AN EVALUATION OF WINTER BIRD POPULATION STUDIES

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THE only large body of data on population sizes of birds in winter is that contained in the winter bird population studies published annually since 1948 in *Audubon Field Notes* (now *American Birds*). The method used in these studies (Kolb, 1965) is that an observer traverses an area of known size six or more times (hereafter termed "visits") during the winter and records all birds observed. After the last visit, the total number of individuals recorded is divided by the number of visits to give an average. This number is then multiplied by the appropriate factor to express results in birds per hundred acres. The same calculations may be made for individual species.

The method appears to have been developed more as a device to make wintertime use of plots established for breeding bird censuses than for any other reason; however, no discussion of the development of the method has been published so far as I know. In the course of conducting such studies it became clear that interpretation of the results was uncertain. This same conclusion has been reached by other workers and, in fact, the difficulty of analysis and comparison has been a persistent theme in the comments by the editor of the winter bird population studies (Kolb, 1961, 1962).

This paper reports results from a model devised to assess the meaning of the figures resulting from the use of the *Audubon Field Notes* (hereafter "AFN") method of studying winter bird populations. I take as a starting point the view that the most desirable datum is density, that is, the number of birds per unit area. For any given area, density changes more or less continually as birds enter the area or leave it. If we visualize a tract of 20 acres on which 10 birds occur but all of which have some portion of their home range lying outside the boundaries of the tract, it is clear that the instantaneous density of the tract can vary between 0, when all of the birds are in those portions of their home ranges off the tract, and 10 when all by chance happen to be on the tract. These figures have some interest but a more valuable figure is some appropriate average of the instantaneous densities. If the average fraction of the home range of the 10 birds included on the study tract was 0.6, then the average density would be 6 birds per 20 acres (assuming that a bird spends equal time in all areas of its home range). An accurate estimate of density would be provided by the AFN method if each bird were recorded on the fraction of visits corresponding to the fraction of its home range included on the tract.

Scientific names of birds mentioned in later sections are Ruffed Grouse, *Bonasa umbellus*; Red-bellied Woodpecker, *Centurus carolinus*; Hairy Wood-

pecker, *Dendrocopos villosus*; Downy Woodpecker, *D. pubescens*; Blue Jay, *Cyanocitta cristata*; Black-capped Chickadee, *Parus atricapillus*; Tufted Titmouse, *P. bicolor*; White-breasted Nuthatch, *Sitta carolinensis*; Brown Creeper, *Certhia familiaris*.

<center>THE MODEL</center>

The basic method used was this: a board was constructed on which were drawn to scale a census tract of 23 acres and the home ranges of eight birds with varying fractions of their home ranges included on the tract. The whole board was the equivalent of about 275 acres and was covered by a grid with coordinates the equivalent of 100 feet apart. The census tract was divided into a grid by lines 200 feet apart (corresponding to every other 100-foot coordinate in the section of the board occupied by the census tract). A simulated observer moved systematically over the tract following the 200-foot coordinates at the same time that a simulated bird (represented by a transparent plastic disk of known diameter) moved within its home range. If the plastic disk touched or overlapped a point occupied by an observer, the bird was considered to be observed and was counted.

Although some simplifications were necessary, the model was made as realistic as possible. Because a primary aim was the eventual assessment of studies conducted from 1966 to 1970 on five study tracts in oak and oak-pine forests of Allegan County, Michigan, the features of the model were based as far as possible on the biological features of the bird community of those areas. On these areas, which varied in size from 9.6 to 18.4 acres, about 20 species of birds were observed on more than 150 visits between November and March. Only 7 species were seen on all five tracts. Populations were low, AFN estimates being in the range from about 5 to 8 birds per study tract or about 30 to 55 birds per hundred acres. Black-capped Chickadee was the most common species with an AFN estimate of about 20 birds per hundred acres. White-breasted Nuthatch, Blue Jay, and Tufted Titmouse were the next most common species.

Specific features of the model were as follows:

1. Home range sizes varied from 9 to 76 acres, with six between 22 and 38 acres (Table 1). These are reasonable sizes for home ranges of forest birds based on our unpublished determinations and the literature (see, for example, Butts, 1931; Fitch, 1958; Kilham, 1969; Robins and Raim, 1971). The percentages of the simulated home ranges lying on the tract varied from 4 to 100 per cent.

2. The initial position of the observer at the beginning of a trial, or simulated visit, was at the southeast corner of the tract. His movement was then systematically across the tract. Systematic movement along coordinates was

TABLE 1

RESULTS OF THE MODEL EVALUATING AFN WINTER BIRD STUDY METHODS.
Trials = 25 except as indicated.

