheeked warblers occupancy across all sites and stations was 0.50 ± 0.19 (SD) and estimates ranged from a low to 0.34 ± 0.16 (SD) to a high of 0.62 ± 0.12 (SD) among sites. Estimated occupancy, adjusted for imperfect detection, and modeled using habitat covariates, was greater than observed (naïve) occupancy at four of six study sites for black-and-white-warblers. Conversely, for golden-cheeked warblers, estimated occupancy was less than naïve occupancy at four of six sites.

For both species the three habitat covariates appear in one or more of the confidence set of occupancy models. The relative importance of the habitat covariates and the site covariate on estimated occupancy was examined by summing the Akaike weights for each model that contained the parameter of interest. For black-and-white warblers, slope (0.58) and canopy cover covariates (0.46) had higher importance weights than aspect (0.26) while for golden-cheeked warblers the slope covariate (0.43) had higher weight than either canopy cover (0.12) or aspect (0.11). For black-and-white warblers, the site covariate weight (0.32) was less than the top habitat covariate weight, while for the golden-cheeked warblers the site covariate had a greater weight (0.68) than any habitat covariate.

Model-averaged estimates of regression coefficients for covariates that influence occupancy, standardized prior to analysis, allow direct comparison of the estimated affects

TABLE 4.—Regression coefficients (\pm SE) for covariates that influence A) the probability of detection, and B) habitat occupancy of black-and-white and golden-cheeked warblers at six study sites in the BCP, TX during 2009. For occupancy, model-averaged estimates and unconditional SE's are based on all models in the candidate set shown in Table 3. Variables are standardized hence coefficients can be compared within species

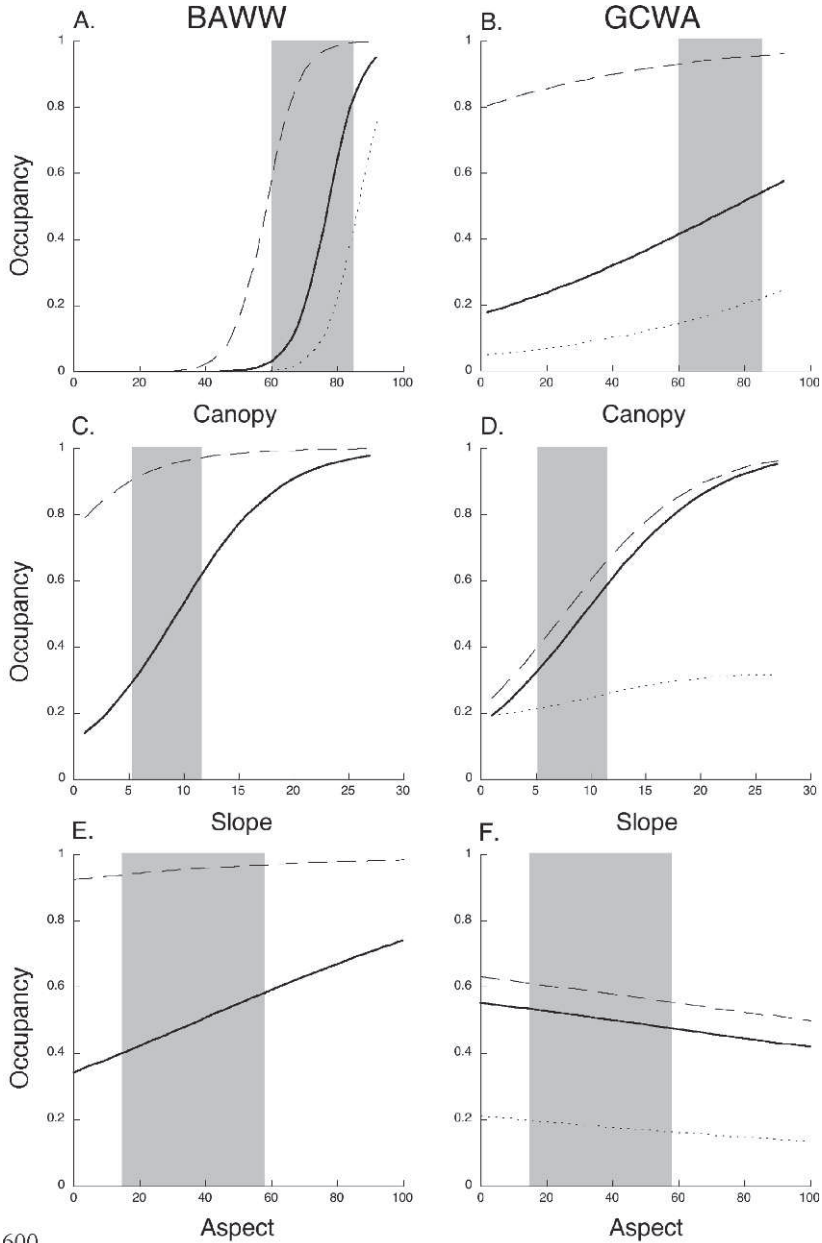
BAWW			GCWA		
Covariate	Estimate	SE	Covariate	Estimate	SE
A. Detection probability					
Canopy cover	0.533	0.199	Canopy cover	0.378	0.102
Slope	0.587	0.152	Slope	0.366	0.106
Time	—	—	Time	0.111	0.080
Time ²	-0.284	0.142	Time ²	—	—
Season	0.015	0.005	Season	0.013	0.003
B. Occupancy					
Canopy cover	3.098	3.421	Canopy cover	0.317	0.360
Slope	0.995	0.391	Slope	0.783	0.365
Aspect	0.558	0.347	Aspect	-0.178	0.333

