QUANTIFYING BIRD-HABITAT USING A RELEVÉ METHOD

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ABSTRACT: The relevé method, a standardized, floristically based vegetation sampling technique developed in Europe, has become a vegetation measurement method used worldwide. Although the relevé method was developed by plant ecologists to classify vegetation, ornithologists have begun to use the method for bird-habitat studies, sometimes including modifications to better sample structural features of a habitat thought to influence bird occupancy. To evaluate the potential for these data to provide information about bird habitat, we compared the use of data acquired using an original relevé method to a modified relevé method to build explanatory bird occupancy models. Furthermore, time and effort required to collect relevé method data were compared against widely used vegetation data collection methods. In 2004-2005, point counts for bird occurrences, relevé vegetation measurements following original methods used by the California Native Plant Society, and a modified relevé method implemented by the California Department of Fish and Game, and time and effort data for both methods were collected in the Sierra Nevada foothill blue oak (*Quercus douglasii*) woodlands of Yuba and Nevada Counties, California. Occupancy models were built using both the original and modified relevé data for three focal bird species important in California's oak woodlands. Site occupancy and probability of detection showed strong associations with covariates collected using the original relevé method for spotted towhee (*Pipilo maculates*), whereas models for white-breasted nuthatch (*Sitta carolinensis*) were best supported using variables collected from both the original and the modified relevé methods. Environmental variables, which were not exclusive to either the original or modified relevé method, best predicted lark sparrow (*Chondestes grammacus*) occupancy and were competitive when compared to models built using relevé data for spotted towhee and white-breasted nuthatch. The modified relevé method, on average, was a more efficient method compared to the original relevé method and other common bird habitat quantification methods. Future research should focus on directly comparing data acquired using relevé methods to those of other bird-habitat quantification methods to test the accuracy of data in building explanatory bird-habitat relationship models.

Key Words: floristics, lark sparrow, occupancy model, physiognomy, spotted towhee, relevé, white-breasted nuthatch

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Avian ecologists need efficient, meaningful measurements for features of a habitat that may influence bird species occupancy (Morrison et al. 2006). In many studies, investigators have used traditional, plot-level quantification methods such as circular-plots (James and Shugart Jr. 1970, Martin et al. 1997), foliage-height diversity (MacArthur and MacArthur 1961, Rotenberry and Wiens 1980), line-intercept transects (Noon 1981), nearest-neighbor (Cottam et al. 1953), point-center quarter plots (Cottam and Curtis 1956), and visual obscurity (Robel et al. 1970). These methods generally provide mechanical estimations of plant cover or structural complexity that are useful in acquiring repeatable measurements over a study area. Although these traditional methods are popular because of their relative accuracy at plot-level scales, they may also be time consuming and, thus expensive. In search of cost-effective and accurate quantification methods, investigators have increasingly used ocular estimates to rapidly quantify vegetation features (Daubenmire 1959, Ralph et al. 1993). One such technique, the relevé method, has been used primarily by vegetation scientists. However, the approach has been adopted by ornithologists and modified for use in bird habitat modeling (Ralph et al. 1993, Heath and Ballard 2003,

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Alexander et al. 2007, Luther et al. 2008, Seavy et al. 2008).

The relevé method, developed in Europe and standardized by the Swiss ecologist Josias Braun-Blanquet (Braun-Blanquet 1964), is a patch-based vegetation sampling technique for describing and classifying vegetation (Poore 1955a, Poore 1955b). It is a semi-quantitative method that relies on ocular estimates of vegetation cover in discrete vegetation patches (Spribille et al. 2001) rather than on the frequency of occurrence of particular plant species within a plot or grid or along a transect. The relevé method is designed to provide a patch-level assessment based on plant-species composition useful for classifying the vegetation cover over large areas (Poore 1955c, Mueller-Dombois and Ellenberg 1974, Sawyer and Keeler-Wolf 1995). Since being introduced, the relevé method has gained popularity among vegetation ecologists and is regularly used to collect information about plant communities for ecological studies (Mucina et al. 1993, Sawyer and Keeler-Wolf 1995, Mucina et al. 2000, Spribille et al. 2001).

Although the relevé method has proven useful for plant ecologists, the method differs from most bird-habitat quantification techniques because it is not designed to sample structural features that may influence habitat use by birds. Two important features of a vegetation community which influence habitat selection of breeding birds are vegetation structure (physiognomy) and plant species composition (floristics, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Rotenberry 1985, MacNally 1990). Therefore, ornithologists applying relevé methods have often modified the protocols to provide both floristic and physiognomy data (Ralph et al. 1993, Heath and Ballard 2003, Alexander et al. 2007, Luther et al. 2008, Seavy et al. 2008).

The relevé method is increasingly being used for vegetation sampling by natural resource agencies and conservation organizations (Ralph et al. 1993, Minnesota Department of Natural Resources 2007). For example, the California Department of Fish and Game (CDFG) and the California Native Plant Society (CNPS) collaborated on a state-wide vegetation sampling effort using a relevé method (Sawyer and Keeler-Wolf 1995). The CNPS has collected vegetation data using relevé methods in an effort to characterize and map vegetation communities throughout California. The CDFG has collaborated with the CNPS by modifying the original CNPS relevé methods by including physiognomic data, which may be useful for quantifying bird habitat. Such efforts generate large-scale and extensive vegetation data that could potentially be useful for understanding bird-habitat relationships. A better understanding of relevé methods and their modifications may enable ornithologists to recommend changes to sampling efforts to help maximize their use for studies of habitat use by birds.

Our overall objective was to test the use of a relevé method in quantifying bird habitat. To address our overall objective, this project had three goals. Our first goal was to examine the overall cost and efficiency of the original CNPS relevé method and the modified CDFG relevé method, compared to two other common bird quantification methods: the circular-plot (James and Shugart 1970), and the Breeding Biology Research and Monitoring Database field protocol (BBIRD, Martin et al. 1997). Our second goal was to determine whether the original CNPS relevé method, which is focused on vegetation composition, or the modified CDFG relevé method, which is focused on vegetation structure is more effective for providing data useful for modeling occupancy patterns of three focal bird species in the woodlands of the Sierra Nevada foothills. Our third goal was to offer recommendations for users of the relevé method to quantify bird habitat.

