The Auk 123(1):33–44, 2006

Printed in USA.

ABUNDANCE AND HABITAT PREFERENCES OF GRAY VIREOS (*VIREO VICINIOR*) ON THE COLORADO PLATEAU

Scott Schlossberg[1]

Program in Ecology and Evolutionary Biology, University of Illinois, Urbana-Champaign, 606 East Healey Street, Champaign, Illinois 61820, USA

Abstract.—The Gray Vireo (*Vireo vicinior*; hereafter "vireo") is a little-studied songbird with small breeding and wintering ranges. Because of uncertainty about vireo populations, conservationists are concerned about the future of this species. The goal of the present study was to provide new data on the ecology of the vireo to help determine its conservation status. During May and June 2001, I studied breeding habitat selection by vireos on the Colorado Plateau in northern Arizona and southern Utah. I surveyed for vireos and collected vegetation data on 31 transects in pinyon–juniper (*Pinus edulis–Juniperus* spp.) woodlands throughout this region. Estimated density of vireos was 0.064 ± 0.011 (mean ± SE) birds ha^{-1}. Analysis at two scales showed that the vireo's primary habitat preference was for areas where junipers predominate over pinyon pine. Vireos also preferred areas with some shrub cover, and they increased with the prevalence of sagebrush (*Artemisia tridentata*) among shrubs. Additionally, vireos were more common at lower elevations, an effect that was largely independent of vegetation characters. Habitats preferred by vireos are widespread in the southwestern United States and may be increasing in extent as woodlands expand into grasslands and shrublands. On the basis of these results, I suggest that vireo populations are relatively safe, at least for the short term. Additional data on vireo demography are needed to ensure the long-term conservation of this species. *Received 26 February 2004, accepted 27 April 2005.*

Key words: Gray Vireo, habitat preferences, pinyon–juniper woodlands, *Vireo vicinior*.

Abundancia y Preferencias de Hábitat de *Vireo vicinior* en la Planicie de Colorado

Resumen.—*Vireo vicinior* es una ave canora con rangos de cría y de invernada pequeños. Debido a la incertidumbre acerca de sus poblaciones, los conservacionistas están preocupados por el futuro de esta especie. El objetivo del presente estudio fue proveer datos nuevos sobre la ecología de *V. vicinior* para ayudar a determinar su estado de conservación. Durante mayo y junio de 2001, estudié la selección de hábitat de nidificación por parte de esta especie en la planicie de Colorado, norte de Arizona y el sur de Utah. Realicé censos de los vireos y recolecté datos sobre la vegetación a través de esta región en 31 transectos en áreas arboladas dominadas por *Pinus edulis* y por especies de *Juniperus*. La densidad de vireos estimada fue de 0.064 ± 0.011 (media ± EE) aves ha^{-1}. Un análisis a dos escalas mostró que *V. vicinior* prefiere principalmente ambientes donde las especies de *Juniperus* son dominantes con respecto a *P. edulis.* Los vireos también prefirieron áreas con cierta cobertura de arbustos, e incrementaron con el aumento en frecuencia de *Artemisia tridentata* entre los arbustos. Además, los vireos fueron más comunes a elevaciones menores, un efecto que en gran medida fue independiente de las características de la vegetación.

---

[1] E-mail: schlssbr@uiuc.edu

Los hábitats preferidos por los vireos están ampliamente distribuidos en el suroeste de los Estados Unidos y su extensión podría estar incrementando a medida que las áreas arboladas se expanden hacia los pastizales y las áreas arbustivas. Con base en estos resultados, sugiero que las poblaciones de *V. vicinior* están relativamente a salvo, al menos en el corto plazo. Es necesario obtener datos adicionales sobre demografía para asegurar la conservación de esta especie a largo plazo.

Information about an organism's life-history, abundance, distribution, and habitat requirements is essential for understanding threats to its survival and for countering those threats (Caughley 1994, Green 1995, Wilson 2000). Lack of such knowledge can lead to inappropriate allocation of scarce resources and poor management decisions (Derrickson et al. 1998). Insufficient knowledge is often cited as a problem for the conservation of poorly known bird communities in remote, tropical regions (Brawn et al. 1998, Grajal and Stenquist 1998). Surprisingly, however, many bird species in North America have received little attention from ornithologists. One such species is the Gray Vireo (*Vireo vicinior*; hereafter "vireo"), a Neotropical migratory songbird that breeds in semiarid pinyon–juniper (*Pinus* spp.–*Juniperus* spp.) woodlands and scrub habitats in the southwestern United States. Few scientific studies have been conducted on the vireo, and most of those have been from the periphery of the species' range (Johnson 1972, Barlow 1977). As a result, only the most basic data on its distribution and breeding biology have been collected (Barlow et al. 1999).

Largely because of this lack of knowledge, conservationists are concerned about the vireo's status. Although Breeding Bird Survey data show a nonsignificant increasing trend for this species over the past 30 years (Sauer et al. 2001), the vireo has a restricted breeding range and, therefore, probably a small global population. As a result, Partners in Flight (2002), the National Audubon Society (2002), and the U.S. Fish and Wildlife Service (2002) have each identified this species as one of special concern.

