

POPULATION DENSITIES OF BIRDS DERIVED FROM TRANSECT COUNTS

JOHN T. EMLÉN

Good estimates of absolute population density as distinct from indices of relative abundance have been virtually unavailable for nonflocking land birds except in the breeding season when singing males, representing mated pairs, restrict themselves to more or less fixed territories where they or their nests can be counted. The lack of efficient and reasonably accurate census methods applicable at any season has seriously hampered the progress of quantitative studies of avian population ecology.

This paper, after reviewing the potentialities and limitations of currently available methods, describes a new method that is, 1) applicable at all seasons, 2) more efficient in terms of area covered per unit of effort than the nest or territory count methods, and 3) comparable in accuracy. The method uses the lateral distribution pattern of all detection points for each species to derive coefficients of detectability with which trail counts may be converted directly to density values in units of birds per 100 acres.

The method was developed over a period of 3 years while the author was gathering data on the ecological distribution of birds in mesquite grasslands in southern Texas, pine forests in Florida and the Bahamas, and mixed woodlands in Wisconsin and Michigan.

AVAILABLE METHODS

Direct counts of birds in circumscribed and measured areas can often be used effectively on flocking species and various nonflocking birds living in exposed situations, but direct and complete enumeration over an area is impossible for the many nonflocking land birds dispersed through the obscuring vegetation of woodlands, fields, and marshes. Simple tallies of individuals detected per unit of effort under closely standardized conditions are valuable as indices from year to year and are relatively easy to obtain (Kendeigh, 1944). Censuses of absolute density, necessary for determinations of biomass and energy functions, require controlled measurements of area as well as population.

Six currently available census methods, plus the new one described in this report, are listed and characterized in Figure 1 and Table 1. In the first of these (A) a fraction of the resident population of a selected tract is captured, marked, and released, then balanced against the coexisting unmarked population in a subsequent tally or tallies. The ratio of marked to total among the observed birds in this tally should equal the ratio of the total number of birds marked to the total number in the population.

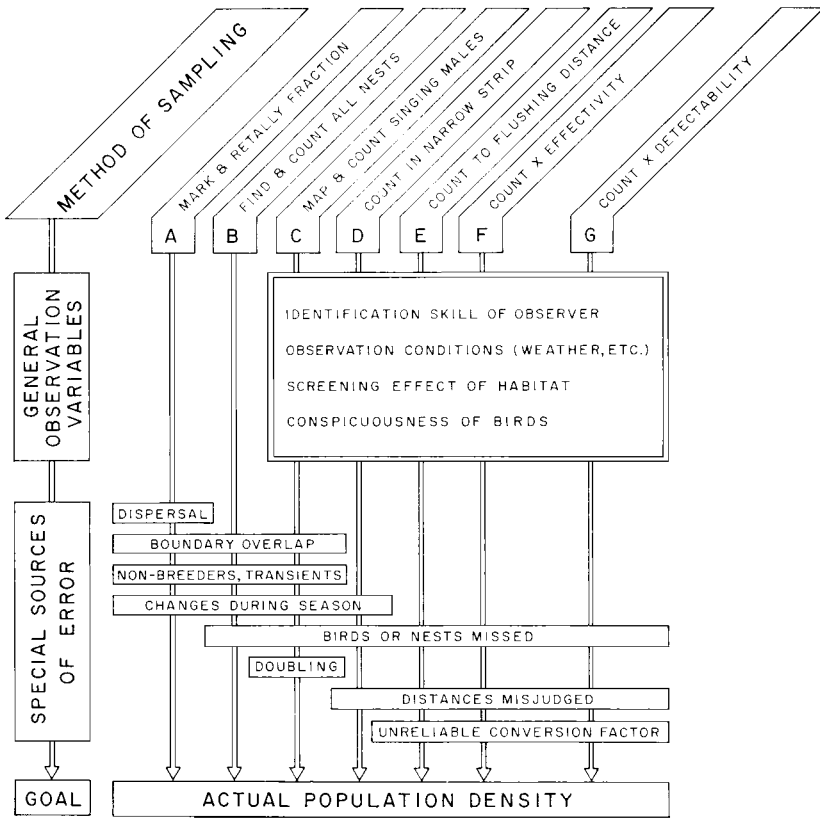


Figure 1. Factors limiting the accuracy and efficiency of census methods for non-flocking terrestrial birds.

In the next four methods (B, C, D, and E) control depends on achieving complete enumeration on small measured plots or narrow strips along a trail. The problem of accounting for each of the elusive residents of the plot is resolved in B by substituting nests for the birds themselves. In C the population indicators are singing territorial males; song perch positions are spotted on maps, and clusters of such positions on composite maps are considered to represent individual territorial males (Williams, 1936; Williamson, 1964). For translation to population density values, each nest (in B) or singing male (in C) may be regarded as roughly equivalent to one pair of resident birds.

Complete coverage of all birds is directly attempted in method D, the count of detections being restricted to a narrow strip of designated width (and area) along the transect trail (Merikallio, 1946, 1958) or to appro-

TABLE 1
CHARACTERISTICS AND EVALUATIONS OF CENSUS METHODS FOR NONFLOCKING TERRESTRIAL BIRDS

	A	B	C	D	E	F	G
Characteristics	Mark portion and tally ratio	Map nests	Map territories	Count in fixed strip	Count to flushing distance	Count \times effectivity	Count \times detectability
Areal unit	Plot	Plot	Plot	Strip (fixed)	Strip = 2 flushing distances	Strip (indef.)	Strip (wide)
Tally unit	Marked obs.: total observation	Nests	Singing males	Max. count for each species	Total count	Singing males	Total count
Conversion	Marked population: tally	$\times 2$ (for ♀ ♀)	$\times 2$ (for ♀ ♀)	(None)	(None)	Divided by effectivity $\times 2$ for ♀ ♀	Divided by C.D.
Subjective evaluations							
Seasonal applicability	Summer-winter	Summer	Summer	All	All	Summer	All
Acres/3 man-hours ¹	10	10	50	100	50	300	300
Replications needed ¹	10	5	10	7	3	3	3
Total man-hours ¹	40	15	35	21	9	9	9
Efficiency (acres/hour)	0.25	0.7	1.4	4.9	5.6	33.0	33.0

¹ Estimated.

priate strip widths assigned to the various species on the basis of characteristic detection distances (Kendeigh, 1956). Adjustments for the inevitable incompleteness of single transects may be made by adopting the largest tally for each species in a series of seven or more transect replications, a process called summation by its inventor (Palmgren, 1930). Again, singing males may be interpreted as roughly equivalent to one pair of resident birds.

