Habitat preferences and interspecific competition: Red-eyed and warbling vireos

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HABITAT PREFERENCES AND INTERSPECIFIC COMPETITION:
RED-EYED AND WARBLING VIREOS

by

Sandra M. Pletschet

B.A., University of California, Santa Cruz, 1981

Presented in Partial Fulfillment of the Requirements
for the Degree of
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1987

Approved by:

[Signatures]
Chairman, Board of Examiners

[Signature]
Dean, Graduate School

March 11, 1987
The habitats and spatial relationships of coexisting Red-eyed Vireos (Vireo olivaceus) and Warbling Vireos (Vireo gilvus) were studied during two breeding seasons in western Montana. Intraspecific territorial overlap was virtually nonexistent. Interspecific territorial overlap was 20.4% in 1984 and 15.1% in 1985 which was less than would be expected if placements were random. Comparison of eight vegetation characteristics showed that the Red-eyed Vireo used habitat with significantly denser cover, especially by trees over 20 meters, than did the Warbling Vireo. Red-eyed Vireos tended to forage in the middle of trees, and to use Quaking Aspens more than Warbling Vireos. Warbling Vireos tended to forage toward the tops of trees and to use willows more than Red-eyed Vireos. Both species sang primarily from the tops of trees.

I did not detect interspecific interaction between the Red-eyed Vireo and the Warbling Vireo. Most of the observed differences between the Red-eyed Vireo and Warbling Vireo can be accounted for by habitat affinities. Distinct habitat preferences by the two species resulted in their spatial separation. Vegetation structure influenced singing and foraging height. My results suggest that ecological segregation does not imply competitive interaction.
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INTRODUCTION

In laboratory experiments, closely-related species rarely coexist. Cause (1934) established protozoan cultures in which lone species flourished, but when congeners were mixed only one species persisted. He related the intensity of competition between coexisting species to the degree of overlap in their resource use. Subsequent laboratory experiments with congeners, such as mice, fruit flies and flour beetles, also resulted in a single species surviving while the others died out (Park 1948, Miller 1967). The competitive exclusion principle, also called Cause's principle, was formulated from these laboratory experiments and states that two or more species can not coexist for long if they use the same limiting resource (Hardin 1960).

Observations of ecologically similar species coexisting in natural communities did not prevent the competitive exclusion principle from gaining general recognition by ecologists. Extrapolation from simple laboratory experiments to complex natural communities was a bold step which carried with it numerous assumptions about the similarities of the two systems. It was assumed that resources are constantly limiting such that competition is relentlessly intense and results in the system stabilizing at equilibrium. Unlike controlled laboratory experiments, natural systems are variable, and resource-defined equilibria may be rare. Many factors besides interspecific competition influence natural communities, such as predation, environmental fluctuation, and history.
The apparent contradiction between laboratory experiments and field observations initiated scores of projects on how similar species coexist in nature. Cause's principle, along with field observations (Grinnell 1904, 1917; Elton 1946; Lack 1944, 1945), led to an expanded concept of the ecological niche as a multidimensional resource space which includes the frequency distribution of resource type, location, and method of utilization (Hutchinson 1959). Numerous field studies have determined that bird species avoid competitive exclusion by resource partitioning in such areas as habitat, food type, foraging tactic, and vertical feeding range. The conclusion has generally been that the observed niche differences are mechanisms of coexistence resulting from competitive pressures (Williamson 1971, Cody 1968, 1974, Schoener 1974, 1983, Diamond 1978).

The existence of niche differences in communities is well established, however there is no consensus on the influence of interspecific competition on the distribution, abundances, and resource use of species in natural communities (Wiens 1977). In most field studies it has been impossible to determine the relative importance of species-specific preadaptations that developed during allopatric speciation and ongoing factors such as competition, predation, physical disturbance, and environmental fluctuation. The array of factors that determines the observed community structure probably varies greatly and depends on the species combination and environmental characteristics (Landres and Mac Mahon 1983).
The role of interspecific competition in maintaining observed avian habitat use patterns and resource partitioning is unsettled. Evidence for avian interspecific competition has been largely indirect and includes: mutually exclusive distributions or reciprocal abundance (Terborgh 1971, Diamond 1973, Terborgh and Weske 1975, Morse 1976); broader habitat ranges where related species are absent (Terborgh 1971, Diamond 1973, Cody 1974, Morse 1976); and overlap in resource use, morphology, and ecology of coexisting species (Lack 1971, Cody 1974). Recently, interspecific competition has been demonstrated more directly by niche and demographic expansion when an ecologically similar species has been removed experimentally (Davis 1973, Williams and Batzli 1979, Dhont and Eyckerman 1980, Reed 1982) and in cases where syntopic species are so similar in their methods of exploiting resources that they defend mutually exclusive territories (Orians and Willson 1964, Murray 1971, Kodric-Brown and Brown 1978, Rice 1978, Catchpole 1978). Intraspecific territorial behavior is well documented in birds and is usually explained in terms of competition for resources (Davies 1978). Cody (1974) has suggested that "the single most effective way to separate entirely the ecological activities of individuals is territoriality".

Studies on ecologically similar, coexisting species have suggested that interspecific interaction can modify the acceptability of habitat (Cody and Walter 1976, Cody 1978, Rice 1978, Sherry 1979). In a recent review of field experiments on interspecific competition, Schoener (1983) found that, with only a few exceptions, habitat overlap is minimal between species which have been demonstrated to compete, while other ecological overlaps, such as morphology and foraging behavior, are
great. He explained this by suggesting that habitats, through territoriality or other interspecific interaction, can be the object of on-going competition resulting in habitat segregation.

Vegetation physiognomy and heterogeneity have repeatedly been shown to be important proximate factors in guiding avian habitat selection (MacArthur and MacArthur 1961, James 1971, Willson 1974, Whitmore 1977). Ultimately, it is presumed that vegetation configuration is associated with critical resources such as food and nest sites. Given this influence, the observed dispersion of ecologically similar species along habitat dimensions has been implicated as a way of avoiding competition for resources (Lack 1971, Shugart and James 1973, Schoener 1974, James 1976). For example, several ecologists have described the ordination of avian guild members along a vertical vegetation axis as a means of achieving ecological separation (Gibb 1954, MacArthur 1958, Williamson 1971). The observed patterns may be the result of different habitat preferences or some form of interspecific competition. Because habitat differences could be maintained or initiated by interspecific competition, these two mechanisms are not mutually exclusive. In the present research, the habitat use and spatial relationships of a pair of coexisting Vireo species are examined and the influence of habitat preferences and interspecific interaction on the observed patterns are considered.