One of the few certainties about the vireo is that its pinyon–juniper habitat is currently undergoing a number of changes that may affect the birds. Since 2001, severe drought has led to mass mortality of pinyon pines (*P. edulis*) over large portions of the Southwest (Breshears et al. 2005). Because trees grow slowly in this habitat, woodlands will be slow to recover (Gottfried and Pieper 2000). Another factor that may affect vireos is altered disturbance regimes caused by livestock grazing and fire suppression. Before European settlers arrived in the Southwest, pinyon–juniper woodlands were generally open savannas with diverse and productive understories (Miller and Wigand 1994, Cole et al. 1997). Because of overgrazing and the subsequent reduction in fire frequency, tree densities have increased, and woodlands today resemble closed-canopy forests more than savannas (Tausch et al. 1981, West 1984). Consequently, this habitat is more homogeneous and more prone to high-intensity fire than before the arrival of livestock in the Southwest (Gruell 1999). Finally, in many areas, pinyon–juniper woodlands are expanding their range, invading areas that were formerly grassland or shrub-steppe (Blackburn and Tueller 1970, Tausch et al. 1981). How all these changes will affect the vireo is not known.

My objective here was to improve our understanding of the vireo's ecology by measuring its abundance and habitat preferences across the central portion of its range. I addressed three questions: (1) How abundant are vireos across this part of their range? (2) How does vegetation structure and composition influence vireo abundance? (3) How does vireo abundance vary with elevation, and is this effect independent of vegetation characteristics? On the basis of my answers to these questions, I assessed how ongoing changes in the vireo's habitats may affect its populations.

Methods

Study region.—Research was conducted in pinyon–juniper woodlands at 31 sites on the southern Colorado Plateau (Fig. 1). The plateau is a large uplifted area characterized by mesas, cliffs, and canyons. Pinyon–juniper woodlands are a characteristic plant community of the Colorado Plateau, occurring at elevations from 1,370 to 2,290 m, where annual precipitation ranges from 305 to 560 mm (Gottfried and

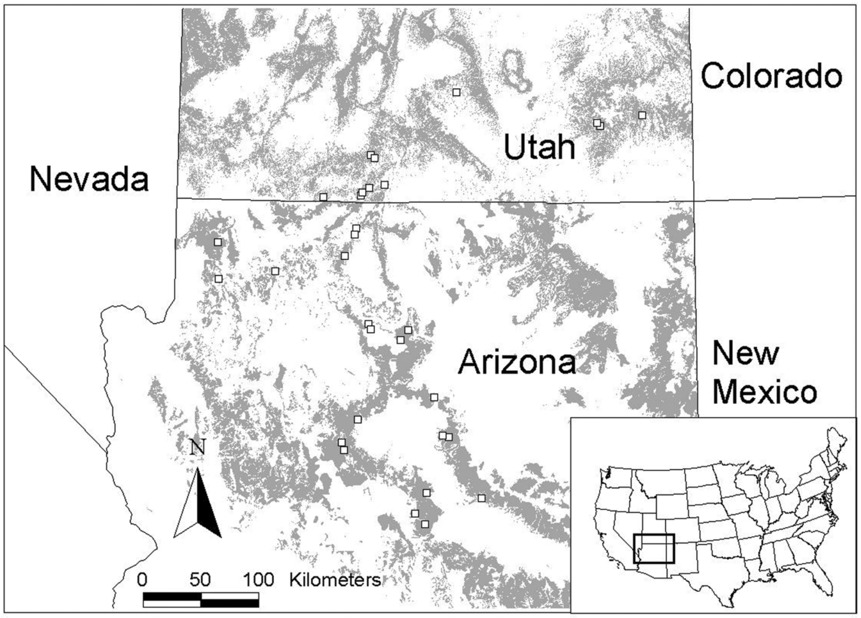

Fig. 1. Study sites (squares) and pinyon–juniper woodlands (shaded) in Arizona and Utah.

Pieper 2000; Fig. 1). These woodlands are short-statured open forests dominated by pinyon pines and various juniper species. At lower elevations, woodlands tend to be more open, with shorter trees; at higher elevations, trees are typically taller and grow more densely. Understory vegetation in pinyon–juniper woodlands varies greatly, depending on soils, tree density, and the disturbance history of a site (Gottfried and Piper 2000).

Site selection.—All field work was conducted on federal lands administered by the National Park Service; Bureau of Land Management; or U.S. Department of Agriculture, Forest Service. The general strategy in selecting sites was to identify areas of pinyon–juniper woodlands using vegetation maps and the expertise of biologists and then to pick specific areas that were amenable to bird surveys (i.e. accessible by roads and lacking steep cliffs or other obstacles). Overall, sites were selected to maximize the range of habitat conditions encountered and with no prior knowledge of the vireo's distribution. I chose three sites in areas that had recently suffered severe fires and two sites in areas dominated by sagebrush (*Artemisia tridentata*) but where pinyon and juniper trees were invading. The remaining sites were in relatively mature woodlands.

Bird surveys.—At each site, I established a transect with random orientation (with the restriction that the transect could not cross any impassable barriers). Transect length varied from 1,000 to 2,500 m (mean ± SE = 2,024 ± 77 m), and birds were counted at points every 250 m along each transect. Bird surveys were conducted between 5 May and 19 June 2001, and each transect was sampled once during a single morning. Beginning within 30 min of sunrise, I conducted an 8-min count of birds at each point, recording the detection distance for each bird seen or heard. I continued along the transect until each point had been surveyed, generally within three hours after sunrise. Seventy-four bird species were recorded during point counts, but only data on vireos are reported here.

