

Final Report on the Breeding Distribution and Habitat Use of Gray and Plumbeous Vireos at Colorado National Monument

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Abstract

Recent observations suggest that Gray Vireo (*Vireo vicinior*) is not ecologically separated from other species of vireos during the breeding season. In western Colorado, this species regularly occupies the same locations as Plumbeous Vireo (*V. Plumbeus*), but details of habitat use and interactions were largely unknown. To illuminate this relationship, I studied the breeding distribution and habitat use of Gray and Plumbeous vireos at Colorado National Monument, Mesa Co., in western Colorado. I conducted ground searches and mapped the territories of singing males and pairs of each in the Monument. I found 160 Gray and 49 Plumbeous vireo territories in 1999 and 172 Gray and 44 Plumbeous vireo territories in 2000. Following breeding activities, I measured habitat variables within territories of both species and within randomly-selected vegetation plots. Four variables – deciduous shrub density, juniper density, juniper height, and piñon height – discriminated among the three groups. Gray Vireo habitat contained the shortest trees and highest densities of junipers and deciduous shrubs; Plumbeous Vireo habitat contained the tallest trees and intermediate densities of junipers and deciduous shrubs; and random habitat contained intermediate height trees and the lowest densities of junipers and deciduous shrubs.

Introduction

Gray Vireo (*Vireo vicinior*) is a species of arid piñon-juniper, mountain, and chaparral habitats. It breeds in the southwestern United States and northwestern Mexico (Philips 1991, AOU 1998), with breeding populations extending into western and southeastern Colorado (Andrews and Righter 1992, AOU 1998). Plumbeous Vireos (*Vireo plumbeus*) are more widespread than Gray Vireos and breed throughout the Rocky Mountains and Great Basin ranges. The species breeds in forests of piñon pines and junipers, and in forests of ponderosa pine (*Pinus ponderosa*) (AOU 1998). To a lesser extent, both species may be found in deciduous trees along streams, but these trees usually lie next to coniferous forests (Chace 1998).

Gray Vireos have been the subject of few studies, leaving many aspects of their nesting biology and ecology unknown. This is particularly true of the habitat relationships of Gray Vireos and other members of the genus *Vireo*. Gray Vireos have been thought to be ecologically separated

from all other vireo species (Bent 1950). They have, however, been found with Black-capped Vireos (*V. articapillus*) in Big Bend National Park, Texas; Bell's Vireo (*V. belli*) in the Bradshaw Mountains, Arizona (Barlow 1967, Barlow et al. 1970); and with Plumbeous Vireos in Kaibab National Forest, Arizona (Barlow 1967, Barlow et al. 1970) and Colorado National Monument, Colorado (Hutchings and Leukering unpubl.).

Hutchings and Leukering (unpubl.) found large populations of Gray and Plumbeous vireos in Colorado National Monument, Colorado, with overlapping distributions. Prompted by these findings, the Rocky Mountain Bird Observatory and the National Park Service initiated a project to inventory Gray and Plumbeous vireos at Colorado National Monument and to describe the habitat use and relationships of the two species. During the 1999 and 2000 nesting seasons, I mapped the breeding territories of both species and measured and compared habitat variables within those territories. This study describes breeding distribution of both species and addresses whether Gray and Plumbeous vireos nesting within the same woodland select different habitat structures for breeding territories.

