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A FIXED-RADIUS POINT COUNT METHOD FOR NONBREEDING AND BREEDING SEASON USE

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ABSTRACT.—We provide a detailed description of a fixed-radius point count method that carries fewer assumptions than most of the currently popular methods of estimating bird density and that can be used during both the nonbreeding and breeding seasons. The method results in three indices of bird abundance, any of which can be used to test for differences in community composition among sites, or for differences in the abundance of a given bird species among sites. These indices are (1) the mean number of detections within 25 m of the observer, (2) the frequency of detections within 25 m of the observer, and (3) the frequency of detections regardless of distance from the observer. The overall ranking of species abundances from a site is similar among the three indices, but discrepancies occur with either rare species that are highly detectable at great distances or common species that are repulsed by, or inconspicuous when near, the observer. We argue that differences in the behavior among species will preclude an accurate ranking of species by abundance through use of this or any other counting method in current use. *Received 3 September 1985, accepted 2 February 1986.*

DESPITE the fact that ratio counts are satisfactory for answering the majority of research questions involving bird counts (Verner 1985), the use of counting methods that result in an estimate of bird density (an absolute measure of number per unit area) has become entrenched. There is growing concern about the violation of numerous assumptions associated with attempts to estimate bird density, which brings the validity of results based on such measures into serious question (Ralph and Scott 1981). There is considerable need, therefore, for investigations into the usefulness of various indices of abundance (counts) that avoid at least some of the assumptions necessary to calculate density while still providing the information needed to answer most research questions.

One counting method that has received relatively little attention is the fixed-radius point count method. Verner (1985: 284), in fact, noted that he was unable to find any reference to use of this method in research. In this paper, we describe the mechanics of a fixed-radius counting method that is similar to, but differs in important respects from, the IPA and EFP point count methods (Blondel et al. 1981) and that can be used to generate data for either a density estimate or a relative index to abundance. Second, we describe the method of calculating three relative measures of species

abundance and discuss how one might test for statistical differences in species abundance among sites. We conclude with a sample application of the method using data from surveys of nonbreeding land-bird communities in Mexico, and compare the results of analyses involving each of the relative indices.

STUDY SITES

During January and February 1984 and 1985, we conducted point counts in each of 39 sites located between Durango and Oaxaca, western Mexico. The precise locations of most sites are not important in the present context, but two sites for which more detailed discussion or analyses follow were the pine-oak woodland within the La Michilía International Biosphere Reserve, located 45 km southwest of Vicente Guerrero, Durango (23°30'N, 104°15'W) and the tropical deciduous forest at the Universidad Nacional Autónoma de México Estación de Biología, located 10 km south of Chamela, Jalisco (19°30'N, 105°03'W).

The pine-oak woodland was dominated by *Quercus chihuahuensis*, *Pinus engelmannii*, and *Arbutus xalapensis*, with *Juniperus deppeana* and *Arctostaphylos pungens* present in the drier sites. Point counts in the woodland fell in one of two categories: "interior" count points surrounded by continuous, unbroken woods, and "edge" count points centered on abrupt woodland edges that were the result of clearings created by road cuts, agricultural fields, or grasslands. Moderate levels of cattle grazing and timber harvesting

were evident. The dominant plant genera in the tropical deciduous forest included *Lonchocarpus*, *Caesalpinia*, *Croton*, *Trichilia*, and *Serjania*. The site was undisturbed, except for 7 km of narrowly cut trails, along which we conducted our bird counts.

THE POINT COUNT METHOD

Data recording procedure.—At each point an observer recorded three kinds of data within a specified time period: (1) the number of individuals of each species detected within a 25-m radius surrounding the observer, (2) the abundance (one or greater than one) of individuals of each species detected beyond the 25-m radius but still within the habitat of interest, and (3) the identity of individuals detected while the observer walked between count points. The latter were recorded as present (+) but were not part of the count data used in subsequent analyses; these data merely contributed to the completeness of our species list for the site.

Birds that originally were detected outside the 25-m radius boundary but that later moved to within 25 m of the observer were recorded as occurring within the fixed-radius circle. On the assumption that all birds within 25 m were detected, this practice would facilitate comparisons among vegetatively different habitats. For example, a bird that first occurred at 50 m and moved to within 25 m during the count would be recorded in both an open and a densely vegetated habitat, even though detection beyond 25 m might have occurred only in the more open habitat.

Point count radius.—Bird densities based on point counts that differ in their fixed radii are not comparable, even though they can be converted to a common number per unit area. Detections that accumulate within a fixed radius during the count period are, in part, the result of birds moving to within the fixed radius, and this rate of accumulation is more likely to be proportional to the circle's circumference than to its area. The precise relationship is unknown, as is the proportion of "inside" detections that result from birds moving to within 25 m during the count. Because of such complexities, we feel the best solution is to select a single, fixed radius for all counts.