Study area

This study was conducted on public lands in Yuba and Nevada counties in the foothills of the Sierra Nevada Mountain Range, California, USA. State lands surveyed included the Spenceville (4635 ha) and Daugherty Hill (1020 ha) Wildlife Areas managed by the CDFG as well as the Sierra Foothill Research and Extension Center (2310 ha) managed by the University of California. The climate of Yuba and Nevada counties is Mediterranean and characterized by hot dry summers and cool wet winters. Annual precipitation averages 50-75 cm and elevations in our study sites range from 93-503 m. There are primarily three vegetation types that are common in our study area. The lower elevation sites are dominated by grasslands and savanna, grading into woodlands, before reaching montane hardwood forests at the highest elevations and depending on features such as slope, aspect, and edaphic attributes. Trees in the study areas included blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), California black oak (*Q. kelloggii*), valley oak (*Q. lobata*), gray pine (*Pinus sabiniana*), ponderosa pine (*P. ponderosa*), and California buckeye (*Aesculus californica*). Shrubs included buckbrush (*Ceanothus cuneatus*), poison oak (*Toxicodendron diversilobum*), whiteleaf manzanita (*Arctostaphylos viscida*), chaparral coffeeberry (*Rhamnus tomentella*), and toyon (*Heteromeles arbutifolia*), and the herbaceous layer was dominated by annual grass species such as soft chess (*Bromus hordeaceus*), ripgut brome (*B. diandrus*), red brome (*B. madritensis*), annual fescue (*Vulpia sp.*), wild oats (*Avena fatua* and *A. barbata*), and medusahead (*Taeniatherum caput-medusae*). Forb species included bigflower agoseris (*Agoseris grandiflora*), purple sanicle (*Sanicula bipinnatifida*), yellow mariposa lily (*Calochortus luteus*), yellow star-thistle (*Centaurea solstitialis*), Italian thistle (*Carduus pycnocephalus*), annual clovers (*Trifolium spp.*), geranium (*Geranium spp.*), and lupine (*Lupinus spp.*).

Sample Points

Sample points were selected from a random sample constituting 5% of several thousand polygons delineated in the Sierra Nevada foothills by the CDFG. Polygons were generated using a geographic information system (GIS) coverage and intersecting data from four biophysical attributes: precipitation, temperature, slope and aspect, and geologic substrate. The 5% sample yielded 150 polygons. Using a GIS, one center point (centroid) was drawn in each of the 150 polygons. Thirty of the 150 centroids were randomly chosen as study locations. At each of the 30 centroids, three sample points for bird and vegetation sampling, spaced 250 m apart in an equilateral triangle centered on the centroid, were plotted with the GIS. The 30 centroids made up a total of 90 sample points. One sample point had to be dropped from the study due to site-access limitations, leaving 89 sample points.

Methods

Bird Counts

Standardized, 100 m fixed-radius point counts (Ralph et al. 1993) were conducted from late March to mid-June 2004 at each of the 89 sample points to characterize the breeding bird community. To distribute observer variability (Ralph et al. 1995), five individuals performed all counts and rotated among sample points. At each sample point, a 10 min bird count was completed, with the first count beginning within 10 min after sunrise. Each sample point was surveyed three times, with roughly two weeks duration between sample point visits. Counts were conducted for 3-3.5 hr after sunrise, permitting surveys at six to nine points per day. Birds counted were those detected visually or aurally within 100 m. Flagging and laser rangefinders were used to mark the 100 m radius boundary and verify bird distances. Birds flying over sample points, heard or seen at neighboring points during counts on the same day or detected beyond the 100 m radius were not counted.

California Partners in Flight (California Partners in Flight 2002) identified 22 species of birds as being associated with California's oak woodlands. Of these species, we selected lark sparrow (*Chondestes grammacus*), and white-breasted nuthatch (*Sitta carolinensis)* for analysis. A third species, spotted towhee (*Pipilo maculates*), was not identified as a focal species in The Oak Woodland Conservation Plan (California Partners in Flight 2002), but was also included in our analysis based on their relative commonness, which was necessary for statistical analysis purposes, and their previously documented use of scrub dominated habitats in California (Grinnell and Miller 1944). These species were chosen as indicator species representing the diversity of the three dominant vegetation types found within our study areas, in the central Sierra Nevada foothills (Grinnell and Miller 1944). In our study area, lark sparrows are associated with open grasslands and savanna (Martin and Parrish 2000), white-breasted nuthatch with oak woodlands (Grubb and Pravosudov 2008), and spotted towhee with montane hardwood forests (Greenlaw 1996).

Relevé Method Vegetation Measurements

At each sample point, a single relevé was conducted following the CNPS methods of vegetation classification, from 31 May to 4 August 2005. Due to logistic difficulties, relevé vegetation data was collected in 2005 and bird point count data were collected in 2004. Cover classes of the woody tree variables most likely changed little over a one year span. There were no significant disturbances (e.g., fire, thinning) at our study areas between the time the vegetation and bird data were collected, and only modest differences from August 1, 2003 to August 1, 2004 in average precipitation 1.90 mm, average high temperature 23.54 °C, and average low temperature 10.70 °C compared to the time frame from August 2, 2004 to August 1 2005 (2.12 mm, 22.54 °C, 10.45 °C respectively; California Irrigation Management

Information System, Browns Valley Station #84, Yuba County, California).

The spatial extent of a CNPS relevé method is based on the habitat sampled. For a woodland sample point, the CNPS uses a 1000 m² (17.5 m radius) circular sub-plot. Most sample points (94%) were dominated by a single vegetation type such as blue oak savanna, blue oak woodland, mixed-blue oak/pine woodland, or montane mixed hardwood. Vegetation was sampled in a 17.5 m radius which was placed either at the bird point counting center point (*N* = 84) or within a 100 m radius in an area that was most representative of the sample point (*N* = 5). Five sample points were dominated by ecotones of dense canopy woodland riparian areas, or open California annual grassland communities. For these points, the percentage of non-woodland present in the 100 m radius sample point was estimated, and a 1000 m² circular sub-plot was positioned accordingly to better sample the non-woodland habitat (e.g., if 80% of the 100 m radius sample point was situated in a creek bed, a circular sub-plot was positioned to include 80% of this vegetation type).

