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A FIELD TEST OF THE VARIABLE CIRCULAR-PLOT CENSUSING METHOD IN A SIERRAN SUBALPINE FOREST HABITAT[1]

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Abstract. The density and distribution of territories were determined for 21 species in a 48-ha Sierran subalpine forest study plot by an intensive program of spot-mapping and nest monitoring. About 10% of the total breeding individuals were color-banded and about 75% of the nests of all species were found. Variable circular-plot (VCP) censuses were simultaneously conducted in the same study plot. The VCP method, with minimum effort (48 stations), could describe community parameters reasonably well and could distinguish common from rare species, but could not correctly determine the relative abundances of the common species, could not correctly describe the distribution of territories within the study plot, and produced errors in density estimates for the common species that ranged from −57% to +65%. When the effort was increased threefold (144 stations), the accuracy of the method was improved so that it produced more or less acceptable relative abundances for even the common species and was marginally capable of describing the distribution of territories for 37% of the species, particularly for those species whose distributions were markedly non-uniform, but it still produced errors in density estimates for the common species that ranged from −67% to +96%. Interestingly, VCP total count often performed nearly as well as the calculated VCP density in determining relative abundances. The accuracy of the VCP method may be expected to be poor for species with low population densities, large territory sizes, high mobilities, and ventriloqual vocalizations, and for habitats that are dense and highly three-dimensional.

Key words: Variable circular-plot census; spot-mapping; nest monitoring; distribution of territories; species density.

INTRODUCTION

The variable circular-plot (VCP) censusing technique has become increasingly popular as a method for estimating bird numbers since it was first introduced by Reynolds et al. (1980). The VCP method has been reported to offer distinct advantages for surveying large geographical regions, particularly in areas of remote and rugged terrain (Scott et al. 1981), as well as for censusing areas where the vegetation occurs in small circumscribed stands that are not suited for line transects (Anderson and Ohmart 1981). Because of the wide range of problems encountered whenever one tries to estimate the numbers of terrestrial birds (Ralph and Scott 1981, Verner 1985), and because of the increasing use being made of the VCP method, it is important that the performance and accuracy of the VCP method be thoroughly assessed.

I previously tested the accuracy of the VCP method in a California coastal scrub habitat where 64% of the individuals of the eight major species were color-banded, and 43% of their nests were found and monitored (DeSante 1981). In this open habitat, the VCP method performed remarkably well; the VCPs underestimated the densities of the eight species by amounts ranging from 2% to 70% and with a mean absolute error of only 25%. Edwards et al. (1981) compared VCPs to sample plots and line transects and found few differences among the methods with regard to various community parameters. They did not, however, compare individual species' densities. Szaro and Jakle (1982) compared the VCP method to spot-mapping in desert riparian and desert scrub habitats in Arizona and also found that the method produced acceptably accurate results.

Recently, Verner and Ritter (1985) completed an extensive comparison of transects and point counts in California oak-pine woodlands and presented considerable evidence that challenged the assumption that VCP density estimates were acceptably accurate. However, because they did not determine the actual den-

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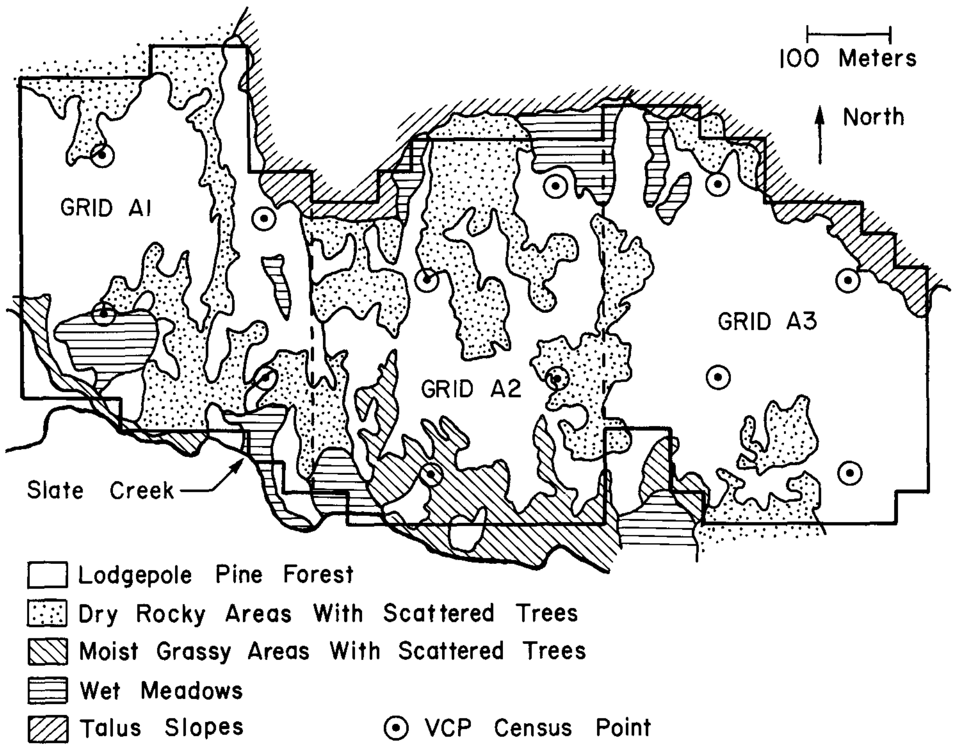

FIGURE 1. Map of the 48-ha subalpine forest study plot located in the Harvey Monroe Hall Natural Area of Inyo National Forest on the east slope of the Sierra Nevada Mountains, Mono County, California.

sities of the various species they could not directly measure the accuracy of the method.

In this paper, I present the results of the VCP method in a subalpine forest habitat and directly compare these results to the "actual" densities of the various species as determined by an intensive program of spot-mapping partially color-banded populations and an intensive program of detailed nest monitoring.

STUDY AREA

The 48-ha study plot (Fig. 1) was located in subalpine forest habitat in the Harvey Monroe Hall Natural Area of the Inyo National Forest on the east slope of the Sierra Nevada Mountains in Mono County, California. The study plot occupied the south-facing slope of Slate Creek Valley, one of the headwater tributaries of Lee Vining Creek, and extended from 3,000 to 3,200 m.

