The Theory and Practice of Line Transects in Animal Ecology by means of Visual and Auditory Recognition

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Introduction

Line transects have been widely used for sampling animal populations, especially in estimating the abundance of birds. But until Yapp (1955), there had been no valid basis for the line transects. Before then some ornithologists had been trying to improve the method in order to obtain more reliable results, but they had done so only empirically. The conventional method that has been frequently used by ornithologists is to count the birds an observer sees or hears as he walks, and to use the number recorded per unit time as an index of relative abundance. But two sorts of errors seem to result from the use of this method. One relates to the conspicuousness of the birds and the other has to do with the mobility both of the observer and the birds. Colquhoun (1940 a, b) discussed this problem and introduced the concept of “conspicuousness.” But his index of conspicuousness can only be determined empirically and it has no general applicability because it may vary with the observer, with the species and with the habitat. He also showed that the number of birds observed per unit time varied with the walking speed of the observer. He compared his number per unit time with the result obtained by a census and obtained a numerical value for his coefficient of correction (vi. et. Nordberg, 1947). But this coefficient could not be made a general law. It had to be determined case by case, and did not provide any theory about the problem of variation in number per unit time nor any general rule for correcting the results in order to compare them with other results obtained by other observers in other places at other times.

Until recently no investigator has made use of the speed of the birds, in other words, no care was taken to correct the number per unit time by making use of the speed so as to compare one result with another. If the figure represented by the number per unit time is to be used for comparative purposes it should give some evidence that the number per unit time is proportional to the actual abundance irrespective of the variations in the speed of the birds, but it gives no such evidence. Then Yapp (1955) put forward his theoretical basis for line transects. According to his theory the absolute density of the birds is calculable if the speed of the birds, the speed of the observer, and the effective radius of the birds, are known; or even when these terms are unknown, the number of birds recorded per unit time can be used as a relative index of abundance provided only that the terms are known beforehand to be constant. He pointed out that any work is of little value in which no information about these terms is made use of in the calculation. But there are certain...
situations in which Yapp's method does not seem easy to use. Therefore I felt it to be necessary to derive another mathematical formula from a slightly different model in which all the factors included in Yapp's formula would be taken into consideration.

In 1956 I conducted several sets of sample counts in a woodland and supplementary data were collected in 1957 and in 1958. I found, when I compared the densities calculated by my formula with those obtained by complete census, that there was a serious discrepancy between them, while I found that the number of birds recorded per unit time was proportional to the actual abundance irrespective of the speed of my birds. My results seem to support that part of the conventional idea which Yapp called into doubt. My results do not seem to bear out the direct application of Yapp's mathematical theory to some situations in the field.

It is, however, not surprising that theory which is based on a very simplified and ideal situation, though mathematically valid, does not fit a complicated actual situation. The important thing is to find how great the discrepancy is and why it occurs.

Acknowledgement

I would like to express my gratitude to Prof. Masatoshi Nitto for his kind leading. I am much indebted to Dr. Motosaburo Masuyama for his help with a criticism of my theoretical formulation.

Sampling Methods and Their Theoretical Justification

An observer walking through a habitat encounters all the birds which happen to be located within his field of perception. This field of perception around the observer moves as he walks, and whatever its shape or range, it has a more or less fixed boundary. Therefore as the observer moves all the individuals which happen to be located within the range of his perception will soon or later come into his perception. In much of the ornithological sampling work done up to now the number per unit time recorded this way (in most cases the number per hour) has been used as an index of the relative abundance of different species or of the same species at different places or at different times (see Grinnell and Storer, 1924; Linsdale, 1928; Dice, 1930; Lack, 1937; Kendeigh, 1944). Of course there may be birds which make contact with the observer more than once by doubling back on their paths. Therefore care has always been taken to avoid this multiple recording of any one individual. But, as mentioned above, this idea was never supported by valid, reasoned explanation taking both the movement of the observer and the birds into account.

Yapp (1955) gave a density-calculating formula derived from the kinetic theory of gasses as follows:

\[(i) \quad D = \frac{z}{2RV}\]
\[(ii) \quad V^2 = \bar{u}^2 + \bar{w}^2\]

where \(D\) stands for the density of the birds, \(z\) the number of encounters between the observer and the birds in unit time, \(R\) the effective radius of the birds, \(\bar{u}\) the average speed of the birds, and \(\bar{w}\) the average speed of the observer.

