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A Range-wide Survey of the Endangered Black-capped Vireo in Texas

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Abstract - *Vireo atricapilla* (Black-capped Vireo) is an endangered migratory songbird with a breeding range that exists predominantly within Texas. Despite the species' listing under the Endangered Species Act in 1987, Black-capped Vireos were largely undocumented in much of the range. We sampled over 10,700 points in Texas, resulting in 2458 Black-capped Vireo detections. We examined the relationship between Black-capped Vireo occurrence and vegetation and broad-scale landscape variables, and we assessed if detections were clustered. Black-capped Vireo detections occurred often on a common soil type but were found where slopes were higher in the western part of the range. We found evidence of clustering in six of our eight study areas but no evidence of habitat metrics driving that clustering. These data improve the current knowledge of Black-capped Vireo distribution and offer opportunities for improved guidance for conservation and management efforts.

Introduction

Successful conservation and management practices require knowledge of an animal's distribution within its range so that the entirety of the population is taken into account and efforts can be targeted to maximize their impact (Colwell and Dodd 1995, Debinski and Brussard 1994, Kantrud and Stewart 1984, Wiens and Rotenberry 1985). This knowledge is especially important for threatened and endangered species whose ranges might be fragmented or limited to portions of their original extent. However, adequately estimating a species' distribution can be challenging for species whose range is primarily located on private lands, where data might be limited. Distribution estimates and management strategies for species occurring mainly on private properties often must be extrapolated from habitat data collected at a few well-studied locations (Miller et al. 2004).

Vireo atricapilla Woodhouse (Black-capped Vireo; hereafter "Vireo") is a migratory songbird with a known breeding range throughout portions of central Texas, isolated areas in Oklahoma (Grzybowski 1986, Wilkins et al. 2006), and the states of Coahuila, Tamaulipas, and Nuevo Leon in Mexico (Farquhar and Gonzalez 2005). In November 1987, the US Fish and Wildlife Service (USFWS) listed the species as endangered under the Endangered Species Act (ESA) due to habitat loss from development, habitat destruction from

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grazing livestock and exotic herbivores, and nest parasitism by the *Molothrus ater* (Brown-headed Cowbird) (Ratzlaff 1987).

At the time of listing in 1987, approximately 350 adult Vireos were counted from surveys in 33 sites across Texas (Marshall et al. 1985). In 2006, the documented Vireo detections in the United States consisted of 6010 males, with almost 80% of these concentrated on just four managed properties: Fort Hood Military Reservation and Kerr Wildlife Management Area in Texas, and the Wichita Mountains National Wildlife Refuge and Fort Sill Military Reservation, which are adjacent, in Oklahoma (Wilkins et al. 2006). Knowledge of Vireo distribution and abundance beyond these public properties is limited, as most of the Vireo's breeding range overlaps private lands and has not been surveyed (Juarez 2004, Magness 2003, Maresh and Rowell 2000, Wilkins et al. 2006). This lack of quantitative information on the Vireo from across its range prevents a reliable evaluation of the species' habitat use and status and limits broad-scale planning and implementation of management actions that would enhance conservation of the species.

Breeding habitat for the Vireo in the US is composed of patches of low, scrubby shrubs and trees that are primarily deciduous and of irregular height with sufficient vegetative cover near the ground to protect the low nest (typically placed about 1 m above ground; Graber 1961, Grzybowski 1995). However, habitat can vary greatly in vegetation composition and other characteristics across the range. The ability to map potential Vireo habitat across its breeding range, and thus improve our knowledge of the species' distribution, would first require analyzing relationships between Vireo occurrence and environmental characteristics. Unfortunately, quantifiable predictors of Vireo habitat—both those that can be measured via remote-sensing and measurements that must be collected on the ground—are largely unknown (Wilkins et al. 2006), and characteristics of the understory are difficult to discern via remote-sensing techniques such as aerial photography and satellite imagery.

As a potential complication for predicting Vireo distribution and habitat use, prior research (Ward and Schlossberg 2004) and field experience (M. Morrison, Texas A&M University, College Station, TX, unpubl. data) indicate there is a tendency for Vireos to form clusters of individuals. Such clustering could be a product of habitat distribution (i.e., the habitat is clustered) or a behavioral process unrelated to habitat features (Block and Brennan 1993, Dall et al. 2005, Hilden 1965, Jones 2001). For example, the presence of conspecifics can act as an indicator of local habitat quality (Danchin and Doligez 2001, Valone 1989). Conspecific attraction could complicate the ability to associate Vireo occupancy with environmental factors by reducing distributional uniformity and, thus, the ability to detect environmental differences between occupied and unoccupied areas.

Our goal was to quantify the distribution and habitat use of the Vireo in Texas based on surveys conducted in 2009 and 2010 on public and private properties. Using both randomly distributed and area-focused survey methods and comparing the results of each, our objectives were to 1) assess the distribution of

Vireos throughout their range in Texas and evaluate their distribution in relation to broad-scale environmental factors, 2) assess the distribution of Vireos within eight study areas to determine whether detections are spatially aggregated on the landscape, and 3) evaluate local-scale vegetation factors to assess Vireo clustering in relation to certain habitat metrics. This study provides the first steps in an effort to model Vireo distribution and habitat within their breeding range.

Methods

As detailed below, we surveyed properties randomly distributed across the range of the Vireo in Texas in 2009 to increase knowledge of their current distribution. To investigate the potential for Vireos to cluster within available habitat, we focused our 2010 survey efforts within eight areas where Vireo were known to occur. Sampling methods differed between years.

Randomly distributed surveys (2009)

To identify areas for Vireo surveys, we first compiled recent (1996 to 2008) Vireo detections from Texas A&M University, Texas Parks and Wildlife Department (TPWD), and other studies on both private and public lands published in the literature or submitted to USFWS (see also Wilkins et al. 2006). Using ESRI ArcGIS 10, we estimated the percent woody canopy cover at each Vireo detection location using the 2001 National Land Cover Database (NLCD; http://landcover.usgs.gov/). Based on the frequency distribution of canopy cover for these Vireo detections, we identified appropriate areas to survey within ecoregions (US Environmental Protection Agency Level III Ecoregions, based on Omernik 1987) as land with 1–40% canopy cover in the Edwards Plateau and Cross Timbers ecoregions and >10% canopy cover in the Chihuahuan Desert ecoregion. Using the Vireo range in Texas, as defined by the US Fish and Wildlife Service's recovery regions as suggested for modification (USFWS 1996), we extracted locations with the appropriate canopy cover values as appropriate survey areas. We also chose to include some areas outside of the Vireo range in our appropriate survey areas based on the canopy cover values. This survey included parts of the Central Great Plains and Southwestern Tablelands ecoregions, which we grouped with the Edwards Plateau and Cross Timbers ecoregions, and the Arizona/New Mexico Mountains, which we grouped with the Chihuahuan Desert ecoregion. Additionally, we excluded from the appropriate survey areas any land-use classes known to be unsuitable for habitat (e.g., cultivated lands, water) and all areas lying within the urban areas layer as delineated from the Texas General Land Office, and the StratMap city limits layer as delineated by the Texas Natural Resources Information System.

