A COMPARISON OF THREE METHODS OF ESTIMATING WINTER BIRD POPULATIONS

By Richard Brewer

Although knowledge of population size is important in the solution of many theoretical and practical ecological problems, accurate estimation of bird density outside the breeding season is difficult. The only sizable body of data attempting such estimates is in the Winter Bird Population Studies published annually since 1948 in *Audubon Field Notes* (AFN) and its successor *American Birds*. Because the AFN method has no clear theoretical basis and interpretation of results is sometimes uncertain (e.g., Kolb, 1961: 358, 1962: 367; Brewer, 1972), I compared it with two other methods for which a rationale can be established but which have not been hitherto described or employed.

I follow Davis (1963) in defining density as an instantaneous measure; it is the number of individuals in a given area at a given time. The bird population of an area changes continually as individuals enter or leave and as they hatch or die. To describe density, what is needed is a series of instantaneous censuses, or an appropriate average of them, or some value arrived at in another way but which can be shown to be equivalent.

Using the first approach, I tried to obtain a continuous record of density for a one-day period. Through the cooperation of several observers, an attempt was made to keep track of all birds on 6.7 ha (16.5 acres) tract of oak forest in Allegan County, Michigan (the Small Oak Area of Brewer et al., 1973) from approximately sunrise to sunset. The second approach was a winter equivalent of the Williams (1947) territory-mapping method. Home ranges of all birds occurring on the same plot were mapped and the fraction of each range on the plot was counted as that individual's contribution to density.

METHODS

AFN Method

The plot was visited 16 times between 18 February and 28 March 1969. (It should be noted that the census dates are all later than the period of 20 December to 10 February recommended for AFN Winter Bird Population Studies. This deviation is not considered important for these comparative studies. In these forests, which do not begin leafing until May, there had been no consistent shift to breeding season spatial organization nor obvious migratory movements by 28 March. The appearance of Dark-eyed Juncos on 23 March is a possible exception.) All but one of the visits were in the A.M., mostly beginning before 0930. Mean length was about 90 minutes. On each count the plot was traversed by following grid lines 61 m apart and plotting on a map each bird seen or heard. Every 61 m (at stakes marking grid intersections) the observer paused for 1.5 minutes. The total number of individuals recorded (all trips) was divided by the number of trips to give a mean (Kolb 1965).

Day-long Census

Two censuses were conducted, on 7 February and 15 March. On these censuses four or five observers were each assigned a sector of the study area (1.2 ha on 7 February, 1.6 on 15 March) which they patrolled continuously from 0840 to 1645 on 7 February and 0817 to 1700 15 March. Locations and movements of all birds observed were plotted on maps of the area, along with times of observation. A complete traverse of an individual's sector required 15–20 minutes if no birds were observed. If birds were seen, the observer remained with them, recording their movements until they left the plot or moved into another observer's sector. In the latter event, the adjacent observer was often able to continue observation of the birds. When all of the observer's records were later combined onto the summary maps, a reasonably clear description was obtained for bird activity on the study area for the entire day.

Treatment of the data took the following form: for each species a schedule was drawn up showing numbers by time. For birds that were seen as they came onto the plot and kept under observation until they left, times used were those actually observed. When, as was frequently the case, birds were not observed until they were already a few to a few hundred feet within the boundaries or birds were lost while still on the plot, 10 minutes were added for the unobserved period. The 10-minute interval was chosen as one half the time required by the observer to cover a sector. The average bird density from sunrise (a) to sunset (b) was calculated as

$$\bar{x} = \frac{\sum_{x=a}^{b} N_x}{b - a}$$

where N is number of individuals and x refers to intervals of 1 minute.