Yapp's theory, though it is originally derived from the kinetic theory of gasses,
is fundamentally based on Poincaré's formula in integral geometry (see Masuyama, 1957). According to Masuyama the number of encounters between the observer and the birds is defined as half the number of points of intersection of two kinds of curves each having its own fixed length, i.e. the path of the observer and the effective radius of the bird or the path of the bird and the boundary of the observer's field of perception. In this theory it is assumed that all parts of the area are equally likely either to contain birds or to be visited by the observer (Skellam, 1958).

One of the most important sampling works is the one that is made in order to obtain the density of a breeding population. In the breeding season most of the birds are territorial, in other words, they are mostly restricted each to its own occupied area. When I tried to derive a mathematical formula based on assumptions, which more closely fit this situation, that every birds has each own definite range of movement within which it moves in a random pattern, that their ranges of movement are distributed at random over the habitat, and that the number of encounters between the observer and the birds is proportional to the speed of the birds relative to the observer, I found that my work resulted in exactly the same formula as Yapp (see appendix for mathematical formulation). So this means that Yapp's formula is also valid when the birds are territorial.

In Yapp's theory a bird must be counted every time it comes into observer's field of perception irrespective of whether he has met it before or not. A schematic representation of the way this is done is shown in Fig. 3 (see transect A) where the encounters are indicated by small open circles. In an actual situation it is often not an easy matter to record such multiple encounters. In a woodland, for instance, there are many obstacles which will prevent the observer from continuous watching of a particular bird. In this situation a bird which comes into the observer's field of perception once may happen to disappear from his sight behind an obstacle, say a mass of foliage, and when it reappears he cannot be sure whether he has made contact with it more than once or not. Moreover in general the conspicuousness of the bird decrease as the distance increases, and the behaviour of the bird just inside or just outside the periphery of the observer's field of perception may be harder to see, with the result that it is difficult to determine the exact number of the points of intersection of the birds' path and the boundary of the observer's field of perception. In such a case the observer can tell only whether or not he has made contact with the bird; not how many times he has made contact. Still one must admit that many trained ornithologists can distinguish one bird from another by behaviour, and that this enabled them not to count the same individuals more than once.

When sampling is conducted in such a way that the observer counts every individual bird he sees or hears along his path (transect) within the range of his perception but does not count any one individual more than once, the density of the birds will be calculated by one of the following formulae:

\[
(I) \quad D = \frac{z}{2w \left( R + L \frac{V - w}{V + w} \right)} \quad (L \leq R)
\]

\[
(II) \quad D = \frac{z}{2w \left( R + L - \frac{2L}{n+1} \frac{(n-1)(L-R)^{n+1}}{(n+1)L^n} \right)} \quad (L < R)
\]

\[
(n = V/w)
\]

(3)
where $D$ is the density of birds; $z$ is the number recorded in unit time; $R$ is the radius of the observer's field of perception; $V$ is the average speed of the birds relative to the observer which is given by Yapp's second formula; $\bar{w}$ the average speed of the observer; $L$ is half the square root of the average area of the range of movement of the birds.

The above formulae will give an approximate value for $D$ when the length of the transect is a certain given amount longer than $L$; if not the formulae will not hold true (the complete statement of these formulae appears in the appendix.). If $L$ is not larger than $R$, formula (I) should be used, otherwise formula (II) should be used.

A schematic figure of this method is shown in fig. 1 (see transect $B$). The small circles indicate the locations where the birds are met and recorded by the observer; small black circles indicate the locations where the birds are met by the observer but not recorded; arrow headed irregular curves indicate the paths of the birds.

The number of encounters between the observer and the birds increases theoretically as the speed of the birds relative to the observer increases. Transect belt $G$ represents a conventional idea which uses the number of birds recorded per unit time as an index indicating the relative abundance of the birds but does not take into account the speed of birds; variability of this index with the speed of the birds is not considered. Transect belt $A$ represents an idea based essentially on Yapp's theory; all the encounters between the observer and the birds are to be recorded; where and how many times an individual bird is met by the observer is a matter of probability which is a function of the density and the average speed of birds; the density of the birds is given by Yapp's first formula. Transect belt $B$ represents the idea that when all the birds met by the observer are to be recorded only once, the density of the birds can be calculated by formula (I) or (II) in the text which also takes the relative speed of the birds into account.

