ESTIMATING BREEDING SEASON BIRD DENSITIES FROM TRANSECT COUNTS

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ABSTRACT.—In this paper I propose that for each species in an area the number of birds detected along a transect trail can be translated into an estimate of absolute density (birds per unit of area) by counting all the detectable (cue-producing) birds in a trailside strip narrow enough to permit detection of all cues produced (the specific census strip), and adjusting this count for the undetectable (silent) birds in the strip by applying a locally and concurrently derived index of the frequency of cue production for the species. Cue frequency is apparently impossible to measure in nonbreeding birds, but if all cues (sightings, calls, etc.) are used, most of the birds in the strip presumably will be detected when the observer advances slowly enough to allow each bird a good chance to make its presence known. In the nonbreeding season the strip width is set for each species at the distance from the trail at which total cue detection starts to decline. In the breeding season cue frequency may be determined for song cues, and strip widths for each species set at a convenient distance within the relatively great distance at which song detection starts to decline. Values obtained by these transect procedures reflect the density of each species at the time the traverse is run; a series of traverses may be made to provide mean values for selected periods through the season.

The method is similar to that described in an earlier paper. New or modified procedures are described for recording detections, establishing specific strip widths, bypassing the calculation of "coefficients of detectability," estimating distances in the field, determining an optimum rate of progress, and measuring the frequency of singing in a representative sample of the population.

Problems of converting adjusted transect counts of singing males to total population density and of applying a combination of all-cue and song-cue procedures to mixed populations of breeding and nonbreeding species are discussed.

A comparison of transect and plot map census methods is presented. In the transect method density estimates are of birds present at a particular time rather than of birds wholly or partially resident at one time or another during a season. The sampling quadrats of transect censuses are elongate rectangles spanning extensive tracts of habitat rather than truncated blocks of representative habitat. The transect method is applicable at any season while the plot map method can be used only during the breeding season when birds are singing on territories. Problems of reliability in the plot map method stemming from individual movements during a survey period and from questions on how to interpret clusters of observation points on territory maps and how to evaluate boundary line territories are replaced in the transect method by problems of accuracy in assuming complete coverage in the all-cue operations and in assigning birds as inside or outside the lateral boundary lines of the census strips. More area can be covered per unit of time in the transect than in the mapping method.—*Department of Zoology, The University of Wisconsin, Madison, Wisconsin 53706.* Accepted 3 November 1975.

THE PROBLEM AND THE MODEL

THE principal access to absolute density values (birds per unit of area) for land birds has been the spot-map method (Williams 1936, Robbins 1970). While reasonably satisfactory for many purposes, spot-mapping procedures are applicable only during the breeding season and on fairly small tracts. Success in estimating absolute densities in large areas has recently been achieved by coordinating absolute data from small mapped plots with relative data from extensive transect counts (Enemar and Sjostrand 1967, 1970), and in 1971 I described a method for translating counts of bird detections along a transect route to absolute density values by applying correction factors for each species based on the distribution of detection points laterally from the transect trail (Emlen 1971). Järvinen and Väisänen (1975) also used the principle of declining detectability with distance, applying three theoretical regres-

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sion curves to the extensive narrow and broad belt census data of Merikallio (1946, 1958) and others on Finnish bird populations.

There is no test of accuracy for my 1971 distance attenuation method, but results appear to be reasonably satisfactory in the nonbreeding season when most birds close to the trailside provide sound or visual cues as the observer passes. It is quite unsatisfactory during the breeding season, however, when many individuals, notably nesting females, remain silent and essentially undetectable even at close range. This paper is concerned primarily with breeding season census problems but reviews various aspects of nonbreeding season transect procedures.

The relation between the number of cues tallied along a transect trail and the absolute density of birds that number represents appears to rest on two variables, both of which can be controlled or measured in many situations: (1) cue attenuation with lateral distance from the trail and (2) the frequency with which birds produce visual or auditory cues detectable by an observer at any range. This paper reexamines and revises the procedures for attenuation control described in my 1971 paper, outlines procedures for measuring cue frequency, and discusses methods for coordinating the two procedures in various situations. It also compares the characteristics, applicability, basic assumptions, advantages, and weaknesses of the transect and the traditional plot-map census methods. The appendix presents some results of preliminary field tests made in Wisconsin using the two methods.

Cue attenuation.—My basic procedure for controlling the attenuation of sound cues and visual cues with distance is to determine for each species the strip width along the trail within which a fully alert observer will detect essentially all cues that are produced. In my 1971 paper I projected the density within this strip to an outer boundary line and used the ratio of the actual count inside that boundary line to the projected total over many miles of transect as a coefficient of detectability for the species. The count within the strip can be used directly as a specific census strip, and this procedure has the advantage of being locality and period specific. In either case distances perpendicular to the trail on either side are estimated for each bird as it is detected, and tallied as dots or other symbols on survey sheets in columns representing narrow strips of terrain paralleling the trail. The symbols in these columns are totaled for each species at the end of a survey or series of surveys, and the accumulated data are plotted as a regression curve with the transect trail serving as the base. Curves typically show fairly level basal plateaus out to from 30 to 200 feet (9–60 m), depending on the species, before declining rapidly or gradually to zero at the limits of detection.