of habitat covariates on occupancy. Comparison of habitat covariates within each species (Table 4) suggests that slope and canopy cover have potentially strong positive influences on occupancy. However, the magnitude of the SE's, adjusted for model uncertainty, for each covariate indicates a high level of variation surrounding the estimates.

Plots of model-predicted occupancy as a function of variation in each habitat covariate provide further insights into the relative effects of habitat variables (Fig. 3). For black-and-white warblers, canopy cover has a strong binary effect on occupancy as predicted occupancy is approximately zero for areas of canopy cover <60% but increases rapidly (to >0.8) as canopy cover approaches 80% (Fig. 3A). This effect is altered slightly depending on the slope of the terrain; with a steeper slope shifting the effect toward greater occupancy at a given canopy cover (Fig. 3A). A similar strong binary response to canopy was not revealed for golden-cheeked warblers although their predicted occupancy does increase steadily with an increase in canopy cover (Fig. 3B). Both species showed similar modeled responses to terrain slope: occupancy is predicted to increase steadily with increasing slope with a possible binary effect evident (Figs. 3C, D). Lastly, the results for aspect indicate that black-and-white warblers are predicted to have a steadily increasing probability of occupying an area as a greater percentage of the area represents mesic (north to northeast facing) habitat (Fig. 3E) whereas golden-cheeked warblers are either unaffected or show only a slight negative response to increasing mesic habitat (Fig. 3F).

DISCUSSION

Both warbler species responded to a general habitat feature that characterizes the physiognomy of the eastern edge of the Edwards Plateau: slope of the terrain. As well both species responded to variation in percent canopy cover of juniper-oak woodlands. That is, neither species occupied all 216 survey stations with high probability. Rather, each species' probability of occupying a survey station depended, in part, on the slope of the terrain and the canopy cover within the immediate area surrounding the station in addition to unspecified site effects. Site effects have previously been shown by Hunt *et al.* (2012) to affect occupancy of golden-cheeked warblers throughout the BCP. Black-and-white warblers



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FIG. 3.—Predicted occupancy of black-and-white and golden-checked warblers as a function of variation in habitat covariates. For each species logistic regression using the coefficients shown in Table 4 was used to estimate occupancy. (3A–B) Predicted occupancy \times canopy cover with slope held constant at its mean (solid line), maximum (dashed line) and minimum value (dotted line). (3C–D) Predicted occupancy \times slope with canopy cover constant at its mean (solid line), maximum (dashed line) and minimum value (dotted line). (3E–F) Predicted occupancy \times aspect with canopy cover

exhibited a strong affinity for steeply sloped areas with occupancy approaching 1.0 given average to high canopy cover. The predicted response to increasing canopy cover was also strong as the species is predicted to be excluded from survey stations when canopy cover is less than 40%. The predicted interrelationship between slope, canopy cover, and occupancy is further evident by the prediction shown in Figure 3C: at the highest observed canopy cover there is little effect of increasing slope on predicted occupancy. Black-and-white warblers thus appear more likely to occupy (establish breeding territories in) areas with relatively steep slopes of 10° or more, although inspection of plots of canopy cover and slope (not shown) show that these same areas always have canopy cover of 50% or greater. This even if black-and-white warblers primarily use slope as a cue for habitat selection in this region, they end up occupying territories that have a relatively dense canopy cover. Therefore, in central Texas at the southwestern edge of the breeding range, black-and-white warblers have retained an association with a habitat composed of a dense forest canopy as in eastern and northern parts of the breeding range (James, 1971; Collins, 1983; Conner *et al.*, 1983; Yahner, 1986; Dettmers *et al.*, 2002).