The study plot was comprised of mature, undisturbed lodgepole pine (*Pinus murrayana*) forest interspersed, particularly in the middle third, with several dry, open, rocky areas with scattered trees and, primarily around the periphery, with a few moist subalpine meadows and small willow (*Salix* sp.) thickets. A rich, moist ground cover of numerous species of forbs, grasses, and sedges, along with scattered shrubs or sub-shrubs (primarily *Ribes, Artemisia, Salix, Holodiscus, Spiraea, Phyllodoce, Potentilla,* and *Ledum*) characterized the eastern two-thirds of the forested areas, while the western third had a similar but much sparser and drier ground cover and shrub layer. Lodgepole pine was the predominant tree species throughout the study area and averaged about 25 m in height and about 0.6 m DBH. A few whitebark pines (*Pinus albicaulis*), often multiple-trunked, were scattered throughout the study plot, but were somewhat more frequent along the upper boundary. The study plot was bordered on the north primarily by talus slopes and steep cliffs, on the south by moist, open, grassy areas with scattered small trees and willow thickets that made up the small floodplain along Slate Creek, and on the east and west by habitat roughly similar to that of the study plot.

METHODS

THE "ACTUAL" DETERMINATION OF BREEDING TERRITORIES

The study plot was divided into three contiguous 16-ha plots orthogonally gridded at 40-m intervals. Grid points were marked with small rock cairns and 60-cm-tall garden stakes with red or yellow flagging. Three observers were responsible for an intensive program of spot-mapping and nest monitoring, one for each 16-ha grid. Detailed spot-mapping censuses, in which were recorded the individual identity (if known), exact location to the nearest 10 m, and coded behaviors of all birds encountered, were run on each grid about five mornings per week for about 5 hr per morning from June through August 1981. A concentrated effort was made during these spot-mapping censuses to locate and monitor, for all species, all nests for all territories that touched the study plot. A total of 540 person-hours was spent in the study area over the course of the 1981 breeding season spot-mapping the birds and monitoring their nests. The extent of this effort and its success (nests were found and monitored for 75% of the breeding territories) made us confident that we determined the actual number and distribution of territories with a high degree of accuracy. Thus, I believe that what is offered here is a valid test of the VCP censusing method rather than a simple comparison between spot-mapping and VCP censusing techniques. It is informative in this regard to note that 122 spot-mapping censuses conducted in North America in 1984 averaged only 25.9 person-hours each for an average plot size of 13.1 ha (Van Velzen and Van Velzen 1985). Our "actual" determination of breeding territories, therefore, involved nearly six times the effort per unit area of an average spot-mapping census.

As yet a further aid to the determination of territories, about 10% of the 1981 breeding birds were individually color-banded. These birds were the surviving and returning birds from a group of birds color-banded in 1979. At that time, over 40% of the breeding birds of the study plot were color-banded.

The proportion of each of the territories that was contained within the 48-ha study plot was estimated to the nearest tenth. (If less than 5% of any territory was contained within the study plot, that territory was ignored unless it was the only territory of that particular species, in which case it was included as a trace.) These proportions were summed for all territories contained within the 48-ha plot and provided the "actual" densities of territories (per 48 ha). These are the densities against which the VCP densities are compared.

THE VARIABLE CIRCULAR-PLOT TECHNIQUE

The details of this method have been described by Reynolds et al. (1980) and DeSante (1981). Twelve permanent VCP stations were established in the study plot at previously established grid points (Fig. 1). All VCP stations were at least 200 m apart. A period of 8 min was spent counting birds at each VCP station following a rest period of one minute to allow for equilibration of bird activity after arrival at each station. Birds were not counted or recorded during travel between stations. Because about 6 min were necessary for travel between stations, each station took roughly 15 min to complete. The entire set of 12 stations thus took about 3 hr to complete. The first station was begun at 0615 PDT on each census morning; the starting location, direction of travel, and observers were varied so that all stations were censused, on average, at the same time each morning. This produced a procedure completely balanced with respect to time, location, and observer, and thus facilitated comparisons between stations.

In order to investigate the effects of sample size and timing of censuses within the season, we utilized two census periods. The first census period was 23 to 26 June 1981, a time when most species in the study plot were incubating eggs. The second census period was 8 to 11 July 1981, a time when most species were tending well-developed nestlings or recently fledged young. To make the comparisons between VCP data and spot-mapping data more accurate, territory maps were constructed from the spot-mapping and nest-monitoring data for each census period.

We used four observers during the first census period (CP #1). Three of these were the same individuals who were conducting the intensive spot-mapping censuses and nest monitoring in the study plot. In order to ensure that they were naive as to the actual number and location of territories, they did not conduct VCPs on their own grids. These three individuals, therefore, each completed only eight VCP stations on each of the four consecutive mornings for a total of 96 stations. A fourth individual, who conducted spot-mapping and nest monitoring on a 16-ha grid that was adjacent to the 48-ha study plot, completed all 12 VCP stations on each of the 4 census mornings. As a result, each of the 12 VCP stations was censused 12 times in CP #1 for a total of 144 stations.

In the second census period we utilized only a single observer who completed all 12 VCP stations on each of 4 consecutive days for a total of 48 stations. Unlike the four individuals who took part in CP #1, this observer was not involved in any spot-mapping or nest monitoring in or near the study plot. He was, however, equally familiar with the calls and songs of all the species that occurred in the study area. All observers were previously experienced in the use of VCPs and all were trained to estimate distances in the study plot for four days immediately prior to censusing. At the end of these four days of training, it was felt

TABLE 1. Total number of territories that touched the 48-ha study plot as determined by intensive spot-mapping and nest monitoring.

Species	Total no. of territories			Territories w/nesting activity		
					For which nests were found	
	All season	CP #1[a]	CP #2[b]	Total no.	No.	%
Dusky Flycatcher *Empidonax oberholseri*	23	23	21	20	19	95.0
Clark's Nutcracker *Nucifraga columbiana*	3	3	3	3	0	0.0
Mountain Chickadee *Parus gambeli*	14	14	14	12	11	91.7
White-breasted Nuthatch *Sitta carolinensis*	2	2	2	2	1	50.0
Brown Creeper *Certhia americana*	1	1	1	1	1	100.0
Rock Wren *Salpinctes obsoletus*	1	1	0	0	0	–
Golden-crowned Kinglet *Regulus satrapa*	1	1	1	1	1	100.0
Ruby-crowned Kinglet *Regulus calendula*	2	2	1	1	1	100.0
Mountain Bluebird *Sialia currucoides*	1	1	0	0	0	–
Townsend's Solitaire *Myadestes townsendi*	1	1	1	1	0	0.0
Hermit Thrush *Catharus guttatus*	10	8	10	8	6	75.0
American Robin *Turdus migratorius*	5	5	4	4	4	100.0
Yellow-rumped Warbler *Dendroica coronata*	17	17	17	16	13	81.3
MacGillivray's Warbler *Oporornis tolmiei*	1	0	1	0	0	–
Wilson's Warbler *Wilsonia pusilla*	1	1	1	0	0	–
Chipping Sparrow *Spizella passerina*	11	8	9	5	2	40.0
White-crowned Sparrow *Zonotrichia leucophrys*	6	6	5	6	4	66.7
Dark-eyed Junco *Junco hyemalis*	31	30	30	28	23	82.1
Pine Grosbeak *Pinicola enucleator*	1	0	1	1	1	100.0
Cassin's Finch *Carpodacus cassinii*	34	30	23	29	21	72.4
Pine Siskin *Carduelis pinus*	14	13	14	14	6	42.9
Total	180	167	159	152	114	75.0

[a] Census period #1: 23 to 26 June, 1981.
[b] Census period #2: 8 to 11 July, 1981.

that all observers were equally accurate in estimating distances of both visual and aural encounters of birds in the study plot.