On the assumption that (1) I miss relatively few cues in the proximal strips immediately adjacent to the trail, and (2) the plateau form of the curve indicates that there is no appreciable additional loss in detection out to the inflection point of the curve, I adopt the inflection point or some convenient point within it on either side of the trail as marking the lateral boundaries of the specific census strip for the species. These lateral boundary lines and the ends of the transect route define the areal base for the density function as well as delimiting the area in which cues can be accepted for density determinations. Specific census strips are thus elongate quadrats within which cue detection approaches completeness. They must not be confused with the areas used in the flushing distance method of King (Leopold 1933, Hayne 1949) in which the estimated distances are along radii emanating forward and laterally from the advancing observer.

In addition to applying the specific census strip directly in place of the derived coefficient of detectability I have made several innovations or modifications of procedure since presenting the transect census model in 1971: (1) To meet the problem of obtaining adequate samples for an uncommon species I may arbitrarily group the available data with those for one or more common species displaying similar cue-attenuation characteristics to derive an approximate value.

(2) Where habitats occur in narrow linear shapes as along a riverbank, a roadway, or an urban city block, I adopt the natural boundary of the habitat to define the census strip except for species in which the specific strip is narrower than the habitat strip.

(3) Where birds are concentrated in flocks it is often difficult to tally each individual as a separate dot on the survey sheet. Under these conditions I estimate the flock size and treat it as a unit, apportioning the lateral distribution points according to my best estimate of the position and dispersion of the flock at the moment it was encountered.

(4) Where, as in the breeding season, the detectability of members of a population fluctuates rapidly and irregularly or varies strongly among individuals, I focus on one or a few of the most stable cue types, such as song, and base my specific strip boundaries and calculations of density exclusively on these. Data obtained by this procedure require special adjustments for cue frequency as described below.

Cue frequency.—Cue attenuation should theoretically be completely controlled by the procedures described in the previous section, the observer simply basing his density calculations for each species on the count obtained in the relatively narrow strip within which his tally of detectable cues approaches completeness. But, entirely aside from cue attenuation, individual birds may still be bypassed because they produce no detectable cues, either visible or audible, while the observer is within detection range. These momentarily undetectable birds cannot be counted directly, but their numbers can be computed if the frequency of cue production (the proportion of observer encounters in which the birds make their presence known by emitting detectable cues) is determined for a representative sample of the strip's population and interpreted as the proportion of detected individuals in the total population of the strip. Thus, in a hypothetical case, if 10 birds of a selected species are detected on a transect count run at a speed that gives the observer 6 min within the detection range of each bird, and it is independently determined that representative members of the population make themselves detectable in 50% of a series of 6 min test periods in which they are continuously within detection range, we can conclude that 10 additional birds were bypassed on the transect count and that the population in the strip is 10 detected plus 10 undetected birds = 20 birds.

The frequency of cue production is difficult to determine under most conditions because when an observer follows them persistantly, birds tend to alter their natural behavior in ways that make them less or more detectable. *Total* cue frequencies (using all visual and sound cues) are, in fact, essentially unattainable, but fortunately during much of the nonbreeding season most of the birds within the narrow specific strip seem to make their presence known if the observer advances slowly and restricts his counts to favorable early morning conditions (Emlen 1971).

Cue frequencies can apparently be estimated with reasonable accuracy during the breeding season if calculations are based exclusively on song. Representative territorial males may be selected as samples and watched continuously over extended periods (Enemar 1959). Or, as it is difficult to recognize truly representative birds, a series of territorial males may be visited repeatedly for shorter periods and their individual song frequencies averaged (Hickey 1943).

When cue frequencies are based exclusively on song cues, transect counts must, of course, also be restricted to songs. The tally will thus be smaller, but the much wider specific census strips that can be employed when only loud vocalizations are used in determining attenuation distances, and the longer bird-observer exposure times available for each territorial singer compensate for the omission of numerous nonsong cues from the calculations.

Density computation.—When cue frequency cannot be measured, as when all cues are used during the nonbreeding season, density must be computed entirely from cue attenuation data. When indices on cue frequency are available, as for song in the breeding season, total density can be computed by multiplying the count of detected (cue-producing) birds in the census strip by the reciprocal of the locally determined cue frequency for the species.

The density values obtained by the specific strip census method, with or without application of cue-frequency data, apply to the population present in the strip at the time the traverse is run. Individual birds that drift back and forth across the boundary lines are included if they happen to be inside, excluded if they are outside when the observer passes. The effects of such transboundary movements will presumably balance out for common species on long traverses, and fluctuations in a stable population should be small in a series of standardized traverses over the same route. Variations in computed density will occur, however, with changes in weather and variations in field procedure such as rate of progress or time of day.