Home range	Percentage on tract	Size (acres)	Occurrence (Percentage of trials recorded)		
			36' radius	75' radius	250' radius
		Normal speed			
J	4	34	0	7	12
A	14	37	4	22*	48
C	30	76	20	56*	92
G	45	38	32	56*	88
D	65	22	24	63*	96
E	65	35	36	64	84
H	100	8.6	24	89*	100
B	100	23	24	68	100
		Half-normal speed			
J	4	34		8	
A	14	37		32	
C	30	76		48	
G	45	38		44	
H	100	8.6		64	
		Twice-normal speed			
J	4	34		12	21**
C	30	76		76	93**
G	45	38		88	100**
D	65	22		64	100**
E	65	35		88	100
H	100	8.6	60***	92	100**

* 27 trials
** 14 trials
*** 20 trials

the method employed in the field by us and by many participants in the AFN studies, but it is not a requirement of the method (Kolb, 1965).

3. The initial position of the bird was determined by the use of randomly chosen numbers indicating a coordinate position on the board. The direction of the bird's first movement was determined randomly from among the eight primary compass directions. After the first movement, the three opposing directions were eliminated for subsequent movements. For example, if the first movement was east, then west, northwest, and southwest were eliminated. The possible actions for the bird on its second movement were six of equal probability: north, northeast, east, southeast, south, and no movement. Tests in the development of the model showed that if all eight directions were re-

tained the simulated bird tended to stay in a restricted area near its initial
position rather than to move over its home range in a manner corresponding
more closely to the actual movements of birds in the field.

Eventually movement of the simulated bird might bring it to the edge of
its home range. At this point all directions were again made available and
the no-movement possibility was eliminated. Certain movements, those which
would take the bird outside its home range, were impossible in this situation
and were rejected; other movements would move the bird along the edge of
its home range. The first move which took it away from the edge into its
home range was used as a new direction and the procedure of discarding the
three opposing points of the compass was again followed (and the no-move-
ment possibility re-instated).

The paths taken by the simulated birds under these procedures seemed
realistic when compared with our maps of actual paths taken by birds in
the field.

4. Three different speeds of movement of the bird relative to the speed of
the observer were used. These were approximately one-half the speed of the
observer (termed "normal speed"), one-fourth the speed of the observer
(half-normal speed), and the same as the speed of the observer (twice-normal
speed). In our censusing of oak forests, the actual speed of the observer
(median values) varied by area from about 56 to 69 feet per minute (fpm),
or about 0.6–0.8 miles per hour (mph). In subsequent sections 67 fpm is
used as the speed of the observer. Although slightly faster than our actual
overall average, it is convenient as a rate taking exactly 3 minutes from one
stake to the next.

The actual movements on the board were as follows: For half and full
speeds the observer went from one grid intersection to the next (200 feet)
in two moves of 100 feet (that is, from one board coordinate to the next).
The bird took one move (normal speed) or two moves (twice-normal speed)
for each move of the observer. The moves of the bird were one-half square.
Going north, south, east, or west, one move of the bird was 50 feet; going
one of the four intermediate directions it was about 71 feet. For half-normal
speed the observer went from one grid intersection to the next (200 feet) in
a single move and at the same time the bird took one move.

At any time the possibilities for movement for the bird were 3 50-foot
moves, 2 71-foot moves, and no movement. Consequently, the average dis-
tance per move was about 49 feet. Twice-normal speed for the bird, accord-
ingly, was about 65 fpm, normal speed 33 fpm, and half-normal speed 16 fpm.

There is relatively little information in the literature on the rate of travel
of birds. Yapp (1956) commented that he had timed feeding winter tit flocks
at speeds from one-eighth to two mph (that is, about 10–175 fpm). Odum

TABLE 2

RATE OF MOVEMENT OF THREE SPECIES OF OAK FOREST BIRDS, ALLEGAN COUNTY, MICH-
IGAN, FEBRUARY–MARCH, 1969.

Species	Number of observations	Total minutes	Feet per minute	
			Range	Median
Downy Woodpecker	7	140	12–71	23
White-breasted Nuthatch	14	229	9–122	30
Black-capped Chickadee	9	149	15–64	42

(1942) reported rates of movement of Black-capped Chickadees, based on all-day observation of flocks, from 18 to 40 fpm. He observed that speeds varied by time of day and by weather conditions and commented that movement was not uniform, periods of rapid movement (up to 350 fpm) alternating with periods of little or no movement.