because the number of territories which overlap the transect belt is a limited number, in other words, the number per unit time obtained by this method, i.e. $z$ in the formulae, increases gradually as the average speed of the birds increases but never exceeds a certain level. Thus

$$\lim_{\bar{w} \to \infty} z = 2\bar{w}(R + L)D$$

but the number per unit time by Yapp's method increases without limit as the average speed of the birds increases. On the other hand if the birds are at rest, the extent of their paths will be negligible, and the number per unit time obtained by the two methods converges:

$$\lim_{\bar{w} \to 0} z = 2\bar{w}RD$$
The conventional method and the idea underlying it can also be shown schematically (see transect C in Fig. 1). There is no difference between my method and the conventional one in as much as an observer records a bird only once along the transect, but there is an essential difference in the underlying idea. If the average speed of birds is slow, the number of encounters between the observer and a particular individual bird will decrease, so that the number of birds which do not encounter will increase, even though their ranges of movement overlap the transect belt (see dotted areas on transect C in Fig. 1). But this number will decrease as the average speed of the birds increases until finally almost all of the birds whose ranges of movement overlap the transect belt are encountered by the observer at least once. Whereas, the conventional idea does not take this relationship into account, in other words, the number per unit time in the conventional idea is assumed to be proportional to the actual abundance irrespective of any change in the average speed of the birds. Therefore if it is expressed graphically it appears as a straight line drawn parallel to the abscissa in Fig. 2 provided that D and \( w \) are given a fixed value (see curve C in Fig. 2). Therefore if the factors determining the number per unit time are the factors included in these mathematical formulae, then the conventional idea seems to be fallacious. But the mathematical formulae would not be applicable if any factor influencing the number per unit time is left out of the formulae. Whether there is such a factor or not can be detected only by comparing the result of a complete census with that of a sample count conducted in the field.
at same time in same place.

The Comparison of the Densities Calculated with the Results Obtained by Sample Counts

In 1956 counts were conducted in a Larch wood (Larix leptolepis) at the University Forest in Fuji throughout the breeding season at two-week intervals from mid-April to the end of July. All of the birds seen or heard along the observer's transect within 25 metres on each side of the observer were recorded. Care was taken not to count the same individual more than once. Most day two counts were made, one in the early morning and the other in the evening, and usually repeated three or four days in succession in the same sampling plot (200×650 metre²). No counts were made on rainy or windy day. After each trip had been completed, the distance walked by the observer was measured on a prepared map and the average walking speed was calculated.

The timing of the average speed of birds was difficult for most of the species concerned so that full discussion is only possible for the Great Tits (Parus major) and the Long-tailed Tits (Aegithalos caudatus); for these species the average speed was estimated fairly accurately. A particular individual or a pair which were colour-ringed were trailed until lost from sight and their locations were plotted on the map at about five-minute intervals (when a great change in their course of movement was observed it was checked even if it occurred within a five-minute interval). After the plotting was over all the plots were joined in succession and the total distance was measured. The average speed was then obtained by dividing the total distance covered by the total time taken (see Table I). As is shown in Table I it varies with the breeding stage of the birds. The maximum speed was recorded at the nestling-period for the Great Tits and at the early part of nest-building period for the Long-tailed Tits. The maximum speeds in both cases were found to be very close. The speed of the Great Tits at the early part of their nest-building period was probably as high as the maximum speed of the Long-tailed Tits at the same stage. But with the Great Tits usually the period lasted only a few days so the speed was not measured. But with the Long-tailed Tits the period lasted much longer. At other periods the average speed was markedly low.

<table>
<thead>
<tr>
<th>Period</th>
<th>Date of observation (in 1958)</th>
<th>Total observation hours (in mins.)</th>
<th>Total distance covered (in mts.)</th>
<th>Average speed (mts/hour)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg-laying</td>
<td>May 10-14</td>
<td>262</td>
<td>2151</td>
<td>493</td>
</tr>
<tr>
<td>Incubation</td>
<td>May 19-24</td>
<td>146</td>
<td>1843</td>
<td>450</td>
</tr>
<tr>
<td>Nestling</td>
<td>June 2-6</td>
<td>320</td>
<td>18473</td>
<td>3464</td>
</tr>
<tr>
<td>The early part of fledgling period</td>
<td>June 13-17</td>
<td>133</td>
<td>321</td>
<td>145</td>
</tr>
<tr>
<td>The latter part of fledgling period</td>
<td>June 18-26</td>
<td>710</td>
<td>3464</td>
<td>293</td>
</tr>
</tbody>
</table>
(b) Long-tailed Tit