We created a 5-km x 5-km grid over Texas and, using a random selection process stratified by ecoregion, we selected a subset (*n* = 240) of those survey squares that overlapped any part of our appropriate survey areas. Additionally, we added a layer of survey squares around public properties with known Vireo detections to help focus some sampling around these protected areas, resulting in a total of 574 squares. Although the subset of squares guided our sampling effort, actual properties sampled were largely determined by our ability to acquire access permission. We first requested access to the public properties, but for private property access, we began selecting squares at random and acquired property ownership information within them using publically available information collected from local county appraisal offices. We could not sample properties with unlisted contact information or where we were denied access. We continued this process until we were granted access in ≈350 survey squares, which based on manpower and time, we estimated to be the absolute maximum number we could survey. Thus, the sampling for surveys in 2009 was limited by property boundaries located within these survey squares. Landowners base their participation on multiple factors that are usually not associated with land-management practices that would influence Vireo abundance (Hilty and Merenlender 2003, Sorice et al. 2011); therefore, we assumed that such access restrictions did not bias our sampling (Collier et al. 2010, 2012; DeBoer and Diamond 2006; Mathewson et al. 2012). Furthermore, we assumed that properties for which we were unable to acquire access were missing from our sample at random (Stevens and Jensen 2007). In some instances where we were unable to obtain property access, we performed roadside surveys.

Area-focused surveys (2010)

In 2010, we selected 8 study areas that were scattered across the breeding range of the Vireo in Texas (Fig. 1): (1) Devil's River: Devil's River State Natural Area, (2) Kickapoo: Kickapoo Caverns State Park and surrounding private properties, (3) Devil's Sinkhole: private properties surrounding Devil's Sinkhole State Natural Area, (4) Kerr: private properties surrounding Kerr Wildlife Management Area (WMA), (5) Mason: private properties surrounding Mason Mountain WMA, (6) Balcones: Balcones Canyonlands National Wildlife Refuge and surrounding private properties, (7) Fort Hood: Fort Hood Military Reservation and nearby private properties, and (8) Taylor: private properties in Taylor County. We chose the first 7 of these locations based on known occurrence of Vireos, as determined by our surveys in 2009 or concurrent research. We included an additional location, Taylor, to expand our sampling in the north-central portion of the range (Fig. 1). Within each of the 8 study areas, we focused on a central location and attempted to gain as much contiguous property access at, and around, that location as possible, including both public and private lands. This sampling strategy allowed us to more thoroughly investigate the possibility that groups of birds were non-randomly distributed over potentially suitable habitat.

Field surveys

We surveyed during the breeding season (1 April–30 June) in 2009 and 2010 from sunrise to 13:00. Our primary objective was to document presence or absence of Vireos at each property rather than provide rigorous abundance estimates. For both years of surveys, we avoided areas of open pasture or dense woodlands (i.e., <1% or >85% canopy cover) while surveying. We surveyed all potential habitat on each property over the course of 1 to 4 days depending on the size of the property. We did not survey during inclement weather (e.g., excessive rain or wind >20 km/h), or any other conditions (e.g., fog) that would inhibit our ability to detect the birds. We required all observers to show proficiency in identifying Vireo by sight and sound before conducting surveys.

During the randomly distributed surveys in 2009, two observers conducted auditory and visual surveys for Vireos within each accessible property or along a fence line in the case of roadway surveys. Both observers covered the same area but did so separate from each other (e.g., starting on opposite sides of a property). They traversed the property slowly and systematically, stopping every 20 minutes for a 5-minute point survey, and recorded all Vireos detected while traversing the property or during the point survey. When Vireos were detected, observers walked to within 5 m of each Vireo and recorded its location using a handheld GPS unit.

For the area-focused surveys in 2010, we created a grid of points (300 m x 300 m) that covered all accessible properties in each of our 8 study areas. We conducted a 5-minute auditory and visual survey at each point with 1 observer and recorded distance (≤100 m and >100 m) and direction to each Vireo detected from that point. In addition, we recorded Vireo locations detected while walking between points. We plotted all Vireo detections using ArcMap. Therefore, our methods yielded point-survey locations and actual Vireo locations in 2009 and resulted in point-survey locations and estimated Vireo locations in 2010.

Vegetation measurements

During our area-focused surveys, we measured vegetation characteristics at each point-survey location to provide an index of vertical structure of woody vegetation and an index for dispersion of woody vegetation (density of vegetation). These metrics represent vegetative indices thought to influence Vireo occurrence (e.g., presence of a browse-line; Grzybowski et al. 1994). We imagined 4 transects radiating from each point, with one transect oriented in the direction of the closest woody vegetation (≥1 m tall) and subsequent transects at 90°, 180°, and 270° from the first transect. For each transect direction, we took measurements on the closest woody plant on that transect, using the dominant plant if multiple plants occurred as a clump. Our vegetation measurements yielded the following metrics: (1) average distance to vegetation: the average distance from the survey point to the closest woody vegetation across the four transects, (2) vegetation height at top: the average height of the woody vegetation across the four transects estimated to the nearest meter, (3) vegetation height at bottom: the average height of the lowest foliage cover of the woody vegetation across the four transects estimated to the nearest 0.1 m, (4) oak index: the number of transects along which an oak species was the closest woody vegetation to the survey point, and (5) juniper index: the number of transects along which a juniper species was the closest woody vegetation to the survey point. All observers received training in these vegetation measures prior to the field season and were required to show proficiency.

Remote sensing and GIS

We quantified remotely sensed habitat characteristics at and around Vireo detections and non-detection locations (defined below, see Analyses) using geospatial analysis tools in ESRI ArcGIS 10 and data layers that provided information on ecoregion, ecosite, and topography. We created a 100-m buffer around