When procedures are standardized, density estimates for a series of specific strip traverses may be averaged to reduce errors caused by small sample sizes, or statistically analysed for information on the completeness of cue detection under various conditions. Palmgren (1930) discussed the averaging of transect-derived density values for an area, noting that in open (no strip boundary) transects or where wide fixed strips are used, the largest count for a species in a series of traverses will approach the actual population level more closely (be more complete) than the mean for the series. This principle applies in situations where the population being counted is assumed to be definitive and where variations in the count are due to variations in the completeness or efficiency of the counting; it does not apply to specific strip counts where the population being counted fluctuates as birds drift back and forth across the boundary line and where all counts are assumed to be essentially complete or at least representative of the birds present within the indicated boundaries when the count was made.

FIELD PROCEDURES FOR THE NONBREEDING SEASON

To estimate densities of nonsinging, nonterritorial populations along a transect route one should use all available cues and follow the procedures described above under cue attenuation. The values will theoretically be complete for all cue-producing (detectable) birds in the specific census strips. Silent and inactive (undetectable) birds will inevitably be bypassed, and no satisfactory technique has yet been devised for estimating them. In the absence of data on cue frequency, best guess adjustments (basal detectability adjustments) may be made for these undetected birds where best estimates are preferable to minimum estimates.

Field Procedures for Breeding Season Populations

To estimate breeding season densities by the specific strip method one should use only song cues and then adjust the tallies of singing males for the unrecorded non-singing males and females. This procedure calls for two separate operations in the field, (1) tallying all song detections and their lateral distances along the route, (2) determining indices of song frequency during the census period. Although these two operations are functionally distinct, the data for each may be collected concurrently along a transect route without prejudice to either set of data and without loss of time.

Counting singing males.—The field procedures for song transects are similar to those used in all-cue transects as described in my 1971 paper, but involve a number of special considerations as discussed below:

(1) *Record all detections.*—Although density calculations in this model are based entirely on song cues, all detected cues should be recorded. Song cues should be clearly differentiated from the others on the tally sheet by some distinctive symbol such as a small circle or the letter s.

(2) *Song strip boundaries.*—Because songs in most species can be heard at relatively great distances, the basal plateaus of lateral regression curves are much broader when based exclusively on song cues than when soft call notes and sightings are also included. Under these circumstances the problems of distance estimation and density calculation can be simplified by setting the boundary lines for the census strip at some convenient arbitrary distance well inside the limits of song detection set by sound attenuation. In the Wisconsin test study (see Appendix) I selected 200 feet on either side of the trail (a 400-foot strip) for most species and 100 feet (200-foot strip) for a few quiet-voiced species.

(3) *Distance estimates.*—As distances from the transect trail to unseen singing birds can rarely be measured, a subjective approach is necessary. Elaborate estimation techniques must be avoided, however, as they involve distractions that can affect the efficiency of distant song detection adversely (Merikallio 1946). Fortunately if a fixed distance well within the absolute limit of detection is set, as advocated in the preceding paragraph, the only critical decision to be made for each observation is relatively simple, whether or not the bird is inside or beyond that prescribed census strip boundary line when first detected. In most cases the correct answer is subjectively obvious, but there may be a good many borderline cases. In any event, every census-taker must face the subjectivity problem squarely and work out a system for himself in which he can test his performance level objectively at frequent intervals. I find that with practice I can almost invariably predict to within 10 or 15% the number of paces (3 feet) it will take me to reach a selected fixed object 200 feet away, the distance to the strip boundary line for most species in breeding season transects. This level of accuracy I am obliged to accept as the best I can do. In making these estimates for self-testing and in actual transect count situations, I find it helpful to cultivate and retain mental images of familiar settings with known dimensions, such as a room in my home, a tennis court base line, a fallen 100-foot tree, or a 100-yard race track straightaway.

To apply these acquired skills to an unseen songbird along a transect route one must first determine the approximate location of the source of the sound with reference to some conspicuous and fixed object in the habitat such as a distinctive tree trunk or a tall shrub, and then estimate the distance of that object from the trail when he is approximately opposite it. Both the locating and the estimating operations