Study Area

The Colorado National Monument, Mesa Co., CO, (hereafter; Monument) is located at the far northern edge of the Uncompahgre Plateau, 10 km west of Grand Junction. The topography of the Monument is dominated by alternating steep-walled canyons and gently sloping mesa tops. Elevations range from 1400 m in canyon bottoms, to 2375 m on upland mesas. The Monument vegetation is dominated by piñon-juniper woodland composed of stands of piñon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Other common plant species include big sagebrush (*Artemisia tridentata*), mountain mahogany (*Cercocarpus montanus*), Utah serviceberry (*Amelanchier utahensis*), singleleaf ash (*Fraxinus anomala*), yucca (*Yucca neomexicana*), Mormon tea (*Ephedra viridis*), Gambel's oak (*Quercus gambelii*), and rabbitbrush (*Chrysothamnus nauseosus*). Average annual rainfall is 277 mm, and minimum and maximum July temperatures are 18EC and 33EC, respectively (Spears and Kleven 1978). Common breeding birds of the area include White-throated Swift (*Aeronautes saxatalis*), Plumbeous Vireo, Gray Vireo, Western Scrub-Jay (*Aphelocoma californica*), Juniper Titmouse (*Baeolophus griseus*), Bushtit (*Psaltiriparus minimus*) Bewick's Wren (*Thryomanes bewickii*), Chipping Sparrow (*Spizella pusilla*), and Brown-headed Cowbird (*Molothrus ater*).

Methods

I conducted a systematic ground search of the Colorado National Monument (83 km²) during the breeding seasons of 1999 and 2000 for Gray and Plumbeous vireos. Searches were conducted between 0600 and 1100 hours, and between 1 May and 30 June. I plotted the locations of all Gray and Plumbeous vireos seen or heard on U.S. Geological Survey quadrangle maps. I used tape playbacks of prerecorded Gray and Plumbeous vireo songs to coax non-singing birds into song, since these birds may have otherwise been overlooked. I considered each singing male and each pair of birds to represent a breeding territory. After plotting locales, I randomly selected 30 locations where each species was detected, and determined the approximate center of those

territories by observing the male's (singing member of the pair) movements for several hours during multiple visits.

Following the completion of the nesting season, I measured habitat variables in each those territories using point-quarter methodology (modified from Martin et al. 1997). I randomly selected a distance and bearing from the approximate center of each territory. From that point, I divided the territory into quarters on the cardinal compass directions. In each quarter, I sampled the nearest juniper, piñon, deciduous shrub, and non-deciduous shrub. For each plant I recorded species, distance from the territory center, height, and crown width. I averaged the measurements in each of the quarters at each vegetation plot and determined the elevation of each territory from topographic maps.

To compare Gray and Plumbeous vireo territories with overall available habitat, I randomly sampled 30 vegetation plots within the Monument. These were selected each year, from a topographic map of the Monument overlaid with a grid of 180 evenly-spaced points (1 km between points). When a point fell on an inaccessible cliff, I selected another random point in the same manner. I quantified variables at the random vegetation plots in an identical manner to those at vireo territories.

Statistical Analyses

I performed analyses on a data set that included vegetation samples of Gray Vireo habitat (N = 60), Plumbeous Vireo habitat (N = 60), and random habitat (N = 60). Before combining the 1999 and 2000 data, I used *t*-tests to ensure there was no significant variation between the two years. I tested the assumption of homogeneous variances (normal bell-shaped distribution) and log-transformed variables with heterogeneous variances (Wilkinson et al. 1996). To test for variables that were highly correlated ($r^2 > \pm 0.7$), I calculated Pearson's product-moment correlation coefficients (Wilkinson et al. 1996) for pairs of all combinations of the variables. I made univariate comparisons of the three habitat types using one-way analyses of variance (ANOVA) and used Tukey's tests for subsequent pairwise habitat comparisons (Wilkinson et al. 1996). I used stepwise discriminant analysis (Wilkinson et al. 1996) to determine if variables could discriminate among Gray Vireo, Plumbeous Vireo, and random habitats. I used predictive discriminant analysis (Wilkinson et al. 1996) to provide a test of the discriminating power of the variables selected by stepwise discriminant analysis. I based estimates of correct classification of habitat types on the jack-knifed classification method (Wilkinson et al. 1996) of resubstitution of data into the discriminant model.