Home-range Method

Because winter home ranges are not necessarily mutually exclusive, the home-range method, unlike the equivalent territory-mapping method for breeding populations, requires that birds be individually recognizable by colorbands or other means. Birds were obtained by trapping. A U.S. Fish and Wildlife Service band was put on one leg and two plastic color bands on the other. Prebaiting and trapping were carried on at two corners of the plot from 17 January to 22 January and at the other two corners from 22 January to 2 February. Also, birds were banded at the only nearby residence 400 m northeast of the plot, where two feeders were in operation throughout this and preceding winters. The brief period of trapping and the switching of stations were designed to avoid, as far as possible, alteration of the bird's normal patterns of movement. Some alterations may have occurred but temporary concentrations resulting from windfalls are probably natural events (Hamerstrom, 1942). The birds banded on or near the plot were Black-capped Chickadee 34

(of which 2 died in traps and are not considered in later sections of this paper), Tufted Titmouse 1, White-breasted Nuthatch 1, Downy Woodpecker 1, and Blue Jay 1. Taken at the feeder 400 m from the plot were Black-capped Chickadee 15, Tufted Titmouse 8, and White-breasted Nuthatch 2.

To allow accurate plotting of bird locations in the field, additional stakes were placed 122 m out on each coordinate line (thereby enclosing about 30 ha). For birds seen farther away from the plot a map including about 250 ha was prepared from an aerial photograph.

The study plot and surrounding area were visited on 24 days between 7 February and 28 March by one to five observers. Birds were identified individually whenever possible; locations, movements, and times were recorded. At the end of the winter, observations of individually identified birds were plotted on summary maps and the size of the home range and the fraction of the home range lying on the plot were measured using random dot overlays (Bruning Areagraphs, 90% precision). By summing the portions of the various home ranges included on the plot, an estimate of population size was obtained. If each individual spends the same amount of time in all parts of its home range, this method should measure mean density. Details of estimation are further discussed in the next section.

RESULTS

AFN Method

Eight species were recorded but the Dark-eyed Junco was seen only once (23 March) and probably had not been in the vicinity most of the study period. An average of 4.7 individuals per visit was observed (Table 1).

TABLE 1.

Frequency and number of birds on the Small Oak Area, 18 February–25 March 1969 (16 visits) by the AFN method.

Species	% of visits observed	Mean number ± SE
Black-capped Chickadee	69	2.1 ± .62
White-breasted Nuthatch	56	1.2 ± .23
Dark-eyed Junco	6	.4 ± .38
Downy Woodpecker	25	.24 ± .25
Hairy Woodpecker	19	.2 ± .10
Blue Jay	19	.2 ± .10
Tufted Titmouse	6	.1 ± .12
Brown Creeper	6	.1 ± .12
All species		4.7 ± .81[1]

[1] Includes one unidentified individual.

Day-long Census

Seven species were recorded, the same as for the AFN method except that the junco was not observed (Table 2). The estimate 7 February was

TABLE 2.

Mean density of birds on the Small Oak Area on two dates in 1969 by the day-long census method, compared with AFN estimates from the 6 dates closest to the day-long censuses.

Species	Numbers			
	February		March	
	Day-long census (7 Feb.)	AFN estimate (18–28 Feb.)	Day-long census (15 March)	AFN estimate (7–23 March)
Black-capped Chickadee	3.1	3.0 ± 1.32[1]	0.5	1.5 ± 0.50
White-breasted Nuthatch	1.0	1.2	0.4	1.2
Tufted Titmouse	0.6	0.3	0.2	—
Blue Jay	<0.1	0.2	0	0.2
Downy Woodpecker	0.3	0.2	0.6	0.5
Brown Creeper	0.1	—	<0.1	0.2
Hairy Woodpecker	0.1	—	<0.1	0.5
Total	5.2	4.8 ± 1.78	1.6	4.0 ± 0.45[2]

[1] ± = SE

[2] Does not include Dark-eyed Junco, 1.0. If this is included total is 5.0 ± 0.89.

for 5.2 birds and on 15 March for 1.6 (chickadees, 3.1 and 0.5). A major difference between the two dates is that there were never large numbers of birds on 15 March (Fig. 1). The largest number on 7 February was 38; during some 100 minutes more than 10 birds were on the plot. On 15 March, however, no more than five birds were detected on the plot at any one time. This difference resulted from the absence of large groups of chickadees on the second date.