Our own observations made on one of our study areas at Allegan (the Small Oak area) in February and March 1969 generally agree with these findings. The observations were made (in connection with studies designed to determine home range boundaries) by following birds for as long as possible and mapping the observations. Measurement of distance was along the actual path followed and speed was calculated using the time elapsed from the first to the last observation of the bird. Obtaining data on speed that are unbiased is difficult. For example, the speed of birds which travel by moving slowly through the forest and then taking a long flight to another area beyond the range of observation will be generally underestimated because the long flights will be omitted from the sample. Also it is important that short observations as well as lengthy ones be included, inasmuch as observations of greater duration may be of birds traveling slowly enough that they can be readily followed. I used a lower limit of four minutes for the practical reason that estimates of speed based on shorter durations might be too inaccurate owing to our recording times only to the nearest minute.

The data seem to indicate that birds may travel at speeds from less than 10 to more than 100 fpm and that variability is appreciable (Table 2). They indicate also that for the time and place they were gathered speeds of three important species of the forest are in the range between 20 and about 40 fpm.

5. Differences in conspicuousness were taken into account by using plastic disks of three radii corresponding to 36, 75, and 250 feet. The circle of 36-foot radius represents a very inconspicuous species, the circle of 250-foot radius, a very conspicuous one. If the disk touched or overlapped the point occupied by the observer or his path in moving from one point to the next,

the bird was counted. This corresponds to a situation in which a bird is totally observable up to a given distance from an observer and is never censusable beyond that distance (curve 1 in Fig. 2 of Eberhardt, 1968), an obviously unrealistic situation. It also corresponds, however, to a situation in which the radii represent median distance of observability (defined as probability of observation). For example, the 75-foot circle represents a situation in which the number of birds nearer than 75 feet that are missed is the same as the number of more distant birds that are observed.

The relationship in the field between observability and distance from the observer is difficult to approach directly. We may visualize the observer in the center of a space that can be subdivided by circles drawn at equal distances going outward from him. The area of the concentric rings so produced increases outward. For example, if 50-foot intervals are used, the ring from 50–100 feet away is larger than the circle from 0–50 feet and the ring from 100–150 feet is larger still. Assuming a homogeneous distribution of birds in the space, the number of birds present in each ring will, accordingly, increase going outward. The increase in area of the concentric rings is linear and so, consequently, is the increase in number of birds present at given distances from the observer. Discussions germane to these ideas but developed in connection with strip censuses are given by Anderson and Pospahala (1970) and Emlen (1971).

If there were no decrease with distance in the ability of an observer to detect birds, the number of birds seen at increasing distances would increase, following curve A in Fig. 1. In fact, we expect observability to decline with distance. Curve B represents a linear decline in observability from 100 per cent at the point occupied by the observer. In this case, the number of birds actually observed would be related to distance from the observer as shown in curve C.

A linear decline in observability with distance is not an unreasonable assumption but other reasonable relationships can be envisaged. I approached the question indirectly in the following manner. During routine visits to the oak forest study areas in the winter of 1968–9, the observer recorded the distance from each stake on each plot at which any bird could be observed by sight or sound. Estimating distances in the field is not easy but was facilitated by the observers' familiarity with the study areas, by the areas being staked at 200-foot (in some cases, 100-foot) intervals, and by the use of maps showing any prominent topographic and vegetational features. Data deemed sufficient for analysis were obtained for the White-breasted Nuthatch (Table 3) on one study area, the Black-capped Chickadee on three study areas, and the Ruffed Grouse on one study area (Table 4).

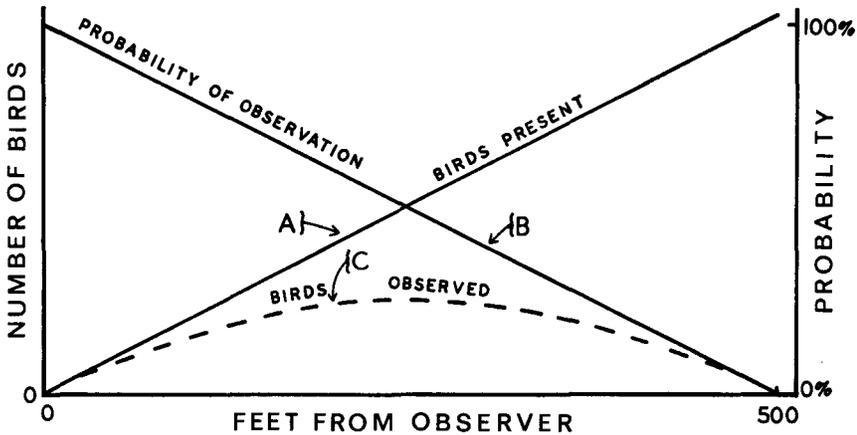Grouping of observations by distance (observations falling at a class

FIG. 1. Relationship between the number of birds present, their probability of being observed (observability), and the number of birds actually observed in ten concentric zones centered on the observer. A linear decline of observability from 100 per cent at distance 0 to 0 per cent at 500 feet is assumed.

boundary, as for example at 100 feet in Table 3, were counted as one-half observation in each class) and plotting the result gives curves corresponding to C in Figure 1. Making the assumption that observation is 100 per cent efficient in the closest zone, the actual number of birds present in each zone can be calculated as in Table 3 (cf. Anderson and Pospahala, 1970: 142–145,

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TABLE 3

RELATIONSHIP OF NUMBER OF WHITE-BREASTED NUTHATCHES OBSERVED AND PROBABILITY OF OBSERVATION TO DISTANCE FROM OBSERVER (LARGE OAK AREA, ALLEGAN CO., MICHIGAN, WINTER 1968-9).