As the radius is decreased, the probability that all individuals will be detected increases but both the number of birds detected and, over a series of point counts, the frequency of bird detections decrease. Thus, the choice of a particular radius represents a compromise. The goal should be to use a radius as large as possible, but within which the detection of all bird species of interest can be reasonably assured, even in dense habitats. We chose a 25-m radius because we planned to compare bird abundances among very different habitat types (from open, desert scrub to tropical evergreen forest). This radius was probably too large to ensure 100% detectability within the

fixed area for the densely vegetated habitats and too small for the more open habitats, where we might have used a greater fixed radius and suffered no loss in detectability. The choice of a fixed radius does not represent a simple optimization problem because basal detectabilities are impossible to calculate accurately. Even if one knew the minimum detectabilities at various fixed radii, the optimal solution would vary from one observer to the next and would vary with the set of habitats under study. With no advance knowledge of either personnel or study sites, the radius had to be chosen subjectively on the basis of previous experience of the investigator and the presumed abilities of the observers. One could also select a radius on the basis of a preliminary plot of the number of detections against radial distance from the observer, but even then it would be difficult to determine that radial distance within which all birds were detected and across which there was no bird movement.

Count duration.—We recorded bird detections immediately upon arrival at the center of the count area and continued to record detections for 10 min. Birds that flushed from within the 25-m-radius circle upon the observer's arrival were recorded as "inside" detections. The approaching observer began, during the last 50 steps before arriving at the center of the counting area, to pinpoint the location from which an individual had flushed. The flushing point was then determined to have been within or outside 25 m after stopping at the count point. Reynolds et al. (1980) suggested waiting until after a 1-min "equilibration" period before recording detections, but this does not necessarily assure the return of birds that flush upon the observer's arrival, especially winter birds that roam continuously and widely.

Birds that were detected but unidentified before the end of the 10-min count period were pursued after the end of the count (if still visible or audible) for an identification. Birds newly discovered at this time were not recorded as part of the count, but were recorded in the same fashion as those discovered between counts (+). When a large flock moved to within 25 m of the observer before the end of the count, we remained stationary until the count period had ended and then took extra time to follow the flock until the flock composition was assessed accurately. In these instances, individuals detected during the count were recorded to have been either within 25 m (if we were confident that they were inside before the end of the count period) or outside 25 m; if the individual was detected only after the end of the count period, then it was recorded merely as present (+). At times it took 30–40 min to estimate accurately the membership of a flock; in fact, we found Gibb's (1960) statement that it takes an average of 1 min per bird to assess the composition of a flock to be quite accurate.

Location of count points.—At a particular study site

we began at a single point and selected a compass direction at random. We used that orientation for one person's route of travel. Additional straight-line routes in the same study area originated from the same point, but were oriented equidistantly throughout the remaining compass directions to provide as uniform a coverage of the available area as possible. One person on a given route generally completed 10 point counts in a day. In some cases, movement along a compass direction would have been extremely difficult, and we substituted nonoverlapping, narrow dirt roads or trails.

The distance between points should be such that the detections from different points remain statistically independent (Reynolds et al. 1980), but this distance represents a compromise between sample-size generation and independence of samples. We placed points at 200-m intervals because the nonoverlapping 100-m radius between adjacent points is beyond the limit of detectability for most small, nonsinging land-bird species (the majority of birds recorded in these counts). There will always be species (e.g. jays, woodpeckers, chachalacas) for which nothing less than separate canyons would be needed to ensure independence of samples, and results generated from those species must be given special consideration.

We also made sure that no count point was less than 200 m from the edge of the habitat type being considered. For some habitats (e.g. small agricultural fields, plantations, riparian areas) this was impossible to accomplish. In those special cases, we recorded detections beyond 25 m only if the bird was judged to be within the habitat of interest, thereby limiting the data available for comparison with other habitats to those from within the 25-m-radius circle.

Number of count points.—We conducted a minimum of 25 counts at any given study site. We never duplicated counts at a particular point and then recorded either the largest tally for each species (Webb et al. 1977, Blondel et al. 1981) or the mean values for each species (Reynolds et al. 1980). Such duplication merely extends the time at a given point and inflates the index of abundance, thus rendering comparisons between sites unjustified unless exactly the same number of repeats were conducted in each site or unless the unbalanced design is explicitly included in the analyses. One advantage of this counting method over others is that a large number of truly independent samples can be generated and analyzed statistically. Duplicate counts may be appropriate in some instances (e.g. to establish relationships between vegetation structure and bird use), but for studies where the goal is to generate indices of abundance for the species that use the habitat, repeat counts erode a major strength of the method because those repeat counts could have represented additional independent samples.