Golden-cheeked warblers were broadly distributed across the six study sites as warblers were detected at least once at 167 of the 216 survey stations (77%). DeBoer and Diamond (2006) revealed an association of golden-cheeked warblers with high juniper canopy cover and more generally landscape composition (percent forested) is considered a primary determinant of occupancy (Magness *et al.*, 2006). Our results affirm the relationship between canopy cover and probability of occupancy as we found that predicted occupancy increased with increased canopy cover (broadleaf and evergreen cover not distinguished) across the total range of canopy cover present across all survey stations (Fig. 3B). However, unlike in black-and white warblers, the relationship between occupancy and increasing canopy cover for golden-cheeked warblers depends on associated values of slope (compare Figs. 3A, B). For example only a minimal increase in occupancy is predicted for golden-cheeked warblers in response to increased canopy cover at high values of slope (Fig. 3B). In contrast occupancy of golden-cheeked warblers is predicted to increase sharply as a function of slope (Fig. 3D) for average to high values of canopy cover. Thus it appears that for golden-cheeked warblers slope is a stronger predictor of habitat use in the BCP than is dense canopy cover.

Given the importance of the habitat variable “aspect” to woodland forest structure in central Texas (Van Auken *et al.*, 1981) we predicted aspect would play a prominent role in predicting occupancy. However despite the variation present within and among study sites we found little evidence to support our hypothesis. Relative Akaike importance weights, model averaged coefficients for aspect, and the predicted response of occupancy to change in aspect all suggested a limited role of aspect in determining occupancy in both species.

Occupancy modeling provides the opportunity to develop indices of abundance that provide information on distribution that represent “improvements” to naïve estimates in that estimates are adjusted for the imperfect detection of the species. Our analysis of the survey data for golden-cheeked warblers previously examined by Hunt *et al.* (2012) affords an opportunity to simultaneously examine, in the context of a single model selection

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constant at its mean (solid line), maximum (dashed line) and minimum value (dotted line). For 3A–3D aspect was held at its mean value; for 3E–F slope was held at its mean value. The shaded region of each graph shows the range of variation in the mean value of the x-axis covariate across study sites

exercise, detection models that do and do not include habitat covariates on detection. Study of the detection process by Hunt *et al.* (2012) indicated two equally competitive models for probability of detection of golden-cheeked warblers: ψ (.) (site, season, time) and ψ (.) (site, season, time²). We found that when compared with detection models that also included the habitat covariates, canopy and slope, the selected models of Hunt *et al.* for probability of detection were not supported (Table 2). We conclude models of detection for the golden-cheeked warbler that include slope and canopy cover assessed at each survey station are superior to models that do not account for variation in habitat among stations.

Occupancy modeling also allows us to provide the first comparative assessment of naïve and estimated occupancy within the BCP reserve for these two warbler species. Black-and-white warblers were seldom encountered (detected) during surveys in comparison to golden-cheeked warblers as black-white warblers naïve occupancy (35%) was less than half of that observed for the golden-cheeked warbler (77%). Thus a naïve survey of the BCP for both species, unadjusted for unequal probability of detection of the two species, would conclude that black-and white warblers are far less common throughout the BCP than golden-cheeked warblers. However, adjusted for imperfect detection, and modeled using habitat covariates, the overall estimated occupancy of the black-and-white warbler at the BCP of 59% far exceeded the naïve estimate. Estimated occupancy was increased for most study sites. Thus we have learned that black-and-white warblers are more common than suggested by encounter rates and can be expected to occupy appropriate habitat throughout the BCP. In contrast, inclusion of habitat covariates for detection and for occupancy (Table 4B) produced an overall estimate of occupancy for the golden-cheeked warbler (50%) that was less than observed naïve occupancy. That is golden-cheeked warbler were observed to be present at many of the study sites above the predicted value based on the model-averaged estimate. Predicted occupancy is simply the probability that the species is present at a given survey station (corrected for probability of detection) given model parameters such as habitat covariates. An imperfect detection history (*e.g.*, the species was detected 1 out of 4 surveys) per station could lead to a predicted occupancy less than 1.0 while naïve occupancy would remain at 1.0. Simply put, naïve occupancy often represents either an overestimation or underestimation of true occupancy. Also, the inclusion of habitat covariates means that predicted occupancy at a given survey station, thus reflected in site means, is dependent on the habitat covariates included in model selection. Additional factors, such as conspecific attraction (Ahlering and Faaborg, 2006) or proximity to favorable habitat not captured by our choice of metrics, may have played a role at some sites leading to higher naïve occupancy than predicted occupancy.