Results

In 1999, I found 160 Gray and 49 Plumbeous vireo territories (Appendix 1); 58% of the former, were in canyon bottoms and 42% were on plateau tops. Of the Plumbeous Vireo territories, 32% were in canyon bottoms and 68% were on plateau tops. In 2000, I found 172 Gray and 44 Plumbeous vireo territories (Appendix 2). Of the Gray Vireo territories, 60% were in canyon bottoms and 40% were on plateau tops. Thirty-one percent of the Plumbeous Vireo territories were in canyon bottoms and 69% were on plateau tops.

Of the measured habitat variables, eight were significantly ($p \leq 0.05$) different among the three habitats (Gray Vireo, Plumbeous Vireo, and random) (Table 1). These were elevation, deciduous shrub density (Mountain Mahogany, Single-leaf Ash, and Utah Serviceberry were the three most abundant deciduous shrubs in the study area) (Appendix 3), juniper density, juniper height, juniper crown width, piñon density, piñon height, and piñon crown width. Gray Vireos utilized habitats at lower elevations with greater deciduous shrub density, and with smaller piñons (height and crown diameter), when compared to random habitat (Table 1). Plumbeous Vireos utilized habitats at higher elevations and with greater juniper density, larger junipers (height and crown diameter), greater piñon density, and larger piñons (height and crown diameter), as compared to habitats at random points (Table 1). Compared to Plumbeous Vireos, Gray Vireos utilized habitats at lower elevations and with greater deciduous shrub density, smaller juniper and piñon densities, and smaller junipers and piñons (height and crown diameter) (Table 1).

Four variables – deciduous shrub density, juniper density, juniper height, and piñon height – were selected by three-group stepwise discriminant analysis for discriminating among Gray Vireo locations, Plumbeous Vireo locations, and random locations (Table 2). Two discriminant functions explained the dispersion of the three groups (Table 2). Discriminant function one (DF1) accounted for 77% of the total dispersion of the three groups; juniper height and piñon height were the dominant variables in DF1 (Table 2). This function may be interpreted as representing a continuum from woodland dominated by short trees, to woodland dominated by tall trees. Species occurring in tall piñon-juniper woodland would be expected to have high group-means scores for this function. Species occurring in short piñon-juniper woodland would be expected to have low group-means scores for this function. Discriminant function two (DF2) accounted for the remaining 23% of the total dispersion of the three groups; deciduous shrub density and juniper density were the dominant variables in DF2 (Table 2). This function may be interpreted as representing a continuum from woodland with high densities of junipers and deciduous shrubs, to woodland with low densities of junipers and deciduous shrubs. Species occurring in shrubby woodland would be expected to have low group-means scores for this function and species occurring in woodland with little shrub understory would be expected to have high group-means scores for this function.

Of the three study groups, Gray Vireos, with group-means scores of -0.783 for DF1, and -0.344 for DF2 (Table 3), were associated with the shortest woodland and the highest densities of deciduous shrubs and junipers. Plumbeous Vireos, with group-means scores of 0.972 for DF1, and -0.191 for DF2 (Table 3), were associated with the tallest woodland and intermediate densities of deciduous shrubs and junipers. Random points, with group-means scores of -0.170 for DF1 and 0.578 for DF2 (Table 3), were associated with intermediate-height woodland and the lowest densities of deciduous shrubs and junipers.

The 95% confidence ellipses (Fig. 1) graphically illustrate these habitat relationships. Such ellipses contain the bi-variate (DF1 and DF2) means of each group 95% of the time. Areas of overlap in the ellipses indicate habitat conditions that would be favorable for the overlapping groups. Based on the parameters defined by DF1 and DF2, Gray Vireos would be expected to occur without Plumbeous Vireos in habitat characterized by short trees and medium to high

densities of deciduous shrubs and junipers (Figure 1). Gray and Plumbeous vireos would be expected to occur together in habitat characterized by medium-height trees and medium to high densities of deciduous shrubs and junipers (Figure 1). Plumbeous vireos would be expected to occur without Gray Vireos in habitat characterized by tall trees and medium to low densities of deciduous shrubs and junipers (Figure 1). Neither vireo species would be expected to occur in habitat characterized by low densities of deciduous shrubs and junipers, regardless of tree heights (Figure 1). As the variance of the discriminant functions is a component of the confidence ellipses, these may also be thought of as measures of the variability in resource use or as measures of habitat-niche breadth (Pianka 1974): The larger the confidence ellipse, the more variable the species is in the use of the resources described by the discriminant functions. Plumbeous Vireo had a slightly larger ellipse than did Gray Vireo, indicating more generalized habitat utilization regarding the dimensions of DF1 and DF2.