In method E all birds are tallied as encountered and their distances from the observer at detection are recorded. The effective size of the census area is then defined in terms of the positions of the recorded birds by adopting the mean distance from the observer as one half the width of the census strip. This method was developed by R. King for game birds that crouch and flush (Leopold, 1933; Hayne, 1949) but has been used in an exploratory way on song birds (Stewart et al., 1952).

In the sixth method (F) and the new method (G) control rests on the degree of completeness of coverage in wide strips. In F completeness is evaluated by reference to observer performance levels on tracts intensively censused for complete coverage by a restricted plot method such as the count of singing territorial males (method C) (Colquhoun, 1940a; Howell, 1951; Enemar, 1959), or by noting the incidence of occurrence of particular individuals in a series of traverses over a transect route (Seierstad et al., 1965). The per cent of completeness indicated for a species by this test is referred to as its *effectivity* (Enemar, 1959). In method G, completeness of coverage is calculated directly for each species from the characteristic distribution pattern of detection points laterally from the census trail and the implications of this distribution for overall detectability within a wide strip (described in the next section of this paper).

All methods have their complications and limitations. With the exception of the first two (A and B), all are beset with confusing observational variables (central block in Figure 1) associated with 1) the experience, acuity, attentiveness, and speed of advance of the observer; 2) the observation conditions related to weather, time of day, etc.; 3) the screening effect of the habitat; and 4) the conspicuousness of the birds as related to their noisiness, movements, size, and color. The first two of these factors are essentially independent variables, best controlled by restricting field work to well-qualified observers and prescribed observation conditions. Graded adjustments for suboptimum conditions, e.g. afternoon hours or cold wet weather, could conceivably provide an alternative to rigid standardization in the second factor. The screening effect of the habitat relates primarily to vegetation density and cannot be controlled by standardization of procedure without seriously restricting the scope of operations. Vegetation type and density should be described and measured on each census tract and the data incorporated as a part of the survey record. It may eventually be

possible to devise a scale of screening values for the various vegetation types (see Table 3). Conspicuousness of the bird varies markedly from species to species and probably reflects distinctive species-characteristic attributes in each case. Each species must therefore be dealt with as a separate entity. The conspicuousness of a species may, of course, vary considerably with seasonal changes in activity and, in some cases, with sex. But such variations should be predictable, and with the accumulation of data a characteristic value or set of values should be assignable to each species. Several workers (Colquhoun, 1940b; Stewart et al., 1952; Enemar, 1959; Williamson, 1964) have recognized this principle and made preliminary moves to establish "coefficients of conspicuousness" for common species.

The first three methods (A, B, and C) when carefully carried out provide relatively good control of the general observational variables described above and may, under favorable conditions, offer relatively high levels of accuracy. Method A poses the difficult requirements that the marked and unmarked components of the population must be equally trappable or observable in the retally procedures, and that no ingress or egress into or from the study plot can occur during the study period. The nest and territory mapping methods, B and C, suffer in efficiency (area covered per man hours of work, Table 1) when conducted intensively, or in accuracy when applied less intensively in open situations (Snow, 1966). The small size of plots necessitated by the excessive time involved in intensive coverage raises further problems of evaluating the inclusion of a large proportion of fractional, boundary-line territories.

Completeness, the criterion of accuracy in B, C, D, and E, is at best an elusive target. Singing males, the critical unit of measurement for methods C, D, and F, change drastically and often quite abruptly in their conspicuousness (song frequency) and local distribution as the breeding season advances. Large numbers of repeat runs are therefore necessary; runs must be spread over many weeks to catch the singing period of all species and individuals, yet concentrated enough to permit valid interpretations of the distribution of recorded song perches in terms of individual territories. After the data are in, the problem of translating the number of singing males or nests to the ultimate population value of birds per unit of area remains, complicated by variables associated with song intensity (Colquhoun, 1940b), nonbreeding resident males, transients, polygamy, irregular movement of individuals across territory boundaries, and large territories only partially incorporated in the tract. The use of maximum counts (summation procedure) in the fixed-strip transect method (D) introduces the possibility of serious error from temporary movements of boundary-line birds into the relatively narrow census strip.

