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BIAS IN DENSITY ESTIMATES DUE TO MOVEMENT OF BIRDS

STEPHEN L. GRANHOLM

ABSTRACT.—While censusing coniferous forest birds in 30-m-radius circular plots, I suspected that frequent movement by birds into and out of the plots might be biasing my results. To quantify the extent of bias, I analyzed data from 142 censuses for three actively calling species that were unlikely to be missed if present on a plot for 5 min. Each census consisted of two consecutive 5-min counts. For the three species, 36 to 72% of all individuals detected were detected in only one of the two counts; thus at least that many moved across plot boundaries during a 10-min period. Density estimates based on a 10-min period were 22 to 56% higher than those based on a 5-min period. My estimates for fixed circular plots were thus biased because they were derived from cumulative rather than instantaneous counts. Movement poses similar problems for variable circular plot, strip transect, and line transect methods. It is difficult to reduce bias due to movement without increasing bias from other sources.

Recently proposed techniques for estimating bird densities have stimulated considerable debate over the relative accuracy of different methods (see especially Ralph and Scott 1981). Available methods include mark-recapture techniques (Seber 1973, Cormack et al. 1979), mapping and counting territories (Williams 1936, Kendeigh 1944, International Bird Census Committee 1970), and several methods based on counting individual birds (see Kendeigh 1944, Emlen 1971, 1977, Fowler and McGinnes 1973, Ramsey and Scott, 1979, 1981, Burnham et al. 1980, Reynolds et al. 1980). Counting methods are straightforward for stationary objects such as plants, but not for highly mobile organisms such as birds, which often move into and out of the census area during the count period. Thus, to be strictly accurate, a count must be instantaneous. In practice, however, it is impossible in most habitats for an observer to detect all birds present at one instant and most methods must rely on a count period of several minutes or more.

In station counts, with a stationary observer, count periods have ranged from 2–20 min (Scott and Ramsey 1981). In transect counts, with the observer moving along a line, the "count period" at any one point depends on the speed of the observer and the distance limits, ahead and behind, within which birds are recorded (Emlen 1971).

A critical assumption for methods based on counts is that so little bird movement occurs during the count period that it does not affect density estimates appreciably. This assumption has received surprisingly little attention in the literature. Burnham et al. (1980) concluded that evasive movement away from the observer before detection is the only serious problem caused by bird movement in line transect surveys, but that it can result in substantial bias. Emlen (1971) pointed out that movement toward, as well as away from, the observer can be a problem with a few species such as hummingbirds. Random movement of birds into fixed plots during the count period was recognized as a problem by Seber (1973). Ramsey and Scott (1978) and Verner (1981) pointed out that random movement poses a similar problem for variable circular plots. Another source of bias is that moving birds are likely to be counted twice (Burnham et al. 1980, Reynolds et al. 1980). Apparently only three studies have provided empirical evidence for the amount of bias created by movement. Breckenridge (1935) and Emlen (1971) both noted that more birds were detected at intermediate than at short distances from transects, suggesting evasive movement by birds. Ramsey and Scott (1978), using variable circular plots, also found more birds at intermediate distances but attributed this to the random movement of distant birds to points within detection range.

In the course of a study using small circular plots, I began to suspect that considerable movement into the plots was occurring during my counts, leading to cumulative rather than instantaneous totals and thus inflating my density figures. In this paper I estimate the degree to which such movement biased my density estimates.

METHODS

CENSUS DATA

I established 24 census points in mature coniferous forests in Yosemite National Park, in the Sierra Nevada of California—12 points in mixed conifer and 12 in red fir forest. My census technique was to stand at a point and record all birds seen and heard within 30 m during each of two consecutive 5-min periods. Two to three flags were placed 30 m from each point to facilitate distance estimation. For birds that I could not see, I first tried to determine which tree and which part of the tree they were in and then estimated the distance to that point. The 142 10-min censuses analyzed in this study (60 in mixed conifer and 82 in red fir forest) were conducted between 05:30 and 09:00 on 7–28 June 1977, during the peak of the breeding season.