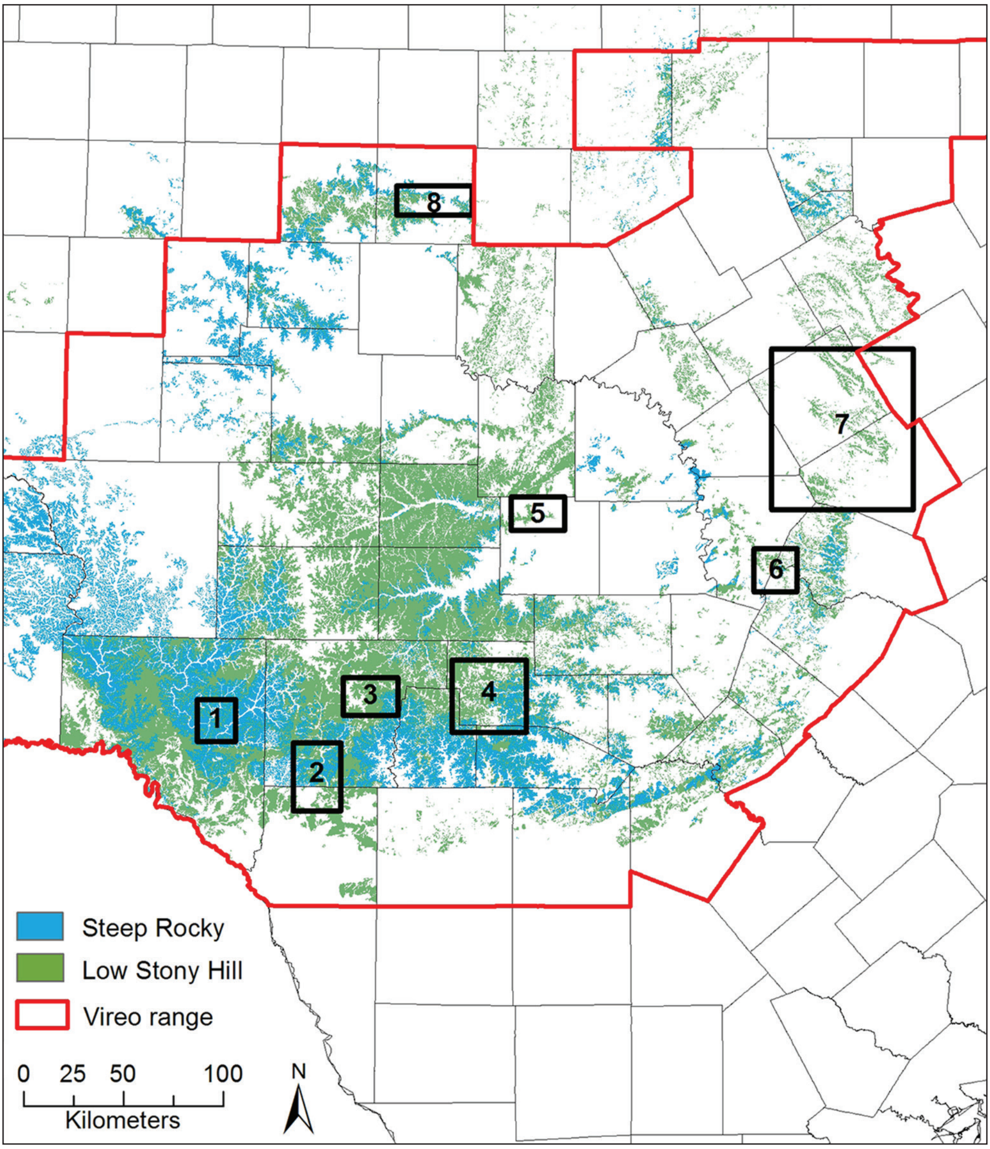

Figure 1. Locations of Texas A&M 2010 area-focused study regions for Black-capped Vireo surveys: 1) Devil's River State Park and surrounding area, 2) Kickapoo Caverns State Park and surrounding area, 3) Devil's Sinkhole State Park and surrounding area, 4) Kerr Wildlife Management Area and surrounding area, 5) Mason County area, 6) Balcones Canyonlands National Wildlife Refuge and surrounding area, 7) Fort Hood Military Reservation and surrounding area, and 8) Taylor County area. Black-capped Vireo breeding range is outlined in red as suggested for revision by the Population and Habitat Viability Assessment Report (USFWS 1996).

each point within which to quantify the characteristics. The 100-m buffer approximated the mean territory size of a Vireo (3 ha; range of mean territory sizes = 1.5 to 3.6 ha; Graber 1961, Tazik 1991).

To categorize the buffered areas according to ecoregion and ecosite, we used the Level III Ecoregions and the Natural Resources Conservation Service (NRCS) ecological site description (ESD; NRCS 2010), respectively. For locations where the ecosite was undefined in the ESD database, we referred to the NRCS soil surveys for the ecosite description. In addition, we calculated the proportion of the landscape within the 100-m buffer that was comprised of a particular ecosite. Ecosites have not been mapped for some areas in the western part of the range; thus, the Arizona/New Mexico Mountains ecoregion and much of the Chihuahuan Desert ecoregion are not included in the ecosite analyses, accounting for the smaller sample size in the Chihuahuan Desert ecoregion for these analyses.

We used the USGS National Elevation Dataset 1/3 arc-second digital elevation models (DEM; 10-m resolution) to derive slope (degrees), planimetric curvature (degrees/100 m), and profile curvature (degrees/100 m) for each 100-m buffer, which indicates the convexity or concavity of the slope (Carson and Kirkby 1972, Schmidt et al. 2003). Profile curvature is the rate of change of slope gradient in the direction of greatest change, where positive values are vertically concave and negative values are vertically convex (Carson and Kirkby 1972, Schmidt et al. 2003). A profile curvature value of zero means the slope is flat (Fig. 2). Planimetric curvature is the rate of change of direction of a contour line, or horizontal convexity (Carson and Kirkby 1972, Schmidt et al. 2003). Positive values for planimetric curvature are horizontally convex (water-diverging slopes)

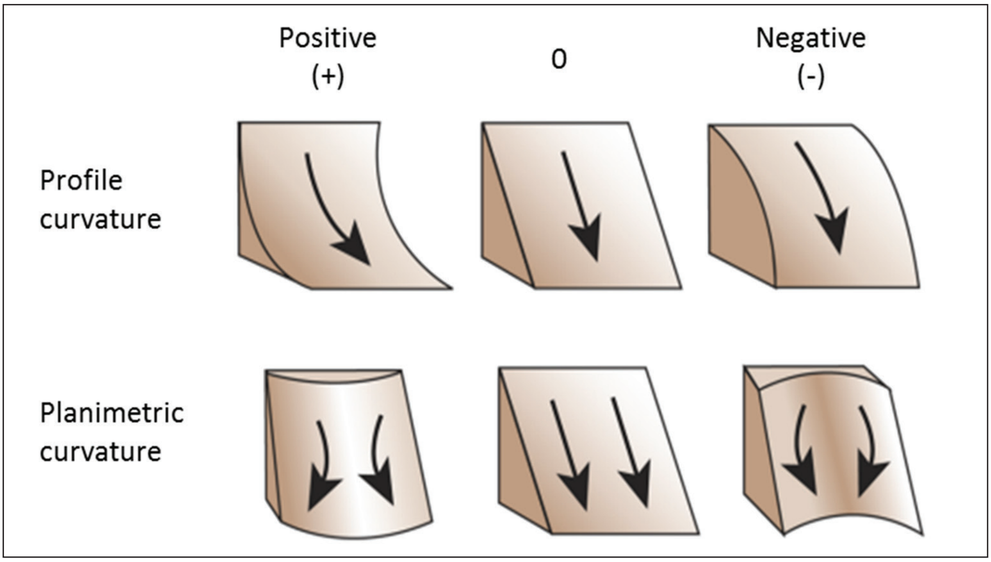

Figure 2. Depictions of profile and planimetric curvature values when the values are positive, zero, or negative. The black arrows indicate the path of objects travelling downhill. Figure adapted from the ESRI support site mapping center (http://blogs.esri.com/Support/blogs/mappingcenter/archive/2010/10/26/Understanding-Curvature-Rasters.aspx).

and negative values are horizontally concave (water-collecting slopes; Fig. 2). From a hydrological standpoint, profile curvature affects the acceleration or deceleration of flow across the land's surface, while planimetric curvature affects the dispersion of water as it flows downhill. Thus, these metrics indicate where water collects and flows, which could influence both the plant growth and food availability for the Vireo.