The Red-eyed Vireo (Vireo olivaceus) and Warbling Vireo (V. gilvus) are arboreal birds that actively glean foliage for insects and other small invertebrates (Hamilton 1962). In southern Ontario, R.D. James (1976) found these two vireo species to be very similar in their
foraging behavior, feeding locations, and nest placement. He noted that ecological separation was accomplished by habitat selection: the Warbling Vireo occupied areas with scattered trees and the Red-eyed Vireo used dense bottomlands. F.C. James (1971) found similar habitat differences between these two vireo species in Arkansas. In the riparian woodlands of western Montana there is considerable overlap in the habitat use by the Red-eyed and Warbling vireo and, as this study demonstrates, both species can be observed foraging and nesting within several meters of each other. Murray (1971) predicted that bird species that normally occupy different habitats are likely to maintain mutually exclusive territories where their habitats come together.

Working separately in northeastern deciduous forests, Rice (1978) and Robinson (1981) found interspecific interaction between coexisting Red-eyed Vireos and Philadelphia Vireos (V. philadelphica) which influenced the habitat use of both species. In Ontario, Rice observed direct aggression between the two species which resulted in their occupation of exclusive, non-overlapping territories. In virtually all respects, such as habitat preference, foraging behavior, and height of feeding and nesting, Rice found these two species to be essentially identical. Therefore, he considered the interspecific aggression between the Red-eyed and Philadelphia vireos to be a means of achieving ecological segregation.

In a New Hampshire deciduous forest, Robinson also found interspecific aggression between the Red-eyed and Philadelphia vireos which he related to resource competition. The intensity of their aggression varied seasonally, as the amount of their vertical overlap
changed, and annually, being most intense in years of high vireo density and nonexistent in years of high caterpillar density. On Robinson's study site, the two species occupied extensively overlapping territories but differed in foraging and nesting height. He explained this difference from Rice's findings by noting that the Ontario forest is structurally simpler than the forest in New Hampshire, resulting in fewer opportunities to segregate vertically and in intensified interspecific aggression. Robinson's research demonstrates that both interspecific interaction and vegetation structure can be important in facilitating coexistence.

My principal objectives are to determine if the Red-eyed and Warbling vireos are ecologically segregated in a Montana riparian woodland and to consider how interspecific interaction, vegetation structure, and habitat preferences potentially influence the observed resource use patterns. I consider two hypotheses, both of which could be accepted or rejected: (1) Interspecific interaction between the Red-eyed and Warbling vireos influences their habitat use and (2) The Red-eyed and Warbling vireos have distinct habitat preferences. The first hypothesis is examined by testing for spatial separation of territories, nests and foraging sites, and segregation along vegetational strata. Habitat preferences are determined by measuring the vegetation characteristics of the areas used by each vireo species.
STUDY SPECIES

The Red-eyed Vireo (REV) and Warbling Vireo (WV) are dull-plumaged passerines with stout bills that have hooked upper mandibles. The plumages of these two species are remarkably similar: Olivegreen to gray upperparts contrasted with buffy flanks, a whitish breast and belly, and a gray crown bordered by a whitish line over the eye. In the field, visual identification can be difficult and the REV's red eye (which is seldom discernable), black line through the eye, and grayer crown contrasting with a greenish back distinguish it from the WV. The REV's body is about 10% longer than the WV's (14-16.5cm compared with 12.5-15cm) and about 30% heavier (17-18gms compared to 11-12gms). The bills of the two species have similar proportions; but the length, depth and width of the REV's bill are approximately 17%, 12% and 10% larger, respectively than those of the WV (James 1976). The females of both species are slightly smaller than the males. Otherwise, the sexes appear to be identical. The songs of the two species are readily distinguishable with the WV having a rambling warble and the REV a series of short distinct phrases. From the time of territory establishment until the young are fledged the males of both species sing continuously throughout the daylight hours. Thus, song is often the most reliable means of field identification.

The sympatric breeding range of REVs and WVs spans southern Canada and northwestern, central and eastern United States. Both species spend the majority of their lives wintering to the south. The REV migrates to South America while the WV winters in Mexico and Central America. These

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vireos arrive in western Montana from mid May to early June and spend between two and three months on their breeding grounds which are generally dense suburban shade trees and woodlands. The males arrive several days before the females and establish territories and attract mates by singing persistently. The territory is defended until several days after the young fledge and all activities, including foraging, mating, and nesting, are conducted within its boundaries. The REV and WV are monogamous, and a strong pair bond is formed and maintained throughout the breeding season.

Once a territory is established and a pair bond formed, the female builds a pensile cup nest on a horizontal branch fork. The REV usually places its nest between 2 and 4 meters up in a shrub or tree, whereas the WV usually nests between 2 and 13 meters (Bent 1950). Both species have a clutch size between 3 and 5, and incubation lasts from 12 to 14 days. WV males and females share incubation and brooding, whereas these duties are the sole responsibility of the female REV. Both sexes of the REV and WV feed their nestlings insects brought in the bill. The young leave the nest between 12 and 16 days after hatching (Harrison 1978).
STUDY SITE

My research was conducted on a 19 hectare riparian woodland located approximately 5 kilometers north of Lolo, Montana (46° 47'N, 114° 06'W) and at an elevation of 850 meters. This study plot is owned and ranched by the Pruyn family (hereafter called the Pruyn Ranch). It is effectively an island of riparian habitat and is bordered to the north and northeast by the Bitterroot River, to the south by a large hay field and to the west by U.S. Highway 93 (Fig. 1). These isolating features limited possible vireo-vireo interactions to those few individuals present on the Pruyn Ranch and facilitated observation of all individual vireos that could have directly influenced each other. Vireo nest locations and territory boundaries were determined for the entire island; however, the majority of my research was conducted on a core area of 14 hectares.

The suitability of the Pruyn Ranch for the present study was initially determined from bird census data collected by Hutto and Mosconi in 1979 and 1980 (at that time the site was owned by Rossignal). These researchers observed that on the Pruyn riparian plot both the Red-eyed and Warbling Vireo were common and often found nesting and feeding in close proximity (Mosconi and Hutto 1981; Hutto, pers. comm.).