ANALYSIS OF MOVEMENT

Data from Mountain Chickadees (*Parus gambeli*), Red-breasted Nuthatches (*Sitta canadensis*), and Golden-crowned Kinglets (*Regulus satrapa*) were used in this analysis. These are common and highly vocal species, unlikely to be missed if within 30 m of an observer for a full 5-min count period. However, 88% of the records of these species were auditory only, and it was nearly impossible to follow the birds' movements visually in these dense, tall forests. Instead I estimated the minimum number of birds that moved across plot boundaries during a 10-min count by comparing the number of each species detected in the first 5-min period with that in the second period. Individuals that were detected during only one of the two periods were assumed to have moved into or out of the plot. For example, if a kinglet was recorded during the first period but not during the second, I assumed it had moved out of the plot. If a kinglet was recorded in each of the two periods, I assumed it was the same individual. It is likely that in some such cases there were two different birds, one having moved out of the plot and the other having moved in. Other cases of movement were undoubtedly overlooked by this analysis. For example, if a bird entered a plot just before the end of the first period and exited early in the second period, and was detected in both cases, my data would provide no evidence of movement. Thus my estimates of the amount of movement are probably underestimates.

The calculations for each species were as follows. Summarizing the results of $c = 142$ 10-min counts I determined n_1, the total number of individuals detected in only one of two consecutive 5-min periods; and n_2, the number of individuals detected both in the first and the second period. The proportion of birds that moved across plot boundaries in 10 min was simply $(n_1)/(n_1 + n_2)$. I also calculated two density estimates for each species, based on the number of individuals detected per 5-min period (D_5) and per 10-min period (D_{10}). If A is the area of the plot, then

$$D_5 = \frac{(n_1 + 2n_2)/2c}{A}, \quad \text{and}$$

$$D_{10} = \frac{(n_1 + n_2)/c}{A}.$$

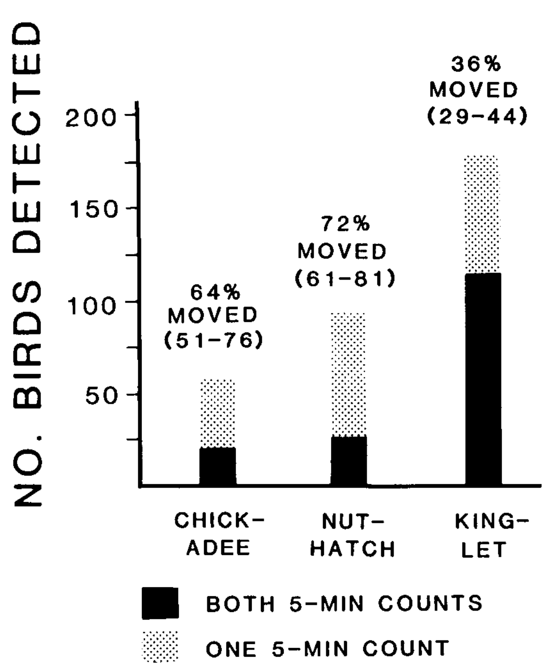

FIGURE 1. Movement of birds based on an analysis of 142 censuses, each consisting of two consecutive 5-min periods, in 30-m-radius plots. I assumed that all birds of these three actively-calling species were detected if present in the plot for 5 min. Thus, if an individual was detected during only one of the two periods, it must have moved into or out of the plot during the 10 min. The 95% confidence interval, based on the binomial distribution, is given in parentheses.