Anaylses

For analyses of the 2009 randomly distributed surveys, we defined detections as actual Vireo locations, while we defined non-detections as survey points where we did not detect Vireos within 200 m. For the 2010 area-focused surveys, for the gridded survey points, if we detected a Vireo within 100-m of the point, we defined the 100-m buffer surrounding each point as detections, regardless of whether we detected the Vireo during a point survey or while moving between points. We defined non-detections as 100-m buffers surrounding survey points where we did not detect Vireos within 100 m of the point.

The two independent but simultaneous surveyors in 2009 resulted in the possibility of each surveyor recording the same bird separately (i.e., 2 location points for the same individual). To reduce the potential of including a single bird twice in the analysis, we subset the 2009 detection points by including in the analysis only those bird locations that were >200 m from each other. We also included in the analysis a subset of non-detection points that fell >200 m from other non-detection points in order to prevent the area of analysis within the 100-m buffers from overlapping.

We report results based on ecoregion for our randomly distributed 2009 surveys and by study area for our 2010 area-focused surveys. We only considered ecosites that were represented in ≥10% of all buffered areas in a study area or that covered ≥10% of the area within the buffers. We compared means using *t*-tests to determine differences in ecosite proportions, remotely-sensed metrics, and vegetation metrics (2010 only) between detection and non-detection locations for each year. We report only statistically significant comparisons.

Spatial distribution

To determine whether Vireos were randomly distributed within our 2010 study areas, we used the centroids of the detection and non-detection buffer locations, spaced at 300 m, and assigned detections a value of 1 and non-detections a value of 0. For each of the 8 study areas, we first tested if the pattern of detections and non-detections was clustered, dispersed, or random using Global Moran's I statistic. The Global Moran's I statistic provides an index value between -1 and 1 and is interpreted similar to Pearson's correlation coefficient, with negative values indicating negative spatial autocorrelation, positive values indicating positive spatial autocorrelation, and values near 0 indicating no spatial autocorrelation (Fortin and Dale 2005). Next, if we detected positive spatial autocorrelation in a study area, we ran a cluster analysis in ArcMap Spatial Statistics (ESRI) using the high/low clustering tool (Getis-ord general G function; Getis and Ord 1992), to determine if detections, or non-detections were aggregated. For both tests, we used row standardization where spatial weights are divided by the sum of the weights of all neighboring survey points.

To determine whether the vegetation or remote-sensing metrics were associated with observed aggregation, we compared the spatial clustering test results with box-plots of each metric. If the spatial analysis indicated that Vireos were aggregated and if box-plots demonstrated obvious differences in the metrics for Vireo detections and non-detections, then we cannot separate clustering of the Vireos from clustering of the habitat because Vireos might be clustering at a different scale than we are examining (Fig. 3). However, if the Vireo detections were spatially clustered but box-plots suggest no obvious differences in any of our metrics between detections and non-detections, then we could reasonably conclude that either the Vireos are aggregating on the landscape for a reason other than habitat availability, or that our metrics are not appropriate for distinguishing between habitat and non-habitat (Fig. 3).

Results

Survey data

In 2009, we surveyed for Vireos within 282 survey squares, on approximately 300 randomly distributed properties in 57 counties and 6 ecoregions in central and west Texas, and detected Vireos in 25 counties (Fig. 4). Roadside surveys were conducted in addition to property surveys in 3 counties. We recorded 460

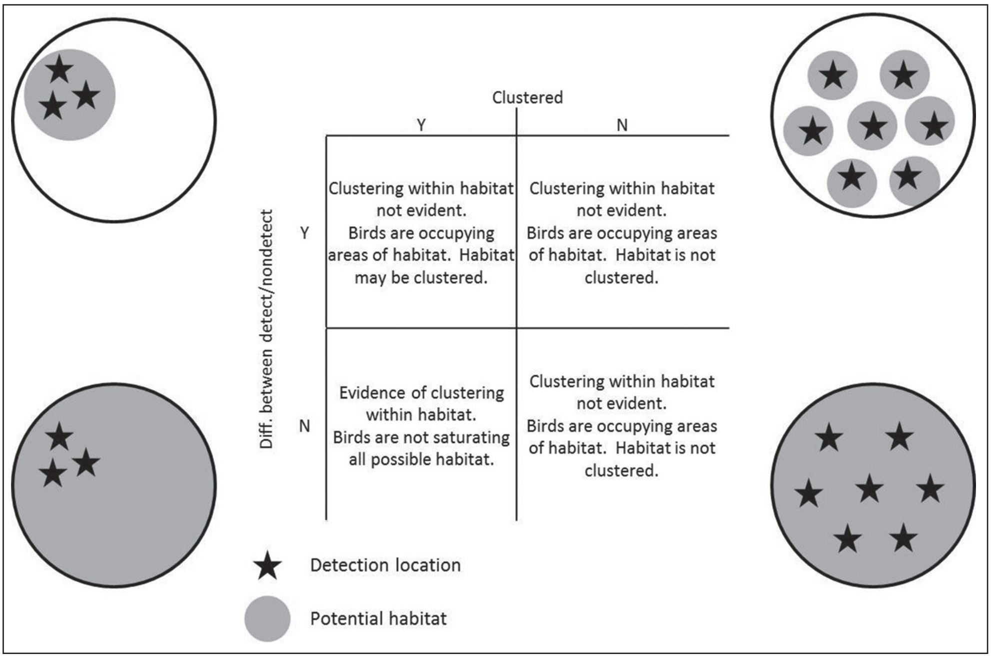

Figure 3. Concept behind clustering analysis and the relation to differences between detection and non-detection locations to get at the underlying cause of clustering. Large circles represent area surveyed. Only when the spatial analysis shows aggregation but no differences are found between detection and non-detection locations can we show evidence that Vireo are clustering for a reason other than habitat, as measured by our metrics.