The Pruyn Ranch has been grazed heavily by both cattle and horses, but during my research it was primarily used as a winter pasture. The vegetation structure was heterogeneous, with areas of open canopy and very little undercover mixed with patches of closed canopy and a dense
understory (Fig. 1). The overall diversity of plant species was low and eight species accounted for virtually all vegetation above one meter. The middle (10-20 meters) and upper (>20 meters) canopies and the sapling or shrub layer (4-10 meters) were dominated by Black Cottonwood (Populus trichocarpa) which covered nearly the entire study site. It was found in 95.9% (N=244) of the 0.06 hectare quadrats sampled. Ponderosa Pine (Pinus ponderosa) was the only other canopy species and it was uncommon (found in 16.4% of the sampled quadrats). Dispersed among the Black Cottonwoods in the shrub layer were willow (Salix sp.), Common Chokecherry (Prunus virginiana), and Black Hawthorn (Crataegus douglasii) with occasional Quaking Aspen (Populus tremuloides). The brush layer (1-4m) was dominated by Red Dogwood (Cornus stolonifera) and Wild Rose (Rosa sp.).
FIGURE 1. Aerial photo of the Pruyn Ranch, Missoula County, Montana. Water surrounds the study site: The Bitterroot River runs along the eastern boundary and the canal encloses the remainder. U.S. Highway 93 can be seen at the top of the photo. The scale is 1:4800.
METHODS

A grid system was established by drawing quadrats, 1cm x 1cm, on a high quality aerial photo of the study plot (1:2400). Using this as a map, natural landmarks, such as fallen trees, water holes, and openings in the vegetation were used to identify my position in the grid system. From these obvious locations, the boundaries of the quadrats were determined by pacing along a compass bearing. Colored and numbered flags were placed at quadrat corners throughout the study site. An aerial photo with the grid system and flag locations was used to determine the location of all vireo sightings.

Early in the breeding season, vireos were caught in mist nets and banded. Tape-recorded song played adjacent to the net was used to attract the birds into the net. Both vireo species responded vigorously to conspecific song. Two color bands were placed on the right leg of each REV and on the left leg of each WV. The opposite leg received a USFWS silver band.

Censusing

Habitat use, nest locations, and territorial boundaries were documented by repeated censusing. Between 15 May and 7 August 1984 I censused three mornings per week resulting in 37 censuses. Four to five censuses were conducted each week during the 1985 breeding season. A total of 58 censuses were done between 9 May and 5 August 1985. Censuses were done in the morning, usually between 0700 and 1100.
To insure that all areas of the study plot received equal census time, I varied my census route daily. A meandering circle best describes the nature of my census path. The direction of circulation was alternated and I varied the manner in which I zigzagged along the circular path. From each route a singing vireo anywhere in the study area could be heard from at least one point along the route. During every census, I attempted to record a minimum of one observation for each vireo pair. If a pair was not found, I put extra effort into locating them during the following census. To allow time for a complete census, I generally followed an individual vireo for only about 15 minutes. Since male vireos sing conspicuously and continually throughout the breeding season, I was able to spend the majority of my field time collecting data rather than looking for birds. Often I was able to follow two singing males (one of each species) simultaneously.

During the 1984 breeding season, census data were collected on horizontal spacing and nest site selection. In 1985, I expanded the information recorded during each observation to include vertical spacing and plant use. First I will discuss the data collected in 1984 and then the 1985 additions will be enumerated. While censusing I recorded on a unique, dated aerial photo the location and movement direction of all vireos seen or heard. The approximate positions of males singing simultaneously were recorded and I was particularly careful to note the location of intraspecific interactions, such as chasing and reciprocal singing. These are significant because they identify unique vireo pairs and territorial boundaries. The location, height, and plant species and height of each nest was recorded. Nests were checked at one to two day
intervals and I recorded the nesting stage as nest building, incubation, nestlings or fledged.

The vireo's behavior, sex, breeding state, and identification and the quadrat of each observation were also noted. Behavior was divided into ten categories: singing, foraging, nest building, sitting on nest, feeding nestlings, feeding fledglings, epigamic, agonistic, resting, and 'other'. Sex was determined by color bands and singing and other behaviors such as incubation, nest building, and copulation. Six breeding states were recognized: territory establishment, nest building, incubation, nestlings, fledglings and unknown. Identification was based on species, color bands, and location. If a vireo was heard but not seen within an established territory, I assumed that it was the vireo known to occupy the area. Similarly, if an unbanded individual or pair was regularly encountered and observed nesting within an area, I assumed that this constituted a stable, territorial pair that survived through the breeding season.

In 1985 an additional three parameters were measured during each census observation. These were vireo height and position and plant species. Vireo height was divided into four categories: 1-4 meters, >4-10 meters, >10-20 meters and above 20 meters. The relative height in the vegetation occupied by the vireo (upper, middle or lower) was recorded as vireo position. Absolute and relative height were both recorded in order to investigate the possible influences of vegetation structure on height use.
Territory Mapping

The playback of conspecific song was used to provoke territory holders into active defense and draw them to the boundaries of their territories (Falls 1981). A high fidelity UHER 4000 Report-L tape recorder was used. Songs were recorded in the field, approximately 15 kilometers from the Pruyn Ranch by using a microphone on a 60cm parabolic reflector. When mapping a territory, I played the tape recorded song near a singing vireo. This initiated the bird to react to the tape as if it were an intruder. As the vireo approached, I moved the recorded song in one direction until the vireo no longer followed. The last location where the vireo sang was recorded on the daily aerial photo as a point on its territorial boundary. Next, I returned the tape recorder to near the territory center and the vireo was lured in another direction until the territory limit was again reached. This pattern was repeated until the outer limits of a territory was established (generally four to six times). These territory boundary locations were designated as 'song-provoked' locations which distinguished them from observational census encounters. The song-provoked locations identified the maximum territory boundaries.

Spatial Data Analysis

Although the distribution of organisms in a community can include many patterns, animals have a tendency to space themselves in one of three general arrangements: (1) in close proximity to one another with relatively large spaces between each animal clump; (2) segregated from one another with each animal spaced evenly relative to all others; (3)
in a haphazard, random arrangement with no apparent relation to one another (Pielou 1969). Unless animals influence each other or are influenced by a common nonrandomly distributed environmental factor, a random distribution is expected.

The observed territory placements and quadrat use were compared with the expected random distribution using chi-square 2 x 2 tests and Cole's Coefficient of interspecific association (Cole 1949). Each test compared the observed and expected frequency of quadrats with both species, REVs alone, WVs alone and with neither. Nest site spacing was analyzed using the ratio R which expresses the amount by which mean distance to nearest neighbor exceeds the value expected under the null hypothesis of random dispersion (Clark and Evans 1954).