A further disadvantage of the intensive plot methods (B and C) and the

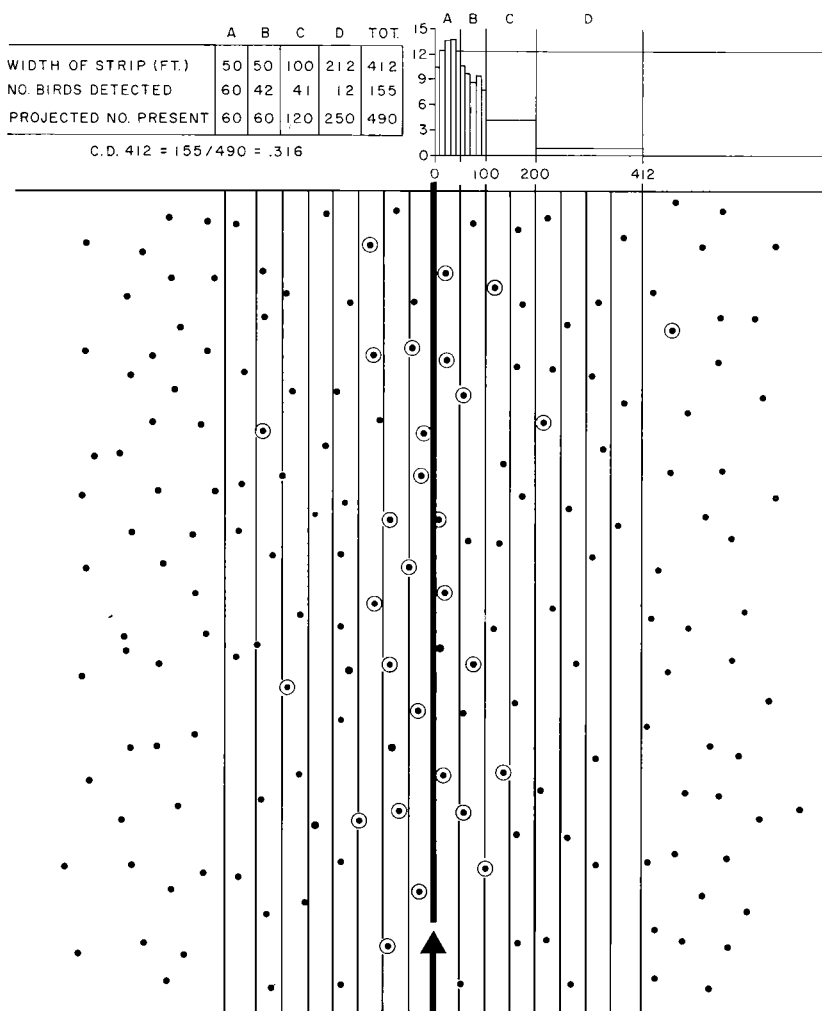


Figure 2. Schematic model of a stand of vegetation with randomly scattered birds (dots) bisected by a transect route (median line). Dots representing birds that are detected by eye or ear are encircled in the model. Lines parallel with the transect route at 50-foot intervals define strips of coverage. Hypothetical counts of birds on a 2-mile traverse of the transect are tabulated and graphed for each strip or substrip at the top right of the figure. A horizontal line at the top of the graph extrapolates the level of the mean of the first five 10-foot substrips (12 birds) horizontally to a boundary line at 412 feet. Assuming complete coverage in these basal substrips, and random distribution of birds, the area below this line represents the population of a 2-mile segment of the 824-foot band (200 acres). This area (total projected population of 490 birds) divided into the area of the columns (155 birds detected) gives the per cent of birds within the band that are detected, i.e. the coefficient of detectability for

dependent strip survey method (F) is their restricted applicability to a few months during the breeding season. Densities of transient populations during migration seasons and of mixed populations of residents and migrants during the winter are therefore entirely beyond the reach of these approaches. The strip transect methods D, E, and G escape this restriction by shifting from fixed indicators of sedentary birds to simple tallies of all birds regardless of their residence status. The critical controls in these latter methods, replacing the segregation and enumeration of distinct individual birds, is the determination of distances from observer to bird, needed for recognizing and rejecting outsiders in D, for establishing the functional strip boundaries in E, and as the basis for evaluating species detectability in G. Instrumental measurements are not feasible in practice, but skills equivalent to a good 6-inch range finder can, in the author's experience, be quickly acquired. An examination of the analysis near the bottom of Figure 1 suggests that the gross of procedural errors inherent in these strip methods is probably no greater than those inherent in the intensive plot methods.

DESCRIPTION OF THE NEW METHOD

The new method, briefly introduced above, involves the determination for each species of a detectability value (or values) hereafter termed the *coefficient of detectability* (C.D.) of the species, and the application of this value to the mean count for the species in a traverse or series of traverses through a census tract.

Coefficients of detectability.—Coefficients of detectability represent the proportion of the population of an area that is ordinarily detected by an observer running a transect. It is a direct reflection of the theoretical "effective radius of the organism" in Yapp's (1956) model of interactions between an observer and the birds along a transect line. Each species appears to have its characteristic C.D. value, varying within limits and in a predictable manner with the seasons and the type of vegetation.

The C.D. value for a population of birds within sight or hearing of a transect route depends on two variables: 1) the distance of the individual birds from the route and 2), their absolute detectability, independent of distance. In the procedures described below, corrections for the first variable are made by applying a *lateral distance conversion* to the count, and for the latter by applying a *basal detectability adjustment*.

Lateral distance conversion.—The lateral distance conversion factor for a species may be determined directly from data on the linear distribution

←

the birds of this stand ($155/490 = 0.316$ in this hypothetical sample). Hypothetical counts of birds on a 2-mile traverse of the transect are tabulated and graphed for each strip or substrip at the top of the figure.