Vireo detections at 11% (*n* = 4056) of the 5-min survey points. The subset of data used in the habitat comparisons included 2322 point-count locations (non-detection points) and 251 Vireo detections (Table 1).

In 2010, we surveyed 6207 survey points on approximately 100 properties within our 8 study areas; surveys occurred across 14 counties and 6 ecoregions. We detected Vireos within 100 m of 942 survey points (Table 2). The percent of

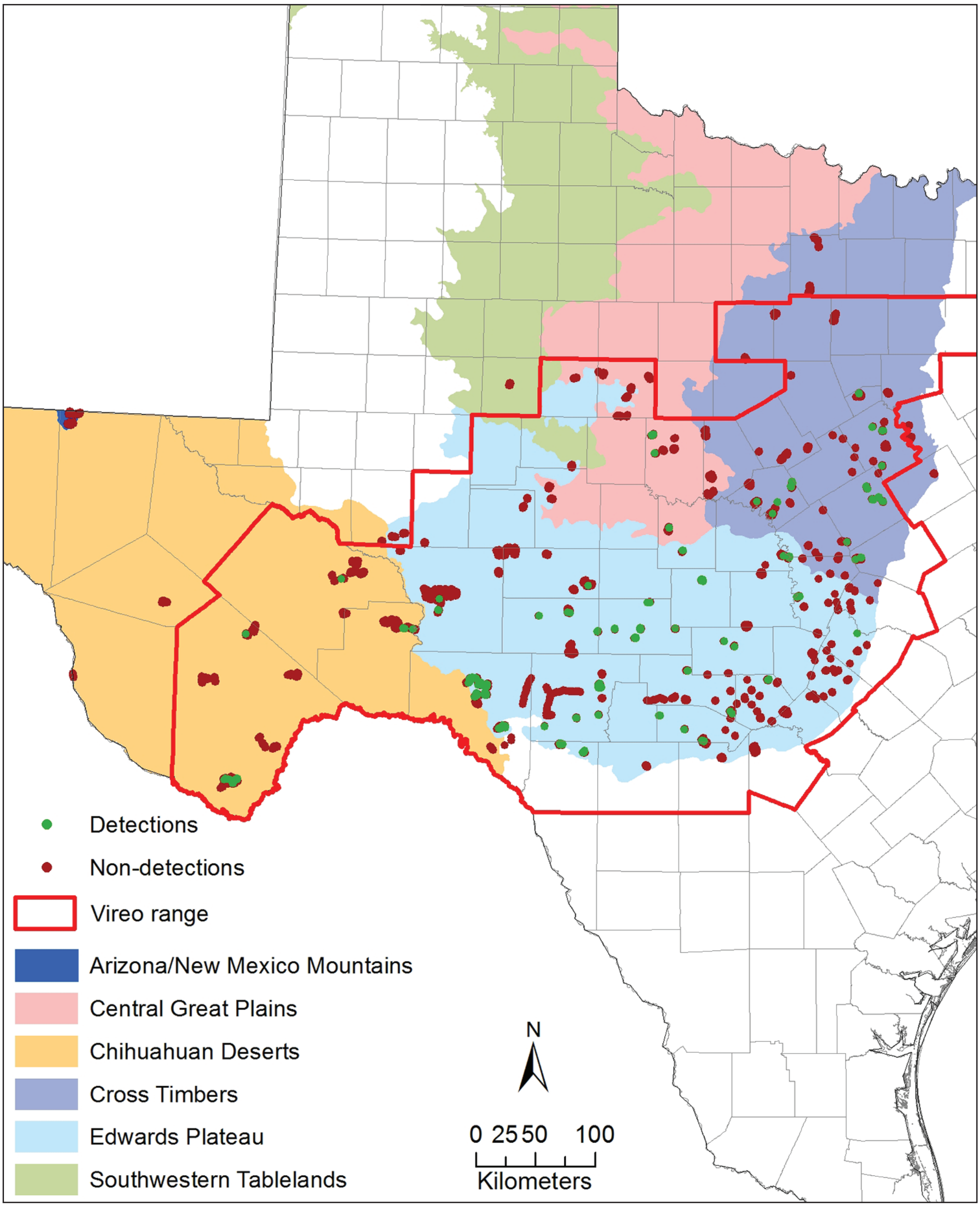

Figure 4. Results from Texas A&M 2009 Black-capped Vireo surveys. Sampling occurred in 57 counties in 8 different ecoregions across the range. Area outlined in red indicates the Vireo's breeding range in Texas as suggested for revision by the Population and Habitat Viability Assessment Report (USFWS 1996).

survey points with detections within our 8 study areas generally decreased from 27% in the west to 9.4% in the east (Table 2).

Remote sensing and GIS

Two main ecosites, Low Stony Hill and Steep Rocky, made up large a percent (>10% each) of the area within our buffers in both years of study (Figs. 1, 5). Low Stony Hill is characterized by relatively gentle slopes (<7°) and shallow, well-drained, moderately permeable soils, whereas Steep Rocky is characterized by similar soils but steep slopes (>7°; NRCS 2010). From our 2009 survey data, a higher average proportion of the detection buffers was comprised of Low Stony Hill than all buffers combined (i.e., available) across the three ecoregions (Fig. 5). However, our 2010 survey results indicated that Low Stony Hill was represented at points with Vireo detections more than

Table 1. Number of points visited and number of Black-capped Vireo detections by Level III ecoregion (based on Omernik 1987) during 2009 randomly distributed surveys. For analyses of detections and non-detections, we used a subset of all points visited (non-detections) and detections where all points were >200 m from each other.

	Total		Subset (>200 m)	
Ecoregion	Survey points	Vireo locations	Survey points (non-detections)	Vireo locations (detections)
Edwards Plateau	1945	355	1139	197
Cross Timbers	1007	51	469	27
Chihuahuan Deserts	688	35	493	24
Central Great Plains	288	19	156	3
Arizona/New Mexico Mountains	115	0	57	0
Southwestern Tablelands	13	0	8	0
Total	4056	460	2322	251

Table 2. Number of 100-m buffers surveyed, number of recorded Vireo detections, and percent of buffers with detections by study area during our surveys in 2010. Buffered points were on a 300-m x 300-m grid; buffers with a Vireo detection recorded within them were defined as detections, whereas those with no Vireo detections were defined as non-detections. Study areas are listed from west to east.

	100-m buffers surveyed				
Study area	Detections	Non-detections	Total	Recorded detections	Percent of buffers with detections
Devil's River	176	476	652	417	27.0%
Kickapoo	249	760	1009	443	24.7%
Devil's Sinkhole	21	440	461	48	4.6%
Kerr	222	1069	1291	389	17.2%
Mason	6	104	110	18	5.5%
Taylor	6	32	38	23	15.8%
Balcones Canyonlands	71	538	609	207	11.7%
Fort Hood	191	1846	2037	453	9.4%
Total	942	5265	6207	1998	15.2%

available at three of the study areas toward the eastern portion of the range (Kerr, Balcones, and Fort Hood) but was represented at detections less than available for the most western study region, Devil's River. No significant difference was detected for the other study areas (Fig. 5).