The statistical requirement of independent data points was met by including in the vertical spacing analysis only those census sightings that were a minimum of 30 minutes apart. For an individual vireo a maximum of three observations during one census were included. I decided on which to include by randomly choosing one data point for each census and then selecting an additional one or two that were 30 minutes before or after the first selected observation. Usually, I had only one data point for an individual per census day. Since my knowledge of nest locations resulted in an enormous number of nest sightings, these data were not considered when selecting the independent subset. I recorded 525 independent observations which were used to derive frequency distributions for height, position, and plant use. Chi-square goodness of fit tests were used to compare frequency distributions of heights and positions of vireo observations and of available plant cover.
Vegetation Analysis

Vegetation structure was quantified by mapping the plant cover, by species, of the 14 hectares where the majority of the vireo data was collected. This was accomplished by using the 244 adjacent 0.058 hectare quadrats that were used to locate vireos during censusing. The study area grid system was drawn on semi-transparent paper and then lined up with the quadrats on a study site aerial photo. Four such composite maps were drawn to record separately the amount of plant cover at bush, shrub, mid-canopy and upper canopy levels. Plant height was determined by using a six meter stick marked brightly at one meter intervals. By extending the measuring stick straight up over my head (I measure 2 meters with my arm extended), plant height below eight meters was determined directly. Tall trees were measured by standing the measuring stick up against the trunk and then viewing this from a distance at least as great as the tree height. From this position, I extended a ruler in front of my eye and by calibrating it to the 6 meter stick, the height of the tree was estimated.

I describe my procedures for mapping the vegetation below. First I determined which quadrat I was in and then the exact location of the plant in question. Since individual trees were distinguishable on the aerial photo, this was not difficult. Next, I identified the plant height categories and species. Finally, for each plant height category, I drew the widest area covered by the plant. This area was measured by pacing and using the 6-meter measuring stick. One millimeter on the map represented 2.4 meters of actual linear distance. When drawing the area covered by a plant on the vegetation map, plant species was recorded by
using a unique color for each species.

The Simpson's index was used to calculate the plant species diversity (PSD) and foliage height diversity (FHD) of each quadrat.

\[ D = \frac{1}{\sum_{i=1}^{s} p_i^2} \]

where \( s \) is the number of categories and \( p_i \) is the proportion of plant cover in the \( i \)th category. The total number of plant species (NPS) and the sum of the four height categories, total plant cover, were also determined for each quadrat. These four measurements and the amount of cover in the four height levels were used to compare the vegetation structure used by the Red-eyed and Warbling vireos. The habitat affinities of each species were characterized with these eight vegetation measurements and the cover by each plant species in the quadrats each species was observed using. Mann-Whitney U tests were used to test for significant differences in each vegetation parameter between the REV and WV.
RESULTS

General Description

The number of REV and WV breeding pairs on the Pruyn study site declined slightly in the 1985 breeding season. There were eight WV and five REV pairs in 1984 and six REV and four WV pairs in 1985. Seven breeding males (4 WV and 3 REVs) and one breeding female (REV) were banded in 1984, and 6 breeding males (3WVs and 3 REVs) and one breeding female (REV) were banded in 1985. Warbling Vireos occupied territories that were spread rather evenly throughout the riparian woodland. In contrast, REV territories were concentrated in the central portion of the study plot and covered only about one-third of the island (Figs. 2 and 3). This preferred area was characterized by dense understory and abundant large cottonwoods growing above 20 meters.

In 1985 males generally placed territories on similar sites as conspecifics had during the previous breeding season. Four of the eight breeding male vireos banded in 1984 returned to breed in 1985. Three individuals (2 REVs and 1 WV) established territories that included at least part of their 1984 sites. Of the 59 quadrats within REV 1985 territories, 50 (83%) had been used by REVs in 1984. WVs included 75 (58.6%) of the quadrats they defended in 1984 in their 128 territorial quadrats of 1985. Between-year comparisons of the quadrats chosen out of the potential quadrats in the study site indicated that each species had a significant positive association between the quadrats used during the two breedings seasons (REV: $\chi^2 = 10.1$, df = 1, P < 0.001; WV: $\chi^2 = 20.1$, df = 1, P < 0.001). Potential quadrats were those that fell within the area.
enclosed by the outermost boundaries of each species territories. For the REV this was 100 quadrats and the WV 197.

Breeding Schedule

On the Pruyn study site in 1984 and 1985, WVs arrived during a two week period in mid May and the REVs arrived in the first week of June (Fig. 4). Figures 2 and 3 show the sequences of WV territory placement. REVs usually established territories and formed pair bonds within a week after arrival, while WVs often spent two weeks. WVs began nesting earlier on average than did REVs. In 1985, for example, when the first two REVs arrived, 5 of 6 WVs were nest building. As a result, most WVs fledged earlier than REVs (Fig. 4).
FIGURES 2, 3. Red-eyed Vireo (dotted lines) and Warbling Vireo (solid lines) territory boundaries. Nest locations (Xs), identities of color-marked vireos (letters), and the sequence of territorial placement (numbers) are shown. Stippling indicates water.
Horizontal Spacing

The degree to which the REV and WV may have influenced each other's horizontal spacing was investigated by comparing a hypothetical random distribution with the observed territory placements, foraging areas, and nest sites. Cole's coefficients indicated negative associations between REV and WV territory placements and foraging areas (Table 1). Horizontal overlap between the territories of the two species on the study plot was 20.4% of the occupied quadrats in 1984 and 15.1% in 1985 (N=198). The decrease in overlap is possibly due to the slight population decline in 1985. I found similar results when considering only those quadrats where foraging by one or both species was observed. The overlaps in foraging quadrats were 8.7% in 1984 and 15.3% in 1985 (N=198). This increase was probably a reflection of the greater amount of time I spent collecting foraging data in 1985.

The number of independent sightings of each vireo species per quadrat were compared to determine the extent of coexistence within quadrats. Quadrats that were frequented by one vireo species were seldom used by the other species (Fig. 5). During each breeding season, there was a significant negative correlation between species in quadrat use (1984: \( r_s = -0.713, P<0.001 \) and 1985: \( r_s = -0.428, P<0.001 \)).

Nearest neighbor analysis was used as final test of the hypothesis of random distribution. The Clark and Evans (1954) index \( R \) was used as a measure of the influence of the position of one nest on the placement of another. \( R \) was compared for both conspecific nest placement and overall nest placement of all individuals. Since renesting occurred in several cases, the data were analyzed separately for first and second
nests. For the 1984 and 1985 breeding seasons, the mean distance between conspecific nests was approximately two times as great as expected with a random nest distribution; while the mean distance between all vireo nests was about 1.5 times the expected. Although within species evenness was expressed more strongly than that between the REV and WV, each R value indicated that nest spacing was significantly more even than the random expectation (Table 2).
TABLE 1. Horizontal Spacing. Analysis of the Red-eyed and Warbling vireos' horizontal spacing using chi-square tests of independence (df=1) and Cole's Coefficient of interspecific association. Sample size for all analyses is 198 quadrats. Territorial quadrats were defended as part of a breeding territory and foraging quadrats were observed being used during independent sightings.