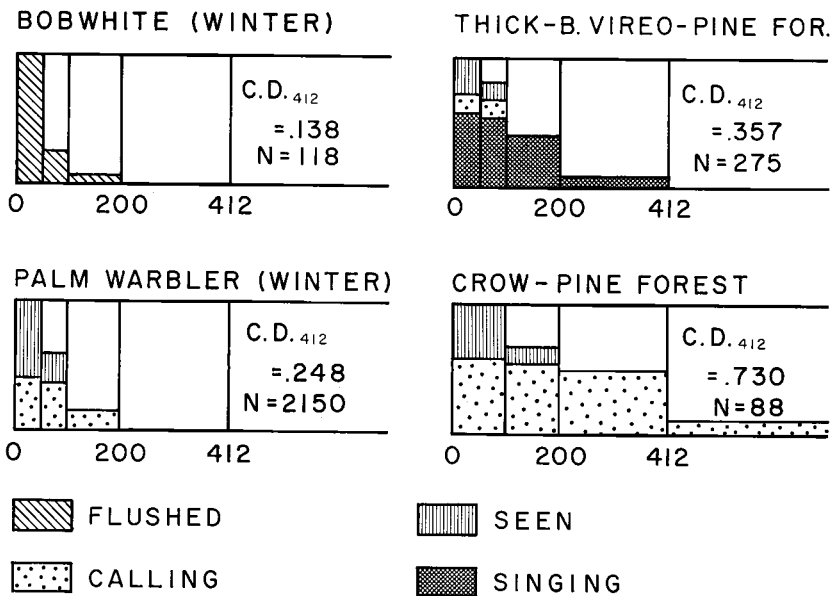


Figure 3. Types and distribution of detections laterally from the transect route in four representative populations. The value for the basal (proximal) strip is plotted as 100 (full column height) in each case, and values for the distal strips are represented proportionately. The Bobwhite sample is of a nonsinging (wintering) population in which the birds were generally detected by flushing at close range; very few detections are made beyond 100-feet laterally, and C.D. values are therefore low. The Palm Warbler sample is of a nonsinging wintering population; tallies beyond 100 feet were nearly all auditory detections of call notes; none were detected beyond 200 feet. The Thick-billed Vireo population on Grand Bahama represents a resident breeding species with a moderately loud song carrying through the forest vegetation for 200 to 300 feet. The Crow sample represents a situation in which visual detection falls off in the first 100 to 200 feet while auditory detection extends laterally for 1000 feet or more producing a high C.D. value.

of detection points laterally from the transect route. The rationale of this procedure is, perhaps, best understood by visualizing a field (the stand) (Figure 2) with randomly scattered objects (the birds) slowly traversed by a recording sensor (the observer) scanning a swathe or band (the area of coverage along the survey route). The objects in this model irregularly emit visual and auditory signals of varying intensity, and the field is irregularly conductive for the signals. The sensor thus detects only a fraction of the signals, the proportion being high close to the route and decreasing laterally.

Plotting the frequency of detection values for successive parallel strips on

either side of the route, a distribution curve is obtained as shown in the graph at the top of Figure 2. In most species this curve maintains a high level for from 40–100 feet, then declines rather precipitously, and finally levels off to approach zero at the limit of detectability of the species. Forms of the curve for representative species are shown in Figure 3.

If we assume for the moment that all birds are detected in the few proximal strips, coefficients of detectability may be derived from these lateral distribution curves by the following steps:

1. Determine the height of the basal plateau by averaging the number of birds counted in each of the 10-foot strips proximal to the point of inflexion of the curve.
2. Extrapolate this plateau level horizontally to a prescribed lateral boundary line defining the limits of the census band (see below).
3. Divide the total count of birds within this boundary by the projected number below the horizontal extrapolation line. The basis for this procedure is that if the count in the proximal strips approaches completeness, it will, when extended to the boundary, represent the projected count of the entire band. The value obtained is the per cent of the total population of the species within the band that is detected, i.e. the coefficient of detectability.

A finite limit must obviously be set to the lateral extension of the survey band but there is no ultimate reason why this limit cannot be remote enough to include all detections. Since, for most species, detections beyond 300 or 400 feet rarely contribute more than an insignificant portion of the total count, however, a more manageable boundary line can be considered. For most species in the studies performed to date an arbitrary cutoff point at 412 feet was adopted, far enough to include nearly all of the visual and auditory observations, yet near enough to be realistic in terms of stand limits. The value, 412 (126 meters), was chosen because a band of this width along either side of a trail and 1 mile in length incorporates just 100 acres, a convenient and widely used base in population density studies. Similarly a lateral boundary distance of 125 meters (410 feet) would incorporate just 100 hectares in 4 km of transect. For loud-voiced species that are commonly detected beyond 412 feet (e.g. flickers, crows, jays, wrens, Mockingbirds) a base of 825 or even 1,650 feet is preferable giving values in terms of individuals per 200 or 400 acres for each mile of transect. For small stands C.D. values for any species may be based on the portion of the lateral distance curve lying proximal to the point representing the mean distance from trail to boundary line (Figure 4).

The translation of a transect count for a given species into a population estimate is effected by dividing the count by the appropriate C.D. value of

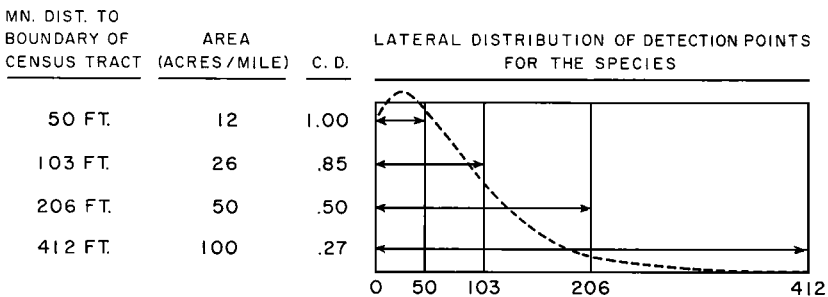


Figure 4. Area and C.D. values for census tracts of various widths for a hypothetical lateral distribution curve of the wintering Palm Warbler type.

the species. Thus, if 40 Palm Warblers are tallied along 5 miles of transect through a Florida pine-palmetto forest in mid-February, and a C.D. 412 value of 0.25 has been established for this species in many miles of winter surveys through similar habitat, the derived estimate per mile, and hence per 100 acres, would be $\frac{40/5}{0.25} = 32$ birds.