Predictive discriminant analysis correctly assigned 60% of the 180 samples into their appropriate groups. Gray Vireo habitat had 71% of its cases correctly classified; 10% of its cases were misclassified as Plumbeous Vireo habitat and 19% as random habitat. Plumbeous Vireo habitat had 63% of its cases correctly classified; 16% of its cases were misclassified as Gray Vireo habitat and 14% as random habitat. Random habitat had 44% of its cases correctly classified; 33% of its cases were misclassified as Gray Vireo habitat, and 23% as Plumbeous Vireo habitat. High misclassification rates for groups suggest a high degree of ecological similarity with the groups with which they were misclassified (Wilkinson et al. 1996).

Discussion

Gray Vireos were fairly evenly distributed throughout the Monument and exhibited a slight preference for canyons. Plumbeous Vireos, on the other hand, were found mostly on plateau tops, with nearly 70% of their breeding territories found in these high-elevation locations during both years. Previous studies suggested that Gray Vireos are separated by elevation from other vireo species. Johnson (1972) found Gray Vireos to inhabit lower elevations than Plumbeous Vireos. Similarly, Oberholser (1974) found Gray Vireos in Texas to inhabit higher elevations than Bell's Vireos and lower elevations than Hutton's and Plumbeous vireos. I found mean elevations of Gray and Plumbeous vireo territories to differ significantly, however, I found the two species' habitats to overlap considerably in elevation. I found Gray Vireos at 1433 - 1981 m and Plumbeous Vireos at 1554 - 2054 m. Despite the fact that they were often found at the same elevations, the two species utilized habitat with significantly different structures, thus suggesting that the species selected habitat based on structure and not elevation: Gray Vireos utilized habitat that combined the attributes of short trees and high deciduous shrub densities, and Plumbeous Vireos utilized habitat that combined the attributes of tall trees and lower deciduous shrub densities.

Cody (1969) describes a model in which moisture and topography in an area act in conjunction to produce a mosaic of vegetation patches making up the preferred habitats of two species. This patchy habitat model seemingly fits the distribution of Gray and Plumbeous vireos at the Monument. Plateau tops were dominated by dense woodlands of tall trees with little shrub understory, and Plumbeous Vireos were most commonly found in these high-elevation areas. However, canyon bottoms, which frequently receive water, had dense patches of tall trees and

Plumbeous Vireos inhabited these low-elevation areas. Gray Vireos were most commonly found at lower elevations that were dominated by short trees and high densities of deciduous shrubs. However, steep slopes at higher elevations had patches of open, shrubby woodland, and Gray Vireos inhabited these high-elevation areas.

Gray and Plumbeous vireos were often found in the same areas, and both species reacted to tape playbacks of the other species' songs, suggesting that they defend territories against each other. Hutchings and Leukering (unpubl.) reported a Plumbeous Vireo chasing a Gray Vireo from a territory at Colorado National Monument. Although in several cases I observed interactions when both species were drawn to tape playbacks, I observed no unprovoked interactions between the two species. In one area, I located a pair of Gray Vireos in the midst of nest building only 115 meters from a Plumbeous Vireo nest with young. In several other locations, I observed both species foraging within 50 meters of each other. Chace (1998) suggested that foraging habits may serve to reduce competitive interaction between vireo species when they occur together. Gray Vireos are thicket foragers (Hamilton 1962), with most prey taken from branches and trunks of small trees or twigs, and from shrubby vegetation (Barlow et al. 1970). Plumbeous Vireos are considered generalist foragers with a wide range of feeding heights and locations (Laudenslayer and Balda 1976, Rusterholtz 1979, Sarzo and Balda 1979). Gray Vireos' preference for high densities of deciduous shrubs, and Plumbeous Vireos' preference for tall trees may serve to reduce competition between the two species, as they may be able to forage in different layers of the same habitat. Although I did not quantify these observations, I observed Gray Vireos foraging almost exclusively in deciduous shrubs. On the other hand, I found Plumbeous Vireos to forage more frequently in trees. Chase (1998) also suggested that size difference may reduce competition by affecting food-size selection or displacement of the smaller species by the larger. Plumbeous Vireos are 25% larger by weight than Gray Vireos and may be able to exploit different resources in the piñon-juniper woodland than Gray Vireos (Chase 1998). It is not clear, however, whether either species excludes the other from habitat.