For our 2009 survey data, Steep Rocky was present only at points in the Edwards Plateau ecoregion, and detection buffers had higher average proportions of Steep Rocky than all buffers combined (Fig. 5). For the 2010 survey locations, detection buffers had higher average proportion of Steep Rocky than all buffers combined for our three western study areas, whereas this ecosite occurred in few, if any, of the central and eastern study areas (Figs. 1, 5).

Several other ecosites differed significantly between Vireo detections and non-detections. The ecosite Draw, which is associated with perennial streams (NRCS 2010), was significantly higher by 58% (absolute percent) at detections than at non-detections in the Chihuahuan Desert ($t_{391} = 6.3$, $P < 0.001$). Only 12% of the total area surveyed in the Chihuahuan Desert ecoregion was categorized as Draw, but Draw made up almost 70% of the area within each detection buffer, on average.

For our 2010 data, Adobe, an upland ecosite characterized by shallow, gravelly, droughty soils and slopes ranging from 0 to 12° (NRCS 2010), showed

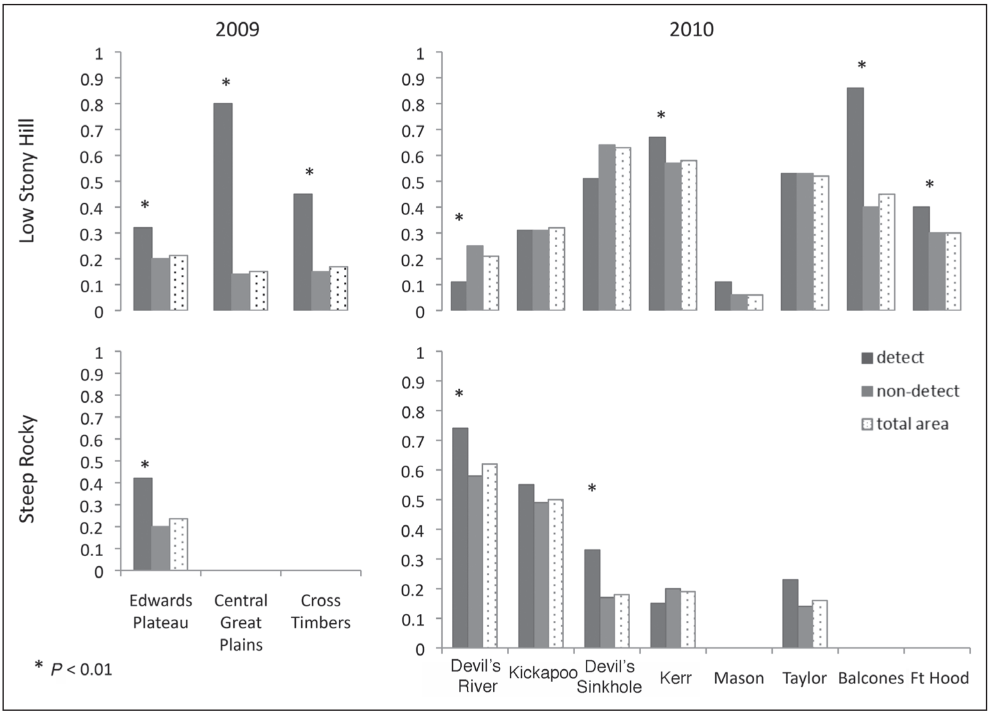

Figure 5. Average proportions of Low Stony Hill and Steep Rocky within 100-m buffers surrounding Black-capped Vireo detection points, non-detection points, and across all points, by ecoregion for surveys conducted in 2009 and for each study area surveyed in 2010. While the white bars (for total area) represent the availability of each ecosite within the study area, the *t*-tests compared the means between detection and non-detection points.

significant differences at three of the eastern study areas, and detection buffers had higher average proportion Adobe than all buffers combined at Mason and Fort Hood (Fig. 6). Additionally, the proportion of Shallow ecosite, characterized by shallow soils with moderate slopes and low water-holding capacity, was significant but lower at detections than non-detections Kickapoo (t_{1007} = 3.7, $P < 0.001$), composing only 6% on average of area within detection buffers and 13% on average of areas within non-detection buffers. Proportion of the ecosite Clay Loam, characterized by flat slopes and fertile soil with high water-holding capacity, was significantly different between detections and non-detections at Balcones (t_{607} = 2.9, P = 0.003), but Clay Loam was not present in any detection buffers and composed only 7% on average of area within non-detection buffers.

For the 2010 surveys, Vireo detections were associated with significantly steeper slopes at Devil's River, Kickapoo, Devil's Sinkhole, Mason, and Fort Hood, while Vireos were associated with less steep slopes at Balcones.

For our 2009 surveys, mean profile curvature was significantly different between Vireo detections and non-detections in the Edwards Plateau, where slopes at detection locations were slightly more concave (Table 3). For our 2010 data, profile curvature was significantly different only at Devil's River, where slopes were again more concave at detection locations (Table 4). Planimetric curvature was significantly different between detection and non-detection points only in the Cross Timbers ecoregion, where detections were on water-collecting (horizontally concave) slopes (Table 3).

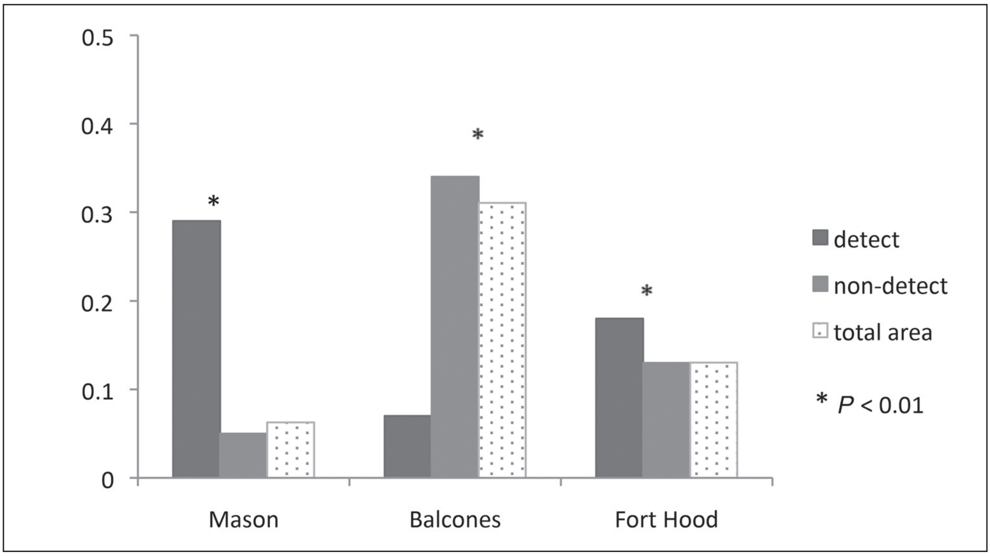

Figure 6. Average proportions of Adobe ecosite (NRCS 2010) within 100-m buffers surrounding Black-capped Vireo detection points, non-detection points, and across all points, by study area surveyed in 2010. While the white bars (for total area) represent the availability of each ecosite within the study area, the *t*-tests compared the means between detection and non-detection points.