Vegetation analysis.—On 30 of 31 transects, I sampled vegetation at each point where I counted birds (extremely fragile soils on one transect precluded measuring vegetation). I focused on woody plants because vireos are primarily foliage dwellers and use trees and shrubs for foraging and nesting (Barlow et al. 1999). At each point-count site, I established four subpoints: a central one at the location of the point count, and three others separated by 120° and located 30 m away from the central point (based on Martin et al. 1997). At each subpoint, I used the point-centered quarter method, which uses the number of trees or shrubs near a point and their average distance from a point as an index of density (Cottam and Curtis 1956). First, I established a circular plot with 15-m radius around each subpoint and divided the plot into four equal quadrants. Within each quadrant, I located the tree nearest the subpoint and recorded its species, distance from the subpoint, height, and average crown width (in the plane perpendicular to a line drawn from the subpoint to the tree). Only trees taller than 0.3 m were counted, including only species that typically grow to a maximum height of ≥4 m (*P. edulis*, *P. ponderosa*, *Juniperus* spp., *Quercus gambelii*, or *Prosopsis glandulosa*). In each quadrant, I also recorded the species, height, crown width, and distance from the subpoint for the nearest shrub, defined as any woody plant that was not a tree but was ≥0.3 m tall. No trees or shrubs were found in some quadrants. I recorded the elevation and geographic position of each point-count location using a Global Positioning System receiver.

Vegetation data were summarized by point by averaging data across the four subpoints. Measures included four variables each for trees and shrubs: height, crown width, distance from the central point, and proportion of quadrants that contained trees or shrubs. For each set of four subpoints, I also calculated the height of the tallest recorded tree, the coefficient of variation (CV) of tree heights, proportion of trees that were pinyon or juniper (these made up 83% of recorded trees), and proportion of shrubs by species.

One potential shortcoming of this sampling scheme is that vegetation was sampled only within 30 m of each point-count location, whereas birds were observed ≤160 m away. This would be a problem, however, only if vegetation were highly heterogeneous. In fact, vegetation tended to be similar at each point within an individual transect (mean CVs for vegetation variables within transects ranged from 18% to 40%). Furthermore, first-order autocorrelations among vegetation variables (comparing each pair of neighboring points) were positive for each variable and significant in 10 of 12 cases (mean $r = 0.48$, range: 0.22–0.75). This strongly suggests that vegetation is fairly homogenous at a scale of 250 m, well beyond the range where vireos were detected (160 m).

Statistical analyses.—Vireo abundance data were analyzed using the program DISTANCE to determine detection rates and estimate densities (Buckland et al. 1993). Sample sizes were not sufficient to compute a detection function for each transect. Thus, I pooled all data to determine a single detection function. Algorithms used to compute detection functions in DISTANCE are robust to the pooling of data across heterogeneous sites (Rosenstock et al. 2002). Because tree density could have influenced my ability to detect birds at a distance, I included the mean distance to trees at each point as a covariate in preliminary DISTANCE models. The final model, selected using Akaike's Information Criterion (AIC), did not include the covariate.

I analyzed the vireo's habitat preferences on two scales, the individual point and the transect. By point, I examined how vegetation measures influenced presence or absence of vireos. To reduce the number of variables, I used *t*-tests (or Mann-Whitney *U*-tests, where appropriate) to screen vegetation variables for differences between occupied and unoccupied points. Variables were retained if results were significant at $P \leq 0.05$. I then used multiple logistic regression to determine which retained variables most influenced the presence of Gray Vireos. To select the final model, I used stepwise regression with forward and backward selection ($P < 0.15$ to enter model, $P > 0.15$ to leave).

Because of disparity in the distribution of the dominant shrub species, I considered the influence of shrub species composition separately from other vegetation variables. Overall, sagebrush was the dominant shrub, comprising 54% of recorded shrubs ($n = 3{,}349$). This species was present on every transect north of 35.5°N latitude ($n = 182$ points, 20 transects) but on no sites south of that latitude ($n = 92$ points, 10 transects). Because of this disparity, I analyzed the influence of shrub species composition separately for these two regions. To be included in the analysis, a shrub had to make up ≥2% of all shrubs recorded and be present at >10% of points. As above, I screened shrub species individually for whether their prevalence differed between occupied and unoccupied points, and retained variables were entered into a multiple logistic regression model.

I also summarized the data by transect to determine how vireo density varied with larger-scale vegetation characteristics. To do this, I averaged vireo densities and vegetation measures across each transect. Because of the disparity in the distribution of sagebrush, I again considered shrub species composition separately from other variables. To reduce the dimensionality of the vegetation data (not including shrub species prevalence), I ran a principal component analysis (PCA) with Varimax rotation. I used the broken-stick criterion to determine which components to retain for analysis (McGarigal et al. 2000). On the basis of the PCA, I computed factor scores for each transect, and I used multiple linear regression to determine which vegetation factors affected vireo density. Because of their lack of significance in exploratory analyses, I did not include interactions or quadratic terms. Because principal component axes are orthogonal, there was no multicollinearity and, therefore, no need to use stepwise selection procedures (Neter et al. 1996). I used *t*-tests to determine which principal components had a significant effect in the regression. To analyze the effects of shrub species on vireo density, I again split the data set between transects with and without sagebrush. Because the distributions of variables were highly non-normal, I simply examined the Spearman rank correlations between vireo density and shrub prevalence by transect.

Previous reports have suggested that vireos are more common at lower elevations (see Barlow et al. 1999). To determine whether vireo densities respond to elevation *per se* or to vegetation features that correlate with elevation, I conducted a separate analysis of the influence of elevation on vireo density at the transect scale. First, I used linear regression to test the relationship between vireo density and elevation. Then, I repeated the analysis of vegetation variables on vireo density, as above, but this time included elevation as a variable in the PCA (the elevation–vegetation model). The purpose of this was to determine whether a model that included vegetation and elevation together fit the data better than a model based solely on vegetation (the vegetation-only model; see above). As above, I used linear regression to select a final model based on the new factor scores. Finally, I used AIC to compare the relative fit of the three models: (1) elevation alone, (2) vegetation-only, and (3) elevation–vegetation. As suggested by Burnham and Anderson (2002), I also included the complete model, with all parameters used in the three models. For this analysis, I excluded one transect because its elevations (1,213 to 1,330 m) were 300 m lower than those of any other site and were below the range in which pinyon–juniper woodlands normally occur (1,370 to 2,290 m; Brown 1994). Appropriate transformations were used throughout to ensure normality of data, and I report all data as means ± SE.