<table>
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</table>

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FIGURE 5. The number of independent observations in each quadrat. Quadrats with no observations of either species (0,0 points) are excluded.
TABLES 2. Nearest Neighbor Analysis. R is the ratio of the observed mean nearest neighbor distance to the mean distance expected with a random nest dispersion. The probability of a greater difference between these two distances is given (P).

<table>
<thead>
<tr>
<th>Year</th>
<th>Statistic</th>
<th>Red-eyed Vireo</th>
<th>Warbling Vireo</th>
<th>Both Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>Area (m²)</td>
<td>58,752</td>
<td>153,216</td>
<td>154,386</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>5</td>
<td>8</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>1.78</td>
<td>1.93</td>
<td>1.63</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>&lt;0.05</td>
<td>&lt;0.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1985</td>
<td>Area (m²)</td>
<td>57,600</td>
<td>113,216</td>
<td>120,960</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>4</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>2.05</td>
<td>1.67</td>
<td>1.43</td>
</tr>
<tr>
<td></td>
<td>First nests</td>
<td>2.35</td>
<td>1.84</td>
<td>1.55</td>
</tr>
<tr>
<td></td>
<td>Second nests</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>&lt;0.02</td>
<td>&lt;0.02</td>
<td>&lt;0.02</td>
</tr>
</tbody>
</table>
**Vertical Spacing**

REVs placed their nests between 2 and 18 meters above the ground with a mean height of 7.1 meters (N = 9). Nest placement by WVs was between 5 and 21 meters with a mean of 12.3 meters (N = 14). There was a significant difference in the nest height of the two vireo species (Z=2.12, P<0.05). REVs placed the majority of their nests at mid-height (57%), while WVs tended to nest toward the tops of trees (57%).

The degree of vertical overlap in singing and foraging between the WV and REV was determined by comparing each species' use of the four height and three position categories. These are referred to as height and position profiles and were derived from 525 independent observations recorded in 1985. Singing males accounted for 368 (70.1%) of these observation and, foraging individuals (who also were often singing males) accounted for 284 (54.1%). To detect vertical shifts, profiles in quadrats used by one species alone were compared with profiles in quadrats occupied by both species.

Singing in the upper third of plants accounted for 78% of all the singing observations of each vireo species (Fig. 6A). When singing in mutually occupied areas, the REV and WV each maintained this tendency (Fig. 6B). There were no significant differences in their singing position profiles. Considering actual heights of all singing observations (Fig. 7A), the REV sang primarily above 20 meters (60.7%); whereas the WV sang with equal frequency above 20 meters (37.1%) and between 10 and 20 meters (39.5%). These singing height differences were highly significant. When only co-occupied quadrats were considered,
each species sang primarily above 20 meters (REV: 62.7% and WV: 54.2%); and there was no significant difference in their singing height profiles (Fig. 7B). This difference between all and co-occupied quadrats was primarily due to shifts by WVs (Fig. 8).

Foraging in the upper two-thirds of plants accounted for over ninety percent of all foraging observations of each species. The REV had a tendency to forage in the middle of plants (55.4%), while the WV tended to forage in the upper third (60.8%) (Fig. 9A). This overall difference between their foraging position profiles was significant (P<0.001). When foraging in mutually occupied areas, the REV and WV each continued to forage primarily in the upper two-thirds of plants (96.6% and 98.0%, respectively); and neither species made a significant change in foraging position (Fig. 10). Nonetheless, their tendencies to partition the middle (REV) and upper (WV) positions decreased and the foraging positions of the REV and WV were not significantly different (Fig. 9B).

As Figure 11A indicates, overall the REV and WV foraged at very similar heights: each foraged primarily between 4 and 20 meters (REV: 66.3% and WV: 62.0%) and with a frequency of about 21% above 20 meters. Their foraging height profiles were slightly different when only foraging observations in co-occupied areas were considered (Fig. 11B). Here, the WV foraged at all four heights with about equal frequency; whereas the REV foraged largely between 4 and 10 meters (43.3%). This difference between all and shared quadrats was primarily due to shifts made by the WV (Fig. 12).
FIGURE 6. Singing position profiles. All observations are considered in 'A' and only those from quadrats used by both species in 'B'. To derive the chi-square values, the lower and middle positions in each comparison were combined (df = 1).
FIGURE 7. Singing height profiles. All observations are considered in 'A' and only those from quadrats used by both species in 'B'. The two lower height categories were combined to derive the chi-square value of profile 'B' (df = 2).
FIGURE 8. Singing height profiles of the Red-eyed Vireo (A) and Warbling Vireo (B). Comparisons are between profiles of quadrats used by both species and by only one species. The chi-square value of 'A' was derived by combining the two lower height classes (df = 1).
FIGURE 9. Foraging position profiles. All observations are considered in 'A' and only those from quadrats used by both species in 'B'. The chi-square value of 'B' was derived by combining the two lower positions (df = 1).
FIGURE 10. Foraging position profiles of the Red-eyed Vireo (A) and Warbling Vireo (B). Comparisons are between profiles of quadrats used by both species and by only one species. Chi-square values were derived by combining the two lower position classes (df = 1).

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FIGURE 11. Foraging height profiles. All observations are considered in 'A' and only those from quadrats used by both species in 'B'.

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FIGURE 12. Foraging height profiles of the Red-eyed Vireo (A) and Warbling Vireo (B). Comparisons are between profiles of quadrats used by both species and by only one species.

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To investigate the correspondence of height use with vegetation structure, I compared each species' foraging and singing height profiles with the proportion of vegetation in each height class, called the foliage height profile. For the quadrats each species was observed using, the mean cover at each of four heights was used in the foliage height profile. For each vireo species, the vegetation cover of used quadrats was distributed equally between the understory (1-10m) and the canopy (>10m); but the REV had a larger proportion of cover above 20 meters than the WV (Fig. 13). The foliage height profiles of the REV and WV were not significantly different.