Vegetation measurements

Although the 2010 survey data suggested several statistically significant differences between Vireo detections and non-detections within three study regions, the differences may not represent biological differences (Table 4). For example, the differences in vegetation height-at-top and height-at-bottom never differed by more than 0.5 m within any study area, and the distance to vegetation from the

Table 3. Results of significant ($P < 0.013$, Bonferroni adjusted) *t*-tests between Black-capped Vireo detection and non-detection points (including means and standard errors) for remote sensing metrics averaged over a 100-m radius circle. Data is from the 2009 randomly distributed surveys.

	Detection			Non-detection			
	n	Mean	SE	*n*	Mean	SE	*P*
Edwards Plateau							
Profile curvature	197	0.08	0.01	1139	0.03	0.00	<0.001
Cross Timbers							
Profile curvature	27	-0.03	0.01	469	0.01	0.00	0.006
Planimetric curvature	27	-0.03	0.01	469	0.01	0.00	<0.001

Table 4. Results of significant ($P < 0.006$, Bonferroni adjusted) *t*-tests between detections and non-detections (including means and standard errors) during the 2010 area-focused surveys for remote-sensing metrics averaged over a 100-m radius and local vegetation metrics taken around each point. Study sites are listed in a general southwestern to northeastern order.

	Detection			Non-detection			
	n	Mean	SE	*n*	Mean	SE	*P*
Devil's River							
Slope	176	13.78	0.45	476	11.86	0.30	0.001
Profile curvature	176	0.10	0.02	476	-0.03	0.01	<0.001
Veg height - Top	174	2.04	0.06	468	1.79	0.03	<0.001
Oak index	174	0.22	0.04	468	0.08	0.01	<0.001
Kickapoo							
Slope	249	8.79	0.27	760	7.55	0.16	<0.001
Veg height - top	242	2.64	0.05	754	3.02	0.04	<0.001
Veg height - bottom	242	0.16	0.02	754	0.23	0.01	0.004
Juniper index	242	1.65	0.08	754	1.92	0.05	0.005
Devil's Sinkhole							
Slope	21	9.50	1.36	440	5.60	0.26	0.002
Kerr							
Dist. to veg	222	7.76	0.38	1069	9.25	0.22	0.004
Veg height - top	222	3.21	0.08	1069	3.85	0.05	<0.001
Veg height - bottom	222	0.33	0.03	1069	0.62	0.02	<0.001
Mason							
Slope	6	4.86	0.94	104	2.61	0.14	0.001
Balcones							
Slope	71	2.76	0.33	538	5.39	0.18	<0.001
Fort Hood							
Slope	191	4.65	0.25	1846	3.56	0.07	<0.001

survey point differed between detections and non-detections by approximately 1 m at Kerr (Table 4).

Spatial distribution

The results of the Getis-ord General G test indicated that the Vireo detection points were clustered ($P < 0.006$, Bonferroni adjusted; Miller 1981) at all study areas except Devil's River, Devil's Sinkhole, and Taylor County (Table 5). We further determined for Devil's River and Devil's Sinkhole that the clustering of both detections as well as non-detections were not the cause of the insignificant *P*-values, as the Moran's I test indicated no clustering was occurring (Devil's River *z*-value = 0.479, $P = 0.532$, Devil's Sinkhole z-value = 0.270, $P = 0.787$) However, a Moran's I test for Taylor County results showed a clustering of both detections and non-detections (z-value = 3.115, $P = 0.002$).

Comparing these results to our remote-sensing and vegetation *t*-tests and associated box plots, we found the metrics showed extensive overlap between detections and non-detections. Slope was the only metric with some difference between detections and non-detections at Balcones, but the average difference was only about 2° (Fig. 7). Sample sizes at Mason and Taylor were too small to draw any conclusions.

Discussion

Using two different strategies for surveying Vireo and describing areas they occupy, our study indicated that while Vireos were rare when surveying across the range, particularly in the western portion of the range, Vireos were locally more abundant within our study areas in the west than in the east. The proportion of survey points from our area-focused surveys that had detections generally increased within our study areas from east to west. However, the results of our randomly distributed surveys showed only a few concentrations of Vireos west of the Devil's River area.

The effect of Low Stony Hill and Steep Rocky ecosites showed a gradient from east to west. Both ecosites, which have a common soil type and differ only

Table 5. Results of the Getis-ord General G test to determine clustering of the Vireo detections within each of our eight 2010 study areas. Clustering was indicated in all study areas except Devil's Sinkhole and Devil's River, where the analysis indicated the pattern was not statistically different from random.

	General G			
Study area	Observed	Expected	Z-value	*P*-value
Devil's River	0.002	0.002	0.475	0.634
Kickapoo	0.002	0.001	11.695	<0.001
Devil's Sinkhole	0.003	0.002	0.354	0.723
Taylor County	0.072	0.027	2.120	0.034
Kerr	0.002	0.001	12.677	<0.001
Mason County	0.039	0.008	11.069	<0.001
Balcones	0.004	0.002	17.758	<0.001
Fort Hood	0.001	0.000	33.654	<0.001

in slope, are clearly associated with Vireo occurrence, but Steep Rocky was used more often in western survey areas where both ecosites occur (Fig. 1). Although we did not find an obvious pattern between Vireo occurrence and slope, our data show that this soil type is used by Vireos when it occurs on slopes in the west and on more level areas in the eastern parts of the range. However, Vireos were generally detected on slightly greater slopes in 2010 in all study areas except Balcones. Vireo breeding habitat in Mexico is described as rocky slopes with shallow soils, consistent with our western study area results (Farquhar and Gonzalez 2005,