Lateral distance patterns of detections and C.D. values may change with the seasons and particularly with the advent of the breeding season when males advertise their presence loudly though intermittently with song, and females retire to obscurity on their nests. At such times song and non-song detections should be tallied and plotted separately. The basal plateau of the lateral distance curve will obviously extend considerably farther from the trail with song detections, producing higher detectability rates and lower population estimates (Table 2). As these tallies and the derived estimates will be restricted to the male element of the population, they should be multiplied by two (assuming an equal sex ratio). Theoretically an estimate of males based on the song detection plateau should match a directly obtained estimate of the total population based on the nonsong detection plateau, but female inconspicuousness at these times may produce serious incompleteness in the latter. In practice, I determine both values when males are singing and adopt the larger of the two as the best estimate. Samples of this method are presented in Table 6, column 3.

Basal detectability adjustment.—The population estimates derived by the procedures described above will obviously be low in proportion to the incompleteness of detections in the relatively narrow strip used to establish the basal plateau of the lateral distribution curve. Where birds are awake and active very few will be missed in at least the proximal 10 to 20 feet of this strip, and as the plotting of detection points characteristically

TABLE 2
LATERAL DISTRIBUTION OF DETECTIONS AND DERIVED VALUES IN A THEORETICAL
POPULATION OF 90 BIRDS (45 MALES AND 45 FEMALES) BEFORE
AND AFTER THE ONSET OF SINGING BY THE MALES

	To 50'	To 100'	To 200'	To 400'	Total	Width of pla- teau	Total to pla- teau	Proj. to 412'	Est. popl.	C.D.	Adj. needed
Winter											
All det.	10	6	1	0	17	50	10	82	82	0.21	1.1
Spring											
Songs only ¹	4	4	7	3	18	200	15	30	60	0.60	1.5
All det. ²	9	4	7	3	23	50	9	75	75	0.31	1.2
All det. ³	5	4	7	3	19	50	5	41	41	0.46	2.2

¹ In this example females are not recorded and the projected population of males is incomplete because of nonsinging individuals. The coefficient of detectability is for males only.

² In this example females are detectable though total detectability is slightly less than in winter. The plateau width is based on nonsong detections though all detections are recorded.

³ This example represents the situations in which females are largely undetectable while males remain conspicuous through movements, call notes, and song.

reveals a plateau out to 50 or more feet, the expected level of completeness will be high. But where birds are intermittently inactive, or where the observer is obliged to depend on the singing of males, a wide base for projection is required, within which a sizeable fraction of the population will not be emitting detectable signals while the observer is within range. Under these conditions many individuals will be bypassed, and a substantial adjustment for incompleteness will be indicated.

The magnitude of adjustments for incompleteness in the basal strip of optimum coverage may be estimated by comparing the converted values for a 412-foot transect strip with population values obtained in the same area by other census methods. As no adequate census method has been developed, our only recourse is to apply several methods concurrently to the same population and compare the results. This has been done on two areas (Table 5). The data in this table, preliminary observations on three more areas, and a few observations from the literature suggest that adjustments for counts of wintering birds should rarely exceed $\times 1.1$ or $\times 1.2$ (Table 2). Breeding bird populations, particularly because of the inactivity of the females and the intermittent singing of the males, require adjustments ranging from $\times 1.1$ to $\times 2.5$ with an average of perhaps about $\times 1.5$.

Pooling data for sample size.—C.D. values should obviously be obtained under conditions closely resembling those of the transect count to be translated, and ideally all the data for the conversion should be recorded in the same area and at the same time as the count. In the tests described in this report, lateral distance measurements were, in fact, tallied concurrently with the records of occurrence, and the values applied directly—the projected basal plateau directly defining the population value.

Results from the best represented species of this study strongly suggest that with the accumulation of records, each species will be found to have one or a few characteristic lateral distribution patterns, and hence C.D. values, accurate within the rather broad limits of acceptability, and applicable over a considerable range of habitats and seasons. As already indicated, basal detectability adjustments for incompleteness may also be species- and season-characteristic. Such broadly based values would theoretically be preferable to those obtained from any single cluster of surveys, since the latter are bound to vary meaninglessly from week to week and site to site because of small sample size. Furthermore if we can establish and adopt a broadly based C.D. value for a species, it will be unnecessary to run large numbers of counts in each census tract; all that will be needed is enough miles of transect, perhaps 10, or even 5, to provide a reasonably reliable mean of detections per mile (birds per 100 acres). Greater confidence can be placed on such a density value than on one based on a statistically inadequate though situationally correct conversion factor.

C.D. values at monthly intervals from several localities are currently being assembled for selected species to test the authenticity of the concept of species-characteristic C.D. values and the variance to be expected. In the meantime figures for well-represented species should be based on means drawn from all available data and, for poorly represented species, on interpolations of values obtained for ecologically and behaviorally similar species.

FIELD PROCEDURES

About 300 C.D. surveys have been conducted by the author in the past 3 years, and about 15,000 detections have been tallied and plotted for lateral distance distribution curves. The field procedures used in these tests are briefly summarized below. They apply equally to the collection of lateral distance data and to transect tallies. In fact, the two operations were combined in all surveys to date.

Sites were selected for stand size (at least 50 acres except in a few special cases) and for general uniformity of physiography and vegetation. Transect routes bisected the survey stands in fairly straight lines at various angles, but existing trails were used where available to reduce distractions caused by obstacles and to provide clear base lines from which to estimate lateral distances. Crisscrossing of routes and repeated traverses were used to obtain adequate samplings in small tracts. Vegetation rows inducing linear distribution patterns of birds, as along bushy fence lines or broad roadways, were crossed at right angles rather than followed.

I did not start to tally data until I had become familiar with the stand and with the field marks and call notes of the local birds (on Grand

Bahama). Where birds could not be identified quickly they were not counted. I invariably worked alone in order to reduce distractions from the job in hand.