Time of day.—To minimize variance associated with

indices of abundance, censuses should be conducted at times when there will be little change in the conspicuousness of birds (Dawson 1981a). We generally began censusing an hour or so after sunrise and finished before 1100 in high-elevation forests and before 1030 in the warmer, low-elevation tropical and desert habitats. Bird detection rates were constant throughout this period (see Results).

Species of interest.—As with any community-wide land-bird census method, we recorded the presence of any land-bird species detected but restricted calculation of indices of abundance to a particular subset of all land-bird species. This subset included those species that were detected reliably through vocal or visual cues they emitted from the vegetation, where one's attention was primarily devoted, and those species whose home ranges were small enough that a reasonable number of independent detections could be assured. This eliminated diurnal raptors (except the American Kestrel, *Falco sparverius*) because of their wide-ranging habits, and nocturnal species (nightjars and owls) because of their cryptic habits. Swifts and swallows also were omitted because of the inconsistent and minor attention given the airspace above the forest, where these aerial feeders normally were detected.

Data evaluation procedure.—We derived three indices of abundance for each species: (1) the mean number of birds detected per 25-m-radius point count ($\times 100$), (2) the frequency of occurrence within a 25-m radius surrounding each count point [$f(25m)$], and (3) the frequency of occurrence within an unlimited radius surrounding each count point [$f(u)$].

Bird density (an absolute measure) often is calculated by converting the average number detected per sample into an average number detected per unit area. A ranking of species by density would be identical to a ranking based on the relative index from which the density was derived, but we believe such a conversion is misleading. Birds are mobile, and they move within detection range from unknown distances at varying intervals throughout the count period (see Granholm 1983). The effective area sampled is, therefore, unknown, and actual density *cannot* be calculated reliably. Fortunately, relative indices normally contain the information needed for comparisons among sites (Verner 1985).

We chose to test for community-wide differences among sites by using the log-linear model approach to analyzing three-way contingency tables [site by species by presence/absence based on either $f(25m)$ or $f(u)$ data; see Sokal and Rohlf 1981: 750]. The test effectively determines whether there is an effect of site on the association between species and their probabilities of occurrence.

Attaching significance to differences in the abundance of single species among sites can be accomplished through use of the nonparametric Mann-

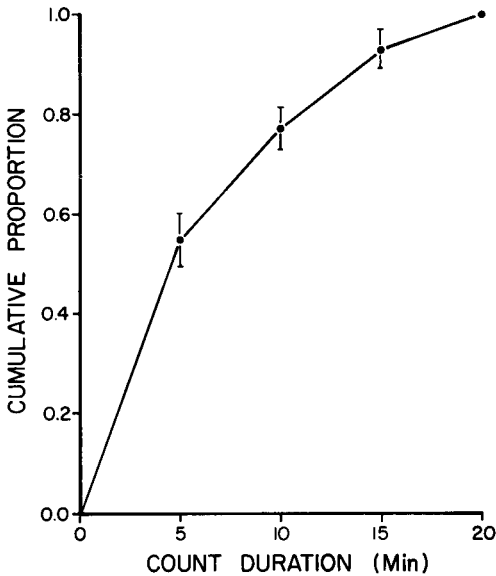


Fig. 1. Relationship between the proportion of the total number of bird species detected in 20 min and the duration of the point count. Data were derived from 10 20-min point counts conducted in the pine-oak woodland of La Michilía. Points indicate means, and bars represent ± 1 SE.

Whitney *U*-test (for a two-site comparison) or a Kruskal-Wallis one-way ANOVA (for a multiple-site comparison) using the mean numbers of detections per count. The frequency data can be analyzed using a model II $R \times C$ contingency test (Sokal and Rohlf 1981: 731-747). One can also determine, in a stepwise manner, the species whose frequencies of occurrence deviate most from expected frequencies generated by the three-way interaction log-linear model (using program BMDP4F, for example; Dixon 1981). The results will differ somewhat, however, from analyses that consider one species at a time because the expected frequencies in the latter case are based, in part, on the abundances of other species in the community. Dawson (1981b) provides further discussion of statistical analyses using relative indices.