RESULTS

Abundance.—Ninety-four vireos were observed during 282 point counts on 31 transects. Distance sampling indicated that overall density of vireos was 0.064 ± 0.011 birds ha^{-1} (95% confidence interval [CI]: 0.046 to 0.089 birds ha^{-1}). Vireos occurred on 69 of 282 points (24.5%) and 20 of 31 transects (64.5%). Estimating the number of breeding pairs from these data was not possible, because the sexes are monomorphic and both males and females sing.

Habitat preferences by point.—Vegetation data were collected at 274 point-count locations on 30 transects. Of the original 12 vegetation variables (excluding shrub species), 6 were retained for analysis with logistic regression (Table 1). The final model for predicting vireo occupancy included two variables: percentage of trees that were junipers and mean distance to shrubs, an indicator of shrub density (overall model: $\chi^2 = 35.3$, df = 2, $P < 0.0001$, concordance = 79%; Table 1). Vireo occupancy increased with the prevalence of junipers (Fig. 2A) and with shrub density (Fig. 2B). For the 182 points on transects with sagebrush, screening led to retention of two shrub species (Table 2). The final logistic regression model included only the positive effect of sagebrush on vireo occupancy ($\chi^2 = 6.55$, df =1, $P = 0.01$, concordance = 62%; Table 2; Fig. 2C). For the 92 points on transects lacking sagebrush, four shrub species were sufficiently abundant for analysis, but none differed in prevalence between occupied and unoccupied sites. Thus, no shrub species influenced the presence of vireos on sites without sagebrush.

Habitat preferences by transect.—At the transect scale, PCA resulted in retention of five components that explained 92.5% of the variance in the vegetation data set. The first factor (pinyon–juniper) contrasted pinyon pines and narrower trees with junipers and wider trees. The second factor (trees) was correlated with two measures

TABLE 1. Effects of vegetation on occupancy of Gray Vireos by point. The *t*-tests indicate differences between points with and without vireos. Logistic regression results are for the final model.

	Initial screening		Multiple logistic regression		
Variable [a]	t	P	Odds ratio [b]	χ^2	P
Pinyon pine (%)	5.84	<0.01			
Juniper (%)	–6.53	<0.01	29.01	28.5	<0.0001
Trees	–0.32	0.75			
Distance to tree	–2.17	0.03			
Tree height	–0.47	0.64			
Tree width	–3.26	<0.01			
CV tree height [c]	2.18	0.03			
Maximum tree height	0.79	0.43			
Shrubs	–0.62	0.54			
Distance to shrub	3.24	<0.01	0.80	7.59	0.006
Shrub height	0.11	0.91			
Shrub width	1.05	0.30			

[a] Variables in bold were entered in the logistic regression model.
[b] Proportional increase in the probability that vireos are present, given a one-unit increase in the predictor variable.
[c] CV = coefficient of variation.

TABLE 2. Effects of shrub species composition on occupancy of Gray Vireos at sites with sagebrush (n = 182). All conventions as in Table 1.

	Initial screening		Multiple logistic regression		
Shrub species	U	P	Odds ratio	χ^2	P
Sagebrush (*Artemisia tridentata*)	2,661.5	0.01	4.068	6.55	0.01
Cliffrose (*Cowania stansburiana*)	3,969.0	0.06			
Gambel's oak (*Quercus gambelii*)	4,109.5	<0.01			
Mormon tea (*Ephedra* spp.)	3,353.0	0.61			

of tree density, total number of trees and distance to tree, as well as maximum tree height. The third factor (tree height) indicated the height of trees as well as the variability in tree height. The fourth factor (shrub size) was a measure of the height and width of shrubs. The final factor (shrubs) reflected the density of shrubs as indicated by the number of shrubs recorded and the distance from the central point.

Multiple regression showed that vireo density was significantly influenced by the vegetation axes in the vegetation-only model (r^2 = 0.54, F = 5.63, df = 5 and 24, P = 0.0014). Of the five components, pinyon–juniper had the strongest effect on vireo density (r = 0.65, t = 4.71, P < 0.0001). Vireo density increased with the proportion of trees that were junipers and with average tree width and decreased with the proportion of pinyon pines (Fig. 3A). Regression also revealed a weak relationship with shrubs (r = 0.41, t = –2.22, P = 0.04), with vireo abundance increasing with shrub density (Fig. 3B).

For the transects with sagebrush, I tested 10 shrub species for rank correlations between their prevalence and vireo density. Only sagebrush had a significant relationship with vireo density (r_s = 0.63, n = 20, P = 0.003). On sites without sagebrush, I tested seven shrub species for correlations with vireo density. I found no significant correlations between shrub prevalence and vireo abundance.