Data gathered following the original CNPS relevé methods corresponded to a traditional relevé method (Sawyer and Keeler-Wolf 1995). The original CNPS relevé method was focused on collecting percent cover data for all environmental, physiognomic, and floristic variables in the following cover class intervals: <1%, 1 – 5%, >5 – 15%, >15 – 25%, >25 – 50%, >50 – 75%, and > 75%. However, to better capture fine-scale differences in habitat features over our study area, we collected percent cover information in continuous measurements to the nearest one percent. Habitat features that occurred in very low percent cover were recorded as 0.01% to acknowledge presence. Detailed percent cover estimates based on the original relevé method included substrate measurements of fine soil (i.e., sand, silt, soil, or dirt < 2 mm in diameter), gravel (i.e., rounded and angular fragments 0.2-7.5 cm diameter, cobble (i.e., rounded and angular fragments > 7.5 – 25 cm in diameter), stone (i.e., rounded and angular coarse fragments > 25 – 60 cm in diameter), boulder (i.e., rounded and angular coarse fragments > 60 cm in diameter), bedrock (i.e., continuous exposed, non-transported rock), litter (i.e., organic matter covering ground), and living stems (i.e., basal area of living stems of plants at the ground surface). Furthermore, information on site history (i.e., land-use or disturbance history), slope, aspect, and elevation of the plot location, vegetation description (i.e., name of vegetation type according to CNPS classification, Sawyer and Keeler-Wolf 1995), and composition (i.e., complete species list of all grasses, forbs, trees and shrubs) were documented at each sample point. The final vegetation composition list generated for a plot is used by the CNPS for final site classification. In addition, to further refine vegetation classifications based on growth state (i.e., early seral, old-growth), the percent cover for each vegetation species at three defined height layers of low (< 0.5 m), mid (0.5 m – 5.0 m), and tall (> 5.0 m) were collected. Height of each unique height layer (i.e., low (< 0.5 m), mid (0.5 m – 5.0 m), and tall (> 5.0 m)) were collected as the maximum height for the low and mid-layers and the minimum height of the tall layer. It was possible for more than one height layer to be represented by one species, (e.g., a blue oak may have seedlings in the low, saplings in the mid, and tree specimens in the tall height layers). Furthermore, percent cover was estimated for lichen and moss partitioned by location within the plot (i.e., epiphytic, ground, or rock), plant growth phenology (i.e., based on vegetative condition classified as early growth or leaf-out, peak growth or leaf-out, or late senescent growth or leaf-out of dominant tree, shrub, and herbaceous species within a stand). The CNPS uses air-photos and field ground truthing to collect information on general descriptions of neighboring vegetation patches (e.g., grassland, chaparral) as well as vegetation patch size. However, these data were not collected for this project due to limited field personnel and lack of remote sensing data.

Physiognomic data collected following the CDFG's suggestions for the modified relevé method included percent cover of the herbaceous layer in four layers: < 10 cm, 10 – 20 cm, 20 – 30 cm, ≥ 30 cm; the shrub layer at four layers < 0.9 m, 0.9 – 1.8 m, 1.8 – 2.4 m, > 2.4 m, and the hardwood and conifer layer at four layers of < 5 m, 5 – 10 m, 10 – 20 m, 20 - 30 m, and > 30 m. Specific plant species were not tabulated. But herbaceous plant types (i.e., grass, forb, sedge, or rush), shrubs, hardwood, or conifer trees were tabulated within each layer. Additionally, shrub decadence was recorded as percent cover for all shrubs that were in the life stage classes characterized as seedling (i.e., < 3 years of growth) young (i.e., < 1% dead), mature (i.e., 1 – 25% dead), and decadent (i.e., > 25% dead). All shrub species were recorded under the height layer variable, as well as the shrub decadence variable. For example, a decadent buckbrush shrub (i.e., > 25% dead) which was in the height layer at 0.9 – 1.8 m, and was covering 15% of a sample plot would be recorded as 15% cover under decadent shrub (i.e., > 25% dead) and 15% under the height layer 0.9 – 1.8 m variable. Although this is a simplified example, most shrub species occurred in different height layers and shrub decadence classes across a relevé sub-plot. Therefore, the variables were not viewed as redundant. The diameter at breast height (dbh) for all trees or snags > 10 cm within the sub-plot were recorded.

Table 1. Selected covariates, expressed as a percent cover for all species specific or height stratum variables or as the frequency or total number of plant species for all richness variables used for occupancy modeling from two vegetation data protocols: the original California Native Plant Society (CNPS) relevé methods and the California Department of Fish and Game (CDFG) modified relevé methods. A third category, environmental variables are covariates that are not exclusive to either the original or modified relevé yet they are hypothesized to be important for bird species occupancy.

Original CNPS Relevé	**Range**	**Mean ± SE**
Tree richness	0 - 4	2.2 ± 0.1
Shrub richness	0 - 3	0.6 ± 0.1
Forb richness	1 - 13	6.1 ± 0.3
Grass richness	2 - 8	4.8 ± 0.1
Herbaceous richness	8 - 23	14.0 ± 0.4
Vegetation richness	10 - 30	18.5 ± 0.4
Quercus wislizenii 0.5 – 5 m %	0 - 52	2.8 ± 0.7
Quercus douglasii > 5 m %	0 - 41	17.7 ± 1.1
Toxicodendron diversilobium 0.5 – 5 m %	0 - 31	3.2 ± 0.6
Total non-native Vegetation %	14 - 83	40.6 ± 1.8
Modified CDFG Relevé		
Hardwood < 5 m %	0 - 52	4.8 ± 0.7
Hardwood 5 – 10 m %	0 - 42	15.9 ± 1.1
Hardwood 10 – 20 m %	0 - 27	7.1 ± 0.6
Conifer 10 – 20 m %	0 - 21	1.5 ± 0.3
Shrub 0.9 – 1.8 m %	0 - 31	2.3 ± 0.6
Shrub Decadent > 25% Dead	0 - 17	1.5 ± 0.3
Herbaceous < 4 cm %	0 - 40	5.0 ± 0.6
Herbaceous ≥ 30 cm %	0 - 61	24.1 ± 1.6
Largest diameter at breast height tree cm	16.3 - 72.6	31.9 ± 0.9
Largest diameter at breast height snag cm	0 - 63.7	6.5 ± 1.1
Environmental Variables		
Elevation m	93 - 505	259.4 ± 12.3
Litter %	0 - 69	24.5 ± 1.6
Bare Ground %	0 - 56	26.0 ± 0.9

Time and Effort

Time and effort (i.e., number of observers needed to complete data collection) was recorded for each full sample point vegetation survey for both the original CNPS and modified CDFG relevé method. Furthermore, to compare the relevé to other field techniques, users of the commonly applied circular-plot method (James and Shugart Jr. 1970) and the Breeding Biology Research and Monitoring BBIRD field protocol (Martin et al. 1997) were surveyed for information based on time and effort for data collection. The circular-plot method (James and Shugart Jr. 1970) was applied in eastern deciduous forests (Rodewald and Yahner 2001) and the BBIRD protocol (Martin et al., 1997) was applied in a Midwestern prairie-savanna-woodland mosaic (Au et al. 2008).