RESULTS AND DISCUSSION

Census methodology.—The duration of the count period represents a compromise between recording all the birds that might eventually occur within the 25-m-radius circle and achieving a reasonable number of independent censuses. The accumulation of species must increase with time and becomes constant when all the species that use the area have been de-

tected. The gain rate of species in the pine-oak woodland of La Michilía in winter was such that after 10 min, we recorded about 75% of all species that we eventually detected in 20 min (Fig. 1). This percentage is nearly identical to that obtained during the breeding season by Hamel (1984), and is similar to what Scott and Ramsey (1981) reported for birds from two Hawaiian forests, where after 10-12 min they recorded 80% of the species that were eventually recorded in 32 min. No matter what the count duration (see Scott and Ramsey 1981 for additional discussion), it is important to realize that counts taken from within a single habitat type but based on unequal durations are not directly comparable because of the relationship between number of detections and time (Fig. 1). Similarly, because species accumulation rates may differ among habitat types, counts of equal duration from distinct habitat types also may not be comparable. The best solution might be to establish species gain-rate curves for each habitat under consideration (like that shown in Fig. 1) and then to use a count duration that achieves the same percentage of the projected species total for each habitat.

We found the suggestion by Morrison et al. (1981) that 4-6 stations are adequate for the complete census of an area to be unsatisfactory. Ten random selections of 5 point counts produced a mean of 42% of the species that were recorded in the entire sample of 104 point counts from the pine-oak at La Michilía. Similarly, 10 5-count samples from the tropical deciduous forest at Chamela produced a mean of 35% of the species that eventually were recorded after 118 point counts. An alternative suggestion that 28-30 stations give reasonable estimates of density and species richness (Reynolds et al. 1980, Blondel et al. 1981) is closer to our results; 25 counts produced an average of 86% of the species eventually recorded at La Michilía and 72% of those eventually recorded at Chamela. Hamel (1984) also detected 80% of the species after 36 (24%) of 150 variable-radius counts.

Analyses of both the mean number of species per count and the mean number of detections per count vs. time of day for the La Michilía and Chamela sites revealed that detection rates were constant throughout these count periods (Table 1).

Detections between points.—In data from the 39

TABLE 1. Mean number of individuals per 25-m-radius count, mean number of species per 25-m-radius count, and mean number of species per unlimited-radius count (Tot spp.) that were detected within several time-of-day categories at the La Michilía and Chamela study sites. Numbers in parentheses are standard errors. Counts from 1984 and 1985 were combined, and the fixed-radius data were log-transformed before conducting ANOVAs.

Time	La Michilía				Chamela			
	<i>n</i>	Individuals ^a	Species ^b	Tot spp. ^c	<i>n</i>	Individuals ^d	Species ^e	Tot spp. ^f
0730-0800	—	—	—	—	22	5.4 (1.2)	3.6 (0.6)	10.6 (0.8)
0800-0830	14	4.6 (1.7)	2.2 (0.5)	8.2 (0.9)	39	6.8 (1.1)	4.2 (0.5)	10.9 (0.5)
0830-0900	42	4.1 (1.0)	2.0 (0.3)	7.1 (0.5)	44	5.4 (0.6)	4.0 (0.4)	10.5 (0.4)
0900-0930	43	5.3 (1.0)	2.4 (0.3)	7.8 (0.5)	42	7.3 (1.1)	5.1 (0.6)	10.6 (0.6)
0930-1000	45	4.5 (0.9)	2.4 (0.4)	7.4 (0.5)	34	8.5 (1.3)	5.5 (0.7)	10.7 (0.6)
1000-1030	41	5.7 (1.4)	2.2 (0.4)	6.3 (0.5)	17	6.1 (1.2)	4.2 (0.8)	8.3 (0.8)
1030-1100	34	6.5 (2.2)	2.4 (0.6)	5.9 (0.6)	—	—	—	—
1100-	20	6.6 (2.8)	2.0 (0.6)	7.1 (0.8)	—	—	—	—

^a ANOVA, $F(6,232) = 0.37$, $P = 0.90$.

^b ANOVA, $F(6,232) = 0.51$, $P = 0.80$.

^c ANOVA, $F(6,232) = 1.69$, $P = 0.12$.

^d ANOVA, $F(5,192) = 0.96$, $P = 0.44$.

^e ANOVA, $F(5,192) = 1.11$, $P = 0.36$.

^f ANOVA, $F(5,192) = 1.73$, $P = 0.13$.

localities the proportion of bird species recorded only between count points averaged less than 0.03; thus, the point count method was effective in the production of a species list, even without between-point tallies. Dawson (1981c) and Hamel (1984) reported similar evaluations of point count methods. At La Michilía we never recorded a species between counts that was not also recorded on at least one count. Table 2, therefore, includes no species recorded as present (+) only. Two additional species, however, were recorded within the study area during field observations outside the morning census period: Wild Turkey (*Meleagris gallopavo*) and Orange-crowned Warbler (*Vermivora celata*).