Progress along the route was on foot and essentially continuous, alternating between slow walking and brief pauses to look and listen. Long stops were avoided to reduce the danger of double recordings, and birds ahead of the advancing observer were not tallied until he had approached to within 100 feet of their position along the trail. Net speeds averaged between $\frac{1}{2}$ and $1\frac{1}{2}$ mph in woodland and between 1 and 2 mph in open country. Interruptions to observe items of special interest were postponed until the formal survey was completed. Detection points were defined as those where a bird was first seen or heard; birds that entered the survey tract after initial detection were not counted. Contrary to a common recommendation for bird-counting operations, squeaking and pishing sounds were used to lure hidden birds into view. Efforts were made to record the lateral distance of the first response of a lured bird, the point of origin rather than the point of identification, and although the effectiveness of the sounds waned when they were used repeatedly on a trail (Emlen, 1969), no correlated change in the pattern of lateral distributions (hence C.D. values) was detected. The slightly higher counts obtained on the first few days of a series as a result of squeaking had only a minor effect on the mean of all counts along the route.

Surveys were made only on days with favorable weather conditions, were started within $\frac{1}{2}$ hour after sunrise, and extended for about 2 hours. Every natural means of detection, visual and auditory, was used and the type of detection recorded with each observation. The location of unseen singing or calling birds was approximated after careful scanning or maneuvering. Lateral distances (at right angles to the route of progress) were estimated in 10-foot intervals to 100 feet, then a single interval from 100 to 200 feet (recorded as +), another from 200 to 400 (412) feet (recorded as ++) and another beyond 412 feet (recorded as +++). After an initial period of self-training with a range finder, I found it best to carry no more than a series of mental references to familiar linear situations, and to check these repeatedly by pacing. Estimates of distances greater than 100 feet were more difficult than short distances, but also less critical for determining C.D. values.

SOME PRELIMINARY RESULTS

A few generalizations and preliminary deductions can be drawn from the field tests run to date. The method appears to be applicable to most non-flocking, temperate zone doves, cuckoos, hummingbirds, woodpeckers, and passerines. It is poorly suited for wide-ranging water birds, shorebirds, and

TABLE 3
ATTENUATION OF DETECTABILITY IN PINE FORESTS WITH A MODERATE UNDERSTORY
ON GRAND BAHAMA ISLAND¹

Detection type	0-50'	50'-100'	100'-200'	200'+	N
All visible detections	73	23	3	1	877
Birds flushed	92	8	0	0	50
Birds seen moving	72	24	3	1	784
Still perching	59	31	10	0	43
All auditory detections	35	29	29	7	2108
Birds calling	48	36	15	1	1029
Birds singing	21	24	41	13	1060
Other sounds	79	16	5	0	19
All detections	46	27	22	5	2985

¹ Incidence of each type of visual and auditory detection is shown in four unequal distance intervals from the trail. Figures represent per cent within each type for all species combined.

hawks, for nocturnal birds, for treetop birds in tall dense forests, and for swifts and swallows that cruise about above the vegetation. Flocking species present special problems and ordinarily are best handled by direct counting within each flock.

Among the species that meet the basic requirements of the method, some create special problems by sneaking away or, on the other hand, by approaching the census taker. The roadrunner exemplifies the former group, and hummingbirds often demonstrate the latter trait. Also many birds close to the trail, in addition to those actually flushed, are probably aroused to vocalize or move, and thus to enhance their detectability. Compensating or even overcompensating for this effect is a tendency for birds of many species to retreat laterally from the line projected ahead of the observer as he advances. Breckenridge (1935) noted this phenomenon, and in the present study counts were commonly higher in the 20-29 and 30-39 foot strips than in the 0-9 and 10-19 foot strips along the trail (top of Figure 2). Bias arising from these behaviors is presumably nullified or at least minimized by averaging the counts out to 50 feet or more in determining the basal plateau level of a lateral distribution curve.

It is too early to attempt to assign general C.D. values or to analyze the seasonal and habitat variations for any species as such, but data are available for a few species in certain regions that seem to show characteristic and suggestive patterns. In these birds, values to the 412-foot lateral distance (C.D. 412) ranged from 0.09 to 0.89. Low values indicating less than 20 per cent coverage were obtained for nonsinging ground feeders that characteristically remained undetected until flushed at close range (wintering Bobwhite Quail, Savannah Sparrows, and Ovenbirds), quiet species frequenting dense brush (nonsinging Song Sparrows and Yellowthroats), and small quiet arboreal and subarboreal birds (Kinglets and Brown Creeper

TABLE 4
C.D. VALUES¹ IN FIVE HABITAT TYPES ON GRAND BAHAMA ISLAND
JANUARY-MARCH 1969

Vegetation type (% cover-high shrubs)	Miles traversed	C.D. 412 (mean)
Dense high thickets (70-90%)	5.3	0.14
Pines with high shrubs (50-60%)	4.8	0.17
Pines with sparse high shrubs (10-20%)	9.1	0.19
Pines with only low shrubs (none)	8.1	0.30
Open pines with low shrubs (none)	12.8	0.25

¹ All species combined.

in the fall and most wintering warblers). Highest values indicating greater than 50 per cent detection to the 412-foot line were produced by large noisy arboreal birds (certain woodpeckers, crows, and jays in winter) and breeding birds with loud clear songs (Cardinal, Carolina Wren, Mockingbird, etc.). These noisy birds may best be evaluated to the 825- or even the 1,650-foot line so that all detections are included.

Except in a few cases sample sizes are still inadequate to permit tests of variance in single populations or to evaluate seasonal or regional variations within a species. In the wintering population of Palm Warblers on Grand Bahama ($N = 2430$) six monthly values (January through March 1968 and 1969) ranged from 0.196 to 0.240 and showed a mean and standard deviation of 0.219 ± 0.015 . During these same 6 months Gnatcatchers on Grand Bahama ($N = 321$) showed a C.D. 412 mean value and standard deviation of 0.197 ± 0.029 . Winter and early spring values for the Pine Warbler on Grand Bahama and the Red-bellied Woodpecker in Florida were 0.311 ± 0.059 ($N = 336$) and 0.560 ± 0.054 ($N = 142$) respectively.