The times provided were based on studies that slightly modified the original protocols. Rodewald and Yahner (2001) supplied information per sub-plot (30- 45 min per sub-plot). They collected circular-plot data at three sub-plots along a transect. Therefore, the time per plot was multiplied by three to produce a 'sample point' estimate of time for vegetation data collection. These estimates do not include time to move between and set-up each of the three sub-plots. Au et al. (2008), supplied effort on sub-plot (30 – 45 min per sub-plot) to complete the BBIRD protocol, including estimates for collecting floristic measurements (i.e., plant species lists which took between 20 min to one and a half hr total per sub-plot). They used two sub-plots per 'sample point'. Their estimates on time were multiplied by two plus the added time to collect vegetation composition data to produce a time per sample point estimate. These estimates do not include time to move between and set-up each of the two sub-plots.

Although vegetation data collection methods compared were carried out in different vegetation types in North America, comparison studies were chosen based on those occurring in similar structure vegetation types to our study area.

Statistical Analysis

Because of the clustered sampling design, it was necessary to test for spatial dependence between individual sample points in each cluster. To test the assumption of independence, semivariograms were built, using the deviance residuals for each focal bird species' presence and absence patterns at each sample point (Legendre and Fortin 1989).

Due to the large number of vegetation covariates collected, we selected a final list for analysis based on *a priori* hypothesized habitat associations for each focal bird species. Specifically, we chose 10 covariates that were collected using the original CNPS relevé protocol and 10 that were collected using the CDFG modified relevé method. Three covariates, elevation, litter, and bare ground were collected in the field and listed as environmental covariates which were not exclusive to either the original or modified relevé method (Table 1). Correlations of variables were assessed using Pearson's product moment correlation coefficient (Pearson 1920). Semivariogram statistics and Pearson's correlations were computed using the R statistical software package (R Development Core Team 2005).

To model the factors associated with focal bird occupancy (ψ) and detection probability (p) related to the original CNPS relevé and modified CDFG relevé method datasets, we performed a single-season, single-species, custom occupancy estimation analysis (MacKenzie et al., 2006) on each of the three species using the PRESENCE statistical software (Hines 2006). All vegetation covariates were transformed for analysis by standardizing the coefficients so the mean value was equal to zero and the standard deviation equal to one (Mackenzie et al., 2006). Thus, the magnitude of an effect a covariate has on bird species occupancy and detection probability can be assessed by the absolute value of the beta coefficient estimates since all covariates were standardized. Occupancy (ψ_a) can be defined as the probability of a species occupying site a, whereas detection (p_{at}) is the probability that a species will be detected at site a at time t (MacKenzie and Kendall 2002).

We started with the most basic null model, $\psi(.),p(.)$, where occupancy and detection probabilities were constant across the sampling period and did not vary with any relevé covariate. Detection probability heterogeneity was then modeled as a function of original CNPS relevé or modified CDFG relevé method covariates, as a linear trend across time between survey periods to account for possible variation in detectability across the sampling period (i.e., decrease in bird song throughout the survey effort), effects of observer bias, or as the full identity matrix (unique detection probability varying over time for each sample period.

After accounting for detection probability, a set of nine *a priori* models were introduced to describe occupancy patterns for each focal bird species based on previously described habitat associations (Grinnell and Miller 1944, Greenlaw 1996, Martin and Parrish 2000, Grubb and Pravosudov 2008). We emphasized additive and quadratic models to describe relationships between bird occupancy and sampling point attributes. Four models were fit using covariates collected using the original CNPS relevé methods and four were fit using the modified CDFG relevé methods. Only models where the standard error of the beta coefficient did not overlap zero were included in final model set for each bird species. The null model was also included in each model set to better determine no effects versus original CNPS relevé or modified CDFG relevé variable effects.

Candidate models composed of different covariates were selected based on an information-theoretic approach outlined by Burnham and Anderson (2002). For species specific model sets that did not have a clear set of best fitting models (AIC_c weights < 0.90), the relative importance of top covariates was assessed by summing the AIC_c weights of all top candidate models containing representative covariates (Burnham and Anderson 2002). Akaike Information Criterion (AIC) scores were converted to the corrected AIC_c to penalize models for over-parameterization (Burnham and Anderson 2004).

To assess model fit to the data, a parametric bootstrap ($N = 10\,000$) test was run on the most global model of the candidate set for each species. This method compares the frequency of observed detection histories relative to expected frequencies if the global model is assumed to be correct (MacKenzie and Bailey 2004). The parametric bootstrap method yielded a variance inflation factor ($\hat{c}$) which was used to determine if there was substantial evidence of lack of fit due to overdispersion within the dataset. Additionally, to examine model performance, the percent deviance explained for the best-fitting model of each species was computed (Burnham and Anderson 2002).

Results

The semivariogram test for spatial dependence revealed that no focal species showed patterns of spatial dependence at the sample point scale. Therefore, we treated each sample point as an independent unit for all analyses. The original CNPS relevé method covariates forb richness and herbaceous richness were correlated ($r = 0.88$, $P < 0.01$). However, both covariates were used throughout the modeling exercise, but were not included in the same explanatory model. The modified CDFG relevé covariates shrub decadent > 25% dead, and shrub 0.9 – 1.8 m were moderately correlated ($r = 0.64$, $P < 0.01$). No other original CNPS relevé or modified CDFG relevé covariate were moderately or highly correlated ($r > 0.60$, $P < 0.01$).

Time and Effort

Time and effort for the original CNPS and the modified CDFG relevé methods were collected and compared with two studies which applied commonly used methods in a effort to examine overall cost (i.e., time + number of observers) of method. The modified CDFG relevé required two observers and was the quickest method for quantifying vegetation features ranging from 30 min in the least homogenous and least structurally diverse habitats to 2 hr in the most structurally diverse vegetation patches compared to the CNPS relevé which also required two observers and ranged between 1 to 3 hr to apply. The original CNPS relevé method was a more time intensive method due to the complete floristic list tabulated within a sub-plot. The circular-plot method required two observers and averaged between 1.5 to 2.5 hr to collect per sample point, while the BBIRD protocol required 2 to 4 observers and ranged between 1.5 to 3.5 hr to apply per sample point.