Relative abundances of species.—The ranking of species by abundance with data from the unlimited-radius counts was correlated with the rankings using either of the other two indices. The combined interior and edge data from La Michilía (Table 2) gave $r = 0.77$ for mean number/count vs. $f(u)$, and $r = 0.82$ for $f(25m)$ vs. $f(u)$. Important discrepancies resulted from species that were detected relatively frequently beyond 25 m but rarely within 25 m. These species were either rare but highly vocal, or common but conspicuous only when at a considerable distance from the observer (i.e. they were shy or inconspicuous when near the observer). For example, in the La Michilía pine-

oak woodland edge, the extremely vocal Gray Silky-flycatcher (*Ptilogonys cinereus*) was not recorded commonly within 25 m (detected on 4% of the counts) and was ranked as one of the rarer species (Table 2). In contrast, it was almost always recorded when the radius was unlimited (70% of the counts) and was the most abundant species according to the $f(u)$ index. More dramatically, the Lilac-crowned Parrot (*Amazona finschi*) was detected within 25 m on only 1% of the 118 point counts conducted at Chamela, but was detected beyond 25 m on 59% of the counts. Similar discrepancies exist with the data from pigeons, doves, woodpeckers, jays, and other species that produce frequent, long-range vocalizations and are otherwise either rare, or common but repulsed by an observer's presence. These kinds of species were detected relatively frequently beyond 25 m, and the ratio of "beyond 25 m" detections to "total" detections (the detection ratio) was relatively large (Table 2). Statistics that depend on an accurate ranking of relative species abundances (such as diversity indices), therefore, should not be used in connection with data derived from high-detection-ratio species because it is difficult to know whether the high detection ratios are a result of inflated $f(u)$ values due to the species' vocal behavior, or due to low $f(25m)$ values resulting from repulsion or shyness when near the observer. The latter problem is common to

TABLE 2. Relative indices of bird abundance from point counts conducted in the pine-oak woodland of La Michilia during January 1984.