Overall, the use of occupancy modeling allows us to infer that black-and-white warblers are relatively common throughout the BCP in comparison to golden-cheeked warblers. Moreover, modeling of occupancy based on habitat covariates allows us to predict the presence of both warbler species throughout BCP as a function of local environment conditions. These results represent a baseline for comparison with future assessments within the BCP that may be motivated by regional changes in the habitats that surround the BCP, changes in habitat within the BCP or long-term climate change particularly for the black-and-white warbler that is at the southern terminus of its geographic range in south-central Texas.

The autecology of each species may provide some insight into the habitat associations revealed in our study. For example the positive and relatively strong association of black-and-white warblers with canopy cover, slope, and aspect might be explained by nesting behavior. Black-and-white warblers are open-cup ground nesters whereas golden-cheeked warblers are canopy nesters. Throughout the BCP, areas of high slope are usually associated

with high canopy cover whereas areas of high canopy cover may occur in areas of low to high slope. For black-and-white warblers, steeper slopes with high canopy cover and a northeastern exposure may provide a slightly more favorable cooler microclimate for nest site selection and (or) egg and nestling development. Certainly, black-and-white warblers in central Texas have to cope with higher ground and surface temperatures than they do in any other parts of their range. Part of their reproductive strategy could involve nesting on steep shaded slopes to lessen exposure of eggs, nestlings, and brooding adults to high temperatures in late afternoon and evening. Additionally, black-and-white warblers often place their nests at the base of shrubs or trees where they may find deeper leaf duff to conceal the nest from predators (Kricher, 1995). Such areas with considerable (non-juniper) leaf ground cover and deeper soil are more prevalent on drainage slopes than on the uplands within central Texas.

Because they nest within a canopy, golden-cheeked warblers may not face these same environmental challenges, and hence their predicted habitat associations are not as strong as those of black-and-white warblers (Fig. 3). A second, nonmutually exclusive hypothesis to explain the differences between the species may relate to variation in tree species composition. In the oak-juniper woodlands of central Texas, drainages (areas with greater slope) contain greater species diversity, particularly of broad-leaf deciduous species (Buechner, 1944; Russell and Fowler, 1999) as has been seen in other regions (Foster, 1988; Enoki and Abe, 2004; Cielo-Filho *et al.*, 2007). Thus a strong affinity for broad leaf tree species, especially those common in other parts of its range, may translate to the black-and-white warbler showing a greater response to canopy cover on the BCP. Additionally, the close association with Ashe juniper (*Juniperus ashei*) by the golden-cheeked warbler (Pulich, 1976; Kroll, 1980; DeBoer and Diamond, 2006) may explain the weaker association with canopy cover given that junipers are widely distributed across canopy cover classes.

Although our study was not designed to definitively identify the causes of the habitat affinities of either species, the study demonstrates the value of occupancy modeling in identifying species' responses to habitat attributes. Previous studies estimating habitat associations of the black-and-white warbler predated the advent of occupancy modeling (James, 1971; Collins, 1983; Conner, 1983; Yahner, 1986; Wilcove, 1988) and as such could not present predicted habitat affinities (such as in Fig. 3) corrected for imperfect detection. Our study also revealed a detection probability for black-and-white warblers ($P = 0.15 \pm 0.042$) lower than that reported by Alldredge *et al.* (2007) ($P = 0.41$) in a different habitat and geographic area. Estimating detection probability has become imperative in many monitoring programs. Likewise, obtaining accurate knowledge of habitat requirements is crucial to the management of most species. Therefore, as a conservation tool, occupancy modeling has tremendous potential because it accomplishes both of these tasks. Occupancy models will be most useful in identifying and quantifying important habitat variables when there is a substantial range of habitat types (or environmental variables) represented at survey stations and predicted occupancy among the stations varies.

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