Home-range Method

The same eight species recorded by the AFN method were observed plus one American Goldfinch seen 19 February (Table 3). The population estimate was 10.8 birds. How the estimates for the Black-capped Chickadee and the Downy Woodpecker were arrived at is given below. Similar methods were employed for the other species.

Of the 35 chickadees banded on the tract or banded elsewhere and seen there, 12 were observed frequently enough to allow a reasonable estimate of home range size. The fractions of the ranges of these birds lying on the tract summed to 4.5. Treatment of the other 23 chickadees was more difficult. Five birds banded on the tract but not seen again were recorded as zero. The other birds, with two to several observations, were assigned fractions of 0.1–0.3. No unbanded birds were recorded

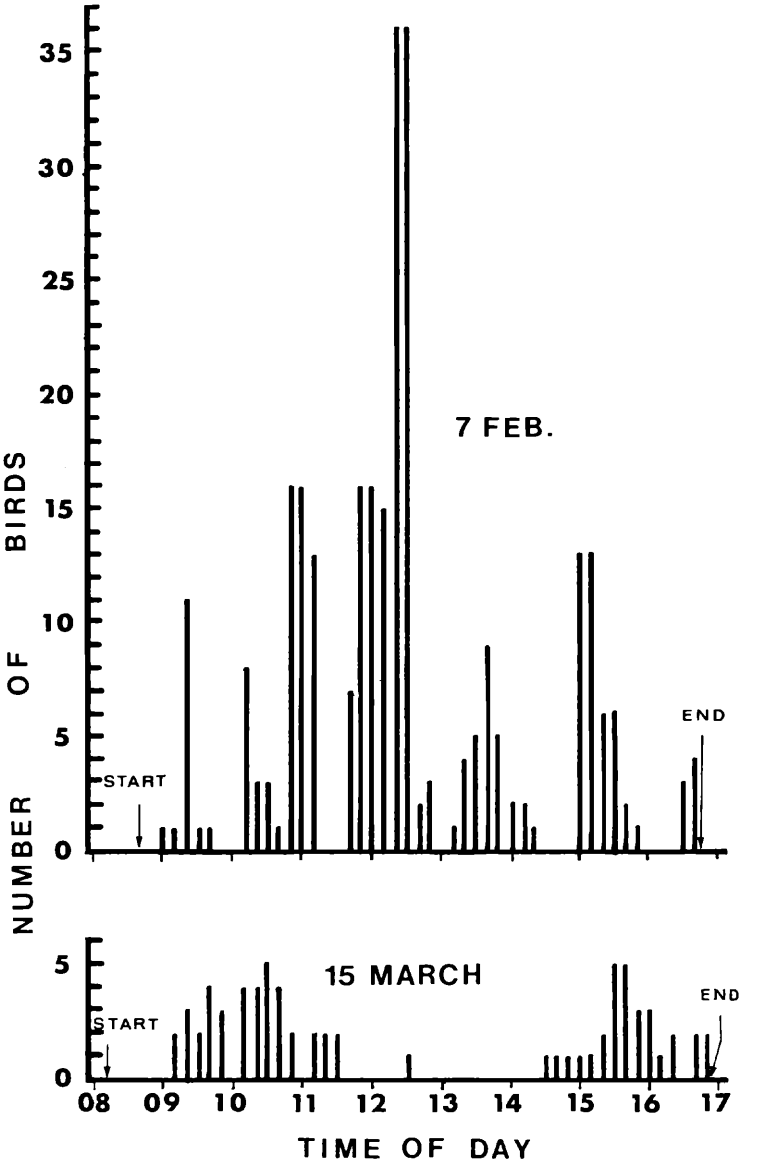

FIGURE 1. Numbers of birds on the Small Oak Area, Allegan Co., MI, at 10-minute intervals on two dates.

on the tract past the trapping period, although some were seen within 30 m of it, and one nested on the tract in the summer of 1969.

Only one Downy Woodpecker was banded. This female was often seen with an unbanded male. There was no indication, such as the si-

TABLE 3.
Mean density of birds on the Small Oak Area 21 January–28 March based on home ranges included on the tract.