TABLE 1

SOME COMPARISONS OF THE PLOT-MAP AND TRANSECT-STRIP CENSUS METHODS

Plot-map method	Transect-strip method
Objectives	
To estimate the number of birds resident during the breeding season.	To estimate the number of birds present during a single census operation.
Nature of the data	
Data units are the territories lying within or partially within (fractions) the plot boundaries.	Data units are the individual detections of birds as the observer moves along the route.
Each visit to the plot contributes data to a single census estimate for the season.	Each traverse of the route provides the complete record for a definitive estimate; the results of repeated traverses can be averaged.
Plots are usually truncated in shape.	Plots are elongate in shape (strips).
Applicability	
Limited to the season when birds are on territories.	Applicable at any season.
Plots must be replicated when objective is to characterize a region or vegetation type.	A long transect plot provides a representative sampling of a region or vegetation type.
Problems of procedure and interpretation	
(Repeated traverses over the same area will reduce errors of omission.)	In the absence of cue frequency data (nonbreeding season) an unknown number of silent (no cue) birds within detection range (the specific strip) will be bypassed in the single traverse that constitutes a definitive transect census.
(No distance estimates are required.)	Lateral distance measurements to detection points are only rough subjective estimates.
Double recording of individuals is difficult to control unless neighboring males sing concurrently.	(Double recording is rarely a problem when following a straight transect course at more than 0.70 mph.)
Determination of territory boundaries on base maps may be difficult especially where territories are contiguous.	(Precise boundary determinations are not required.)
Determination of the fraction of boundary line territories lying within a plot requires knowledge of the transboundary extensions.	(No territory evaluations are required.)
Individual territorial birds may enter, leave or shift within a plot between spaced visits.	(Intervisit changes are minimal when intervals are short.)
Efficiency (hypothetical) in hours	
For a 24-acre plot (birds resident through the breeding season)	For a 24-acre (0.5 mi × 400 feet) strip segment (birds present during three 5-day periods)
Staking and mapping — 10 hr.	Mapping — 2 hr.
Vegetation survey — 4 hr.	Vegetation survey — 4 hr.
8 surveys × 2 hr. — 16 hr.	15 traverses × 0.6 hr. — 9 hr.
Total — 30 hr.	Total — 15 hr.

are best accomplished by moving along the trail and sighting towards the object or the sound source from several spaced points. A clearly visible and reasonably straight trail is important as a reference base for this operation. Major landmarks previously plotted to scale on a strip map of the route (see next subsection) greatly facilitate all distance estimates in the tract.

(4) *Rate of advance.*—The rate of progress along the trail and the distance ahead and to the rear within which songs should be recorded are critical insofar as they determine the length of time the observer is exposed to each bird on the census strip. A net walking speed of about 0.75 mph combined with a 200-foot limit for recording birds, fore and aft, allows 6 min for each bird. Where 200 feet is also used as the lateral distance to the strip boundary (see consideration *2* above), the observer is, in effect, concentrating his attention on the birds in a slowly advancing 400-foot square area in which he is centered.

TABLE 2

CENSUS DATA FOR A 48-ACRE STAND OF MIXED WOODLAND IN WISCONSIN[1]

	Total count per mile[2]	Width of specific strip[3]	Total count in specific strip[4]	Song count in 200-foot strip[5]	Song frequency[6]	Territories in 200-foot strip[7]
Mourning Dove (*Zenaida macroura*)	2.0	40 + 40	0.5	0.64	0.40	2.0
Yellow-billed Cuckoo (*Coccyzus americanus*)	0.1	200 + 200	0.2s	0.09	v[8]	—
Common Flicker (*Colaptes auratus*)	1.9	60 + 60	0.9	0.45	0.15	3.1
Red-bellied Woodpecker (*Melanerpes carolinus*)	0.4	100 + 100	0.2	—	—	0.5
Downy Woodpecker (*Picoides pubescens*)	2.2	100 + 100	1.3	—	—	4.0
Great Crested Flycatcher (*Myiarchus crinitus*)	0.6	200 + 200	0.2	—	—	0.4
Blue Jay (*Cyanocitta cristata*)	13.0	100 + 100	8.4	—	—	8.2
Black-capped Chickadee (*Parus atricapillus*)	16.2	60 + 60	10.4	—	—	8.8
White-breasted Nuthatch (*Sitta carolinensis*)	0.2	200 + 200	0.1	—	—	0.2
Red-breasted Nuthatch (*S. canadensis*)	1.1	100 + 100	0.9	—	—	1.0
House Wren (*Troglodytes aedon*)	3.1	200 + 200	3.8s	1.91	0.66	3.0
Gray Catbird (*Dumetella carolinensis*)	5.2	40 + 40	1.6	1.68	0.44	7.9
Brown Thrasher (*Toxostoma rufum*)	4.3	60 + 60	2.9	0.91	0.19	6.0
American Robin (*Turdus migratorius*)	6.3	40 + 40	3.3	0.91	0.13	8.1
Wood Thrush (*Hylocichla mustelina*)	3.0	200 + 200	3.5s	1.77	0.52	3.6
Cedar Waxwing (*Bombycilla cedrorum*)	0.6	50 + 50	0.6	—	—	1.0
European Starling (*Sturnus vulgaris*)	0.3	100 + 100	0.2	—	v	—
Common Yellowthroat (*Geothlypis trichas*)	0.6	200 + 200	0.6s	0.32	0.27	1.0
Red-winged Blackbird (*Agelaius phoeniceus*)	0.4	200 + 200	0.5s	0.23	0.60	—
Northern Oriole (*Icterus galbula*)	0.3	100 + 100	0.3	0.09	0.10	0.8
Common Grackle (*Quiscalus quiscula*)	7.7	40 + 40	4.2	—	v	—
Brown-headed Cowbird (*Molothrus ater*)	4.7	50 + 50	2.2	1.95	0.51	3.5
Cardinal (*Cardinalis cardinalis*)	6.4	60 + 60	3.0	2.91	0.59	7.0
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	2.4	50 + 50	0.8	0.86	0.28	4.2
Indigo Bunting (*Passerina cyanea*)	0.8	200 + 200	0.8s	0.41	0.53	0.9