Elevation.—At the transect level, elevation was negatively correlated with vireo density (r = –0.71, n = 30, P < 0.0001; Fig. 4). This finding is consistent with the fact that elevation had a strong relationship with pinyon–juniper (r = –0.70, n = 30, P < 0.001) but not with any other principal component (all $|r| < 0.16$, n = 30, all P > 0.40). A second PCA, including vegetation variables and elevation (the elevation–vegetation model), produced results very similar to the

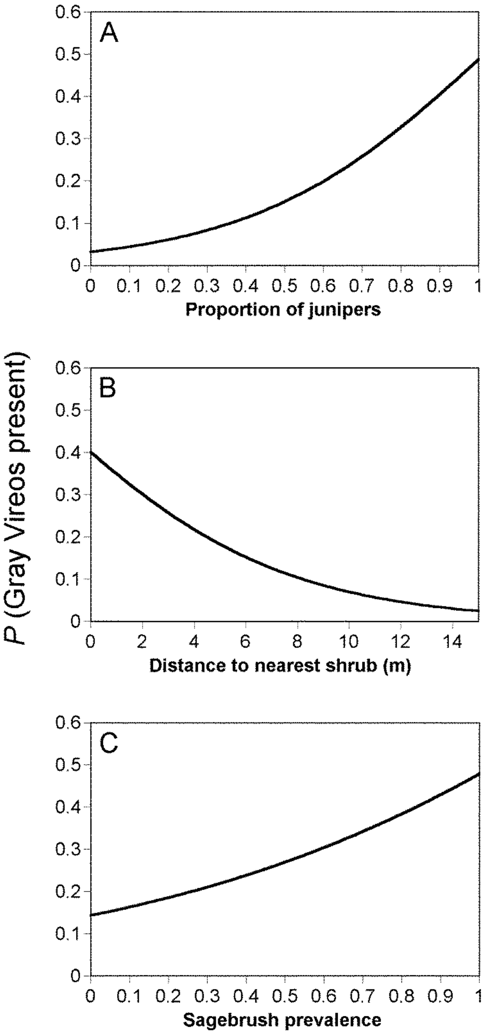

FIG. 2. Results from logistic regression of vegetation variables on Gray Vireo occupancy for (A) juniper prevalence, (B) distance to nearest shrub, and (C) sagebrush prevalence (for transects with sagebrush).

vegetation-only results. Five components were retained, explaining 91.5% of the variation in the original data set (Table 3). Elevation loaded strongly on the component axis (pinyon–juniper–elevation) that included tree species composition. Other axes were largely as in the vegetation-only PCA. Linear regression showed that of the five components, only the pinyon–juniper–elevation axis and the trees axis influenced vireo density (overall model: $r^2 = 0.55$, $F = 5.71$, df = 5 and 23, $P = 0.001$; Table 4).

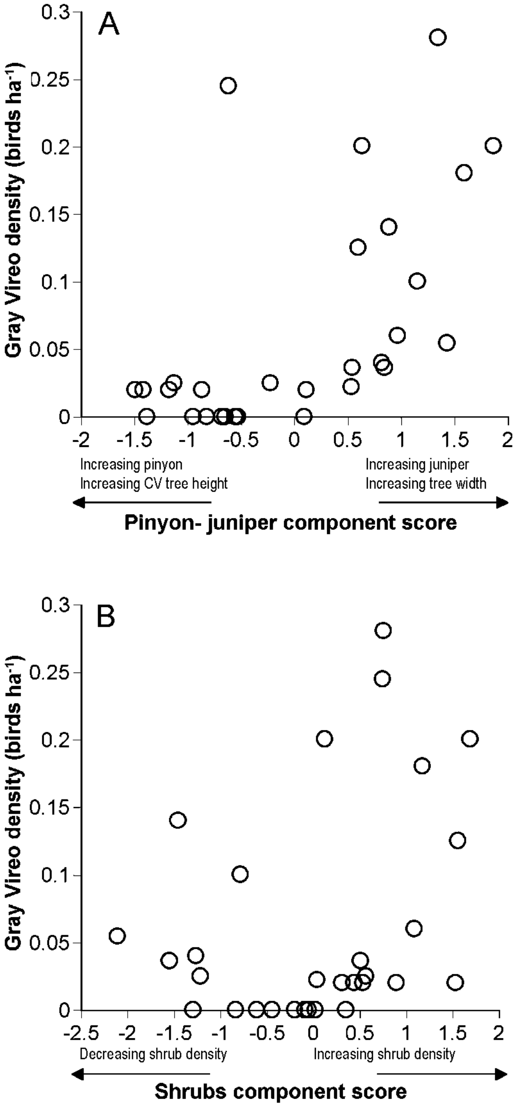

FIG. 3. Relationship between Gray Vireo density and component scores for (A) the pinyon–juniper component axis and (B) the shrubs component axis for the vegetation-only model.

I used AIC to compare the relative fit of the best vegetation-only model (pinyon–juniper and shrubs), the elevation-only model, the best elevation–vegetation model (pinyon–juniper–elevation and trees), and the full model including all parameters (Table 5). The model with the highest support was the vegetation–elevation model. Support was strong (total weight = 0.85), however, for both models that included elevation. By

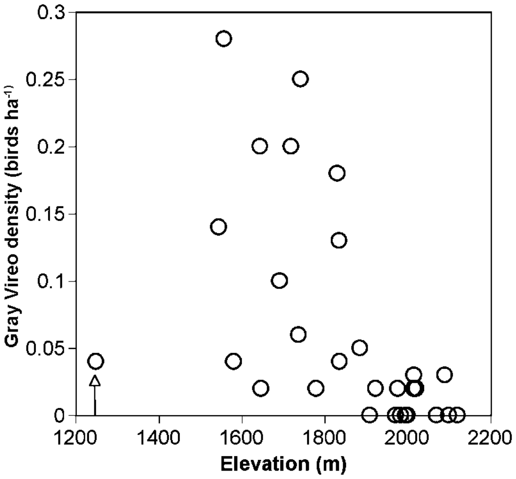

FIG. 4. Relationship between elevation and Gray Vireo density. Arrow indicates an outlier site that was not included in analyses.

contrast, the vegetation-only model had a weight of just 0.13, indicating low support. This suggests that elevation has a strong effect on vireo density and that this is, to a certain extent, independent of the vegetation parameters that I measured.