Sample sizes are still too small to evaluate the seasonal changes within

TABLE 5
COEFFICIENTS OF DETECTABILITY (C.D. 412) FOR BREEDING BIRD SPECIES
IN NORTHERN MINNESOTA AND NORTHERN MICHIGAN

	Northern Minnesota ¹ (1955-SCK)	Northern Michigan ² (1969-JTE)
Great Crested Flycatcher	0.93 (5) ³	0.80 (23) ³
Least Flycatcher	0.36 (73)	0.52 (13)
Eastern Wood Pewee	0.46 (35)	0.51 (65)
Red-eyed Vireo	0.52 (73)	0.42 (65)
Ovenbird	0.58 (28)	0.55 (73)
Scarlet Tanager	0.47 (10)	0.56 (14)
Rose-breasted Grosbeak	0.47 (14)	0.60 (7)

¹ Kendeigh (1956).

² This study.

³ Values in parentheses are number of birds recorded.

TABLE 6
COMPARISON OF BREEDING POPULATION ESTIMATES (BIRDS PER 100 ACRES)
OBTAINED BY THREE METHODS¹

	Method C mapping (terr. × 2)	Method D sum- mation (max. count) ²	Method G C.D. conversion		Indicated adjustment for incom- pleteness (col. 1/ col. 3) ⁴
			(all de- tections)	(songs × 2) ³	
Grand Bahama pine forest:					
Ground Dove	11	12.8	—	7.6	1.4
Zenaida Dove	9	4.8	6.2	—	1.4
Cuban Emerald Hummingbird	29	19.4	44.1	—	0.7
Hairy Woodpecker	6	16.9	6.4	—	0.9
Greater Antillean Pewee	14	12.9	8.4	—	1.7
Loggerhead Flycatcher	0.6	2.4	0.2	—	—
Stolid Flycatcher	3	9.6	—	3.5	0.9
Blue-Gray Gnatcatcher	31	16.9	21.4	—	1.4
Red-legged Thrush	4	9.6	4.1	—	—
Bahaman Yellowthroat	17	19.4	16.9	—	1.0
Thick-billed Vireo	34	44.0	—	29.0	1.2
Olive-capped Warbler	14	19.5	15.5	—	0.9
Yellow-throated Warbler	11	14.3	9.8	—	1.1
Pine Warbler	14	22.0	16.9	—	0.8
Bananaquit	29	22.0	21.2	—	1.4
Striped-headed Tanager	40	34.0	41.2	—	1.0
Black faced Grassquit	11	12.0	8.4	—	1.3
TOTAL (17 species)	278	292.3	263		1.06
Michigan deciduous forest:					
Mourning Dove	2	1.2	—	0.8	—
Black-billed Cuckoo	1	0	—	0.2	—
Hairy Woodpecker	2	1.2	0.3	—	—
Eastern Kingbird	2	2.4	—	0.5	—
Great Crested Flycatcher	6	7.3	—	3.8	—
Least Flycatcher	2	4.8	—	4.1	—
Eastern Wood Pewee	20	22.0	—	16.5	1.2
Blue Jay	6	2.2	4.1	—	—
Common Crow	2	0	—	—	—
Black-capped Chickadee	4	1.2	0.3	—	—
White-breasted Nuthatch	1	1.2	0.1	—	—
Red-breasted Nuthatch	1	1.2	0.3	—	—
Brown Thrasher	2	0	—	0.6	—
Robin	4	6.0	2.8	—	—
Hermit Thrush	3	7.2	—	2.8	—
Veery	8	9.7	4.0	—	—
Cedar Waxwing	6	2.4	1.9	—	—
Red-eyed Vireo	20	25.4	—	17.7	1.1
Black-and-white Warbler	1	2.4	—	0.3	—
Black-throated Green Warbler	1	2.4	0.6	—	—
Pine Warbler	3	2.4	—	0.6	—

¹ Data were taken on two census tracts: a 35-acre stand of pineland on Grand Bahama Island, surveyed on 7 mornings between 15 and 23 April 1969, and a 49-acre stand of aspen, oak, etc. in northern Michigan, surveyed on 8 mornings between 10 and 14 June 1969.

² In method D the number of singing males within 200 feet of the trail was doubled and added to the number of nonsong detections, then multiplied by 2 to conform to the strip width of method G.

³ In method G the highest of the two derived values was adopted as explained in the text.

⁴ In column 4 the values obtained by method G are related to those obtained by method C. There is no final reference for completeness.

TABLE 6 (Continued)

	Method C mapping (terr. × 2)	Method D sum- mation (max. count) ²	Method G C.D. conversion		Indicated adjustment for incom- pleteness (col. 1/ col. 3) ⁴
			(all de- tections)	(songs × 2) ³	
Michigan deciduous forest:					
Myrtle Warbler	4	3.6	1.6	—	—
Ovenbird	22	24.0	—	17.7	1.2
Brown-headed Cowbird	10	11.0	—	4.1	2.4
Scarlet Tanager	6	4.8	—	2.5	—
Rose-breasted Grosbeak	6	4.8	—	1.3	—
Indigo Bunting	2	4.8	—	2.2	—
American Goldfinch	3	1.2	0.3	—	—
Vesper Sparrow	4	7.2	—	1.0	—
Chipping Sparrow	6	4.8	—	1.9	—
TOTAL (30 species)	160	173.8	95		1.69

any species, but in the Bobwhite Quail and Mockingbird, C.D. 412 values roughly doubled with the advent of the singing season. Ovenbirds on their breeding grounds in Michigan had C.D. values about four times those derived from nonsinging birds on their wintering grounds in Florida and Grand Bahama.