[1] Twenty traverses along a 1.10-mile transect route through a 48-acre stand in Madison, 18 June to 7 July 1974.
[2] All birds detected by sightings, calls or songs—per mile.
[3] Distance between inflection points for the species on each side of trail—in feet.
[4] All birds detected by sightings, calls or songs within the specific strip, or songs detected (indicated by s) × 2, whichever is larger.
[5] All males detected by song within 200 feet (100 feet for Catbird)—per mile.
[6] Proportion of 6 min. territory crossings in which the resident bird sang.
[7] Sum of whole or fractional territories as determined by clusters of points representing song sites within 200 feet of trail on date when the species population was at maximum.
[8] v = nonresident vagrants.

TABLE 2—*Continued*

	Total count per mile[2]	Width of specific strip[3]	Total count in specific strip[4]	Song count in 200-foot strip[5]	Song frequency[6]	Territories in 200-foot strip[7]
American Goldfinch (*Spinus tristis*)	1.0	50 + 50	0.5	0.18	0.25	0.9
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	3.1	50 + 50	1.0	1.73	0.72	0.8
Field Sparrow (*Spizella pusilla*)	2.6	200 + 200	2.7	1.36	0.60	2.8
Song Sparrow (*Melospiza melodia*)	0.4	200 + 200	0.4s	0.14	0.75	0.3

(5) *Number of traverses.*—Because the calculated values obtained in these transect censuses apply to the number of birds in the strip at the moment of counting, traverses over a route may be repeated and averaged. To avoid complications related to seasonal or breeding cycle changes, such traverse replications should be made within a limited period, ideally on successive days. For reasons explained in the next subsection, the number of replications in a series is limited to about 5 when song frequency measurements are involved. Double (10) or triple (15) series may, of course, be used. Where a composite record for an entire breeding season is desired, as in traditional spot-mapping censuses, several series of counts will be needed, perhaps one 5-day series every 2 weeks.

Determining song frequencies.—The conversion of transect counts of singing males to population densities requires measures of mean song frequency for the area and season in which the counts were made. A series of observation periods at territories located along the census route can provide a record of the mean incidence of singing by their resident occupants. This operation can be coordinated with the transect count operation to provide song incidence records efficiently for the same population and periods as those covered by the count.

A simple strip map of the route (scale about 1:2400) showing prominent landmarks to 200 feet laterally should be prepared at the start. I carry a set of such strip maps, one for each resident species, on my clipboard beneath the census tally sheet for the day. On these maps I plot the position of each detection point as a colored symbol and draw lines to indicate a bird's movements from perch to perch. I use a different color on the maps for each traverse, and as I can clearly discriminate only five colors of small dots on a map, I set five as the number of traverses in a series. Each map thus provides the complete record for a species over a series of 5 traverses. Obvious clusters of differently colored symbols and lines delineate the territories of localized males on these maps, and song frequencies can be read directly as the number of color-distinct song symbols in a cluster (from 0 to 5) divided by the number of visits or checks of the territory in a series—always five. In this system a species with six recognizable territories along a strip provides a sample size of $6 \times 5 = 30$ song checks. Mean frequency values obtained in this way will be too high if the count of territories is incomplete because of the presence of nonsinging males (zero frequency) that fail to reveal themselves by any cue during the five visits to their territory, or that are detected by nonsong cues only once or twice and classed as nonterritorial birds.

The additional time needed for the double entry of detections in this coordinated transect-song check procedure is negligible, and the attention needed for carefully

TABLE 3

THREE DENSITY ESTIMATES (BIRDS PER 100 ACRES) BASED ON THE CENSUS DATA PRESENTED IN TABLE 2[1]