The REV sang in the canopy with a frequency of 86% and the WV with a frequency of 77%. Since the canopy accounted for only about half of vegetation cover, there was a significant difference between each species' singing height profile and foliage height profile (REV: \(\chi^2 = 46.4, \text{df}=3, P<0.001\), WV: \(\chi^2 = 29.6, \text{df}=3, P<0.001\)). Foraging by each species was primarily between 4 and 20 meters and seldom below 4 meters. Thus, the REV's and WV's foraging height profiles were each significantly different from their foliage height profiles (REV: \(\chi^2 = 25.7, \text{df}=3, P>0.001\); WV: \(\chi^2 = 20.2, \text{df}=3, P>0.001\)). When areas that WV shared with the REV are compared with areas the WV used alone, the proportion of vegetation cover above 20 meters was greater and that between 10 and 20 meters was less. The foliage height profiles of exclusive WV areas and coexistence areas were significantly different (Fig. 14B). There was not a significant difference between the foliage height profile of quadrats the REV used alone and quadrats it shared with the WV (Fig. 14A).
FIGURE 13. Foliage height profiles. All quadrats used by either vireo species are considered (Red-eyed Vireo n = 52, Warbling Vireo n = 106).

\[ \chi^2 = 2.14, \ p > 0.3 \]
FIGURE 14. Foliage height profiles of the quadrats used by Red-eyed Vireos (A) (n = 52) and Warbling Vireos (B) (n = 106). Comparisons are between quadrats used by both species and by only one species.
Plant Species Use

Foraging in Black Cottonwoods accounted for 82 percent of all foraging observations of each vireo species (Fig. 15B). Singing was also primarily done in Black Cottonwoods: 95% of REV and 88% of WV singing (Fig. 15A). When three plant categories were considered (Black Cottonwood, broadleaf shrub, and Quaking Aspen), there was a significant difference between plant species used for foraging ($\chi^2 = 10.5$, df=2, $P<0.01$) and for singing ($\chi^2 = 15.1$, df=2, $P<0.01$). This difference was largely due to the WV's tendency to use willows while the REV used Quaking Aspens. A small sample size of foraging and singing in plants other than Black Cottonwoods prevented conclusive determination of changes in plant species use between co-occupied and exclusive areas.

All 14 WV nests and 7 of 9 REV nests were placed in Black Cottonwoods. One REV nest was found in Common Chokecherry and the other in Red Dogwood. The height of the plant used by WVs for nesting ranged from 9 to 29 meters with a mean of 18.9 meters. REVs used plants between 3 and 22 meters tall with a mean of 14.1 meters. There was no significant difference in the height of the plant the two vireo species used for nesting ($Z=1.27$, $P>0.2$).
FIGURE 15. Plant species use for singing observations (A) and foraging observations (B).
Habitat Characteristics

On the Pruyn study site the REV placed territories in habitat with relatively dense vegetation from the ground level to above 20 meters. The WV used this structurally complex habitat less extensively and tended to set up territories in open vegetation with little understory and few trees above 20 meters. Habitat characteristics were determined by measuring eight vegetation parameters in the quadrats that each species was observed foraging in during independent sightings (Table 3). For each year, significant habitat differences were found between the REV and WV: total vegetation cover and, in particular, cover above twenty meters and between one and four meters were greater in the habitat used by REVs.

The extent of habitat separation was greater in 1985, when 7 of the 8 measurements were significantly different. The only measurement that was similar for each species during each breeding season was the vegetation cover between 10 and 20 meters. Comparisons of the eight vegetation parameters between years indicated that neither the REV nor the WV made any significant habitat changes. For most vegetation characteristics, a slight increase between years by one species was accompanied by a slight decrease by the other species.

Since the REV and WV differed in their overall habitat use yet coexisted in 21 quadrats in 1985, I determined how the vegetation parameters in the shared quadrats compared with the quadrats each species used alone (Table 4). Vegetation characteristics in the co-occupied quadrats were similar to those the REV occupied alone and significantly different to those occupied by the WV alone. For both
species, cover between 10 and 20 meters deviated slightly from this trend.

Three plant species accounted for over 80% of the vegetation cover in the quadrats used by each vireo species: Black Cottonwood (58-63%), Red Dogwood (9-13%), and willow (7-12%). For each year, there was significantly more Black Cottonwood and Red Dogwood cover on REV territories (1984: Z=3.02, P<0.01 and Z=2.08, P<0.05; 1985: Z=3.75, P<0.001 and Z=1.79, P<0.07). In 1984 the WV had significantly more willow cover (Z=2.18, P<0.05).
TABLE 3. Vegetation characteristics of the quadrats in which each vireo species was observed foraging. Sample sizes in 1984 and 1985 are 48 and 52 Red-eyed Vireo and 54 and 106 Warbling Vireo quadrats, respectively. All covers are percent and total cover is the sum of the four height category covers.

<table>
<thead>
<tr>
<th>Vegetation parameter</th>
<th>Red-eyed Vireo</th>
<th>Warbling Vireo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Year</td>
<td>Range</td>
</tr>
<tr>
<td>Total Cover</td>
<td>1984</td>
<td>45-185</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>45-190</td>
</tr>
<tr>
<td>Cover 1-4m</td>
<td>1984</td>
<td>0-60</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>0-60</td>
</tr>
<tr>
<td>Cover 4-10m</td>
<td>1984</td>
<td>0-75</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>0-75</td>
</tr>
<tr>
<td>Cover 10-20m</td>
<td>1984</td>
<td>0-60</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>0-50</td>
</tr>
<tr>
<td>Cover &gt;20m</td>
<td>1984</td>
<td>0-95</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>0-95</td>
</tr>
<tr>
<td>Foliage Height</td>
<td>1984</td>
<td>1.1-3.9</td>
</tr>
<tr>
<td>Diversity</td>
<td>1985</td>
<td>1.1-3.9</td>
</tr>
<tr>
<td>Plant Species</td>
<td>1984</td>
<td>1.0-2.9</td>
</tr>
<tr>
<td>Diversity</td>
<td>1985</td>
<td>1.0-3.8</td>
</tr>
<tr>
<td>Number of Plant Species</td>
<td>1984</td>
<td>1-6</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>1-6</td>
</tr>
</tbody>
</table>

*Mann-Whitney U test corrected for ties
\( ^{d} \) Two-tailed P: * = P<0.1, ** = P<0.05, *** = P<0.001, NS = not significant
TABLE 4. Vegetation characteristics of 1985 quadrats used for foraging by one vireo species alone compared with those used by both. All covers are precents and total cover is the sum of the four height category covers.