All individuals of all species encountered during the 8-min counting periods were recorded, regardless of distance from the observer. The numbers of "singing males" and "all other observations" were recorded separately and together equaled the numbers of "all birds." Total count refers to all individuals counted by all observers during all 8-min counting periods at all VCP stations during each census period. VCP densities were calculated from the count of singing males within the basal radius, unless the total count of all birds was greater than two times the total count of singing males, in which case VCP densities were calculated from the count of all birds within the basal radius. The basal radius was determined for each species as the inside radius of the first band that had a density significantly less than the density of the previous bands. Significance was determined by likelihood ratio-testing with a critical value of four (Ramsey and Scott 1979). Ten-meter band widths were used throughout.

Statistical comparisons were made between VCP and "actual" densities using Pearson product-moment correlations and Spearman rank correlations. A significance level of $P \leq 0.05$ was used for all comparisons.

RESULTS

The results of the intensive program of spot-mapping and nest monitoring are presented in Table 1 for the total number of territories that touched any part of the 48-ha study plot. Twenty-three species held territories or home ranges in the study plot during the summer of 1981. Twenty-one of these are treated in this paper and are shown (along with their scientific names) in Table 1. The two additional species that occurred in the plot but that are not treated are Great Horned Owl (*Bubo virginianus*), represented by an apparently unmated male with a home range that seemed to include most of the study plot but, because of nocturnal habits, was not adequately censused by either method, and Calliope Hummingbird (*Stellula calliope*), represented by a female that nested in the southeast portion of the study plot but was recorded away from her nest on only two occasions so that the actual extent of her territory was unknown.

A total of 180 territories of these 21 species was present in the study plot during the 1981 breeding season. Of these, 152 showed some nesting activity. The other 28 territories primarily involved unmated males. Nests were found and monitored for 114 (75.0%) of the 152 breeding territories. The number of fledglings was determined for each of the 38 breeding territories for which no nest was found. These detailed nest and fledgling data provide considerable assurance that the number and distribution of territories were accurately determined.

The 180 total territories involved 335 total individuals of which 31 (9.3%) wore color bands that were placed on them during the summer of 1979. These color-banded birds included Dusky Flycatchers (*Empidonax oberholseri*)—7, Mountain Chickadees (*Parus gambeli*)—4, Hermit Thrushes (*Catharus guttatus*)—6, Yellow-rumped Warblers (*Dendroica coronata*)—2, White-crowned Sparrow (*Zonotrichia leucophrys*)—1, Dark-eyed Juncos (*Junco hyemalis*)—6, and Cassin's Finches (*Carpodacus cassinii*)—5. The presence of these color-banded individuals also aided in the determination of the number and distribution of territories.

The seasonal dynamics in the density of birds in the study plot can be seen by the fact that only 167 of the 180 territories were active during census period #1 (23 to 26 June) and only 159 were active in census period #2 (8 to 11 July). The reduced numbers during CP #1 reflected the late arrival of a number of breeding pairs of Fringillids including Pine Grosbeak (*Pinicola enucleator*) and Pine Siskin (*Carduelis pinus*), as well as the late arrival of a few unmated male Hermit Thrushes, Chipping Sparrows (*Spizella passerina*), and a MacGillivray's Warbler (*Oporornis tolmiei*). The still lower numbers during CP #2, especially for Cassin's Finches, reflect the early departure of a number of males that failed to attract mates and the departure of a few pairs that failed in their first nesting attempt.

COMMUNITY PARAMETERS

The results of the VCP method for certain community parameters are presented in Table 2 for both census periods #1 and #2. In CP #1, the total density of territories was underestimated by only 6.5%. In CP #2, the underestimation of the density of territories was somewhat greater, 16.7%, still a reasonably small error. In both census periods, the species richness as determined from the VCPs was exactly the same as the "actual" species richness, 19 species. In each census period, however, one rare species was picked up on the VCPs by the observation of only one bird so that a density value could not be calculated. Furthermore, in CP #2, the VCPs completely missed one rare species but picked up two apparently floating individuals of a different rare species whose territory had disappeared from the study plot between census periods #1 and #2. Despite these minor discrepancies, however, the VCPs were capable of picking up virtually all of the resident species.

TABLE 2. Field test of the variable circular-plot censusing method: results for community parameters.

Parameter	"Actual"[a]	VCP	% Error[b]
Census period #1[c]			
Total density of territories (/48 ha)	135.8	126.9	−6.5
Species richness	19	19	0.0
Species diversity ($1/\Sigma\, \rho_i^2$)	8.39	7.80	−7.0
Census period #2[d]			
Total density of territories (/48 ha)	132.1	110.1	−16.7
Species richness	19	19[e]	0.0
Species diversity ($1/\Sigma\, \rho_i^2$)	9.03	8.04	−11.0

[a] As determined by intensive spot-mapping and nest monitoring.
[b] Negative errors indicate underestimations, positive errors indicate overestimations.
[c] 23 to 26 June 1981. VCP data from 12 stations each censused 12 times = 144 stations.
[d] 8 to 11 July 1981. VCP data from 12 stations each censused 4 times = 48 stations.
[e] Does not include one species that was completely missed by the VCPs, but includes another species, represented by two VCP observations, for which no territory existed in census period #2.

Table 2 indicates that the "actual" species diversities (calculated as $1/\Sigma\, \rho_i^2$ where ρ_i is the proportion of the total population contributed by the ith species) were slightly higher in CP #2 than in CP #1. This is because species diversity calculated in this manner is highly dependent upon the most abundant species. The presence of unmated males in these most abundant species, therefore, has the effect of further increasing their abundance and thus decreasing both the "evenness" of the bird community and the species diversity. Many of these unmated males departed shortly after CP #1 so that the evenness and, therefore, also the species diversity was increased in CP #2. Table 2 also indicates that the VCPs underestimated species diversity by only 7% in CP #1 and by only 11% in CP #2. These underestimations of species diversity were the result of the fact that some of the most abundant species were overestimated by the VCPs so that the evenness was decreased. Despite these various errors, it is clear that the VCP method performed remarkably well in estimating community parameters in a subalpine forest breeding bird community.

INDIVIDUAL SPECIES' DENSITIES

Let us now examine how well the VCP method performed in estimating the densities of individual species. First, let us concentrate on CP #1 (Table 3) and examine those species whose VCP densities were determined from counts of singing males. The densities of ter-

TABLE 3. Field test of the variable circular-plot censusing method: results for individual species for Census Period #1[a].