DISCUSSION

Abundance.—The estimated density of vireos on my study sites, 0.064 ± 0.017 birds ha^{-1}, is very similar to estimates from other studies of this species. The Colorado Bureau of Land Management (1995) estimated 0.06 birds ha^{-1} in Colorado. Weathers (1983) reported 0.04 birds ha^{-1} in California, and Grinnell and Swarth (1913; cited in Weathers 1983) found 0.063 birds ha^{-1} in the same region. The close correspondence among these results is striking and suggests that vireos occur at similar densities throughout their range. The density of vireos is significantly lower than that of other small insectivorous songbirds breeding in pinyon–juniper woodlands (LaRue 1994, Colorado Bureau of Land Management 1995, S. Schlossberg unpubl. data). Why vireos occur at such low densities is not known, but the relatively large size of the birds' breeding territories may be a factor. Vireo territories have been reported to range in size from 2 to 10 ha (Barlow et al. 1999). No explanation has been proposed for the large size of vireo territories.

Habitat preferences.—Analysis at two different scales, the point and the transect, led to the same

TABLE 3. Principal component analysis of vegetation measures, including elevation. Component loadings in bold are significant by the criterion of loading >0.5.

	Factor				
	Pinyon–juniper–elevation	Tree height	Shrubs	Trees	Shrub size
Eigenvalue	3.66	2.61	1.89	1.82	1.91
Variance explained (%)	28.20	20.10	14.60	14.00	14.70
Cumulative variance	28.20	48.20	62.80	76.80	91.50
Variable	Component loading				
Pinyon pine (%)	**0.950**	0.051	0.066	0.097	0.039
Juniper (%)	**–0.947**	–0.125	–0.025	–0.112	–0.071
Elevation	**0.842**	0.075	–0.089	0.053	0.206
Tree width	**–0.793**	0.121	–0.153	–0.417	0.137
Maximum tree height	0.088	**0.943**	–0.085	0.193	0.150
Tree height	–0.203	**0.929**	–0.125	–0.056	0.166
CV tree height [a]	0.474	**0.818**	–0.075	0.025	–0.097
Distance to shrub	0.089	0.129	**–0.959**	–0.028	–0.076
Shrubs	0.157	–0.085	**0.934**	–0.070	0.144
Trees	0.058	0.010	–0.043	**0.937**	0.173
Distance to tree	–0.442	–0.181	0.012	**–0.814**	0.009
Shrub height	–0.036	0.022	–0.096	–0.012	**–0.974**
Shrub width	–0.146	–0.301	–0.151	–0.185	**–0.881**

[a] CV = coefficient of variation.

Table 4. Linear regression of vegetation–elevation principal components on Gray Vireo density.

Parameter	Estimate	SE	t [a]	P
Pinyon–juniper–elevation	–0.129	0.022	–5.96	<0.0001
Trees	0.057	0.022	2.62	0.0140
Tree height	0.011	0.022	0.51	0.6100
Shrub size	0.022	0.022	0.07	0.9500
Shrubs	0.008	0.022	0.38	0.7100

[a] df = 28.

Table 5. AIC analysis of models explaining Gray Vireo density as a function of vegetation and elevation.

Model	Model components	K [a]	AIC_c [b]	ΔAIC_c [c]	Weight [d]
Elevation–vegetation	Pinyon–juniper–elevation + trees	4	–47.1	0.0	0.50
Elevation only	Elevation	3	–46.4	0.7	0.35
Vegetation only	Pinyon–juniper + shrubs	4	–44.5	2.7	0.13
Full	All [e]	7	–40.6	6.5	0.02

[a] Number of parameters in model (including constant and error).

[b] Akaike's information criterion adjusted for small sample size.

[c] Difference between model AIC_c and the minimum AIC_c.

[d] Akaike weight indicating relative support for the model.

[e] Complete model including all parameters above.

conclusion: Ideal habitat for the vireo is lower-elevation woodland dominated by junipers and with shrub cover including a high proportion of sagebrush. Of these habitat elements, the preponderance of junipers was consistently the most important. This habitat preference explains, in part, why vireo density was inversely related to elevation. Junipers, because they are more drought-tolerant than pinyon pines, tend to predominate at lower elevations, whereas the more cold-tolerant pinyons increase with elevation (Tausch et al. 1981, Martens et al. 2001). One reason why vireos may prefer areas with junipers is that the birds often nest in small to medium-sized junipers (2–5 m tall; S. W. Hutchings and A. R. Leukering unpubl. data).

Vireos preferred areas with some shrub cover, though the relationship between vireo abundance and shrub density was weak. Analysis of shrub species preferences showed that in areas with sagebrush, the birds increase with the prevalence of sagebrush. Vireos, however, were also found at many sites lacking sagebrush. At these locations, no preferences for shrub species were apparent. Shrubs may be important to vireos because, although the birds generally forage and nest in trees, they occasionally nest in taller shrubs (>1.5 m tall) and will feed in shrubs (S. Schlossberg unpubl. data). Still, the birds occurred at some sites that had very little shrub cover, so shrubs are not a required habitat feature for vireos. Whether shrub cover influences the vireo's nesting success is not known.