	Transect method		
	Based on all detected cues[2]	Based on song cues and adjusted for song frequency[3]	Plot-map method[4]
Mourning Dove	4.8	6.6	7.5
Yellow-billed Cuckoo	0.4	v	v
Common Flicker	6.0	12.4	11.7
Red-bellied Woodpecker	0.9	—	1.9
Downy Woodpecker	5.2	—	15.0
Great Crested Flycatcher	0.4	—	1.5
Blue Jay	17.2[5]	—	30.1
Black-capped Chickadee	25.1[6]	—	33.1
White-breasted Nuthatch	0.2	—	0.8
Red-breasted Nuthatch	3.4	—	3.8
House Wren	7.8	11.9	11.7
Gray Catbird	15.7	31.4	29.7
Brown Thrasher	20.1	19.7	22.8
American Robin	32.2	28.8	30.8
Wood Thrush	7.4	14.0	13.7
Cedar Waxwing	4.9	—	4.1
European Starling	0.9	v	v
Common Yellowthroat	1.3	4.9	3.8
Red-winged Blackbird	1.0	1.6	1.3
Northern Oriole	1.1	3.7	3.4
Common Grackle	41.0	v	v
Brown-headed Cowbird	18.4	15.7[7]	20.7[7]
Cardinal	21.0	20.3	26.3
Rose-breasted Grosbeak	6.4	12.6	15.8
Indigo Bunting	1.7	3.2	3.4
American Goldfinch	3.7	3.0	3.8
Rufous-sided Towhee	7.5	6.0[8]	4.9[8]
Field Sparrow	5.7	9.4	10.5
Song Sparrow	0.7	0.8	1.1

[1] No values are given in column 2 for nonsinging species and in columns 2 and 3 for species that were represented only by vagrants (v).
[2] Calculated for 100 acres from column 3 in Table 2.
[3] Calculated from column 4 in Table 2 and adjusted for song frequency (column 5) and for undetected females.
[4] Calculated from column 6 in Table 2 and adjusted for undetected females.
[5] Fledged juveniles (est. 2 per average family flock of 4) have been subtracted.
[6] Fledged juveniles (est. 4 per average family flock of 6) have been substracted.
[7] Observed sex ratios of cowbirds suggest an average of about two females per male. Male territories were very large and difficult to plot.
[8] Only one of the two singing males on the tract was paired.

placing the symbol on the map is complementary to, rather than competitive with that needed for assigning a lateral distance value on the tally sheet.

Conversion to absolute density estimates.—The adjustment or conversion factor for a count of singing males in a song-cue transect strip is the reciprocal of the song incidence for that population and period. This holds for both high and low song frequencies, a low frequency simply indicating the need for a large adjustment. The method is thus applicable over wide ranges of singing activity.

Densities computed for a song-cue strip should be converted to standard units such as birds per 100 acres or square kilometers. Where the strip width for a species has been set as 200 feet on either side of the trail, one mile of strip will cover 48.5 acres. Conversion to birds per 100 acres in this case is accomplished by multiplying the density in the strip by 100/48.5 = 2.06.

To obtain total population density for a species, the value obtained for male density must be adjusted for the uncounted females. For monogamous singing species in the Wisconsin test area I applied the imprecise but not unreasonable assumptions that the song tallies reflected both resident and vagrant males, and that

TABLE 4

SINGING INCIDENCE OF TERRITORIAL MALES AT MADISON, WISCONSIN, DURING FIVE PERIODS BETWEEN 18 JUNE AND 17 AUGUST 1974.[1]

	18–29 June		1–7 July		14–19 July		21 July–5 August		12–17 August	
	Inc.	N	Inc.	N	Inc.	N	Inc.	N	Inc.	N
Mourning Dove	0.37	(30)	0.43	(40)	0.43	(30)	0.27	(30)	0.33	(30)
Common Flicker	0.30	(30)	0.15	(40)	0.18	(40)	+	X	+	X
House Wren	0.70	(50)	0.64	(80)	0.50	(60)	0.60	(20)	—	X
Gray Catbird	0.50	(100)	0.38	(90)	0.31	(110)	—	(90)	—	(120)
Brown Thrasher	0.18	(80)	0.20	(60)	0.03	(80)	—	(60)	—	(70)
American Robin	0.06	(80)	0.19	(90)	0.23	(90)	0.40	(10)	—	X
Wood Thrush	0.58	(80)	0.43	(60)	0.43	(80)	0.23	(60)	0.03	(30)
Common Yellowthroat	0.35	(20)	0.20	(20)	0.40	(20)	0.20	(10)	—	X
Brown-headed Cowbird	0.60	(50)	0.37	(30)	—	X	—	X	—	X
Cardinal	0.64	(80)	0.54	(80)	0.41	(80)	0.35	(60)	0.40	(50)
Rose-breasted Grosbeak	0.45	(40)	0.10	(50)	0.04	(50)	—	X	—	X
Indigo Bunting	0.65	(20)	0.35	(20)	0.30	(10)	—	X	—	X
American Goldfinch	0.10	(20)	0.15	(20)	0.35	(20)	0.13	(30)	0.10	(30)
Rufous-sided Towhee	0.80	(20)	0.65	(20)	0.80	(20)	0.70	(10)	0.50	(20)
Field Sparrow	0.70	(30)	0.50	(30)	0.37	(30)	0.55	(20)	0.35	(20)
Song Sparrow	0.80	(10)	0.70	(10)	0.20	(10)	0.10	(10)	—	X

[1] Values are the proportions of 4–6-min. early morning visits to (crossings through) territories during which the resident bird sang. Numbers in parentheses give the sample size for each value (territories × visits).

the overall sex ratio in the populations was roughly equal. On this basis I simply multiplied the computed male density by two.