Occupancy Analysis

The parametric bootstrap test ($N = 10\,000$) did not indicate lack of fit ($\hat{c} < 2.0$) for the global model for any of the three focal bird species. As expected, the null model $\psi(.),p(.)$ resulted in varying parameter estimates of occupancy and detection among the different species (Fig. 1). Spotted towhees had the highest detection rate which lead to the lowest adjustment for the estimate of occupancy relative to the original naïve estimate. Estimated detection probabilities were lower for white-breasted nuthatches and lark sparrows. Thus, the magnitude of difference between the estimated occupancy and the naïve estimate were greater. Detection probability, modeled by effects of observer bias was the most well supported model for lark sparrows (AIC_c weight = 1.00; $\beta_{\text{Observer 1}} = 0.53 \pm 0.49$, $\beta_{\text{Observer 2}} = -0.89 \pm 0.40$, $\beta_{\text{Observer 3}} = -0.43 \pm 0.41$, $\beta_{\text{Observer 4}} = -1.3 \pm 0.49$, $\beta_{\text{Observer 5}} = -1.9 \pm 0.45$), and white-breasted nuthatches (AIC_c weight = 1.00; $\beta_{\text{Observer 1}} = 1.1 \pm 0.41$, $\beta_{\text{Observer 2}} = 0.27 \pm 0.21$, $\beta_{\text{Observer 3}} = -0.56 \pm 0.41$, $\beta_{\text{Observer 4}} = -1.1 \pm 0.42$, $\beta_{\text{Observer 5}} = -0.67 \pm 0.31$). The covariate, vegetation richness, collected using the original CNPS relevé method (AIC_c weight

= 0.99; $\beta_{\text{Vegetation richness}} = 1.21 \pm 0.28$) best explained detection probability for spotted towhees.

Original Relevé vs Modified Relevé

For lark sparrows, the summed AIC_c weights comparing models derived from the CDFG modified protocols were better supported than models generated from the original CNPS relevé variables (Table 2). For white-breasted nuthatches, models using covariates from both the original and modified relevé protocols were competitive. For spotted towhees, models composed of covariates collected using the original relevé performed better. For all three bird species, environmental variables explained probability of sample point occupancy better than covariates collected using the original or modified relevé methods.

For lark sparrows, the top-ranking models to explain occupancy included the environmental covariates litter %, and bare ground %, and the CDFG modified relevé covariate largest diameter at breast height tree cm, which accounted for a combined AIC_c weight of 0.90 (Table 3). There was a positive association for the covariates largest diameter at breast height tree cm, and litter %, but a negative association with bare ground % (Table 4). The best-fitting model explained 14.83% of the deviance in the data for lark sparrows.

The top models for white-breasted nuthatch included the environmental variable elevation m, which accounted for a combined AIC_c weight of 0.42, *Quercus douglasiii* Tall %, combined AIC_c weight = 0.38, largest diameter at breast height snag cm, combined AIC_c weight = 0.35, and hardwood 5 – 10 %, AIC_c weight = 0.25 (Table 3). The slopes for elevation m, largest diameter at breast height snag cm, and vegetation richness were positive, additionally, the slope for *Quercus douglasiii* Tall %, and hardwood 5 – 10 % was positive (Table 4). The best-fitting model explained 10.17% of the deviance in the data for white-breasted nuthatches.

The top models for spotted towhee included the environmental variable elevation m, and the covariates shrub richness, and vegetation richness which were quantified using the original CNPS relevé method and accounted for a combined AIC_c weight of 0.93 (Table 3). The slope for shrub richness and vegetation richness was positive, whereas the slope for elevation m was negative (Table 4). The best-fitting model explained 24.63% of the deviance in the data for spotted towhees.

Discussion

Relevé Method and Model Performance

The results of this study suggest that both the original CNPS and the modified CDFG relevé methods can be used to model occupancy of birds in Sierra Nevada foothill blue oak woodlands. Our results, using covariates from both the original CNPS relevé and the CDFG modified protocol, were consistent with past findings that suggest that both floristics and physiognomy are important in avian site selection at plot-level scales (Rotenberry 1985, MacNally 1990). Although traditional relevé methods are intended to be used for vegetation classification, we found that their application to wildlife habitat evaluation can be enhanced by including physiognomic variables. In addition, we found that the CDFG modified relevé method was a more efficient bird habitat quantification method in terms of time needed to collect habitat data, compared with the original CNPS relevé, the James and Shugart Jr. circular-plot (1970), or the BBIRD protocol (Martin et al. 1997).

We found the simplified and commonly understood

Table 2. Summed AICc weights of eight candidate models. Four models were composed of covariates collected using the original CNPS relevé method, and four models composed of covariates collected using the modified CDFG relevé method. A third group, environmental variables, are covariates which are not exclusive to either the original of modified relevé method.

	CNPS original relevé	CDFG modified relevé	Environmental variables
lark sparrow	0.02	0.20	0.98
spotted towhee	0.94	0.06	1.00
white-breasted nuthatch	0.42	0.41	0.56

Table 3. Model selection rankings from a set of nine models for three focal species to explain occupancy (ψ) and probability of detection (p) in Sierra Nevada foothill woodlands, California, USA.