Though vireos are generally tree-dwellers, only the vegetation–elevation model showed a relationship between vireo abundance and tree density. No such relationship was found in the vegetation-only model. Furthermore, the effect of tree density on vireo abundance in the vegetation–elevation model was weak. This suggests that tree density is not a major factor in habitat selection by vireos, so long as some trees are present. In my study area, vireos are not found in areas lacking trees (S. Schlossberg pers. obs.). This habitat preference was not apparent in the data because nearly all study sites had some trees.

Elevation had a strong effect on the abundance of vireos in the present study. If elevation was important only because it correlated with vegetation features preferred by vireos, then the vegetation–elevation model should have performed equivalently to the vegetation-only model. In contrast, AIC analysis showed that models including elevation did a better job of explaining vireo abundance than the model that included only vegetation. Although part of the vireo's preference for lower elevations may be attributable to the negative correlation between elevation and juniper abundance, these results suggest that elevation affects vireo abundance independently from vegetation. Thus, all else being equal, lower-elevation sites are more important for vireos than higher-elevation sites. Data showed that vireos were uncommon above 1,900 m and increased in abundance from 1,900 to 1,500 m (Fig. 4). Sites within this elevation range should be given priority when considering conservation of this species.

The present study did not reveal why vireos select low-elevation areas. One possible explanation is competitive exclusion by the congeneric Plumbeous Vireo (*V. plumbeus*), typically found at higher elevations than Gray Vireos (Sedgwick 1987). Observers have reported that Gray and Plumbeous vireos can be syntopic (Barlow et al. 1970, S. Schlossberg pers. obs.), but experimental tests of competition between the two species have not been conducted. Another possibility is that Gray Vireos are physiologically adapted to the warmer temperatures found at lower elevations (see Cooper and Gessaman 2004).

The regional scope of the present study stands in contrast to the smaller-scale approach typically used to study avian habitat associations. Admittedly, a small-scale study may be best for understanding fine-scale habitat associations. Such a study, however, could produce results that do not apply in other portions of the species' range. By making conclusions about region-wide habitat preferences, the present study should be useful to managers over a wide area. One limitation of these findings is that study areas were restricted to pinyon–juniper woodlands on the Colorado Plateau. Although vireos are found almost exclusively in this habitat type in Arizona and Utah, because of the focus of my study, results are meaningful only within this habitat. Applying these findings in California and Texas, on the periphery of the vireo's range, would not be justifiable, because vireos use different habitats in those areas (Barlow et al. 1999).

Assessment of potential threats to vireo habitat.— In light of the data on vireo habitat preferences, we can better understand how potential changes in pinyon–juniper woodlands may affect vireo populations. Currently, southwestern pinyon–juniper woodlands are experiencing three major changes. First, since 2001, pinyon pines have been dying in large numbers because of drought and a bark-beetle (*Ips confusus*) outbreak (Breshears et al. 2005). The vireo's preference for areas where junipers dominate suggests that losing pinyon pines, thereby increasing the relative abundance of junipers, could improve habitat suitability for vireos. Preliminary data, however, suggest that vireos have not increased in abundance where pinyon pines have died (S. Schlossberg unpubl. data). This may be because most dead pinyon pines are still standing (S. Schlossberg pers. obs.), so vireos do not perceive the increased dominance of junipers. Furthermore, pinyon pines are most abundant at higher elevations within pinyon–juniper woodlands, so areas that experience significant pine mortality may not be suitable for vireos because of their elevation. Additional data are needed to determine how the pinyon pine die-off will affect vireos, but my results do not provide any reason to believe that pine mortality threatens the birds.

Second, overgrazing and fire suppression in woodlands have allowed trees to increase greatly in density (West 1984), leading to reduced understory productivity. Data showed that vireos have weak preferences for both higher tree densities and for higher shrub densities. Although loss of understory shrubs could be harmful to vireos, increased tree density may actually benefit the birds. Thus, the effects of increased tree density and loss of shrubs may cancel one another out. Given that the birds' preferences for higher tree and shrub densities were both weak, increased tree density is unlikely to have a major effect on vireo habitat use. At the same time, however, increased tree density may lead to more high-intensity fires in pinyon–juniper woodlands. In the present study, results from three sites that had recently experienced major fires showed that birds avoid areas where trees have been killed but will use adjacent, unaffected areas (S. Schlossberg unpubl. data). Major fires would likely be detrimental to vireos because the birds avoid areas lacking trees.

Finally, pinyon and juniper trees have recently invaded large areas of grassland and shrubsteppe (Blackburn and Tueller 1970, Tausch et al. 1981). As a result, the extent of pinyon–juniper woodlands in the Southwest is currently at a historical high (West 1984). The expansion of woodlands is almost certainly positive for vireos because they will use relatively young woodlands where trees have invaded more open habitats, especially in sagebrush shrublands. Furthermore, the expansion of pinyon–juniper woodlands is primarily occurring at the lower elevations preferred by vireos (Tausch et al. 1981). Thus, the potential area of vireo habitat is increasing because of tree invasion of more open habitats.

Conservation status.—Although vireos occur at low densities, their preferred habitat—low-elevation woodlands with many junipers and a sagebrush understory—is abundant and probably increasing in the Southwest. Furthermore, many of the ongoing changes in pinyon–juniper woodlands, especially the expansion of woodlands into open areas, are likely to benefit vireos. A simple population model for vireos in my study area, covering ~20% of the species' breeding range, produced a population estimate of 183,000 birds (S. Schlossberg unpubl. data). Taken together, these findings suggest that vireo populations and their habitats are relatively safe for the time being. The present study, however, represents only a snapshot in time, and trends for this species remain uncertain (Sauer et al. 2001). Future priorities for research on this species should include determination of demographic parameters and improved monitoring of populations (e.g. by adding more Breeding Bird Survey routes in vireo habitat). Although peripheral populations in California, Texas, and Colorado may be of conservation concern (Barlow et al. 1999), the vireo as a species does not appear to warrant special consideration at this time.