Procedures for nonsinging species.—A number of species in a breeding community such as the woodpeckers and jays may have nothing equivalent to the loud and frequent advertisement songs of most song birds, yet remain localized as pairs or small flocks for at least part of the breeding season. Such species can be treated as nonterritorial birds by recording all cues and assuming nearly complete cue frequency within the specific census strip of the species (the nonbreeding season procedure) or, when these birds are foraging in flocks or pairs on delimited home ranges, they can be sampled for total cue frequency in the same manner that singing species are sampled for song frequency. The frequency value can then be applied to the tally of pairs or flocks within the census strip of the species to provide a density estimate for pair or flock units. Adjustment of this estimate to total adult density for the species may then be accomplished by multiplying the number of flocks by an independently derived value of mean flock size. This procedure alleviates the practical problem of counting the individuals in each flock when encountered in the field.

FIELD PROCEDURES FOR MIXED AND TRANSITION POPULATIONS

The seasonal transition from breeding to nonbreeding condition and back is gradual in populations of any given species, and an avian community characteristically contains both breeding and nonbreeding species through much of the year. Thus a census taker will often be confronted with a mixture of species, some needing the all-cue method without frequency adjustments and others eligible for the song-cue method incorporating measurements of song frequency. The choice will generally be determined by the uniformity and frequency of cue production by the birds at the time, and the opportunities available for recognizing and keeping tabs on individual birds as required by cue-frequency measurement procedures. With field operations standardized and restricted to optimum weather conditions, reasonably high uniformity and frequency of cue production can be assumed for most species through much of the nonbreeding season and, for some, throughout the year. Opportunities for individual recognition are provided when individuals isolate themselves on distinct and exclusive territories where they can be visited and checked periodically, and this occurs for many species in the breeding season and for a few throughout the year.

As communities often contain representatives of both categories simultaneously and as a species may change from one category to the other rather rapidly, field procedures should be designed to cover the data requirements for each. This raises no serious problems, and a tally sheet can be planned that provides space for recording all the pertinent information for each procedure. Strip maps are, of course, required for song-frequency measurements and should be included with the tally sheet whenever the use of this procedure for one or more species seems indicated. The choice between simple cue attenuation (all cues) and song-frequency procedures can then be made after the fieldwork is completed with full data in hand. Where density values are obtained for a species by both methods simultaneously, a selection between the two can be made on the basis of size and clarity of the data samples supporting each and on considerations of the basic reliability of the two procedures (see Appendix).

Discussion

The transect method differs from the familiar territory mapping method (see Robbins 1970) in the nature of the density values obtained, in aspects of reliability and accuracy, and in overall efficiency. The summary and comparison of the two methods presented in Table 1 may be useful in selecting the best approach for various types of ecological and behavioral studies. Some of the major considerations are discussed in greater detail below.

Density values.—Transect censuses provide data on the number of birds of each species on a transect plot (strip) at the time the traverse is made. Repeated traverses along the same route within the span of a week or two provide replicate samples of the same population suitable for averaging and other statistical treatments. By contrast, the territory mapping method provides a composite record of the number of individuals of each species resident on the selected plot at one time or another during a breeding season. Repeated visits to the plot increase the completeness of the record but do not constitute replications and cannot be averaged. In the transect method time-bracketed series may be repeated on the same plot at spaced intervals to provide data for an overall record for the season, while in the territory mapping method, provided adequate data are collected, the record may be broken down by periods to provide information on direct species associations or on changes in community structure and distribution as the season advances.

Where the objective of a census operation is to determine mean density values over a large area or an extensive habitat type, a long rectangular strip transecting the area, as provided by the transect method, will produce a better sampling than a compact, truncated plot (of the same size). Where the objective is to measure the populations on a small island or an isolated block of distinctive habitat too small to accommodate an elongate transect strip, the mapping method is preferable.

Where a record of seasonal changes through a full year is desired the territory mapping method is inapplicable. The specific-strip transect method as described in this report may be applied, although the necessary changes of procedure between the breeding and nonbreeding seasons may give rise to errors.

Reliability and accuracy.—Territories that overlap census plot boundary lines present problems for evaluating densities by the territory mapping method. This problem assumes major proportions when species' territories are large in relation to the census plot. Unless information is obtained on the boundaries of such territories outside the plot, the fraction inside, and hence the number of birds represented, cannot be reliably evaluated. The problem of boundary line territories is bypassed in the transect strip method as the census units are simply birds present inside the strip at the moment of counting. For song frequency determinations in the breeding season the samples can be restricted to resident birds whose territories lie across or near the trail and who can thus be assumed to remain continuously within hearing range.