Number of birds estimated as actually present in each zone is calculated by determining density for zone 1 (0.00077 per square foot in this case) and multiplying this value by the area of the other zones.

Zone (Distances in feet)	Area of zone (square feet)	No. of observations	No. birds calculated as present	Probability of observation
1 (0–100)	31416	6	6	100
2 (100–200)	94248	5.5	18	31
3 (200–300)	157080	5	30	17
4 (300–400)	219912	2.5	42	6
5 (400–500)	282744	1	54	2
6 (500–600)	345576	0	66	0
7 (600–700)	408408	1	78	1

TABLE 4

RELATIONSHIP OF NUMBER OF BLACK-CAPPED CHICKADEES AND RUFFED GROUSE OBSERVED
AND PROBABILITY OF OBSERVATION TO DISTANCE, ALLEGAN CO., MICHIGAN, WINTER 1968-9.

Zone (distances in feet)	Black-capped Chickadee						Ruffed grouse	
	Large Oak		Small Oak		Large Pine		Small Pine	
	No. Obs.	Prob.	No. Obs.	Prob.	No. Obs.	Prob.	No. Obs.	Prob.
1 (0–40)	2	100	5	100	6.5	100	4	100
2 (40–80)	5	83	7	47	11.5	60	6	50
3 (80–120)	1	10	5	20	2.5	8	1.5	8
4 (120–160)	1	7	2	6	1.5	3	0.5	2
5 (160–200)	0	0	—	—	—	—	—	—
6 (200–240)	1	4	—	—	—	—	—	—

and Emlen, 1971: 329–333). If these figures were plotted they would corre-
spond to curve A of Fig. 1. Dividing the number of birds observed by the
number calculated to be present gives a curve relating probability of obser-
vation of distance (Table 3), corresponding to curve B of Figure 1. The
assumption of 100 per cent efficiency in zone 1 is probably erroneous (see,
for example, Enemar, 1959: 78–89, and Emlen, 1971), but this will not
affect the shape of the probability curve derived. The shape would be affected
if the distribution of birds were not homogeneous around the observer; bias
might be serious if the presence of the observer affected the distribution by
attracting birds or driving them away. My impression is that for winter
studies in oak forest this was not a serious problem in that any such move-
ments tended to be within zone 1 rather than between zones.

The results suggest that probability of observation declines rapidly at first
and then more slowly (Tables 3 and 4). It is clear that a straight-line rela-
tionship does not hold over the whole distance from zero to the limits of
observation. A negative exponential relationship like that suggested by Gates
et al. (1968) for the flushing of Ruffed Grouse is a possibility, but it is also
possible that the relationship is a reversed sigmoid curve like curve in Fig.
2 of Eberhardt (1968), with a short upper limb hidden within zone 1.

I return now to the suggestion that the radius used for the plastic disk
simulating a bird should represent the median distance of observability. This
distance, at which the number of near birds missed is equal to the number
of far birds seen, shifts depending upon the observability curve. Calculation
of the median distance of observability appears to require a knowledge of
this curve, information which, as I have indicated, is not readily obtained.
One can, however, fairly readily obtain actual distances of observation in

TABLE 5

DATA FOR COMPARISON OF MEDIAN DISTANCE OF OBSERVATION AND MEDIAN DISTANCE
OF OBSERVABILITY, USING AN ARBITRARY DENSITY OF 0.0026 BIRDS PER SQUARE FOOT AND
AN ARBITRARY REVERSE SIGMOID RELATIONSHIP BETWEEN PROBABILITY OF OBSERVATION
AND DISTANCE FROM OBSERVER.