Species	Woodland interior (n = 57)			Woodland edge (n = 47)			All sites (n = 1,650)
	Mean ^a	f(25m) ^b	f(u) ^c	Mean ^a	f(25m) ^b	f(u) ^c	Detection ratio ^d
<i>Falco sparverius</i>	0.0	0.00	0.00	4.3	0.04	0.13	0.86 (66)
<i>Columba fasciata</i>	7.0	0.04	0.44	17.0	0.06	0.55	0.90 (101)
<i>Zenaidura macroura</i>	0.0	0.00	0.00	0.0	0.00	0.02	0.77 (57)
<i>Selasphorus platycercus</i>	0.0	0.00	0.00	2.1	0.02	0.04	0.56 (16)
<i>Eugenes fulgens</i>	0.0	0.00	0.00	2.1	0.02	0.02	0.19 (54)
Unidentified hummingbird sp.	8.8	0.09	0.12	2.1	0.02	0.02	0.37 (313)
<i>Melanerpes formicivorus</i>	10.5	0.09	0.35	25.5	0.17	0.57	0.80 (258)
<i>Trogon elegans</i>	0.0	0.00	0.00	0.0	0.00	0.04	0.81 (75)
<i>Sphyrapicus varius</i>	0.0	0.00	0.00	6.4	0.06	0.06	0.48 (29)
<i>Picoides villosus</i>	3.5	0.04	0.11	6.4	0.06	0.17	0.62 (73)
<i>Picoides stricklandi</i>	1.8	0.02	0.02	0.0	0.00	0.00	0.54 (123)
<i>Colaptes auratus</i>	3.5	0.04	0.39	4.2	0.04	0.64	0.92 (324)
<i>Lepidocolaptes leucogaster</i>	1.8	0.02	0.02	0.0	0.00	0.00	0.67 (94)
<i>Mitrephanes phaeocercus</i>	1.8	0.02	0.02	0.0	0.00	0.00	0.66 (89)
<i>Empidonax affinis</i>	0.0	0.00	0.10	4.3	0.04	0.04	0.39 (28)
<i>Cyanocitta stelleri</i>	0.0	0.00	0.25	38.3	0.19	0.53	0.82 (200)
<i>Aphelocoma ultramarina</i>	42.1	0.04	0.32	42.6	0.11	0.30	0.86 (200)
<i>Corvus corax</i>	1.8	0.02	0.61	2.1	0.02	0.40	0.97 (149)
<i>Parus sclateri</i>	42.1	0.21	0.33	46.8	0.28	0.34	0.41 (208)
<i>Parus wollweberi</i>	29.8	0.12	0.18	8.5	0.02	0.06	0.47 (55)
<i>Psaltriparus minimus</i>	8.8	0.02	0.02	0.0	0.00	0.02	0.44 (55)
<i>Sitta carolinensis</i>	38.6	0.21	0.56	25.5	0.15	0.60	0.75 (263)
<i>Sitta pygmaea</i>	7.0	0.02	0.02	0.0	0.00	0.00	0.59 (78)
<i>Certhia americana</i>	3.5	0.02	0.04	8.5	0.04	0.06	0.47 (151)
<i>Thryomanes bewickii</i>	0.0	0.00	0.00	4.3	0.04	0.04	0.40 (5)
<i>Troglodytes aedon</i>	0.0	0.00	0.00	10.6	0.11	0.15	0.43 (116)
<i>Regulus calendula</i>	57.9	0.42	0.49	57.4	0.45	0.53	0.28 (505)
<i>Sialia mexicana</i>	7.0	0.02	0.32	40.4	0.13	0.38	0.85 (143)
<i>Catharus guttatus</i>	7.0	0.05	0.07	2.1	0.02	0.02	0.26 (58)
<i>Turdus migratorius</i>	17.5	0.14	0.56	25.5	0.19	0.64	0.77 (274)
<i>Myadestes townsendi</i>	0.0	0.00	0.00	0.0	0.00	0.02	— (1)
<i>Ptilogonys cinereus</i>	43.9	0.12	0.84	8.5	0.04	0.70	0.88 (234)
<i>Phainopepla nitens</i>	7.0	0.04	0.12	8.5	0.04	0.17	0.68 (40)
<i>Vireo solitarius</i>	5.3	0.04	0.05	0.0	0.00	0.00	0.16 (79)
<i>Vireo huttoni</i>	15.8	0.14	0.23	2.1	0.02	0.09	0.40 (132)
<i>Peucedramus taeniatus</i>	0.0	0.00	0.02	0.0	0.00	0.00	0.59 (218)
<i>Dendroica coronata</i>	1.8	0.02	0.04	4.3	0.04	0.04	0.45 (322)
<i>Dendroica nigrescens</i>	3.5	0.04	0.05	0.0	0.00	0.00	0.16 (110)
<i>Myioborus pictus</i>	3.5	0.04	0.07	2.1	0.02	0.09	0.62 (136)
<i>Euphonia elegantissima</i>	17.5	0.02	0.02	0.0	0.00	0.00	0.56 (9)
<i>Piranga flava</i>	0.0	0.00	0.02	0.0	0.00	0.00	0.42 (89)
<i>Pipilo erythrophthalmus</i>	3.5	0.02	0.02	14.9	0.06	0.09	0.55 (76)
<i>Pipilo fuscus</i>	0.0	0.00	0.00	36.2	0.21	0.23	0.33 (30)
<i>Oriturus superciliosus</i>	0.0	0.00	0.00	21.3	0.04	0.04	0.39 (31)
<i>Spizella passerina</i>	5.3	0.04	0.04	80.9	0.11	0.15	0.41 (44)
<i>Junco phaeonotus</i>	33.3	0.19	0.28	276.6	0.62	0.66	0.35 (237)
<i>Carpodacus mexicanus</i>	0.0	0.00	0.04	0.0	0.00	0.09	0.81 (36)
<i>Carduelis pinus</i>	0.0	0.00	0.04	0.0	0.00	0.00	0.79 (53)
<i>Coccothraustes vespertinus</i>	0.0	0.00	0.02	0.0	0.00	0.00	0.60 (5)

^a Mean number of individuals per 25-m-radius point count ($\times 100$).

^b The proportion of 25-m-radius counts within which the species was detected.

^c The proportion of unlimited-radius counts within which the species was detected.

^d The number of point counts at which a given species was recorded only beyond the 25-m radius divided by the total number of counts (n) at which the species was recorded, whether within or beyond 25 m. The sample for each species (given in parentheses) was taken from among 1,650 counts and 39 sites scattered throughout western Mexico in 1984 and 1985.

all methods and is not widely appreciated. The influence of an observer on the movement of birds is one of the most devastating factors affecting attempts to calculate community-wide relative densities. Many large birds, raptors, and shy understory birds simply avoid detection. Therefore, their density and biomass will always be underestimated relative to other species when derived from a single method of counting. This makes such calculations highly suspect. Even relative abundances derived from spot mapping are biased in this way because species with relatively few detections are less likely to have the minimum number of registrations needed to identify a cluster and, consequently, the number of territories will be underestimated.

A community-wide analysis.—We conducted 57 and 47 counts in the La Michilía pine-oak interior and edge communities, respectively. A total of 38 species was detected in each of the two communities, and each had 11 species not recorded within the other community type (Table 2). The two communities were statistically different in their species compositions as determined from three-way contingency analyses [f(25m): $G = 109.4$, $df = 40$, $P < 0.01$; f(u): $G = 138.0$, $df = 48$, $P < 0.01$]. Although the overall result was the same for each analysis, the unlimited-radius count data were certainly non-independent for some species.