Species	Density
Black-capped Chickadee, *Parus atricapillus*	6.6
White-breasted Nuthatch, *Sitta carolinensis*	0.7
Tufted Titmouse, *Parus bicolor*	1.2
Blue Jay, *Cyanocitta cristata*	<0.1
Downy Woodpecker, *Picoides pubescens*	1.0
Brown Creeper, *Certhia familiaris*	0.1
Hairy Woodpecker, *Picoides villosus*	1.1
Dark-eyed Junco, *Junco hyemalis*	<0.1
American Goldfinch, *Carduelis tristis*	<0.1
Total	10.8

multaneous observation of more than two birds or the observation of an unbanded female, that the home ranges of any other individuals touched the tract. There were, however, records of a male and a female, both unbanded, to the north. Our observations suggested home ranges of about 19 ha for the female and somewhat less than 10 ha for the male, in both cases including the whole study plot; the included fractions summed to 1.0 birds.

DISCUSSION

The three estimates of population size differed (Table 4). The largest value is the nearly 11 birds estimated by the home-range method. The AFN data are variable but, even so, the home-range estimate lies well outside the AFN 95% confidence interval of 3.0–6.4. The average of the two day-long censuses is 3.4, which is within the 95% confidence limits for the AFN method. A better comparison is between each day-

TABLE 4.
Comparison of the three methods.

Trait	Method		
	AFN	Day-long census	Home-range
Number of species observed	8	7	9
Mean density, all species	4.7 ± 0.81	3.4	10.8
Mean density, Black-capped Chickadee	2.1 ± 0.62	1.8	6.7
Approximate man-hours	24	75	150[1]

[1] Does not include the time of AFN and day-long censuses (99 hours) during which observations of banded birds were made.

long census and the six AFN visits closest in time (Table 2). The February values are very similar but the March day-long census figure is lower and outside the 95% confidence interval (2.8–5.2) for the AFN method.

In my opinion, the figures for the all-day censuses provide a fairly close approach to the actual mean density on the plot for those two days. The estimate is affected by the correction applied for birds observed only after entering the plot or lost to sight before leaving it. Omitting the correction entirely drops the estimate on 7 February to 3.3 and on 15 March to 1.1. The true average density for those two days probably lay between these values and the corrected values, that is, between 3.3–5.2 and 1.1–1.6.

The difference between the two dates is probably real, but it is unclear whether the low 15 March value is representative of a substantially lower population or whether it was simply a day when the plot was used very little by the birds having ranges touching it. I suspect that the latter was more important. The suggestion is sometimes made that birds such as chickadees "have more or less regular beats which they cover approximately on schedule" (McAtee, 1920). Our observations correspond with those of Butts (1931) who found more variable movements. Bartholomew (1967) showed that Bobwhites (*Colinus virginianus,*) which have home ranges similar in size to chickadees, may travel over only a small portion of their range during a given day; the same appears to be true for Ruffed Grouse, *Bonasa umbellus* (Marshall, 1965). The winter of 1968–1969 was snowy, with a continuous, deep snow cover from about Christmas until late February. By 15 March, a sunny day mostly above freezing, all north slopes and much of the level ground were still snow covered. Our observations suggested that on such days, chickadees and some of the other species tended to spend long periods feeding around bare, sunny patches.

The estimate yielded by the home-range method seems far too high. This is puzzling, and I can only list some possible explanations. (1) Much of the difference, I believe, is related to the preceding discussion. The premise that birds use all portions of their home range equally is probably often wrong. Studies of Gottfried and Franks (1975) and Robins and Raim (1970) have shown that Dark-eyed Juncos and Black-capped Chickadees may concentrate activities in some parts of their home range and do little more than travel through others.

(2) If home ranges shifted so that, for example, one home range included the plot in February, then shifted away, and another home range shifted to the plot in March, both ranges would be counted in calculating density by the home-range method. (Given sufficient data, such shifts could be accommodated by calculating home ranges for periods shorter than the whole season). Arguing against this as an important factor in these data is the fact that most individuals that contributed heavily to the density estimate were seen throughout the census period. For example, of the 12 chickadees with well-known home ranges, 9 were

observed on or near the plot from the date of trapping past the date of the last day-long census.