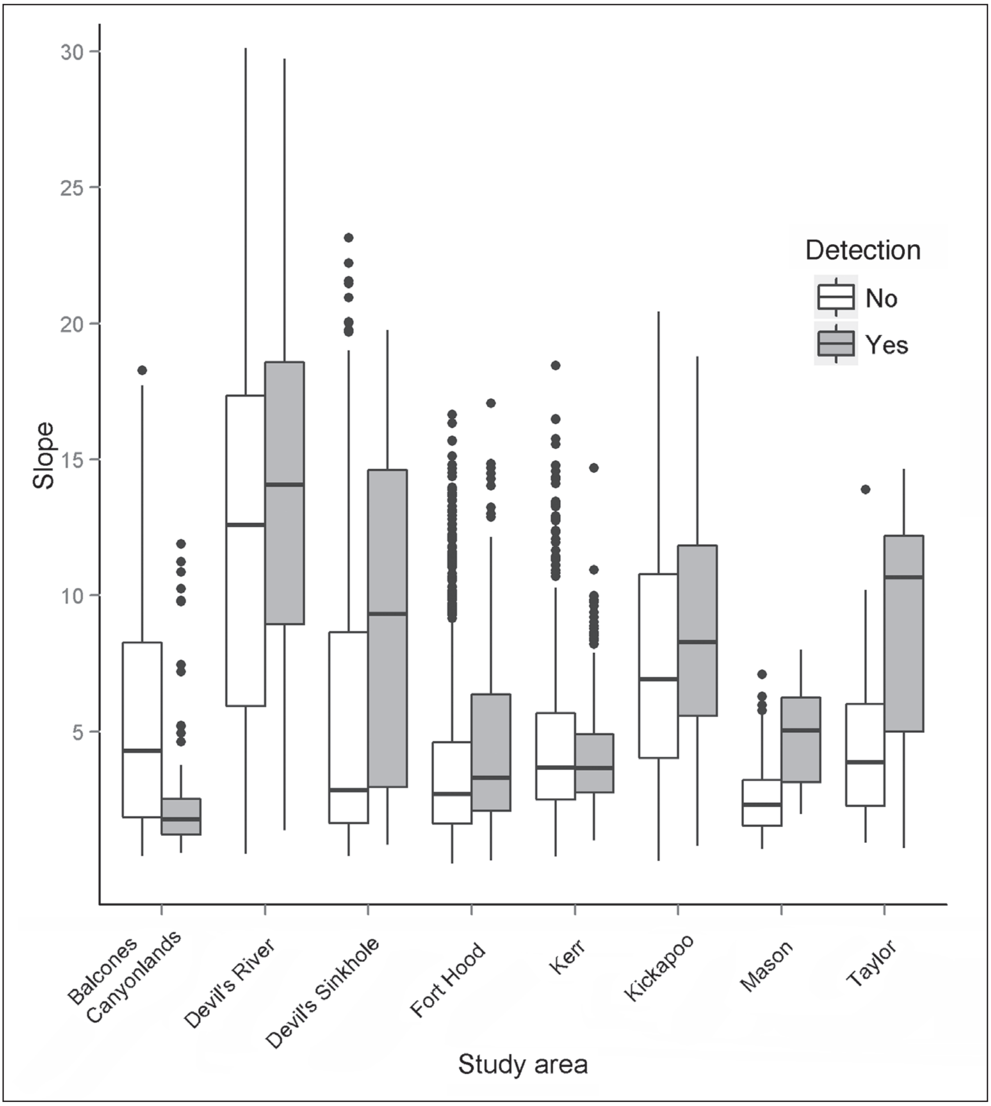

Figure 7. Box plots of average slope at each study site, comparing differences between detections and non-detections. Sample sizes are too small in Mason and Taylor to draw any conclusions from the differences. Average slope at Balcones differed with relatively little overlap, but the difference is only 2°, which is probably not biologically relevant. Boxplots for other metrics showed a similar inability to differentiate between detections and nondetections.

Graber 1961). Soil types have been used to help delineate avian habitat (Gottschalk et al. 2005, Vander Haegen et al. 2000), but ecosites have only recently been investigated for use in avian studies (Marshall 2011).

Differences in climate could help account for these east–west gradients in the proportion of occupied survey points and the effect of ecosite. As the climate becomes more arid from east to west, where and how vegetation grows will differ. Vegetation types that would grow on flatter areas in the east may only grow in drainages where water collects in the west, where rainfall is much lower. Similarly, soils with higher runoff would be more likely to support smaller vegetation in the west as compared to the east where there is more rainfall. Additionally, from east to west, the dominant vegetation differs in species composition, climax states, and structural characteristics. For example, climax vegetation in the west is predominately shrubs due in part to lack of rainfall compared to the east where the climax vegetation can become tall and dense woodland in the absence of natural or man-made disturbances (e.g., fire). Therefore, Vireo habitat is maintained without disturbance in the west (Farquhar and Gonzalez 2005) and requires disturbance in the east (Grzybowski et al. 1984). However, once the climate becomes too arid, the vegetation requirements for potential Vireo habitat can no longer be supported. This factor may explain the relative lack of detections farther west than the Devils River study area. Detections in the Chihuahuan Desert ecoregion were either in areas of higher elevation where the climate would be less arid, such as in the Chisos Mountains of the Big Bend area or in drainages where water collects and could support more vegetation.

Although there were some statistically significant differences between Vireo detections and non-detections in the study regions, vegetation characteristics were generally similar. We also found substantial overlap in the remotely sensed spatial metrics. Although the *t*-tests were significant, the box plots showed no distinct separation between areas with Vireo detection or non-detection. Further, the results of our spatial cluster analysis showed that Vireo detection points were spatially aggregated in all locations except Devil's River and Devil's Sinkhole, although the small sample sizes in Mason and Taylor make those results inconclusive. It is possible that the metrics we examined are not capturing a difference that the Vireos are cueing in on (e.g., food availability).

However, these results lend support to the idea that Vireos are clustering on the landscape and not occupying all potential habitat, potentially a product of conspecific attraction (Ward and Schlossberg 2004). Future work will further assess the Vireo aggregations to determine how the Vireos distribute themselves within areas at finer spatial scales in relation to each other and in relation to different habitat variables.

While many of our metrics showed significant differences between detection and non-detection locations within most of the ecoregions and study areas, we did not find many significant patterns across regions or across years. These results could be because our metrics were not appropriate for defining habitat or because Vireo habitat is so diverse across the range, it is just inherently difficult to measure or predict. Additionally, our metrics might be poor predictors of habitat when considered individually, but some combination of metrics might be more predictive of Vireo habitat. Future efforts will investigate multivariate analysis of our metrics and attempt to model habitat rangewide.

The ability to link Vireo occurrence and remotely sensed metrics such as soil type (using ecosites) allows us to estimate Vireo distribution and begin to map potential habitat within the range of the Vireo, providing better guidance for conservation and management efforts. Additionally, the potential that Vireo are clustering due to conspecific attraction could account for the apparent rangewide rarity of Vireo yet local frequency of detections found during our surveys, and this clustering has implications for management (Ahlering and Faaborg 2006). For instance, management practices that create new Vireo habitat may be more successful in recruiting Vireos if located adjacent to occupied habitat. Additional information is needed to determine how Vireo will disperse from one season to the next to further determine the implications of this clustering behavior and to predict habitat occupancy if new habitat is created.

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