RESULTS

Considerable movement was detected for all three species. As indicated in Figure 1, 72% of the nuthatches, 64% of the chickadees, and 36% of the kinglets that I observed in the plots were detected in only one of two consecutive 5-min periods. Based on the assumptions stated above, this means *at least* those percentages moved across plot boundaries during the 10-min counts. For all three species, the 10-min density estimate was significantly higher than the 5-min estimate: by 56% (44–68%) for nuthatches, 47% (35–61%) for chickadees, and 22% (17–28%) for kinglets (Fig. 2). The values in parentheses were calculated by using the maximum and minimum estimates of cross-

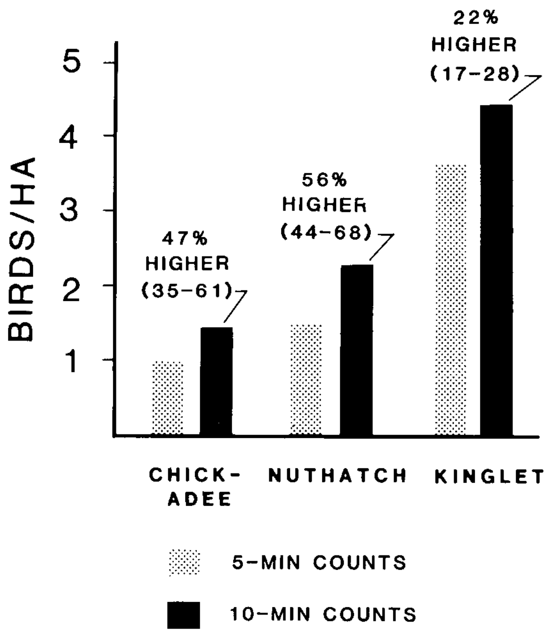

FIGURE 2. Density based on 5-min versus 10-min counts. The values in parentheses were calculated on the basis of the 95% confidence limits shown in Figure 1.

boundary movement, from the confidence intervals shown in Figure 1.

DISCUSSION

FIXED CIRCULAR PLOTS

The reason that density was overestimated is clear. To be accurate, the 10-min count should have approximated an instantaneous count. However, the count included not only those individuals that were present at the instant when the count began, but also all the birds that subsequently entered the plot within 10 min. (A few birds probably left the plot before being detected, but that would affect the 5-min and 10-min estimates equally and thus would not affect the comparison.) Because the rate of influx was high, the density was greatly overestimated. It follows that the 5-min count also overestimated density, to the extent that birds moved into the plot during that shorter time interval. Ideally I should also have determined the bias in the 5-min estimate by comparing it to results from a shorter count period. However, shorter periods were considered too brief to reliably detect all individuals (of the three species) in the plot. A count period longer than 10 min would, of course, result in greater bias. I could not estimate the actual amount of bias in the 10-min density estimates because I did not know the absolute bird densities on my plots.

I believe that density overestimation due to movement for most passerine species in Sierran coniferous forests would be greater than that for kinglets. For species such as Steller's Jay (*Cyanocitta stelleri*), Pine Siskin (*Carduelis pinus*), and Red Crossbill (*Loxia curvirostra*), which range widely and move frequently when foraging, bias would probably be even greater than that for Red-breasted Nuthatches. Raptors, swifts, and swallows are not usually censused by the methods discussed in this paper, due to obvious problems created by movement and large home ranges.

My study contained two potentially serious sources of error. Although I was experienced in estimating the 30-m distance, I undoubtedly made occasional errors in judging a bird "in" or "out." I believe such errors did not affect my results, because I tried to make independent judgments about the location of birds during the two consecutive periods, and the errors probably cancelled each other. A potentially more serious bias would occur if birds were present but not detected. From my own experience and discussions with other ornithologists familiar with these habitats (E. C. Beedy and J. Verner, pers. comm.), I believe that chickadees, nuthatches, and kinglets were unlikely to be missed unless they were sitting quietly on a nest.

I do not believe nests were an important source of bias, for three reasons: (1) Most plots probably did not contain a nest, because the breeding territories of all three species were probably much larger than the 0.28-ha plots. Estimates of territory size for Mountain Chickadees have ranged from means of 1.05 ha (Szaro and Balda 1979) and 1.5 ha (Laudenslayer and Balda 1976) to over 8 ha for a single territory (Minock 1971). The first two estimates were based on the spot-map method and are probably minimum estimates. I could find no information on territory size of the other two species, but judging from that of other small foliage-gleaning forest passerines (see Verner et al. 1980), it is probably at least 1 ha. In my 24 plots I found only three Red-breasted Nuthatch nests and no nests of the other two species. (2) Most visits to the nest would not bias my results. The only situation that would inflate my estimate of movement would occur when a bird was detected during one 5-min period and missed during the other (because it was in the plot but quietly sitting on the nest). (3) Late in the breeding cycle, when the nestlings were large and noisy, a parent's visit to the nest was not likely to go unnoticed.