<table>
<thead>
<tr>
<th>Vegetation parameter</th>
<th>Both Species (N = 21)</th>
<th>Red-eyed Vireo (N = 31)</th>
<th>Warbling Vireo (N = 85)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (SD)</td>
<td>Mean (SD)</td>
<td>Za Pb</td>
</tr>
<tr>
<td>Total Cover</td>
<td>115 (32)</td>
<td>116 (33)</td>
<td>0.31 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>78 (34) 3.94 ***</td>
</tr>
<tr>
<td>Cover 1-4m</td>
<td>30 (12)</td>
<td>23 (14)</td>
<td>1.58 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>19 (18) 2.99 **</td>
</tr>
<tr>
<td>Cover 4-10m</td>
<td>23 (12)</td>
<td>30 (22)</td>
<td>1.19 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>18 (17) 2.14 **</td>
</tr>
<tr>
<td>Cover 10-20m</td>
<td>15 (13)</td>
<td>24 (16)</td>
<td>1.85 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>23 (17) 1.74 *</td>
</tr>
<tr>
<td>Cover &gt;20m</td>
<td>46 (25)</td>
<td>38 (25)</td>
<td>1.10 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>20 (22) 4.07 ***</td>
</tr>
<tr>
<td>Foliage Height Diversity</td>
<td>2.9 (0.63)</td>
<td>2.9 (0.84)</td>
<td>0.20 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.4 (0.75) 2.67 **</td>
</tr>
<tr>
<td>Plant Species Diversity</td>
<td>2.2 (0.60)</td>
<td>2.0 (0.52)</td>
<td>0.88 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.7 (0.71) 2.68 **</td>
</tr>
<tr>
<td>Number of Plant Species</td>
<td>3.6 (0.87)</td>
<td>3.5 (1.3)</td>
<td>0.41 NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.7 (1.4) 2.43 **</td>
</tr>
</tbody>
</table>

* Mann-Whitney U test corrected for ties
** Two-tailed P: * = P<0.1, ** = P<0.05, *** = P<0.001, NS = not significant
DISCUSSION

Horizontal Spacing and Habitat Preferences

There is general consensus among biologists that animals place territories in relation to habitat preferences and the position of conspecifics. The influence guild species have on each other appears to vary with species composition, time, and location (Robinson 1981, Rice et al 1983, Morse 1985). My results do not support the hypothesis that interaction between the REV and WV influenced their horizontal spacing on the Pruyn Ranch in 1984 or 1985; but does support the hypothesis that these vireo species had different habitat preferences.

In 1984 and 1985 on the Pruyn ranch the REV and WV spaced their territories more evenly than independent placement would predict. Because both species foraged throughout their territories and nested within their territorial boundaries, foraging and nesting sites were also segregated. This non-random horizontal spacing was largely due to the REV's concentration in the central portion of the study area which had relatively dense vegetation cover. Localization of the REV suggests three possibilities. First, the central dense vegetation was preferred by both species, but the REV, in part, excluded the WV from it. Second, this section was not preferred by either species but competition from the WV confined the REV to it. Third, the habitat preferences of the two vireo species were significantly different. Interaction between the REV and WV for territorial space assumes that the habitat preferences of both species were similar.
Birds generally place territories on the most optimal habitat available, and less suitable areas are used when optimal areas are occupied by conspecifics or another competitor (Fretwell 1972). The WVs arrived on the study site before the REVs and, without any possible REV interaction, set up territories in the open vegetation located at the periphery of the study site. For example, in 1985 the first three WVs to arrive established territories that were almost completely nonoverlapping with future REV territories. When REVs arrived, most WVs were nest building on territories which remained constant despite the REV influx. Clearly, the WVs based territory placement on their affinity for the peripheral open vegetation and were not measurably influenced by REVs.

Once WVs had occupied most of the peripheral open vegetation, newly arriving WVs began to settle in the central dense vegetation which was also eventually occupied by REVs. The use of this different vegetation may have resulted from WVs being forced into the dense vegetation when all the preferred open habitat was occupied by conspecifics. Similar instances of individuals being forced into less suitable habitat by intraspecific population pressure have been found in Chaffinches (Fringilla coelebs), Goldcrests (Regulus regulus), and Blue Tits (Parus coeruleus) (Cody 1985).

Though less convincing, my results also suggest that the WV was not affecting the territory placement of the REV. While the REVs tended to use areas unoccupied by WVs, this separation was not complete and, in each breeding season, 40% of REV territorial space was also used by WVs. Therefore, if interaction with the WV was influential, WVs prevented
REVs from using open vegetation while allowing for coexistence in dense vegetation. Orians and Willson (1964) found a similar situation with blackbirds. The socially dominant Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) occupied all preferred vegetation alone, but shared less preferred habitat with the subordinant Red-winged Blackbird (*Agelaius phoeniceus*). In this case and in nearly all others that have been studied in detail, the larger of the interacting species has been found to be dominant (Orians 1961, Morse 1974, Sherry 1979, Robinson 1981). Since the REV is on average 30% heavier and 10% longer than the WV, it is unlikely that the WV would be physically able to confine the REV to less preferred habitat. Assuming REVs were dominant, they would have been able to choose their preferred habitat to the greatest extent possible. If REVs preferred open vegetation, overlap with the WV would have most likely been in open vegetation.

The REV population size was smaller than the WV and they arrived en masse and all settled in the central dense vegetation. The similarity of the habitat REVs used alone and shared with WVs suggests that all REVs were using their preferred habitat and that the REV's habitat requirements were more specific than those of the WV. The difference between species in the variability of the habitat used could have been due to differences in the specificity of habitat requirements or to the difference in population sizes or both. It is unclear if REVs could have increased their population size and settled into the peripheral open habitat used solely by the WVs. REVs used many vegetational layers: they sang primarily from the tops of trees above 20 meters, foraged primarily in the middle of plants between 4 and 20 meters, and
placed their nests low in the canopy, on average at 7 meters. It is possible that the REVs height use resulted from the complex nature of the vegetation they inhabited. When using this central complex habitat, WVs slightly expanded their use of the vegetation strata, but never to the extent of the REV. The foraging height profile and singing height profile of the REV were each different from its foliage height profile. This indicates that the REV height use was not generally related to the plant profile. The REV's use of diverse vegetational strata probably limited REVs to the denser and more complex habitat.