Model	**ΔAICc**	w_i	**K**
lark sparrow			
ψ(Litter %$^{\wedge 2}$ + Bare Ground %),*p*(Observer)	0	0.78	9
ψ(Largest diameter tree at breast height cm + Litter %$^{\wedge 2}$),*p*(Observer)	3.70	0.12	9
ψ(Hardwood 10 – 20 m %$^{\wedge 2}$ + Bare Ground % + Litter %),*p*(Observer)	6.10	0.04	10
ψ(Herbaceous < 4 cm + Bare Ground %),*p*(Observer)	5.98	0.04	8
ψ(*Quercus douglasii* Tall %$^{\wedge 2}$ + Bare Ground %),*p*(Observer)	7.68	0.02	9
ψ(Tree richness + Herbaceous richness),*p*(Observer)	11.16	0	8
ψ(*Quercus douglasii* Tall %$^{\wedge 2}$ + Total non-native Vegetation %),*p*(Observer)	12.00	0	9
ψ(*Quercus douglasii* Tall %$^{\wedge 2}$ + Forb richness + Grass richness),*p*(Observer)	16.72	0	10
ψ(.),*p*(.)	23.96	0	2
spotted towhee			
ψ(Elevation m + Shrub richness),*p*(Vegetation richness)	0	0.82	5
ψ(Elevation m + Vegetation richness),*p*(Vegetation richness)	3.94	0.11	5
ψ(Elevation m + Shrub 0.9 – 1.8 m %),*p*(.)	5.19	0.06	4
ψ(Herbaceous ≥ 30 cm % + Shrub 0.9 – 1.8 m %),*p*(.)	20.91	0	4
ψ(Shrub 0.9 – 1.8 m % + Shrub Decadent > 25% Dead),*p*(.)	20.99	0	4
ψ(Hardwood < 5 m % + Shrub Decadent > 25% Dead),*p*(.)	24.37	0	4
ψ(*Quercus wislizenii* Medium % + *Toxicodendron diversilobium* Medium %),*p*(Vegetation richness)	27.93	0	5
ψ(Litter % + Herbaceous richness),*p*(Vegetation richness)	44.54	0	5
ψ(.),*p*(.)	44.41	0	2
white-breasted nuthatch			
ψ(Elevation m + Hardwood 5 – 10 m % + Largest diameter at breast height snag cm),*p*(Observer)	0	0.25	9
ψ(*Quercus douglasii* Tall %),*p*(Observer)	0.47	0.20	7
ψ(Elevation m + Litter % + Bare Ground %),*p*(Observer)	0.79	0.17	9
ψ(*Quercus douglasii* Tall % + Litter %),*p*(Observer)	1.81	0.10	8
ψ(Largest diameter at breast height snag cm),*p*(Observer)	1.82	0.10	7
ψ(*Quercus douglasii* Tall % + Tree richness),*p*(Observer)	2.25	0.08	8
ψ(Conifer 10 – 20 m %),*p*(Observer)	2.88	0.06	7
ψ(Litter$^{\wedge 2}$ + Tree richness),*p*(Observer)	3.61	0.04	9
ψ(.),*p*(.)	18.28	0	2

covariates that were included in both the original CNPS and modified CDFG relevé methods related well to descriptions of current and desired conditions for bird species that are found in land management plans and treatment prescriptions (California Partners in Flight 2002, Rich et al. 2004). Thus, these results illuminate the importance of data collected using the original and modified relevé methods for linking to management issues for priority bird species with Partners in Flight conservation objectives (Rich et al. 2004).

Table 4. Beta coefficient parameter estimates for site occupancy (ψ) modeled using variables collected following the California Native Plant Society (CNPS) original relevé methods and the California Department of Fish and Game (CDFG) modified relevé methods in addition to environmental variables for three bird species in Sierra Nevada foothill woodlands.

	lark sparrow	**spotted towhee**	**white-breasted nuthatch**
CNPS original relevé			
Tree richness	-0.98		-0.49
Shrub richness		1.44	
Forb richness	0.07		
Grass richness	-0.05		
Herbaceous richness	-0.02	0.31	
Vegetation richness		0.95	
Quercus wislizenii Medium %		2.07	
Quercus douglasii Tall %	1.36		0.73
Quercus douglasii Tall %$^{\wedge 2}$	-1.66		
Toxicodendron diversilobium Medium %		2.28	
Total non-native Vegetation %	0.54		
CDFG modified relevé			
Hardwood < 5 m %		1.17	
Hardwood 5 – 10 m %			1.42
Hardwood 10 – 20 m %	0.59		
Hardwood 10 – 20 m %$^{\wedge 2}$	-0.64		
Conifer 10 – 20 m %			-0.30
Shrub 0.9 – 1.8 m %		5.07	
Shrub Decadent > 25% Dead		1.00	
Herbaceous < 4 cm %	1.16		
Herbaceous ≥ 30 cm %		-0.40	
Largest diameter tree cm	1.20		
Largest diameter snag cm			-0.54
Environmental Variables			
Elevation m			-0.84
Litter %	-6.61	1.96	0.47
Litter %$^{\wedge 2}$	7.20		-2.70
Bare Ground %	-1.03		

Time and Effort

Efficiently quantifying habitat is a critical goal for all field ornithologists. The original CNPS relevé method, on average, took 30 min to one hr longer to collect when compared to the modified CDFG relevé method. The original CNPS method is more time consuming because it requires an extensive floristic list of all vegetative species within a circular sub-plot. The CNPS is interested in classifying vegetation communities based on the presence and absence, and frequency of common and rare plants (Sawyer and Keeler-Wolf 1995). Furthermore, detailed structural information is not collected with this method. The modified CDFG relevé method is a more efficient method primarily because it is focused on collecting dominant structural features of a habitat patch such as diameter at breast height of trees, and percent canopy cover of general vegetation features (i.e., hardwood, conifer, and shrub) and not on collecting floristic lists. Since uncommon plants are rarely thought to influence habitat occupancy by bird species, the CDFG did not require rare plant species to be quantified. The relevé methods were similar in effort (i.e., number of observers). However, the modified CDFG relevé method was more efficient in total time to collect data compared to common ornithological methods for quantifying bird habitat. Rodewald and Yahner (2001) noted a modified version of the James and Shugart Jr. (1970) circular-plot method took roughly 1.5 – 2.5 hr to apply at three sub-plots along a transect, whereas, Au et al. (2008) described a modified version of the BBIRD protocol (Martin et al. 1997) to take up to a third longer than the relevé methods in quantifying bird habitat in a prairie-savanna mosaic. The estimates for these methods did not include time to move between sub-plots, including sub-plot set-up, which would increase overall quantification time depending on the complexity of the habitat and terrain.

Original Relevé

The original CNSP relevé method provided data which led to well supported models for the spotted towhee, and competitive models for the white-breasted nuthatch (Table 2). The original CNPS relevé is centered on floristics. The role of floristics on partitioning assemblages of bird species within and between habitats has been well studied (MacNally 1990, Rodewald and Abrams 2002, Fleishman et al. 2003). The customary viewpoint is that at relatively broad scales, vegetation composition is suggested to influence bird community composition (Rotenberry 1985, Rodewald and Abrams 2002). However, at fine-scales, Holmes and Robinson (1981) have shown that floristics also influences food availability and foraging preferences of bird species. Thus, the results of these studies suggest vegetation composition is an important proximate cue for bird species used for selecting habitat at varying spatial scales. Our results support the importance of floristics to bird species during the breeding season. We found spotted towhee to be highly associated with the frequency of shrub species. Our study areas in the Sierra Nevada foothills are relatively homogenous with total number of shrub species. However, this floristic variable was the best predictor of spotted towhee occupancy. Additionally, the white-breasted nuthatch was positively associated with the presence of blue oaks, yet negatively associated with the total number of tree species. This finding supports the results of Block (1990) and Block and Morrison (1990) who also found that blue oak is an important tree for foraging white-breasted nuthatch during the breeding season in a similar study area within the region. Although the original CNPS relevé method was not designed to explain bird-habitat relationships, we found that the method includes variables related to the floristic composition of a habitat that can be useful for describing occupancy patterns of focal bird species.