A second source of error in the territory mapping method is in the interpretation of clusters of observation points as territories. This becomes particularly difficult where a species is abundant and territories are contiguous. Supplementary notations of concurrent singing by neighboring territory holders and of behavioral interactions between such neighbors are very useful in locating boundary lines in these cases, but interpretations of the same set of data by several experienced observers may still differ considerably (Svensson 1974, Best 1975, Mannes and Alpers 1975). Transect counts do not require any interpretation of territory boundaries, and the samples for song-frequency measurements may be selected judiciously to avoid territories in confusing situations.

While the transect method escapes the hazards of misinterpreting boundary line overlaps and point clusters on census maps, a fair comparison of the two systems must balance threats to reliability against the threats to accuracy posed by the investigator's inability to verify the two basic assumptions of the variable-strip transect method, completeness of count close to the trail, and even distribution laterally from the trail. Theoretically the former can be covered by adjustments for cue frequency during the breeding season, but remains a serious factor of unknown and variable magnitude at other times; the latter must be controlled as far as possible by selecting census tracts with broad stretches of essentially uniform habitat structure.

Efficiency.—The relative efficiency of the two methods in terms of time and effort is difficult to judge because a single composite density value for a season cannot be equated readily with a series of time-bracketed values distributed through the same season. Using hypothetical values, however, I estimate in Table 1 that to obtain a single composite density value by the mapping method requires roughly twice as many hours as a series of three time-bracketed mean density values based on five transects each. This apparently greater efficiency of the transect method must, of course, be weighed against considerations of the nature of the values desired for any particular study.

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APPENDIX

As a test for the breeding season transect method described in this paper I conducted a field study combining transect and plot map methods on a tract of mixed woodland in the University of Wisconsin arboretum at Madison, Wisconsin in the summer of 1974. I ran 20 traverses along a 1.10 mile transect route through the tract between 18 June and 7 July, and added 30 traverses between 8 July and 17 August. The census data collected on the first 20 traverses are presented in Table 2, and density estimates calculated from them by the total-cue method, the adjusted song-cue method, and the plot map method are presented in Table 3.

All traverses (1 or 2 per day) were made during the first 3 h of daylight while walking at an average speed of 0.70 to 0.80 mph along a well-marked trail that looped through the tract. All detections of movements, call notes, and songs for each species were tallied on prepared sheets in columns representing 10-foot strips to 100 feet, then a 100-foot and a 200-foot strip to 400 feet. All detections were also recorded as colored symbols on strip maps of the route to provide the basis for song-frequency measurements. A separate map was used for each five traverses for each species, and the symbols for each traverse were recorded in different colors. The song frequency for a species (column 5 in Table 2) was calculated from these maps by multiplying the number of different colored song symbols in each selected territory (territory crossings during which the bird was singing) by the number of selected territories on the map. The total number of territories (column 6 in Table 2) was my best estimate of the sum of whole and fractional territories lying within the strip.

The values derived by the adjusted song-cue and plot-map methods (columns 2 and 3 respectively in Table 3) correspond closely for most species. As the two are based on different sets of data this correspondence gives credence to the possibility that both reflect the actual density during the census period quite well. It also suggests that the length of the census period, 20 days, was not long enough to reveal any appreciable differences between the maximum density level during the period as measured by the plot-map method and the mean density level for the period as measured by the transect method. Which of the two sets of results is more accurate in terms of the objectives of its respective method rests on the error sources inherent in the two methods as considered in the discussion section of this paper.

Values obtained by the total cue transect method (not adjusted for cue frequency) presented in column 1 of Table 3 are, with two exceptions, lower than those obtained by the other methods, and in a few cases substantially lower. This, of course, is to be expected during the breeding season when resident birds are highly irregular in cue production. In some species it may be attributed in large part to the low detectability of female during the breeding season, but in at least the seven species where song detections (multiplied by 2 to cover females) were used because they gave higher values than the unadjusted values based on all cues (see footnote 3 in Table 2) it clearly involved nonsinging resident males. When adjusted for song frequency (column 5 in Table 2) these values are equated with the song-cue transect values. The total-cue and song-cue methods, of course, cover nonterritorial birds deliberately omitted in the plot-map method.

The song-frequency indices used for transect censuses in this paper (occurrence in 4–6 min periods) presumably reflect species-characteristic behavioral traits that will vary in more or less predictable patterns for each species with time of day and stage of the nesting cycle. Individual variations will inevitably occur but, roughly standardized for time of day when frequencies are not changing rapidly, mean values for the populations on a census tract may be expected to show predictable progressive changes as the breeding season advances. If this prediction can be verified with the accumulation of data, it may be possible to apply values for a specified segment of the season to song counts along a census route without recording local song frequencies for every operation.

Song frequencies for 16 species on the Madison census tract are presented in Table 4 for five periods between 18 June and 17 August of 1974. Ten traverses were run in each period to provide sample sizes of 10x the number of sample territories for each species. Incidence values (frequencies) declined for most species as the season advanced. Records for early June would doubtless reveal higher frequencies for these species. Irregular fluctuations presumably reflect the smallness of the sample sizes.