Species	Density of territories (/48 ha) "Actual"[b]	VCP[c]	Diff.[d]	% Error[d]	Basal radius r (m)	VCP count[e] Total	Within r
A. Species whose VCP densities were determined from counts of singing males only.							
Cassin's Finch*	26.9	16.5 ± 2.2	−10.4	−38.6	90	208	126
Dark-eyed Junco*	23.0	16.5 ± 3.2	−6.5	−28.2	60	104	56
Yellow-rumped Warbler*	15.3	14.7 ± 2.0	−0.6	−3.6	100	205	139
Chipping Sparrow	6.9	1.5 ± 1.0	−5.4	−78.6	60	9	5
Hermit Thrush*	5.7	2.8 ± 0.7	−2.9	−51.6	100	53	26
White-crowned Sparrow*	3.8	1.3 ± 0.4	−2.5	−67.0	120	31	17
Ruby-crowned Kinglet*	1.6	1.5 ± 0.5	−0.1	−3.3	120	37	21
Subtotal	83.2	54.8	−28.4	−34.1			
Common species*	76.3	53.3	−23.0	−30.1			
B. Species whose VCP densities were determined from counts of all birds.							
Dusky Flycatcher*	17.1	28.5 ± 3.7	+11.4	+66.8	40	223	86
Mountain Chickadee*	12.0	14.9 ± 2.9	+2.9	+24.3	40	101	45
Pine Siskin*	12.0	13.6 ± 2.7	+1.6	+13.2	50	96	64
American Robin*	3.4	6.6 ± 1.4	+3.2	+95.0	40	83	20
Clark's Nutcracker*	2.1	4.1 ± 0.7	+2.0	+95.9	70	138	38
White-breasted Nuthatch	2.0	0.5 ± 0.2	−1.5	−77.6	150	21	19
Golden-crowned Kinglet	1.0	0.3 ± 0.5	−0.7	−66.8	40	2	1
Brown Creeper	0.9	0.6 ± 0.8	−0.3	−34.5	40	6	5
Mountain Bluebird	0.8	2.7 ± 2.1	+1.9	+231.6	30	4	3
Wilson's Warbler	0.8	—	—	—	—	1	—
Townsend's Solitaire	0.5	0.3 ± 0.2	−0.2	−36.3	100	8	6
Rock Wren	T[f]	0.1 ± 0.1	+0.1	—	190	5	4
Subtotal	52.6	72.2	+19.6	+37.2			
Common species*	46.6	67.7	+21.1	+45.3			
Grand total	135.8	126.9	−8.9	−6.5			
Total common species*	122.9	121.1	−1.8	−1.5			

* Common species: those whose VCP total count was greater than 25.
[a] 23 to 26 June 1981. VCP data from 12 stations each censused 12 times = 144 stations.
[b] As determined by intensive spot-mapping and nest monitoring.
[c] Density ± 95% confidence interval.
[d] Negative values indicate underestimations, positive values indicate overestimations.
[e] Number of birds (either singing males or all birds) detected by VCPs.
[f] Trace: actual density considerably less than 0.05.

ritories for all seven species in this subgroup were underestimated by amounts ranging from 3.3 to 78.6%. Only two species, Ruby-crowned Kinglet (*Regulus calendula*) and Yellow-rumped Warbler, were underestimated by less than 25%. Males of both of these species were very persistent singers, and during CP #1 all females of these species in the study plot were incubating eggs. These factors apparently contributed to the accurate VCP estimates of their densities. Only two other species, Dark-eyed Junco and Cassin's Finch, were underestimated by less than 50%. These were also rather persistent singers but, while most finch nests during CP #1 contained eggs, most junco nests at this time were hatching, a factor that greatly decreased the amount of singing in male juncos. Overall, the total density of this subgroup of seven species was underestimated by 34.1%.

Reynolds (pers. comm.) has recommended that the minimum number of observations per species (total count) needed to calculate a meaningful basal radius should be at least 25. Six of the seven species in this first subgroup fulfilled this requirement and are designated as "common" species. The total density of these six species was underestimated by 30.1%. The remaining species, Chipping Sparrow, was represented by a total count of only 9 observations and thus its basal radius, calculated VCP density, and consequent percent error are all somewhat suspect. Nevertheless, it is clear from its very low VCP count compared to other species in this subgroup and its considerably higher "actual" density compared to others in this subgroup, that the density of Chipping Sparrows was seriously underestimated by the VCPs.

Turning now to those species whose VCP densities were determined by counts of all birds, we see that the densities of all five common species were overestimated by amounts ranging from 13.2 to 95.9%. The total density of these five species was overestimated by 45.3%. Not all species in this subgroup, however, were overestimated. Most of the rarer species were underestimated by fairly substantial amounts, but one rare species, Mountain Bluebird (*Sialia currucoides*), was severely overestimated. In fact, only two species in this entire subgroup,

TABLE 4. Field test of the variable circular-plot censusing method: results for individual species for Census Period #2[a].

Species	Density of territories (/48 ha) "Actual"[b]	VCP[c]	Diff.[d]	% Error[d]	Basal radius r (m)	VCP count[e] Total	Within r
A. Species whose VCP densities were determined from counts of singing males only.							
Dark-eyed Junco*	23.1	10.0 ± 2.2	−13.1	−56.7	110	80	38
Yellow-rumped Warbler*	15.0	19.4 ± 4.1	+4.4	+29.3	80	88	39
Chipping Sparrow	8.5	1.6 ± 0.7	−6.9	−81.0	190	16	15
Hermit Thrush*	7.8	12.9 ± 3.3	+5.1	+65.3	110	60	49
White-crowned Sparrow*	3.0	1.6 ± 0.5	−1.4	−46.9	100	34	5
Brown Creeper	1.0	2.0 ± 1.3	+1.0	+99.0	100	3	2
Golden-crowned Kinglet	1.0	0.7 ± 0.6	−0.3	−35.1	70	4	1
Ruby-crowned Kinglet	0.8	1.3 ± 1.3	+0.5	+59.2	80	3	2
Subtotal	60.2	49.4	−10.8	−17.9			
Common species*	48.9	43.9	−5.0	−10.3			
B. Species whose VCP densities were determined from counts of all birds.							
Cassin's Finch*	20.6	16.8 ± 3.2	−3.8	−18.5	60	105	38
Dusky Flycatcher*	16.4	19.7 ± 5.0	+3.3	+20.3	50	60	31
Pine Siskin*	13.3	8.9 ± 2.6	−4.4	−32.7	40	45	9
Mountain Chickadee*	11.9	9.7 ± 2.2	−2.2	−18.3	60	75	22
American Robin	2.7	1.9 ± 1.3	−0.8	−27.8	70	9	6
Clark's Nutcracker	2.2	0.8 ± 0.3	−1.4	−63.3	160	24	13
White-breasted Nuthatch	2.0	1.1 ± 0.4	−0.9	−47.1	160	22	17
Wilson's Warbler	1.0	0.0	−1.0	−100.0	—	0	—
MacGillivray's Warbler	0.8	—	—	—	—	1	—
Townsend's Solitaire	0.7	0.3 ± 0.5	−0.4	−53.6	70	2	1
Pine Grosbeak	0.3	1.3 ± 0.8	+1.0	+324.4	100	10	8
Mountain Bluebird	0	0.0 ± 0.1	0.0	—	220	2	1
Subtotal	71.9	60.7	−11.2	−15.6			
Common species*	62.2	55.1	−7.1	−11.4			
Grand Total	132.1	110.1	−22.0	−16.7			
Total common species*	111.1	99.1	−12.0	−10.8			