Acknowledgments

Thanks to E. Conrad for assistance in the field and to Sigma Xi for a grant-in-aid of research. J. Chynoweth, M. Herder, S. Rosenstock, and G. Sheppard assisted me in selecting study sites and choosing field methods. The manuscript was improved greatly by comments from J. Brawn, S. Robinson, M. Ward, and J. Foster. During preparation of this manuscript, I was supported by a National Science Foundation Graduate Research Fellowship.

Literature Cited

Barlow, J. C. 1977. Effects of habitat attrition on vireo distribution and population density in the northern Chihuahuan Desert. Pages 591–596 *in* Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region, United States and Mexico (R. H. Wauer and D. H. Riskind, Eds.). U.S. Department of the Interior, National Park Service, Washington, D.C.

Barlow, J. C., R. D. James, and N. Williams. 1970. Habitat co-occupancy among some vireos of the subgenus *Vireo* (Aves: Vireonidae). Canadian Journal of Zoology 48:395–398.

Barlow, J. C., S. N. Leckie, and C. T. Baril. 1999. Gray Vireo (*Vireo vicinior*). *In* The Birds of North America, no. 447 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Blackburn, W. H., and P. T. Tueller. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51:841–848.

Brawn, J. D., S. K. Robinson, D. F. Stotz, and W. D. Robinson. 1998. Research needs for the conservation of Neotropical birds. Pages 323–335 *in* Avian Conservation: Research and Management (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, D.C.

Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, and others. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences USA 102:15144–15148.

Brown, D. E. 1994. Great Basin conifer woodland. Pages 52–57 *in* Biotic Communities: Southwestern United States and Northwestern Mexico (D. E. Brown, Ed.). University of Utah Press, Salt Lake City.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, New York.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63: 215–244.

Cole, K. L., N. Henderson, and D. S. Shafer. 1997. Holocene vegetation and historic grazing impacts at Capitol Reef National Park reconstructed using packrat middens. Great Basin Naturalist 57:315–326.

Colorado Bureau of Land Management. 1995. Analysis of the Colorado BLM nongame bird monitoring point count transects. Bureau of Land Management, Grand Junction, Colorado.

Cooper, S. J., and J. A. Gessaman. 2004. Thermoregulation and habitat preference in Mountain Chickadees and Juniper Titmice. Condor 106:852–861.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Derrickson, S. R., S. R. Beissinger, and N. F. R. Snyder. 1998. Directions in endangered species research. Pages 111–123 *in* Avian Conservation: Research and Management (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, D.C.

Gottfried, G. J., and R. D. Pieper. 2000. Pinyon–juniper rangelands. Pages 153–212 *in* Livestock Management in the American Southwest: Ecology, Society, and Economics (R. Jemison and C. Raish, Eds.). Elsevier, New York.

Grajal, A., and S. Stenquist. 1998. Research applications for bird conservation in the Neotropics. Pages 337–343 *in* Avian Conservation: Research and Management (J. M. Marzluff and R. Sallabanks, Eds.). Island Press, Washington, DC.

Green, R. E. 1995. Diagnosing causes of bird population declines. Ibis 137:S47–S55.

Gruell, G. E. 1999. Historical and modern roles of fire in pinyon–juniper. Pages 24–28 *in* Ecology and Management of Pinyon–Juniper Communities within the Interior West (S. B. Monsen and R. Stevens, Eds.). U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-9.

Johnson, N. K. 1972. Breeding distribution and habitat preference of the Gray Vireo in Nevada. California Birds 3:73–78.

LaRue, C. T. 1994. Birds of northern Black Mesa, Navajo County, Arizona. Great Basin Naturalist 54:1–63.

Martens, S. N., D. D. Breshears, and F. J. Barnes. 2001. Development of species dominance along an elevational gradient: Population dynamics of *Pinus edulis* and *Juniperus monosperma*. International Journal of Plant Sciences 162:777–783.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer-Verlag, New York.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon–juniper woodlands. BioScience 44:465–474.

National Audubon Society. 2002. Audubon Watchlist 2002: An early warning system for bird conservation. [Online.] Available at www.audubon.org/bird/watchlist/.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied Linear Statistical Models, 4th ed. Irwin, Chicago.

Partners in Flight. 2002. Species Assessment Database. [Online.] Available at www.rmbo.org/pif/pifdb.html.

Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Landbird counting techniques: Current practices and an alternative. Auk 119:46–53.

Sauer, J. R., J. E. Hines, and J. Fallon. 2001. The North American Breeding Bird Survey, Results and Analysis 1966–2000, version 2001.2. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland.

Sedgwick, J. A. 1987. Avian habitat relationships in pinyon–juniper woodland. Wilson Bulletin 99:413–431.

Tausch, R. J., N. E. West, and A. A. Nabi. 1981. Tree age and dominance patterns in Great Basin pinyon–juniper woodlands. Journal of Range Management 34:259–264.

U.S. Fish and Wildlife Service. 2002. Birds of conservation concern 2002. Division of Migratory Bird Management, Arlington, Virginia.

Weathers, W. W. 1983. Birds of Southern California's Deep Canyon. University of California Press, Berkeley.

West, N. E. 1984. Successional patterns and productivity potentials of pinyon–juniper ecosystems. Pages 1301–1332 *in* Developing Strategies for Rangeland Management: A Report. Westview Press, Boulder, Colorado.

Wilson, E. O. 2000. On the future of conservation biology. Conservation Biology 14:1–3.

Associate Editor: E. K. Bollinger