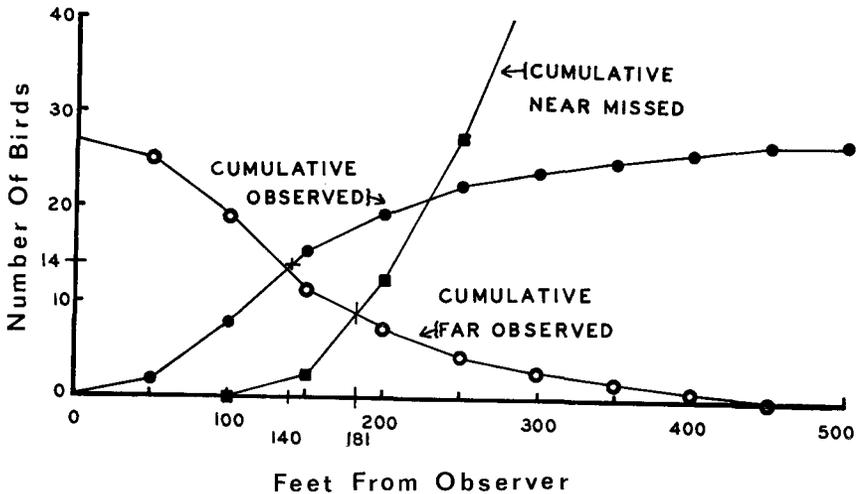| Distance from observer (feet)	Number of birds present	Probability of observation	Number of birds seen	Cumulative numbers		
				Birds seen	Near birds missed	Far birds seen
0–50	2	0.99	2	2	0	27
50–100	6	0.95	6	8	0	25
100–150	10	0.75	7.5	15.5	2.5	19
150–200	14	0.30	4	19.5	12.5	11.5
200–250	18	0.15	3	22.5	27.5	7.5
250–300	22	0.07	1.5	24	48.0	4.5
300–350	26.5	0.05	1	25	73.5	3
350–400	31	0.03	1	26	103.5	2
400–450	35	0.02	1	27	137.5	1
450–500	39	0.01	0	27	176.5	0

Fig. 2. Comparison of median distance of observation and median distance of observability for data in Table 5. Median distance of observation is the distance below which and above which half of the birds were observed. A total of 27 birds was observed; consequently, the median is the distance at which the 14th bird was seen, or about 140 feet. Median distance of observability is the distance at which the number of near birds missed is equal to the number of far birds observed, or about 181 feet.

some manner such as that described on page 266; from such data one can
calculate a median distance of observation. The median distance of observa-
tion is the distance below which and above which half of the actual observa-
tions lie. I have investigated the relationship between the median distance of
observation and the median distance of observability using models based on
various observability curves. Table 5 and Fig. 2 illustrate the method for an
arbitrary reverse sigmoid relationship between observability and distance.
Graphical solution (Fig. 2) indicates that the median distance of observation
is about 140 feet and the median distance of observability is about 181 feet.
All of the observability curves which I have tested, including most of the
biologically reasonable ones, yielded a similar relationship of the median
distance of observation lying within the median distance of observability;
the quantitative relationship between them, however, varied considerably de-
pending on the exact nature of the observability curve. For birds in oak
forests the median distance of observation lies between 40 and 200 feet and
several are clustered between 50 and 100 feet (Table 6; see also the appro-
priate species in Table 9 of Kendeigh, 1944. The latter figures apparently
are means rather than medians; because of the occasional bird observed at
a great distance, the mean will usually exceed the median for data of this
sort.) Presumably these medians are all in some degree underestimations
of the median distance of observability. In sum, the oak forest data seem to
justify the radii of 36 feet as a very inconspicuous species, 250 feet as a very
conspicuous one, and 75 as a species of average conspicuousness.

6. As soon as a given simulated bird was tallied, the trial was discon-
tinued; this corresponds to a situation in which an observer can invariably
avoid counting the same bird more than once on a visit. This is undoubtedly
unrealistic, but I have no information on the frequency with which birds
are counted more than once, nor on how often birds are not counted in the
belief that they had already been recorded.

Fourteen to 27 (mostly 25) trials, or simulated visits, were used for each
home range under each set of radius/speed conditions. In all, 1000 simulated
visits were used (Table 1).

RESULTS

The relationship of basic importance is that between the percentage of
visits on which a bird is recorded (hereafter this percentage is called "occur-
rence") and the percentage of the bird's home range lying on the study tract.
For the AFN method to indicate accurately the contribution of a given indi-
vidual bird to the density of birds on the tract, the two values must agree.
This relationship is indicated by the diagonal line in Figs. 3 and 4.