A natural experiment occurred in 1985 when there were fewer individuals of each species on the Pruyn Ranch than there had been in 1984. If the REV and WV were competing for the same vegetation characteristics, interspecific competition would have lessened and the availability of this commonly preferred habitat would have increased in 1985. This probably would have resulted in an increase in the similarity of the habitat used by each species. If each species had unique habitat affinities, intraspecific competition would have been the primary influence regulating territory placement and, with fewer conspecifics in 1985, each species would have been able to use its preferred habitat to a greater extent. This probably would have resulted in the differences between species in habitat being greater in 1985. The latter of these two possibilities is what I observed and suggests that the segregated territory placement of the REV and WV was due to differences in their habitat preferences.
My results support the hypothesis that the observed horizontal segregation was due to habitat affinities. During each breeding season I detected significant differences in the habitat used by each species. Also, for each species there was no change between years in habitat use. During the 1984 and 1985 breeding seasons the REV and WV appear to have based their habitat choices on individual affinities and interspecific interaction was not influential. F.C. James (1971) and R.D. James (1976) found the REV and WV to separate along habitat dimensions similar to those I have documented. My findings contrast with coexisting Red-eyed and Philadelphia vireos who have similar habitat preferences and compete for the same space (Rice 1978, Robinson 1981).

**Vertical Spacing**

Although the REV and WV sang primarily from the tops of trees, overall, each sang at different heights. This appears to have been primarily the result of differences in the vegetation structure used by each species. While the foliage height profiles of the two species were not different, the amount of cover above 20 meters in REV territories was much greater and offered the REV more opportunities to sing at a greater height.

When observations from quadrats both species used were considered, their singing height profiles were similar. This change was primarily due to the WV's increase (by 22.4%) in singing above 20 meters. The WV made this shift despite the REV's singing at this height with a frequency of 62.7%. Co-occupied areas had a greater amount and proportion of vegetation above 20 meters than did areas the WV used.
alone. The WV's affinity for singing from the tops of trees probably resulted in its singing at a greater height when in an area with a higher canopy.

These findings suggest that the actual singing height was influenced by vegetation height and an affinity for singing from the tops of trees and not by interspecific interaction. Position appears to be a better indicator of singing height preference than actual height.

Foraging height is considered an important component in resource allocation within avian communities (MacArthur 1958, Cody 1974). Overall, the foraging height profiles of the REV and WV were similar; yet their positions in the canopy were different. WVs foraged primarily in the upper third of plants and REVs foraged in the middle. These findings are consistent with Robinson (1981) who found that REVs foraged primarily in the middle canopy and Hamilton (1962) who found that the WV preferred to forage in the tops of trees.

The overall similarity in REV and WV foraging height was probably a reflection of differences in vegetation structure of the areas each species used for foraging. Black Cottonwoods greater than 20 meters were more common on REV territories than on WV territories. Thus, while foraging in the middle of a tree, REVs foraged at about the same height as WVs. James (1976) also did not find a difference in the foraging height of the REV and WV; but found that the trees used by the REV were on average 50% taller than those of the WV. Although he did not consider their vertical positions, I can infer from his data that the REVs were foraging in the middle of trees, while WVs were toward the top.
The overall difference in foraging position could be due to species specific affinities or to interaction between the REV and WV or to both. Most of foraging observations were of vireos in quadrats not used by the other vireo species (74.6% of WV and 67.4% of REV). That is, the closest conspecific was generally at least 24 meters away and often much further. Over such distances, direct vireo interaction that could have influenced their foraging positions was unlikely. Therefore, I consider the overall foraging position profiles of each species to be primarily due to unique affinities.

When I considered only the quadrats used for foraging by both species, the number of observations is small (30 REV and 48 WV) and conclusions based on these data are tentative. Nonetheless, a few trends are worth noting. The only significant change by either species between exclusive areas and shared areas were shifts in foraging height by the WV. For each height class, the change in foraging by the WV was in the same direction as the change in the proportion of vegetation cover. In particular, the WV foraged with greater frequency above 20 meters (by 12.5%) and below 4 meters (by 14.6%) and the proportion of the total vegetation cover in these two height classes also increased (by 15.3% and 2.8%, respectively). Likewise, foraging and the proportion of vegetation in the two middle height classes each decreased (10-20m: 21.6% and 15.6%; 4-10m: 5.6% and 2.5%, respectively). This suggests that the WV changed its foraging height in response to changes in vegetation structure.
The WV's increase in foraging below 4 meters in shared areas was much greater than the corresponding increase in vegetation cover. This suggests that another factor was influential. The WV shifted its foraging away from the two height classes most frequently used by the REV and it is possible that interaction with the REV initiated these shifts. Nonetheless, in co-occupied areas half of the WV shifts were in the same direction as changes made by the REV. The only major changes made by both species in the same height class were both decreases and corresponded to decreases in vegetation proportion for each species. From my results, it is unclear if the WV foraging height shifts were responses to interaction with the REV or to changes in vegetation structure or both.

In summary, my results show that the WV and REV have similar singing position affinities and different foraging position affinities and that vegetation structure influences singing and foraging height. Interspecific interaction did not influence singing profiles. It is unclear what, if any, role interaction between the REV and WV played in their foraging profiles.
Studies have shown that insectivorous birds often forage preferentially on certain plant species (Holmes and Robinson 1981, Airola and Barrett 1985). The WV and REV each foraged primarily in Black Cottonwoods. This was probably because vireos are primarily arboreal birds and Black Cottonwoods were the only common tree on the Pruyn Ranch. Although, in 1985, willow and Quaking Aspen cover were similar for each vireo species, WVs used willows more than REVs and REVs used Quaking Aspen more than WVs. This indicates that there was some difference in the plant species each vireo species preferred to use. The influence of interspecific competition and preadapted affinities on their plant species preferences is unclear. Overall, differential plant species use was probably of only minor importance in ecologically separating the WV and REV.
Concluding Remarks

Ecologically similar species, especially congeners, generally have distinct habitat preferences (James 1971, Anderson and Shugart 1974, Whitmore 1977, Cody 1974, 1985, Morse 1985). When such species coexist in the same habitat they often use complementary vegetational strata (MacArther 1958, Robinson 1981). From this habitat and height segregation, interspecific competition, or its consequences, is often inferred (Cody 1974, Diamond 1978). An alternative view, seldom considered, is that species are occupying habitats independently of one another (Wiens 1977). Sherry and Holmes (1985) measured the dispersion of forest birds and their habitat use and concluded that habitat selection was the result of diverse biological processes. By measuring the spatial and temporal relationship of the REV and WV and the corresponding habitat use, I have shown that their distinct habitat and height preferences were not necessarily correlated with interspecific competition. My results support recent warnings by ecologists: it is wrong to assume that observed complementary differences in resources use between coexisting species are due to competitive pressure.
LITERATURE CITED