Modified Relevé

The modified CDFG relevé method provided data which led to competitive models for the white-breasted nuthatch and better supported models for the lark sparrow when compared to covariates collected using the original CNPS relevé method (Table 2). The modified CDFG relevé method is centered on physiognomy. Vegetation physiognomy has long been thought to be an important habitat attribute influencing bird diversity (MacArthur and MacArthur 1961) and habitat selection of breeding birds (Cody 1981, Cody 1985). Although our model support was not overwhelming for the influence of the physiognomic variables on focal bird species occupancy, we did find support that physiognomy is indeed an important attribute of habitat influencing bird distributions. To add further support to the significance of physiognomy to bird species during the breeding season in California oak woodlands, Block (1990, 1991) documented the importance of vegetation structure, in addition to composition, for foraging bird species throughout northern Sierra Nevada foothill woodlands. Block found species such as the ash-throated flycatcher (*Myiarchus* *cinerascens*), and western bluebird (*Sialia mexicana*) consistently used tree species with large diameters. The variables included in the modified CDFG relevé method showed strong, expected coefficient estimates for the focal study species (Table 4). Spotted towhee is a shrub associated species (Greenlaw 1996). Although the floristic variable shrub richness was included in the most well supported model for explaining occupancy for this species, we found positive associations with the two physiognomic CDFG modified relevé shrub variables, shrub 0.9 – 1.8 m %, and shrub decadent > 25, % as well as the structure variable hardwood < 5 m %. For the open canopy associated lark sparrow, we found a positive association with the largest diameter at breast height tree cm. The largest diameter trees occur in open savanna stands in our study area. Grinnell and Miller (1944) described similar habitat relationships for these species, documenting the affinity of lark sparrow to open habitats, and spotted towhee to shrubby plant communities.

Models for white-breasted nuthatch occupancy were competitive between covariates collected using original and modified relevé methods. The covariate hardwood 5 – 10 m % was included in the most well supported model explaining white-breasted nuthatch occupancy. This covariate had a positive correlation which was expected based on previously described habitat attributes for this species in woodlands of California (Grinnell and Miller 1944). However, the largest diameter at breast height snag was negatively associated with white-breasted nuthatch which was unexpected. The white-breasted nuthatch is a cavity nesting species (Grubb and Pravosudov 2008). Furthermore, cavities were hypothesized to be more abundant where large snags were present. Thus, we expected white-breasted nuthatch to be associated with this covariate. It is possible non vegetative factors, such as the presence of predators such as cooper's hawks (*Accipiter cooperii*), the higher risk of nest-parasitism from brown-headed cowbirds (*Molothrus ater*), or the abundance of highly aggressive competitors such as European starlings (*Sturnus vulgaris*) may have influenced site occupancy for white-breasted nuthatches. Thus, the modified CNPS relevé protocol appears useful in quantifying physiognomic habitat features which are important for site-occupancy of our focal species. However, other non-structural factors, which are not quantified using the relevé methods may be influential for distributing the focal species throughout the study area.

Occupancy Modeling

As with many species, detectability of birds can be highly variable based on changing behavioral patterns (Krebs 1971, Hutto 1985, Pagen et al. 2000), environmental conditions (Trzcinski et al. 1999), or differences in observer abilities to correctly identify species during surveys (Cunningham et al. 1999). Without accounting for the probability of detection being less than one, ornithologist may be relying on biased data, leading to erroneous conclusions (Gu and Swihart 2004, MacKenzie et al. 2006). Using the occupancy modeling approach, we found the variation in detection probability greatly influenced estimates of site-occupancy (Fig. 1). The spotted towhee and white-breasted nuthatch had higher detection probabilities than the lark sparrow, which lead to minor adjustments in null estimates of site-occupancy. Whereas for lark sparrows, detectability was low, thus leading to a high estimate of site-occupancy across our study area. Species with low detection probability may be much more common than originally estimated based on naïve estimates of site occupancy. Our results also supported previous work suggesting heterogeneity in observer abilities may influence detectability of bird species (Cunningham et al. 1999). For lark sparrow, and white-breasted nuthatch, detection probability was best explained by the covariate observer. These findings suggest the difference in abilities of observers should be modeled to correctly account for estimates of occupancy. Furthermore, accounting for detection probability may enhance the capacity of investigators searching for site-specific covariates which may influence bird occupancy (MacKenzie et al. 2006).

Relevé Scale Considerations

Recognizing scale issues is important when using a relevé method because habitat features can differ markedly over geographic areas thus influencing wildlife-habitat relationship patterns (Block 1989, Block and Morrison 1991, Morrison et al. 1991). The CNPS uses a 1000 m^2 (17.5 m radius) circular sub-plot for each relevé located within a wooded vegetation community. Although many vegetation and habitat variables can be collected within a 17.5 m radius plot, some species may respond to features at different scales. For example, in Monterey County, Nuttall's woodpeckers (*Picoides nuttallii*), which are a woodland associated species in the Sierra Nevada foothills, had an average territory size of about 65 ha (Miller and Bock 1972). Plot-level vegetation measurements may fail to capture habitat features over larger areas which may better predict occupancy for species with large territory sizes. If using the CNPS relevé approach to model species with larger territories, investigators should consider data collection on more than one relevé sub-plot within the area (e.g., point count circle) of interest.

Other users of the modified relevé method have used 50 m radius plots to quantify habitat (Ralph et al. 1993, Alexander et al. 2007, Luther et al. 2008, Seavy et al. 2008). Although our results suggested occurrence patterns of bird species can be predicted based on vegetation features quantified using a modified relevé method, we recommend caution when using relevé methods for smaller plots, such as the CNPS 17.5 m radius. We urge users to carefully consider *a priori* habitat associations of study species, specifically focusing on breeding season territory sizes and the resources that may influence use by particular bird species. Researchers should expand plot sizes, or use multiple smaller plots within an area of interest (e.g., 100 m radius bird point count station), to better quantify habitat features thought to influence bird species occupancy.