* Common species: those whose VCP total count was greater than 25.
[a] 7 to 11 July 1981. VCP data from 12 stations each censused 4 times = 48 stations.
[b] As determined by intensive spot-mapping and nest monitoring.
[c] Density ± 95% confidence interval.
[d] Negative values indicate underestimations, positive values indicate overestimations.
[e] Number of birds (either singing males or all birds) detected by VCPs.

Mountain Chickadee and Pine Siskin, were estimated to within 25%, and only two other species, Brown Creeper (*Certhia americana*) and Townsend's Solitaire (*Myadestes townsendi*), were estimated to within 50%. Overall, the total density of the 12 species in this subgroup was overestimated by 37.2%.

When we look at the total for all 19 species we see that the various overestimation errors tended to cancel the various underestimation errors so that the total density was only underestimated by 6.5%. If we examine the 11 common species we see that the same thing happened and that the total density was underestimated by only 1.5%. It must be stressed, however, that despite these very accurate VCP estimates of total density, the VCP estimates for the densities of individual species generally showed substantial errors. In fact, the mean absolute error of the VCP density estimates of the 19 species in CP #1 was 61.8% while the mean absolute error for the 11 common species was 44.4%. It is true, of course, that mean absolute error is a biased measure because underestimation errors are bounded at 100% while overestimation errors are effectively unbounded. Furthermore, errors calculated from VCP density estimates of rare species are suspect because the basal radius values upon which the density estimates are based are themselves suspect. Nevertheless, the mean absolute error calculated for the 11 common species should be meaningful because (a) none of the common species had overestimation errors exceeding 100% and (b) all of the basal radii for these species were calculated from total counts of over 25 observations.

The results of census period #2 (Table 4) show some differences and many similarities. Recall, however, that the data for CP #2 were derived from only 48 stations while the data for CP #1 were derived from a total of 144 stations. Let us first examine those species whose VCP densities were determined by counts of singing males. In this case four species were underestimated while another four species were overestimated. Of the four common species, two were overestimated and two were underestimated. Errors ranged from −81.0% to +99.0% for all eight species and from

TABLE 5. Spearman rank correlations (r_s) between "actual" densities of territories[a] and VCP densities or VCP total counts.

Species group	Number of species	Using VCP densities		Using VCP total counts	
		r_s	P	r_s	P
A. Census period #1[b]					
All species					
Determined by counts of singing males	7	0.813	<0.05	0.714	NS
Determined by counts of all birds	12	0.895	<0.001	0.790	<0.01
Total species	19	0.879	<0.001	0.865	<0.001
Common species only*					
Determined by counts of singing males	6	0.929	<0.01	0.886	<0.02
Determined by counts of all birds	5	0.975	<0.01	0.375	NS
Total common species	11	0.855	<0.001	0.761	<0.01
B. Census period #2[c]					
All species					
Determined by counts of singing males	8	0.720	<0.05	0.887	<0.01
Determined by counts of all birds	12	0.802	<0.01	0.792	<0.01
Total species	20	0.833	<0.001	0.857	<0.001
Common species only*					
Determined by counts of singing males	4	0.400	NS	0.800	NS
Determined by counts of all birds	4	0.600	NS	0.400	NS
Total common species	8	0.548	NS	0.286	NS

* Common species: those whose VCP total count was greater than 25.
[a] As determined by intensive spot-mapping and nest monitoring.
[b] 23 to 26 June 1981. VCP data from 12 stations each censused 12 times = 144 stations.
[c] 7 to 11 July 1981. VCP data from 12 stations each censused 4 times = 48 stations.

−56.7% to +65.3% for the four common species. Not a single species was estimated to within 25% error and only three species, Golden-crowned Kinglet (*R. satrapa*), Yellow-rumped Warbler, and White-crowned Sparrow, were estimated to within 50% error. Because overestimation errors tended to cancel underestimation errors, the total density of the eight species in this subgroup was underestimated by 17.9%, while the total density of the four common species was underestimated by only 7.8%.

Nine of the 12 species whose VCP densities were calculated from counts of all birds, including three of the four common species in this subgroup, had VCP densities that were underestimated in CP #2. Three of these 12 species, however, Dusky Flycatcher, Mountain Chickadee, and Cassin's Finch, were estimated to within 25% and an additional three species, White-breasted Nuthatch (*Sitta carolinensis*), American Robin (*Turdus migratorius*) and Pine Siskin, were estimated to within 50%. Overall, the total density of the 12 species in this subgroup was underestimated by 15.6% while the total density of four common species was underestimated by 11.4%.

Again, because underestimation errors tended to cancel overestimation errors, the total density for all 20 species in CP #2 was underestimated by only 16.7% while the total density of the eight common species was underestimated by only 9.8%. Nevertheless, the mean absolute error of all 20 species in CP #2 was 67.3% and the mean absolute error of the eight common species in CP #2 was 36.0%.

Because the errors in estimating the densities of individual species seemed fairly substantial, at least on a percent error basis, it was appropriate to inquire whether or not the VCP method could rank the species in the correct order of abundance. Spearman rank correlations were calculated between "actual" and VCP densities and are shown for both census periods in Table 5. Separate rank correlations were calculated for all species and for common species only. Within each of these subgroups, separate rank correlations were also calculated for those species whose densities were determined by counts of singing males, for those species whose densities were determined by counts of all birds, and for total species. Six rank correlations, therefore, were calculated for each census period.

Table 5 indicates that all six rank correlations using VCP densities were significant in CP #1. The strongest rank correlations, however, occurred for all species determined by counts of all birds and for all total species, not only because the sample sizes were greatest in these subgroups but also because the species in these subgroups had the greatest spread in abundance and included both very common and very rare species. In CP #2, significant rank correlations were also obtained for all three of the all-species subgroups but *no* significant rank correlations were obtained for any of the common-species-only subgroups. I

TABLE 6. Pearson product-moment correlations (r) between "actual" densities of territories[a] and VCP densities or VCP total counts.