I conclude that my estimates of bias due to movement are reasonably accurate, at least as minimum values. Probably the only truly accurate method for assessing the amount of movement would be radiotelemetry.

OTHER METHODS BASED ON COUNTS

Bird movement also poses serious problems for other bird census methods based on counts. With variable circular plots several methods exist for calculating density, all based on the number of individuals detected and their distances from the census point. Simulation studies of the method of Ramsey and Scott (1979, 1981) showed that density overestimation could be substantial and was greater for fast-moving species and long count periods (Scott and Ramsey 1981). However, this bias was less than that for fixed plots. It is likely that bird movement similarly affects other density estimation procedures using variable circular plots, including the method of Reynolds et al. (1980).

With strip transects, an observer counts birds within a moving rectangle whose dimensions are determined by the width of the transect and the distance limits, ahead and behind, within which birds are recorded. The "count period" is the length of time that a motionless bird is within the rectangle. Density estimates derived from strip transects are biased by movement of birds to the extent that birds move into the moving rectangle during the count period. Because the strip width in many previous studies was less than or equal to the diameter of my plots (60 m), I suspect that bias was significant. For example, Salt (1957) used a fixed strip width of 60 yards and Beedy (1981) used 30 m. With the variable strip transect method, strip widths ranged from 18–120 m for Emlen (1977) and 50–126 m for Dickson (1978), depending on the species. If Emlen's 6-min count period is typical of strip transect studies, then there is less time for in-out movement than with my 10-min station counts, but bias could still be substantial. Few observers have reported their distance limits fore and aft for recording birds, leading me to suspect that they had no limits. If so, their count periods would be longer, and bias due to movement would be greater, than in Emlen's study.

In line-transect surveys no lateral boundaries are specified, and density estimates are based on the total number of detections and the distribution of detection distances. As with other methods, the error due to bird movement would be greater the longer the count period and the faster the movement. Burnham et al. (1980:21) recognized that "if the subject of the study is a highly mobile animal (such as a passerine bird), serious problems due to movement can arise, often to the extent of rendering line transect sampling useless for such species."

REDUCING BIAS DUE TO MOVEMENT

With all methods, an observer must make a special effort to avoid recording the same bird twice and to detect birds before they move. Burnham et al. (1980) suggested scanning the transect line farther ahead. Note that this also increased the count period, thus increasing the bias due to movement. A compromise solution is to census only a moving rectangle in front of the observer. Emlen (1971) and Reynolds et al. (1980) compensated for evasive bird movement by calculating the average bird density out to a distance beyond the avoidance movement. It is equally important to avoid attracting birds and thereby overestimating density. Burnham et al. (1980:130) also suggested, on mathematical grounds, that if movement is relatively minor then using "a monotonically decreasing estimator like the exponential polynomial" is a satisfactory way to reduce bias.

Probably the most effective ways to reduce bias due to movement are to use larger plots and shorten the count period. Larger circular plots or wider strip transects minimize the ratio of perimeter to area, reducing the relative amount of cross-boundary movement during a count (and also reducing the chance that a bird will leave the plot entirely when avoiding an observer). An analogous approach with variable-plot or plotless methods is to limit the census to birds emitting long-distance cues, e.g., singing males. This would have the same effect as enlarging the census plot. The major problem with larger fixed plots is that more birds may be missed; also there may be more error due to birds recorded twice and inaccurate distance estimation (Scott et al. 1981).

Shortening the count period allows less time for birds to move into the censused area and thus can reduce bias due to movement. With transect methods, this means that an observer must move faster and/or set shorter distance limits fore and aft. Schweder (1977) demonstrated that if the observer's speed is fast relative to that of the animal, then movement is not a serious problem for line transect censuses. Thus, in certain situations bias can be reduced by censusing from a vehicle, such as a car, boat, or airplane. Scott and Ramsey (1981) suggested using count periods of different lengths for species with dramatically different rates of movement.