(3) Home ranges could have been underestimated or misinterpreted. This seems least likely for the chickadees, which contributed 60% of the density estimate, but it is a better possibility for other species for which some individuals occurring on or near the plot were unbanded. Underestimation of home-range size will tend to produce overestimates of the fraction of the home-range included on the tract and, thereby, overestimates of density. For banded birds, underestimation of home-range size is, of course, more likely than overestimation. Nevertheless, our estimates of home-range size were similar to those in the literature (Brewer, 1978).

For nomadic birds or others for which a definite home range cannot be determined, the home-range method will not estimate density; examples in this study are the Dark-eyed Junco and American Goldfinch. Such birds are, of course, poorly handled by the AFN method also, which tends to overestimate any such species that are recorded. This is because such species are usually aggregated. They are, accordingly, represented by one or a few flocks or by no birds at all. Very common nomadic species may be adequately sampled; the others will tend to be overestimated (if a flock happens to be recorded) or underestimated (if no flock is seen).

The highly variable density during the course of a winter day is of interest (Fig. 1), as is the substantial amount of time when 6.7 ha of midlatitude oak forest is empty of birds. It might be argued, in view of this, that areas of 6–8 ha are unsatisfactorily small for conducting winter population studies. Although choosing areas as large as possible may be desirable from the standpoint of minimizing atypical situations, the view seems otherwise to have little merit. The relationship between the percentage of a bird's home range included on a study plot and the likelihood of the bird being encountered on a visit to the plot is complex (Brewer, 1972: Fig. 3); merely increasing the fraction of birds whose ranges are wholly included on the plot does not necessarily increase the accuracy of density estimation by the AFN method. In any case, a forest of 6–8 ha does have an avian density, varying (based on these data) from zero to many birds during the course of a winter day. The average density for the forest is not likely to be identical to the density for the whole landscape over which some of the birds may range and for some purposes, such as estimating the avian contribution to energy flow, accurate determinations of density for the forest alone may be necessary.

CONCLUSIONS AND RECOMMENDATIONS

1. Any of the three methods is likely to give a virtually complete species list, except for wandering or erratic species.

2. A home-range method is not likely to be generally useful. It is too time-consuming and not demonstrably accurate. In connection with other studies of a single species it may be useful, especially if accomplished

using biotelemetry. The use of many small traps, as described by Merritt (1975), might also be a possibility if the trapping period was kept short.

3. The day-long census method probably gives, for the day on which it is conducted, a close approximation to density, but it is too time-consuming and too restricted in time to be of general use. It might be of interest for certain kinds of research and as a *macho* activity of a bird club similar to, but of more scientific value than, such activities as century counts. The assurance of accuracy could be increased by having a large number of cooperators so that sector size could be reduced or so that two persons could patrol each sector in opposite directions. Interpretation of day-long census results is easier if some part of the bird population is color-marked or -banded.

4. The AFN method, in oak forest in Michigan, seemed to give estimates that were close to mean density figures, but it probably overestimates conspicuous birds and underestimates inconspicuous ones (Brewer, 1972). It seems to be a useful intensive approach to obtaining quantitative information on winter populations. Although the relationship of the numbers obtained to density may vary among species, habitats, seasons, and observers, for many purposes this may not be a serious drawback.

5. Transects (Forbes, 1907; Forbes and Gross, 1923; Graber and Graber, 1963; Enemar and Sjöstrand, 1970; Emlen, 1971; Robbins and Bystrak, 1974) may be useful for extensive work on winter populations. With the exception of the Forbes census in some habitats these require calibration by species, habitat, season, and observer to obtain density estimates. The most promising method of correcting transect data to obtain density is that developed by Anderson and Pospahala (1970) and Emlen (1971). In many cases, the level of precision so achieved and the increment of usefulness may not be great enough to justify the time required, so that transects, like the AFN method, may be most useful for indicating approximate or relative abundance.

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