Species	Number of species	Using VCP densities r	Using VCP densities P	Using VCP total counts r	Using VCP total counts P
A. Census period #1[b]					
All species					
Determined by counts of singing males	7	0.949	<0.01	0.800	<0.05
Determined by counts of all birds	12	0.971	<0.001	0.828	<0.001
Total species	19	0.855	<0.001	0.844	<0.001
Common species only*					
Determined by counts of singing males	6	0.956	<0.01	0.803	<0.05
Determined by counts of all birds	5	0.946	<0.02	0.536	NS
Total common species	11	0.783	<0.01	0.760	<0.01
B. Census period #2[c]					
All species					
Determined by counts of singing males	8	0.689	NS	0.861	<0.01
Determined by counts of all birds	12	0.962	<0.001	0.944	<0.001
Total species	20	0.851	<0.001	0.821	<0.001
Common species only*					
Determined by counts of singing males	4	0.467	NS	0.845	NS
Determined by counts of all birds	4	0.750	NS	0.696	NS
Total common species	8	0.555	NS	0.402	NS

* Common species: those whose VCP total count was greater than 25.
[a] As determined by intensive spot-mapping and nest monitoring.
[b] 23 to 26 June 1981. VCP data from 12 stations each censused 12 times = 144 stations.
[c] 7 to 11 July 1981. VCP data from 12 stations each censused 4 times = 48 stations.

conclude, therefore, that the VCP method applied with a minimum of effort (48 stations) in a subalpine forest habitat was capable of distinguishing common from rare species but was incapable of correctly ranking the relative abundance of the common species. When the effort was increased threefold (144 stations), the VCP method was found to be capable not only of distinguishing common from rare species but also capable of ranking the common species more or less correctly according to their relative abundances.

Because the effort needed to estimate distances during VCP counts is substantial, I was curious to discover how well the VCP method performed using just the total counts without regard to distance estimations. These data are also presented in Table 5. In CP #1, the VCP total counts always produced poorer rank correlations than did the calculated VCP densities, but nonetheless produced significant correlations in four out of six cases. Surprisingly, in three of the six cases in CP #2, VCP total counts produced rank correlations that were actually better than the rank correlations produced by calculated VCP densities.

It was also appropriate to inquire how well the calculated VCP densities were correlated to the "actual" densities. Pearson product-moment correlations (Table 6) were calculated for all the same subgroups for which rank correlations were performed. In CP #1, significant correlations were again found for all six subgroups. The best correlations were, of course, obtained for all species determined by counts of all birds and for all total species, again because the sample sizes were greatest and because these subgroups had the greatest range in densities. The correlations obtained in CP #2 were, in all cases, at least somewhat poorer. In fact, the correlations were not significant for any of the common-species-only subgroups nor for all species determined by counts of singing-males subgroup. Again I conclude that the VCP method, when applied with a minimum of effort (48 stations) in a subalpine forest habitat, was capable only of distinguishing common from rare species and was incapable of providing reasonably accurate estimates of relative density. When the effort was increased threefold (144 stations), however, the VCP method was found to be capable of producing more or less accurate relative densities.

Table 6 also indicates that, in CP #1, VCP total counts produced product-moment correlations that, while generally poorer than those produced by calculated VCP densities, nevertheless were significant in about five out of six cases. Moreover, in CP #2, VCP total counts produced product-moment correlations that were actually more significant than calculated VCP densities in two out of six cases.

DISTRIBUTION OF TERRITORIES

Finally, I inquired how well the VCP method could describe the distribution of territories among the 12 VCP stations. Circles of basal radius r for each species were drawn around

TABLE 7. Pearson product-moment correlations between "actual" densities of territories[a] and VCP densities at each of the twelve VCP stations.

	Census period #1[b]					Census period #2				
Species	VCP density by	Y-int	Slope	r	P	VCP density by	Y-int	Slope	r	P
Dusky Flycatcher	AB[d]	0.058	1.744	0.749	<0.01	AB[d]	0.475	0.395	0.277	NS
Clark's Nut-cracker	AB	0.285	−0.040	−0.274	NS	AB	0.160	0.202	0.116	NS
Mountain Chicka-dee	AB	0.454	−0.425	−0.466	NS	AB	0.128	0.529	0.423	NS
White-breasted Nuthatch	AB	0.095	0.002	0.409	NS	AB	0.330	0.019	0.205	NS
Brown Creeper	AB	0.028	0.069	0.294	NS	SM[e]	0.009	0.485	0.502	NS
Rock Wren	AB	0.005	0.670	0.941	<0.001	—	—	—	—	—
Golden-crowned Kinglet	AB	−0.002	0.275	0.887	<0.001	SM	0.014	0.192	0.237	NS
Ruby-crowned Kinglet	SM[e]	0.038	0.686	0.635	<0.05	SM	0.045	−0.091	−0.091	NS
Mountain Bluebird	AB	0.023	−0.284	−0.125	NS	—	—	—	—	—
Townsend's Soli-taire	AB	0.026	0.234	0.321	NS	AB	0.022	−0.029	−0.031	NS
Hermit Thrush	SM	0.180	0.000	0.000	NS	SM	0.984	0.057	0.037	NS
American Robin	AB	0.042	1.450	0.489	NS	AB	0.078	0.237	0.364	NS
Yellow-rumped Warbler	SM	0.191	0.763	0.520	NS	SM	1.237	−0.641	−0.176	NS
MacGillivray's Warbler	—	—	—	—	—	AB	−0.008	0.583	0.944	<0.001
Wilson's Warbler	AB	0.007	−0.056	−0.091	NS	—	—	—	—	—
Chipping Sparrow	SM	0.025	0.045	0.171	NS	SM	0.162	0.071	0.313	NS
White-crowned Sparrow	SM	0.036	0.271	0.622	<0.05	SM	0.011	0.497	0.555	NS
Dark-eyed Junco	SM	0.357	0.051	0.051	NS	SM	0.394	0.218	0.269	NS
Pine Grosbeak	—	—	—	—	—	AB	0.136	3.636	0.322	NS
Cassin's Finch	SM	0.210	0.525	0.688	<0.02	AB	0.467	0.378	0.275	NS
Pine Siskin	AB	0.156	1.088	0.613	<0.05	AB	0.131	0.148	0.311	NS

[a] As determined by intensive spot-mapping and nest monitoring.
[b] 23 to 26 June 1981. Each of the 12 VCP stations were censused 12 times.
[c] 7 to 11 July 1981. Each of the 12 VCP stations were censused 4 times.
[d] AB: VCP density determined by counts of all birds.
[e] SM: VCP density determined by counts of singing males only.

the VCP points on each species' territory maps. The "actual" number of territories (estimated to the nearest 0.05 territory) contained within these circles was then counted. The mean VCP density within each of these circles was compared to these "actual" values by calculating Pearson product-moment correlations for the 12 VCP stations. The results of this analysis are shown for both census periods in Table 7.