The species that deviated most strongly from expected frequencies generated by the three-way log-linear models were [for f(25m) counts] Hutton's Vireo (*Vireo huttoni*), Bridled Titmouse (*Parus wollweberi*), Gray Silky-flycatcher, and [for f(u) counts] Brown Towhee (*Pipilo fuscus*), House Wren (*Troglodytes aedon*), and Yellow-eyed Junco (*Junco phaeonotus*). Clearly, the species that contributed most to the community-wide difference depended upon whether fixed-radius or unlimited-radius data were used for the analysis. The absolute abundances of the same species listed above may not differ significantly between community types on the basis of single-species analyses (see below) because community-wide analyses detect significant differences between communities in the relative as well as absolute abundance of species.

Single-species analyses.—A species-by-species comparison of the La Michilía interior and edge communities produced similar results based on either the mean number per count or the f(25m)

statistic. The frequencies of occurrence differed significantly for the Steller's Jay (*Cyanocitta stelleri*), House Wren, Brown Towhee, and Yellow-eyed Junco, while the mean numbers per count differed for the same 4 species plus Western Bluebird (*Sialia mexicana*) and Hutton's Vireo (Table 3).

The results from these two fixed-radius indices were similar to, but differed in important respects from, the results of analysis using the unlimited-radius data. Although there were only three discrepancies between results from the unlimited-radius and the fixed-radius measures in terms of statistical significance (American Kestrel; Acorn Woodpecker, *Melanerpes formicivorus*; and Northern Flicker, *Colaptes auratus*), for three additional species there was a 3-fold difference in the probability levels associated with the two indices (Gray-breasted Jay, *Aphelocoma ultramarina*; Common Raven, *Corvus corax*; and Western Bluebird) (Table 3). The abundances of 2 of the 6 species (Gray-breasted Jay and Western Bluebird) were more similar between woodland interior and edge according to the unlimited-radius indices of abundance than according to the fixed-radius indices, whereas the abundances of the remaining 4 species (American Kestrel, Acorn Woodpecker, Northern Flicker, and Common Raven) were more similar according to the fixed-radius indices (Table 3). Each of the 6 species was characterized by a relatively high detection ratio (of the 49 species listed in Table 2, all 6 species had detection ratios that rank among the top 10). Individuals of these species were either relatively inconspicuous when close to the observer or relatively conspicuous when distant. The simplest explanation for differences of this magnitude is that the frequencies of detection within 25 m were so low that the statistical analyses produced results that were unreliable and substantially different from the results based on f(u) data. Whatever the proper explanation, it is important to appreciate that in the case of high-detection-ratio species, unlimited-radius data may be more reliable than data from the fixed-width samples, despite the lack of complete independence among f(u) samples. Unlimited-radius samples therefore may prove indispensable not only for generating more complete species lists, but also for detecting differences in the abundances of these high-detection-ratio species.

TABLE 3. Probability levels (*P*-values) associated with the species-by-species tests for differences in bird abundances between interior and edge counts at La Michilia.