Foliage, particularly in the tall shrub stratum (eye and ear level of the observer) rapidly attenuates the detection of bird sounds and movements laterally from the transect route. Birds that can readily be detected aurally to 400 feet or more in an open situation may be undetectable at 200 feet in dense high brush. In a sample of lateral distance data from the Grand Bahama pine forests (Table 3) visual detectability for all species together in the second 50-foot strip was about 30 per cent of that in the basal 50 feet, and then dropped to about 2 per cent beyond the 100-foot line. Auditory detectability in the same sample declined to 83 per cent beyond 50 feet and to 41 per cent beyond 100 feet, but for singing alone there was no appreciable decline inside the 200-foot line. In a comparison of results from various forest types on Grand Bahama, overall C.D. values (all species combined) were about twice as high in open pine forests with low palmetto shrubs as in dense, high shrub thickets (Table 4).

To date no other ornithologists have followed my field procedures over the same or similar routes to test for interobserver variability, but a useful comparison can be drawn from data presented by Kendeigh (1956) on the frequency of detection points at various distances from his survey trail in northern Minnesota. C.D. values derived from these data correspond reasonably well with values I obtained for the same species in northern Michigan in 1969 (Table 5).

Direct tests of the accuracy of the C.D. conversion method are not possible as there is no known way to obtain a complete and accurate census of nonflocking land birds as a reference. Howell (1951) and Enemar (1959) placed great reliance in the territory mapping method (C in Figure 1) in deriving their effectivity values for transect counts. After conducting several such territory mapping surveys, noting the wide-range of interpretations that can be extracted from composite maps of song perches, and evaluating the problems of nonbreeders, transients, large partially incorporated territories, etc., I do not have sufficient faith in the method to accept it as a final reference. I have, however, made direct comparisons of the territory mapping method, the maximum count in a fixed strip (summation) method, and the C.D. conversion method (C, D, and G in Figure 1) in a pineland stand on Grand Bahama and in a deciduous forest in northern Michigan (Table 6). Although I relate the values obtained by the C.D. method to those obtained by territory mapping, I am inclined to think that the former is more sensitive and balanced for most of the uncommon species and perhaps more "foolproof" for most of the abundant species in which territories are contiguous. This does not mean that adjustments for completeness are not needed. With appropriate adjustments the final values will apparently resemble those obtained directly by territory mapping in general order of magnitude.

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SUMMARY

Census methods for nonflocking land birds are reviewed and a new method is described that is applicable at all seasons, is more efficient than the intensive plot methods, and is apparently comparable in accuracy. In the new method foot transect counts are made in which all detections, visual and aural, out to the limit of detectability are tallied. The count for each species is then multiplied by a conversion factor (coefficient of detectability) representing the per cent of the population that is normally detected by these procedures. Conversion values are derived directly from distribution curves of detection points laterally from the observer's trail. Conversion values are finally adjusted for incompleteness in the strip of optimum coverage close to the transect trail. Field procedures used in testing the

new method are described and samples of preliminary results are presented and evaluated.

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Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706. Accepted 6 April 1970.

Appendix. Scientific names of birds referred to in text and tables

Bobwhite	<i>Colinus virginianus</i>
Mourning Dove	<i>Zenaidura macroura</i>
Zenaida Dove	<i>Zenaida aurita</i>
Ground Dove	<i>Columbigallina passerina</i>
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>
Cuban Emerald Hummingbird	<i>Chlorostilbon ricordii</i>
Hairy Woodpecker	<i>Dendrocopos villosus</i>
Loggerhead Flycatcher	<i>Tyrannus caudifasciatus</i>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>
Stolid Flycatcher	<i>Myiarchus stolidus</i>
Least Flycatcher	<i>Empidonax minimus</i>
Eastern Wood Pewee	<i>Contopus virens</i>
Greater Antillean Pewee	<i>Contopus caribaeus</i>
Blue Jay	<i>Cyanocitta cristata</i>
Common Crow	<i>Corvus brachyrhynchos</i>
Black-capped Chickadee	<i>Parus atricapillus</i>
White-breasted Nuthatch	<i>Sitta carolinensis</i>
Red-breasted Nuthatch	<i>Sitta canadensis</i>
Brown Thrasher	<i>Toxostoma rufum</i>
Robin	<i>Turdus migratorius</i>
Red-legged Thrush	<i>Mimocichla plumbea</i>
Hermit Thrush	<i>Hylocichla guttata</i>
Veery	<i>Hylocichla fuscescens</i>
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
Cedar Waxwing	<i>Bombycilla cedrorum</i>
Bananaquit	<i>Coereba flaveola</i>
Thick-billed Vireo	<i>Vireo crassirostris</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Black-and-white Warbler	<i>Mniotilta varia</i>
Myrtle Warbler	<i>Dendroica coronata</i>
Black-throated Green Warbler	<i>Dendroica virens</i>
Yellow-throated Warbler	<i>Dendroica dominica</i>
Olive-capped Warbler	<i>Dendroica pityophila</i>
Palm Warbler	<i>Dendroica palmarum</i>
Pine Warbler	<i>Dendroica pinus</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Yellowthroat	<i>Geothlypis trichas</i>
Bahaman Yellowthroat	<i>Geothlypis rostrata</i>
Brown-headed Cowbird	<i>Molothrus ater</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Striped-headed Tanager	<i>Spindalis zena</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Indigo Bunting	<i>Passerina cyanea</i>
American Goldfinch	<i>Spinus tristis</i>
Black-faced Grassquit	<i>Tiaris bicolor</i>
Vesper Sparrow	<i>Poocetes gramineus</i>
Chipping Sparrow	<i>Spizella passerina</i>