Only seven of the 19 species showed significant positive correlations in CP #1. Three of these seven species (Rock Wren [*Salpinctes obsoletus*], Golden-crowned Kinglet, and Ruby-crowned Kinglet) had very low densities (only one or two territories) and only occurred in a limited part of the study plot. Three others of these seven species (White-crowned Sparrow, Cassin's Finch, and Pine Siskin) had higher densities but also showed pronounced non-uniform (clumped) distributions of territories. Only one of the seven species (Dusky Flycatcher) had both a high density and a nearly uniform distribution in the study plot. In CP #2, only one of the 19 species, MacGillivray's Warbler, showed a significant positive correlation. This species also had a very low density and occurred in only a very small part of the study plot. In summary, the VCP method with a minimum effort (48 stations) in a subalpine forest habitat could not effectively describe the distribution of territories within the study plot. Even with a threefold increase in effort (144 stations), the method could only marginally describe the distribution of territories and then usually only for those species that had pronounced non-uniform distributions of territories within the study plot. This is an especially important result because, after all, it is the number of birds within range of the observer at each point that forms the real basis for comparison with the "actual" densities.

Table 7 also indicates that the majority of Y-intercepts for the Pearson product-moment correlations were greater than zero and most slopes were less than one. Since perfect correlation should produce a Y-intercept of zero and a slope of one, the indication is that the VCP method tended to overestimate density where a species was less common and to underestimate density where a species was more common.

DISCUSSION

Before considering the accuracy of the VCP method, let us first consider its efficiency. Recall that the average spot-mapping Breeding Bird Census plot in 1984 required approximately 2 hr/ha to complete (Van Velzen and Van Velzen 1985). Our 48-ha study plot would thus require about 96 hours of effort for standard spot-mapping. (Recall also that we spent 540 hours on our study plot intensively spot-mapping and nest monitoring in order to obtain "actual" densities.) In CP #2 we completed 48 VCP stations in 12 hours while in CP #1 we completed 144 VCP stations in 36 hours. Accuracy aside, these figures do indicate that the VCP method is time-efficient, ranging from only 12% to 37% of the time required for standard spot-mapping. If, however, the number of stations would have to be doubled in order to be able to deal with more of the rarer species, much of the efficiency of the method would be lost.

The results presented earlier indicate that the VCP method, using a relatively small number of stations (48) in a subalpine forest habitat, could distinguish common from rare species but was generally incapable of correctly determining the absolute abundance of most species. The mean absolute error in the densities of eight common species was 36%. Furthermore, the VCP method under these conditions could not correctly rank the common species and thus could not determine the relative or even the ordinal abundances of these common species. Moreover, the VCP method under these conditions was generally incapable of correctly describing the distribution of territories within the study area. However, because the various overestimation errors tended to cancel the errors of underestimation, the VCP method, even with this minimum effort, could describe various community parameters, including total density, species richness, and species diversity, with reasonable accuracy.

When the number of stations was increased threefold to 144, the accuracy of the VCP method was improved so that it more or less correctly ranked the various species, including the common species, and thus produced acceptable measures of ordinal and apparently even relative abundance. Nevertheless, the VCP method, even with this added effort, was incapable of correctly determining the absolute abundances of most species. The mean absolute error in the densities of 11 common species was 44%. With this added effort the VCP method was marginally capable of describing the distribution of territories for about 37% of the species but generally only for those species whose distributions were markedly nonuniform.

The results of this study, therefore, tend to support some aspects of the work of Verner and Ritter (1985) in that it found that the VCP method could not produce accurate estimates of absolute density. The present work, however, does not completely support Verner and Ritter's loss of confidence in the ability of the VCP method to produce reliable estimates of relative density. With an adequate sample size (144 stations) and in the peak of the breeding season, particularly in the incubation phase of the nesting cycle, we found that the VCP method could produce reasonably acceptable estimates of relative density in a subalpine forest habitat. The present results, however, do tend to conflict somewhat with those of Szaro and Jakle (1982) who compared the VCP method with spot-mapping in desert riparian and desert scrub habitats and found mean absolute errors of 17% and 37% respectively, and with previous work by DeSante (1981) who tested the VCP method in a California coastal scrub habitat and found that it produced a mean absolute error of 25%. In contrast, even with common species in the subalpine habitat, the VCP method produced a mean absolute error of 36 to 44%, over half again as great as those earlier studies. Why did the VCP method seem to perform better in the desert riparian, desert scrub, and coastal scrub habitats than in the subalpine forest habitat? To find out let us examine the potential sources of error in the VCP method.

First, individual birds within the basal area may be missed, leading to an underestimation of density. Birds may be missed, for example, if they fail to call, sing, or show themselves during the 8-min counting period at each point. This factor may have contributed to the greater error in CP #2 than in CP #1 (the total density of all species combined was underestimated by 16.7% in CP #2 as compared to only 6.5% in CP #1). The likely reason for this was that, for nearly all species, singing generally tended to be less in CP #2 when they had nestlings or fledglings than in CP #1 when they were incubating eggs. Wilson and Bart (1985) also indicated that the timing of censusing within the phenology of the nesting season could be a source of as much as 25% error in the relative density of House Wrens (*Troglodytes aedon*). Similarly, Sayre et al. (1980) found that a 25% difference in the proportion of mated versus unmated Mourning Doves (*Zenaida ma-*

croura) could produce a 37% error in the apparent density of the population simply because of differences in cooing rates between mated and unmated birds. Mayfield (1981) documented analogous problems with various wood warbler species. Individual birds could also be missed if two birds countersinging close together were counted as one. This error would tend to increase with increasing densities and decreasing territory sizes. Although missing individual birds could have contributed to some of the error in the subalpine, it seems unlikely that it was the primary reason why VCPs performed less well there than in the coastal scrub.

There is, however, another more subtle way in which birds within the basal area may be missed in the tall forest habitat—simply by singing from high in the forest canopy. Such a bird, if it were nearly overhead, would be recorded as if it were only 10 m away and, although it has a substantial likelihood of being missed, will be artificially included in the first band with nearby birds that are close to the ground and that have a much lower likelihood of being overlooked.