For all conditions occurrence was positively related to the percentage of
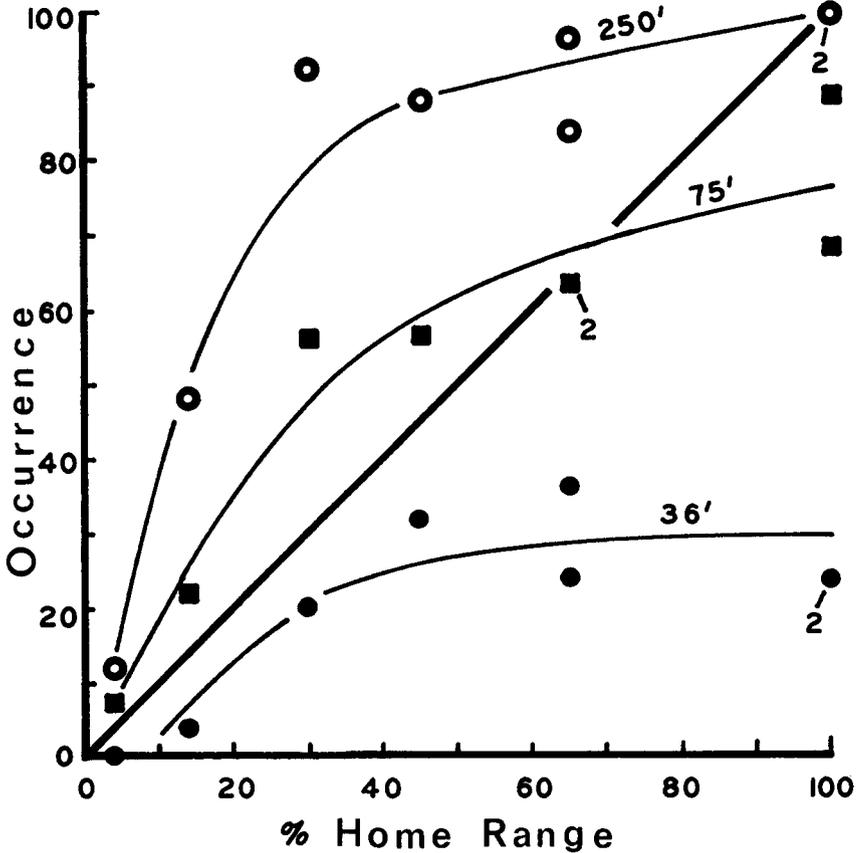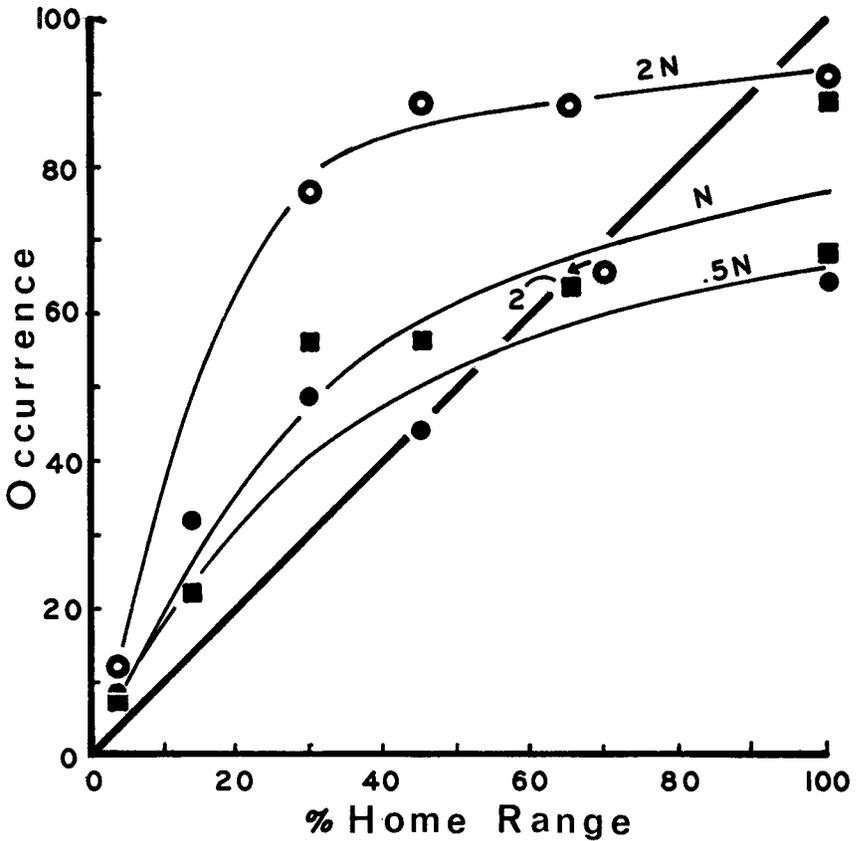
FIG. 3. Relationship between occurrence (percentage of simulated visits on which a bird was counted) and percentage of the bird's home range on the study tract (birds moving at normal speed) for highly conspicuous birds (circle, 250-foot radius of observability), moderately conspicuous birds (squares, 75-foot radius), and inconspicuous birds (dots, 36-foot radius). Lines were fitted by eye.

the home range on the tract. In no case, however, did the curve relating occurrence to home range follow the required diagonal (Figs. 3 and 4, Table 1). Both conspicuousness of the bird and its speed relative to that of the observer influenced occurrence. The closest approach to the diagonal and, thus, the closest approach to an accurate reflection of density was given by the combination of a 75–foot median distance of observability and normal speed. All of the other combinations gave curves lying further from the diagonal.