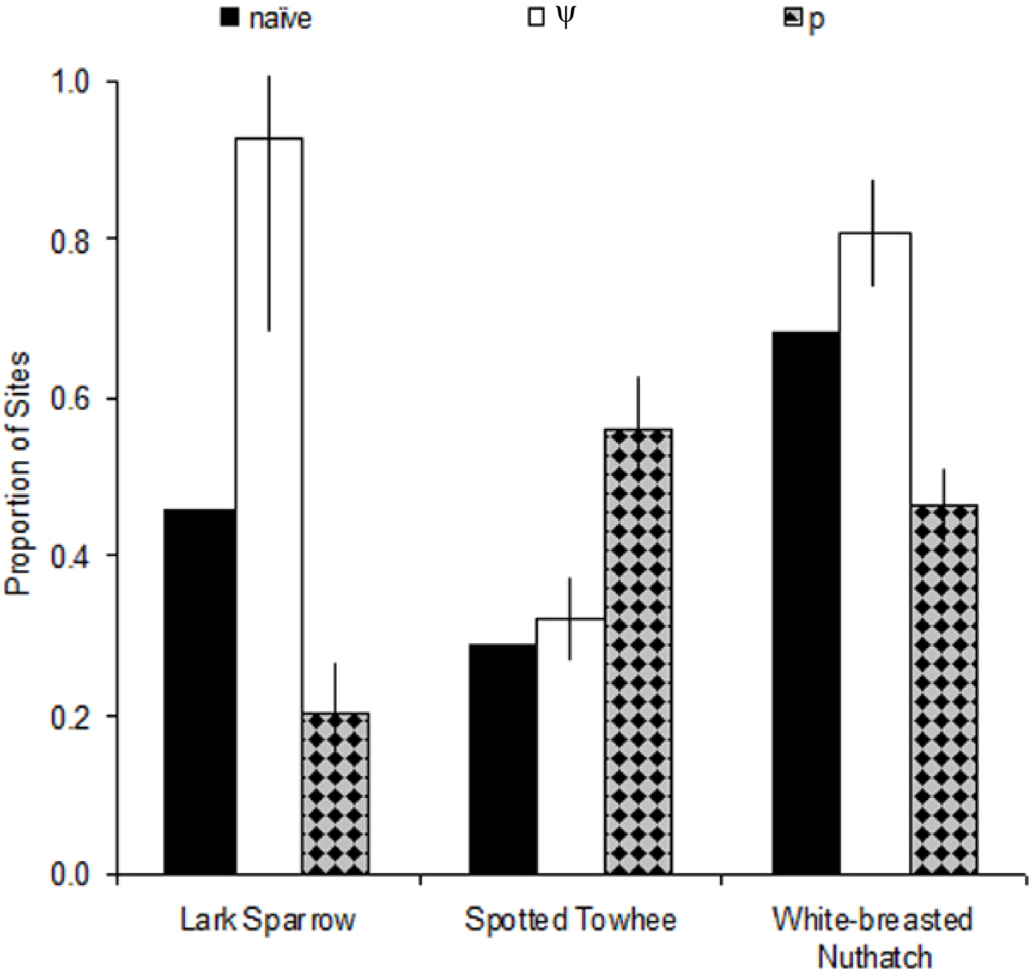

Fig. 1. Parameter estimates (with standard error bars) for proportion of sites occupied ψ(.), and detection probability p(.), for three birds in central Sierra Nevada foothill woodlands. Naïve detection rates (unadjusted proportion of sites with at least one detection) are included to show contrast with modeled occupancy estimates.

Relevé Sub-Plot Placement Recommendations

Extensive vegetation sampling efforts, such as that undertaken by the CNPS, are often aimed primarily at classifying vegetation in homogenous stands to characterize the conditions of unique sites that may harbor rare and endemic plant species (Sawyer and Keeler-Wolf 1995). In contrast, ornithologists routinely place point-count stations in areas that include edge habitats. We recommend that users of a modified relevé method be flexible enough in their choice of sampling sites, incorporating ecotones and transitional vegetation communities (e.g., area of disturbance or primary succession within a homogenous vegetation type). Some bird species may be responding to edge effects or other features of habitat heterogeneity that may be missed if only homogenous patches are sampled.

In addition to the previous recommendation regarding size of relevé sub-plot, we recommend users to carefully consider using additional sub-plots to capture the variation in heterogeneous habitats. Smith et al. (2008) highlight the importance of using multiple sub-plots to capture habitat heterogeneity for predicting occupancy patterns of bird species in heterogeneous forests. In homogenous habitat patches, Smith et al. (2008) document the need for fewer sub-plots to capture habitat variability which may be influencing site-occupancy for focal study species. Additional sub-plots would increase the time needed to collect relevé data. However, these modifications may enable field ornithologists to better capture vegetation features across varying landscapes.

Relevé Modification with Vegetation Structure Data

Based on the findings of this study, including the work of previous authors who have noted the important of vegetation physiognomy to birds throughout the breeding season (Cody 1981, Cody 1985, Rotenberry 1985, MacNally 1990), we recommend users of a relevé method to include, or to continue incorporating measurements of vegetation structure which are thought to influence bird occupancy. Furthermore, in addition to percent cover estimates of broad physiognomic classes (i.e., hardwood, and shrub), users of relevé methods could append additional methods for quantifying vegetation structure, such as foliage-height diversity (MacArthur and MacArthur 1961).

Using the occupancy modeling approach, we assessed the usefulness of the vegetation data collected using an original and a modified relevé method for modeling habitat relationships of three focal bird species. We found that data collected using a modified relevé method were effective for modeling occupancy for two species of birds, but occupancy patterns for one species were better predicted using data collected using the original relevé protocol. Environmental variables such as elevation were selected in the most well supported models for all three species indicating their importance for explaining bird-habitat occupancy relationships. Relevé methods were more efficient to collect compared to studies which applied the James and Shugart Jr. circular-plot (1970), and the BBIRD protocol (Martin et al. 1997). For the three focal species, we did find a low percent of deviance explained from the modeling exercise. It is possible other habitat quantification methods could potentially provide data which would explain more deviance while building explanatory bird-occupancy models. However, many of our *a priori* hypothesized models were well supported suggesting the relevé methods were capable of quantifying features influencing bird-habitat occupancy. Our results suggest data collected using relevé methods can be used to accurately model wildlife habitat associations, but we recommend including structural variables that may not be included in the original relevé method protocols and urge investigators to carefully consider habitat associations and territory sizes of their study species when determining the size of their study plots.

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