The second potential error is that an individual bird may be counted twice, thus leading to errors of overestimation. The most obvious way in which this could happen is when a bird moves across its territory during the 8 min and is counted as two different birds. It is reasonable to expect that the larger the territories or the more mobile the species, the greater will be this tendency toward overestimation. This may indeed have contributed to the greater errors in the subalpine forest habitat than in the coastal scrub habitat for three reasons. First, the average density per species in the Sierran subalpine (15.7 territories/km^2) was only one third of that in the California coastal scrub (46.6 territories/km^2) and lower densities are generally associated with larger territories. Indeed, the territory size of the most abundant subalpine species, Dark-eyed Junco, averaged nearly twice that of the most abundant coastal scrub species (Song Sparrow, *Melospiza melodia*). Second, large species tend to have large territories and more large species were present in the subalpine than in the coastal scrub. Note, for example, the substantial overestimation of American Robin and Clark's Nutcracker (*Nucifraga columbiana*) in CP #1 (Table 3). Third, overestimation errors should tend to be more frequent for more mobile species. In this regard, a number of subalpine species such as Clark's Nutcracker, Mountain Bluebird, and Pine Siskin, are extremely mobile and were often picked up by the VCPs in overhead flight. All three were overestimated in CP #1. It is interesting, in fact, to note that not a single species was overestimated in coastal scrub habitat while about one third of the species were overestimated in the subalpine forest habitat in each census period.

The tendency toward increased overestimation with increased mobility can perhaps be seen within a single subalpine species, Yellow-rumped Warbler. During CP #1, all females of this species were incubating eggs, and their mates sang persistently for long periods of time from very small areas, often from a single tree. This presents an ideal situation for estimating density by VCPs based on singing males. Interestingly, in CP #1, this species was *underestimated* by only 3.5%. In CP #2, all pairs were involved in feeding nestlings or young fledglings and would characteristically make frequent long flights from foraging areas in one part of the territory to the nest or fledglings which were often located on the other side of the territory. The male Yellow-rumped Warblers, however, continued to sing persistently during both of these periods and regularly sang from opposite sides of their territory only a few seconds apart. During CP #2, this species was *overestimated* by 29.3%.

The third and perhaps most serious potential errors of the VCP method are errors in distance estimation, particularly errors of distance underestimation. In fact, a 25% underestimate of distance will produce a 78% overestimate of density while a 25% overestimate of distance will produce only a 36% underestimate of density. Errors in distance estimation may be expected to increase as (a) distance markers become less visible, (b) the birds themselves become less visible, and (c) the birds become more ventriloqual. In this regard, the previous test of the VCP method in the California coastal scrub habitat (DeSante 1981) may have been conducted under nearly optimal conditions for accurate distance estimation. In the coastal scrub study, virtually the entire array of color coded grid markers (2-m-tall rebar 30 m apart) was visible from any VCP station. Furthermore, most individuals sang from exposed perches on top of the 1- to 2-m-tall coastal scrub so that they were easily visible and their locations and distances were exactly determinable.

In contrast, in the Sierran subalpine forest habitat, most grid markers (small rock cairns with approximately 60-cm-tall garden stakes 40 m apart) were generally invisible from any given VCP station. A single grid marker 40 m away could be seen from a few of the stations but never were more than two markers visible from any station. Furthermore, because of the dense three-dimensional nature of the habitat, individual birds could very rarely be seen even when singing persistently. Moreover, certain Sierran species, most notably Hermit Thrushes, had highly ventriloqual vocalizations so that it was virtually impossible to estimate distances correctly. It was a regular occurrence to have a singing Hermit Thrush "move" from 40 m to as much as 160 m away simply by changing his voice and turning his head. It is little wonder that the accuracy of the VCP method was less in the subalpine than in the coastal scrub.

A fourth potential error is that the calculation of VCP density could be based on the selection of an inappropriate basal radius. This could most easily be caused by sampling error in the frequency distribution of distances. Errors of this type would likely become more frequent and potentially more severe as the sample size decreases, that is, as the density decreases. The low densities of many subalpine species, as compared to the much higher densities of most coastal scrub species, could easily have increased the frequency of such errors. In particular, the extremely low total count (<10) of a number of rare species in both census periods makes the calculation of basal radius (and thus also of density and subsequent percent error) for these species somewhat suspect. The only way in which the VCP method can deal effectively with such rare species is if the sample size, that is, the number of stations or the number of times a station is censused, is greatly increased. For some of these rare species, the number of stations, and thus the total effort expended, would have to be increased by a factor of 5 to 10 or even greater. This, to some extent, is counterproductive to the basic purpose of VCP censusing—to obtain reasonably accurate estimates of density in remote or circumscribed areas with an efficiency of time and personnel. Clearly, the VCP method cannot be recommended for censusing such rare species.

Another factor in our experimental protocol that could have led to errors in the determination of basal radii is that we sampled our study plot with 12 permanent VCP stations rather than 12 floating VCP stations randomly chosen each census day from all possible grid points. In some cases the latter method might tend to provide improved coverage of the study plot and might also tend to minimize biases in determining the basal radii of less common species by allowing them to be detected at varying distances, that is, from various points, on subsequent censuses. This would be especially true for those less common species that tend to have relatively small effective detection distances. In fact, however, many of our study species had basal radii in the neighborhood of 100 m, roughly half the distance between our VCP stations, so that the entire study plot was very nearly effectively sampled by our 12 permanent stations. It seems doubtful that a protocol of floating VCP stations would have significantly increased the accuracy of the VCP method in our study plot, at least not for the common species nor for those with relatively large detection distances.

Of special interest is the fact that VCP total counts often performed nearly as well as the calculated VCP densities in ranking species or in determining relative abundances. This suggests that either (1) detectability did not vary much between species, or (2) there was so much "fuzz" because of distance estimation errors, etc., that basal areas were relatively meaningless. In either case, the VCP total count appeared to contribute more to the density estimate than did the measure of basal area. This should be encouraging to those wishing to utilize point-count data without distance estimations in order to obtain ordinal or relative abundance determinations.

Two additional points, however, must be mentioned in this regard. First, our total counts were derived from data taken with distance estimates. Because it is likely that some birds were missed in our total counts due to the concentration required to estimate the distances to the birds, it could be expected that total counts derived from data taken without distance estimates would produce slightly higher numbers especially for the more common species. Second, because our total counts included all birds encountered regardless of distance from the observer, it is likely that they included a few birds outside the study plot, especially for those VCP stations nearer to the edge of the study plot and for those species with larger effective detection distances. This potential source of error was virtually negligible with regard to VCP estimates of density because these estimates included only birds within the basal radius which, for most VCP stations and for most species, was well within the boundaries of the study plot.

In summary, potential errors in the VCP method may be expected to increase when and where (1) the population densities of the species decrease, (2) the territory sizes of the species increase, (3) the mobility and degree of ventriloqual vocalizations of the species increase, (4) the habitat becomes more three-dimensional and more dense thereby obscuring both the birds and any distance markers that are set out, and (5) the timing of the census period becomes increasingly later than the time when the majority of the birds are in the incubation phase of their nesting cycle. The first of these problems can presumably be made somewhat less severe by increased effort. The remaining problems, however, are intrinsically very difficult to overcome.

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