FIG. 4. Relationship between occurrence (percentage of simulated visits on which a bird was counted) and percentage of the bird's home range on the study tract for birds (moderate conspicuousness) moving at normal speed (squares), twice-normal speed (circles), and half-normal speed (dots). Lines were fitted by eye.

For any conspicuousness: speed combination the basic curve relating occurrence to per cent home range on the tract showed a fairly sharp initial rise and then tended to level off (Figs. 3 and 4, Table 1). The AFN method, accordingly, is relatively insensitive to changes in percentage of home range on the tract from 30 or 40 to 100 per cent.

Occurrence increased with increased conspicuousness but the exact relationship was complex. The same increase, either actual or proportionate, in median distance of observability was more effective in increasing occurrence when the increase was in the range from 36 to 75 feet than when in the range

from 75 to 250 feet (Table 1). Also, the increase in occurrence was greater for a given increase in median distance of observability for birds with large percentages of their home range on the tract than for those with small (Table 1).

Occurrence increased with increased speed of the bird relative to that of the observer (Fig. 4, Table 1). Increasing to twice-normal the speed of birds with a median distance of observability of 75 feet moved their curve far above the diagonal into about the same position occupied by highly conspicuous birds (250-foot radius) traveling at normal speed.

There was no consistent indication that size of home range had an effect on occurrence (cf. home ranges D with E and H with B in Table 1).

<div align="center">DISCUSSION</div>

It is clear that the AFN method fails in most situations to indicate accurately the contribution of an individual bird to the avian population of a study tract. To recapitulate, the relationship between occurrence and percentage of home range on the tract is non-linear, such that occurrence increases only slightly for home ranges 100 per cent on the tract compared with those 40 per cent on the tract. Occurrence is also affected by the conspicuousness of the bird and the speed of the bird relative to that of the observer.

Other things being equal, the 75-foot radius of observability gave best results. I suspect that this is true because this value, among the three used, most nearly approximates half the distance between census-plot coordinates. With the 36-foot radius a bird may be within a square adjacent to the observer and escape observation. With the 250-foot radius, a bird may be beyond the adjoining coordinate and still be observed; consequently, if the bird has any substantial part of its range on the tract, the probability of tallying the bird at some time during the visit becomes very high, approaching 100 per cent once half or more of the home range is included on the tract (Table 1, Fig. 3). It is a matter of some interest that, with the 75-foot radius, even birds whose home ranges are wholly on the tract, whether contained within it or coincident with it, were not invariably encountered on a visit (Table 1). This was made possible by the movements of the bird producing a path that avoided the observer.

Presumably a bird which remained stationary for the length of a visit and which was of sufficient conspicuousness to be seen from one point on the tract, if it were on the tract, would be recorded on the number of trials corresponding to its percentage of home range on the tract. Increasing the speed of the bird increases its exposure to the observer, at least for home ranges having a small percentage of their area on the tract and, thus, results in these birds being observed too often. Allowing birds with a very high percentage

of their home range on the tract to move, however, introduces the possibility of their eluding the observer, as described above. It is unclear whether birds moving at one-fourth the speed of the observer are censused much more poorly than birds moving at one-half the speed of the observer (Table 1, Fig. 4); it is, however, clear that birds moving at the same speed as the observer are generally observed far too often.

The aim of the AFN method is to estimate abundance—ideally density—of the total bird community and its constituent species. This is slightly different from the question of how well the method assesses the contribution to density of an individual bird and is worth examining directly. To begin with, very conspicuous birds and birds having speeds equal to that of the observer will almost invariably be overestimated. The Blue Jay is probably an example of a species which will be overestimated. Very inconspicuous birds (the Brown Creeper, perhaps) will invariably be underestimated, possibly excepting cases in which they are very fast moving.

Birds of medium conspicuousness and moving at speeds one-half to one-fourth that of the observer will produce estimates that may be close to the actual density on the tract. The occurrence curve for such birds cuts the diagonal in such a way that birds having a small percentage of their home range on the tract will be overestimated and birds having a large percentage will be underestimated. If birds of both categories occur on the tract, the errors will be in opposing directions. It would be too much to expect that the errors would cancel one another but the tendency would be in this direction. Unfortunately, the extent and direction of the final error will be impossible to calculate.