Species	Relative index		
	Mean ^a	f(25m) ^b	f(u) ^b
<i>Falco sparverius</i>	0.12	0.39	0.02
<i>Columba fasciata</i>	0.49	0.82	0.33
<i>Zenaida macroura</i>	—	—	0.92
<i>Selasphorus platycercus</i>	0.27	0.92	0.39
<i>Eugenes fulgens</i>	0.27	0.93	0.92
Unidentified hummingbird sp.	0.15	0.31	0.12
<i>Melanerpes formicivorus</i>	0.19	0.33	0.04
<i>Trogon elegans</i>	—	—	0.39
<i>Sphyrapicus varius</i>	0.05	0.18	0.18
<i>Picoides villosus</i>	0.50	0.82	0.50
<i>Picoides stricklandi</i>	0.36	1.00	1.00
<i>Colaptes auratus</i>	0.84	1.00	0.04
<i>Lepidocolaptes leucogaster</i>	0.36	1.00	1.00
<i>Mitrephanes phaeocercus</i>	0.36	1.00	1.00
<i>Empidonax affinis</i>	0.12	0.39	0.60
<i>Cyanocitta stelleri</i>	0.00	0.00	0.01
<i>Aphelocoma ultramarina</i>	0.17	0.29	1.00
<i>Corvus corax</i>	0.89	1.00	0.05
<i>Parus sclateri</i>	0.52	0.58	1.00
<i>Parus wollweberi</i>	0.06	0.12	0.16
<i>Psaltriparus minimus</i>	0.36	1.00	1.00
<i>Sitta carolinensis</i>	0.40	0.58	0.88
<i>Sitta pygmaea</i>	0.36	1.00	1.00
<i>Certhia americana</i>	0.45	0.87	0.82
<i>Thryomanes bewickii</i>	0.12	0.39	0.39
<i>Troglodytes aedon</i>	0.01	0.04	0.01
<i>Regulus calendula</i>	0.84	0.95	0.83
<i>Sialia mexicana</i>	0.03	0.07	0.61
<i>Catharus guttatus</i>	0.41	0.75	0.48
<i>Turdus migratorius</i>	0.51	0.66	0.55
<i>Myadestes townsendi</i>	—	—	0.92
<i>Ptilononyx cinereus</i>	0.15	0.27	0.14
<i>Phainopepla nitens</i>	0.84	1.00	0.69
<i>Vireo solitarius</i>	0.20	0.56	0.31
<i>Vireo huttoni</i>	0.03	0.07	0.09
<i>Peucedramus taeniatus</i>	—	—	1.00
<i>Dendroica coronata</i>	0.45	0.87	1.00
<i>Dendroica nigrescens</i>	0.20	0.56	0.31
<i>Myioborus pictus</i>	0.68	1.00	1.00
<i>Euphonia elegantissima</i>	0.36	1.00	1.00
<i>Piranga flava</i>	—	—	1.00
<i>Pipilo erythrophthalmus</i>	0.22	0.48	0.25
<i>Pipilo fuscus</i>	0.00	0.00	0.00
<i>Oriturus superciliosus</i>	0.12	0.39	0.39
<i>Spizella passerina</i>	0.13	0.29	0.10
<i>Junco phaeonotus</i>	0.00	0.00	0.00
<i>Carpodacus mexicanus</i>	—	—	0.51
<i>Carduelis pinus</i>	—	—	0.56
<i>Coccothraustes vespertinus</i>	—	—	1.00

^a *P*-values based on Mann-Whitney *U*-tests.

^b *P*-values based on Chi-square tests (with Yates' correction).

Comparative evaluation.—There is strong reason to believe that data derived from the variable-width line transect (Emlen 1971) and the variable-radius circular plot (Reynolds et al. 1980) methods cannot be converted into reliable absolute density estimates. This holds because the distance to detected birds cannot be estimated accurately on the basis of aural cues alone (the majority of detections in both summer and winter) (Dawson 1981c, Richards 1981, Scott et al. 1981, Hamel 1984); because detectability profiles do not represent accurately a bird's probability of detection at a given distance from randomly placed transects or points (Conant et al. 1981, Hutto and Mosconi 1981); because the number of detections needed to generate an interpretable profile is greater than is collected for the majority of species; and because it is often impossible to obtain an accurate count of birds within large flocks, especially when they occur at some distance from the observer. Moreover, if these considerations are coupled with the fact that censuses involve a finite period of time during which individuals move into detection range from an unknown distance (Granholm 1983), the error of converting numbers detected into a number per unit area (density) becomes even more apparent.

Although these problems may be avoided by using the point count method, some additional problems persist. These are best understood if we imagine finding that the mean number per count or the frequency of occurrence of species *X* differs significantly between two sites. This could result from sampling error due to low sample sizes, differences in species detectability among sites, differences in the area censused among sites, differences in behavior, or actual bird-density differences between sites.

Sampling error can be minimized by ensuring that at least 30 counts are conducted in each site. There will always be species too rare to circumvent this problem, but 25–30 counts should be adequate as a minimum. The proportion of species with relatively few detections is certainly no worse than the proportion of species for which meaningful detectability profiles can be drawn for use with the popular variable-distance counting methods. Area and detectability differences can be minimized by ensuring that the same area is censused in both locations, and that the area is one in which the

detectability of all birds is uniformly high. We have tried to achieve this goal in our winter studies through the use of fixed-radius (25 m) plots. Behavioral differences might be a particularly important problem if mean flock size differed between two sites, because rate of flock movement is positively correlated with flock size (Morse 1970, Buskirk et al. 1972). The effect of such a difference can be reduced by minimizing the time spent at a sample point. A 20-min sample period, which is characteristic of the IPA and EFP methods, would be less desirable than 10-min samples on this basis, and on the basis of other considerations (Dawson 1981a). The effects of detectability and behavioral differences also could be minimized by using count durations in each site that achieve a fixed (say, 80%) sample of the projected total for that habitat.

The fixed-radius point count method we have described is not without problems, but we believe the problems are fewer and less severe than those associated with the currently popular methods. Relative indices such as the one we describe are excellent not only for determining broad, continental, or regional patterns of bird species distribution (Wiens and Rotenberry 1981), but for reliable measures in local studies as well.

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