Numerous aspects of Gray and Plumbeous vireo habitat relationships remain unknown. Among these are the exact natures of the foraging habits of both species, the interactions of both species during territory formation and defense, and if either species excludes the other from habitat. Further research would help to clarify these issues.

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Table 1. Means of habitat variables measured at Colorado National Monument. *P* values are for ANOVA.

Values in each row with similar letters are not significantly different (Tukey's $P > 0.05$)

Habitat variable	Gray Vireo	Plumbeous Vireo	Random	<i>P</i>
Elevation (m)	1700.5 a	1916.6 b	1834.9 c	<0.001
Deciduous shrub point-quarter distance (dm)	142.8 a	414.3 b	515.1 b	<0.001
Juniper point-quarter distance (dm)	70.6 a	60.7 b	81.4 a	<0.001
Juniper height (dm)	26.0 a	36.6 b	28.5 a	<0.001
Juniper crown width (dm)	26.7 a	31.3 b	27.0 a	0.005
Piñon point-quarter distance (dm)	103.8 a	71.9 b	90.7 a	<0.001
Piñon height (dm)	19.4 a	36.5 b	25.5 c	<0.001
Piñon crown width (dm)	16.9 a	29.1 b	21.8 c	<0.001

Table 2. Canonical discriminant function loadings for habitat variables.

Habitat variable	DF1	DF2
Deciduous shrub point-quarter distance	0.268	0.803
Juniper point-quarter distance	-0.376	0.712
Juniper height	0.627	-0.195
Piñon height	0.479	0.086

Table 3. Canonical scores of group means.

Habitat Type	DF1	DF2
Gray Vireo	-0.783	-0.344
Plumbeous Vireo	0.972	-0.191
Random	-0.170	0.578

Appendix3. Shrubs recorded at Colorado National Monument by the point-quarter method of measuring vegetation from the center of a plot.

Deciduous shrub species	Percent of total (N=651)
Cliff Rose (<i>Cowania stansburiana</i>)	0.9
Fremont Cottonwood (<i>Populus fremontii</i>)	2.6
Greasewood (<i>Sarcobatus vermiculatus</i>)	6.2
Gambel Oak (<i>Quercus gambelii</i>)	1.2
Mountain Mahogany (<i>Cercocarpus montanus</i>)	44.2
Rabbitbrush (<i>Chrysothamnus nauseosus</i>)	4.7
Russian Olive (<i>Elaeagnus angustifolia</i>)	0.5
Utah Serviceberry (<i>Amelanchier utahensis</i>)	8.0
Singleleaf Ash (<i>Fraxinus anomala</i>)	22.4
Snakeweed (<i>Gutierrezia sarothrae</i>)	4.4
Snowberry (<i>Symphoricarpos oreophilus</i>)	1.8
Squawbush (<i>Rhus trilobata</i>)	2.6
Tamarisk (<i>Tamarix pentandra</i>)	0.1
Willow (<i>Salix exigua</i>)	0.4
Non-deciduous shrub Species	Percent of total (N=360)
Mormon Tea (<i>Ephedra viridis</i>)	50.6
Big Sagebrush (<i>Artemisia tridentata</i>)	49.4