Shortening the count period, however, increases the risk of missing birds on fixed plots. This poses a serious problem for variable circular plot and variable strip transect methods as well, if there is no substantial basal region of near-perfect detectability. Because it is not usually practical to measure the actual amount of bias, one must subjectively choose the count period and plot size that one believes will reduce overall bias to an acceptable level. In dense, tall vegetation such as the coniferous forests I studied, I would doubt the accuracy of any method unless it were calibrated against bird populations of known density.

In some circumstances it is possible to make an instantaneous count. With some species in open situations, photographs can be used (Nettleship 1976, Birkhead and Nettleship 1980). In the case of fixed circular plot censuses, another possible approach is to record all birds detected on the plot during a specified count period and then, at the end of the period, make a judgment as to which birds are still present. Only those birds remaining would be used for the density estimate. Alternatively, all birds could be counted except those that moved into the count area after the count began. These approaches might be practical in open habitats, especially if the observer(s) were positioned to view the entire plot continuously. But in most circumstances it would be too difficult to detect all movement into or out of the plot.

CONCLUSIONS

The quantitative estimates of bias reported here suggest that movement of birds is a more serious problem than generally recognized for density measurements based on counts. Investigators should acknowledge the probable bias created by movement, at least for active species. If a census method is considered robust to bird movement, that assumption should be tested empirically.

Bias due to movement can be reduced by several different design features, particularly by minimizing the count period and maximizing the plot size. But these "solutions" to the problem of movement also increase bias due to missed birds, birds recorded twice, and inaccurate distance estimation. The choice of plot size and count period must reflect a compromise solution to these competing problems.

Although bias can be reduced, it is likely to remain substantial. More studies testing the accuracy of various methods on populations of known density (e.g., DeSante 1981, Hildén 1981) are the most vital prerequisites for refining bird census methods based on counts. Such studies estimate the overall bias, resulting from problems such as missed birds and inaccurate distance estimation as well as bird movement. Until more is known about all sources of bias, results of methods based on counts should be regarded as relative rather than absolute measures of bird densities.

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Department of Zoology, University of California, Davis, California 95616. Present address: 1031 Ventura Avenue, Albany, California 94706. Received 19 April 1982. Final acceptance 8 August 1982.

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RECENT PUBLICATIONS

Gulls: A guide to identification.—P. J. Grant. 1982. Buteo Books. 280 p. $32.50. Source: Buteo Books, P.O. Box 481, Vermillion, SD 57069. This book republishes the authoritative series of articles on gull plumages and identification that appeared in *British Birds* (v. 71–74, 1978–1981). New are more than 170 monochrome photographs (for a total of 376), and improved drawings. It covers 23 gulls from the Middle East, Europe, and eastern North America. The absence of western North American species renders the book less useful in the nearctic. A world map shows the distribution of those species that are covered. An introductory chapter on gull plumage includes topography, British terminology, and an imprecise description of the sequence of plumages and molts. A thoroughly accurate and welcome guide to the immature and difficult plumages of the species covered. References, index of photographs.—J. Tate.

Wildfowl 33.—Edited by G. V. T. Matthews and M. A. Ogilvie. 1982. Wildfowl Trust, Slimbridge. 176 p. Paper cover. $13.00. Source: Administrative Officer, Wildfowl Trust, Slimbridge, Gloucestershire GL2 7BT, England. Thanks to its now-worldwide scope and revised format, this annual has become an important outlet for scientific papers about anseriform birds. Resembling recent issues (noted in Condor 84:21 and earlier), the latest volume contains 25 articles, nearly one-third of which concern species in the Americas. Ornithologists who wish to receive future volumes should note that only copies to meet known requirements will be printed. While a certain number will be produced for booksellers, those who wish to ensure a copy of No. 34 are encouraged to order and pay for it before 15 September 1983.