Possibly some species of birds of the oak forests fit reasonably well the conditions of conspicuousness and speed which allow fair estimates of density (Tables 2 and 6). More information on conspicuousness and speed could be used, however, before drawing such a conclusion. These topics are worth some further research. Persons making AFN studies could contribute data on conspicuousness and help to interpret their own figures by recording distances at which birds are observed. It is certain that variations in speed and conspicuousness will affect estimates greatly; consequently, if a bird is fast moving at one period of the year and slow at another, or if it is more conspicuous in one vegetation type than another, the figures derived in these separate situations will not be comparable.

One important consideration in the winter study of populations not dealt with directly in the model is the tendency of many species to occur in flocks. If only mathematical considerations were involved, the effect would be simply to increase variability over the situation in which each bird moves independently. This is undoubtedly one of the reasons for the visit-to-visit vari-

TABLE 6

MEDIAN DISTANCE OF OBSERVATION FOR SEVERAL OAK FOREST BIRDS. THE STUDY AREAS
WERE LARGE OAK (LO), SMALL OAK (SO), LARGE PINE (LP), SMALL PINE (SP),
AND GREENBRIER (GB).

Species (Study Area)	No. of observations	Median distance (feet)
Brown Creeper (LP)	3	40
Brown Creeper (SO)	3	90
Ruffed Grouse (SP)	12	50
Black-capped Chickadee (LP)	22	60
Black-capped Chickadee (SO)	19	60
Black-capped Chickadee (LO)	10	50–75
Tufted Titmouse (GB)	5	70
Tufted Titmouse (LO)	9	100
White-breasted Nuthatch (GB)	7	70
White-breasted Nuthatch (LO)	21	200
Blue Jay (LO)	15	175
Red-bellied Woodpecker (LO)	9	200

ability in actual counts which, in my field experience, is substantial. In light
of this variability, the six visits minimally required by the AFN method may,
by chance, give very atypical results and will give a variance so large that
statistical demonstrations of any except enormous differences between years
or areas may be impossible. Other, biological, considerations may, however,
also be involved. Probably the presence of a bird in a flock increases its
likelihood of being seen. This is so because the flock tends to be more con-
spicuous than a single bird and once any member of a flock is detected, the
observer is likely to observe most or all of the other members. Individual
conspicuousness and flock conspicuousness may, then, be different things.
Values such as those given in Table 6 will, however, tend to reflect the con-
spicuousness of the usual unit (flocks for chickadees, individuals for creepers,
twosomes for nuthatches) so that we are led again to the conclusion that the
most important effect of conspecific flocking on AFN results will be to in-
crease variability.

Because of the severe biasing effect of bird speeds that are high relative to
the observer's speed, I would recommend that in conducting AFN studies the
observer move at the most rapid pace compatible with his ability to detect
birds in his vicinity. Doubtless this pace will vary among habitats. It is per-
haps worth emphasizing that this recommendation is designed to increase the
likelihood that AFN figures will approximate densities; if the aim is to in-
clude as many as possible of the birds whose ranges touch the tract, an ex-

tremely slow pace would be best but the estimates derived will then be over-estimates for all except the very inconspicuous species.

This discussion has emphasized the fact that AFN figures are full of imponderables. It may be desirable to conclude with a point that, if not optimistic, is at least moderately firm. In the special situation in which the study tract is so isolated or circumscribed that all birds have their home ranges entirely within it, all species except the most conspicuous ones will be underestimated.

SUMMARY

A model was designed to evaluate estimates of bird numbers derived by methods em-ployed in *Audubon Field Notes* winter bird population studies. Strictly accurate esti-mates of density would result if the percentage of visits to a study tract on which a bird was seen (called "occurrence") was the same as the percentage of that bird's home range lying on the tract. This linear relationship was not found; instead occurrence tended to level off at percentages above 40. Occurrence was also affected by the con-spicuousness of the bird and by the speed of movement of the bird relative to that of the observer.

It was concluded that in field situations fulfilling the conditions of the model very conspicuous birds would be overestimated and very inconspicuous birds underestimated. Estimates for species of medium conspicuousness might be fair approximations of actual density, owing to the tendency of the method to underestimate the contribution to density of birds with a high percentage of their home range on the tract and to overestimate the contribution of birds with a low percentage. These conclusions hold for birds moving slowly relative to the observer. Density of birds moving as fast as the observer will be drastically overestimated, except for very inconspicuous species.

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(From the author's abstract) "Observations of hunter performance provide information on specific differences in crippling losses and on factors governing the choice by hunters of what ducks they shot at, how effectively they shot at different times during the season and in various kinds of weather and what proportions of the ducks brought down were retrieved and kept."—G.A.H.