<table>
<thead>
<tr>
<th>Period</th>
<th>Date of observation (in 1957)</th>
<th>Total observation hours (in mins.)</th>
<th>Total distance covered (in mts.)</th>
<th>Average speed (mts/hour)</th>
</tr>
</thead>
<tbody>
<tr>
<td>The early part of nest-building period</td>
<td>Apr. 24–26</td>
<td>350</td>
<td>21804</td>
<td>3738</td>
</tr>
<tr>
<td>The latter part of nest-building period</td>
<td>May 16–21</td>
<td>380</td>
<td>8984</td>
<td>1419</td>
</tr>
<tr>
<td>The feeding flock at a common feeding area</td>
<td>May 16–21</td>
<td>130</td>
<td>808</td>
<td>378</td>
</tr>
</tbody>
</table>

There was a technical difficulty in determining the average speed of the birds which were at different breeding stages, because the average speeds were different. For example, at the middle of June, the Great Tit population consisted of two pairs in the egg-laying period, five pairs in incubation, three pairs with their fledglings out of the nest, and two pairs without nesting-activity. Therefore I calculated the average speeds at each breeding stage weighted by the number of pairs in each stage (see Table II). On the other hand, all the pairs of Long-tailed Tits showed good coincidence throughout the period of the breeding stage. The Great Tits showed good coincidence only at the beginning of May.

<table>
<thead>
<tr>
<th>Date (in 1956)</th>
<th>( \bar{w} )</th>
<th>( \bar{u} )</th>
<th>( \bar{V} )</th>
<th>( \bar{z} )</th>
<th>( \frac{\sigma^2}{\bar{z}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 2–5</td>
<td>820</td>
<td>470</td>
<td>945</td>
<td>2.02</td>
<td>0.350</td>
</tr>
<tr>
<td>May 22–27</td>
<td>870</td>
<td>1390</td>
<td>1640</td>
<td>2.20</td>
<td>0.235</td>
</tr>
<tr>
<td>June 14–17</td>
<td>810</td>
<td>410</td>
<td>919</td>
<td>1.74</td>
<td>0.212</td>
</tr>
<tr>
<td>July 3–7</td>
<td>940</td>
<td>1430</td>
<td>1714</td>
<td>1.64</td>
<td>0.931</td>
</tr>
<tr>
<td>July 24–27</td>
<td>920</td>
<td>750</td>
<td>1187</td>
<td>1.20</td>
<td>0.224</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Date (in 1956)</th>
<th>( \bar{w} )</th>
<th>( \bar{\bar{u}} )</th>
<th>( \bar{V} )</th>
<th>( \bar{z} )</th>
<th>( \frac{\sigma^2}{\bar{z}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr. 10–14</td>
<td>1360</td>
<td>2140</td>
<td>2536</td>
<td>1.53</td>
<td>0.492</td>
</tr>
<tr>
<td>May 2–5</td>
<td>820</td>
<td>350</td>
<td>935</td>
<td>0.87</td>
<td>0.167</td>
</tr>
<tr>
<td>May 22–27</td>
<td>870</td>
<td>3740</td>
<td>3840</td>
<td>0.93</td>
<td>0.170</td>
</tr>
</tbody>
</table>

Note: \( \bar{w} \)=the average speed of the observer; \( \bar{u} \)=the average speed of the birds; \( \bar{V} \)=the average speed of the birds relative to the observer; \( \bar{z} \)=the average number of birds recorded per hour; \( \sigma^2 \)=the square root of the average area of territories.

As no attempt was made to measure the territory sizes in 1956, they were made in the following two years. The seven territories of the Great Tits were 3.4, 2.8, 1.5, 1.4, 1.3, 1.1, 1.1ha, and the two territories of the Long-tailed Tits were both 3.2ha. The square root of the average of these sizes was used as \( 2L \) in calculating the densities (see formulae (I) and (II)). There seems to be no difficulty in using these average sizes obtained from such small samples as above as representative especially in the latter species, because it appears that these magnitude do not differ from
other pairs of the same species which I have observed in other cases before and since, though they were not measured such an precise way as present case, nor have I observed a significant change in the population density in the three years that might affect the territory size.

The basic data prepared for the calculation of the densities of the Great and the Long-tailed Tits at various breeding stages are shown in Table II. There are three sets of such data taken for the Long-tailed Tits from April to May and five sets taken from May to July for the Great Tits. The average speed of the observer was fairly constant from one set of counting trips to another but on April 10-14 it was exceptionally higher.

As the counting trips were made repeatedly along the same transect in the same sample plot, the number per hour was determined after each trip had been completed, in Table II indicating the average number per hour obtained in each set of trips (six or seven trips in a set). The number per hour obtained this way fluctuated from one trip to another so that the variances are shown in the same table. Clearly these variances are by no means identical with those mentioned by Masuyama (1957) and skel-lam (1958) which were proportional to the variance of the spatial distribution of the population sampled. The average size of the ranges of movement of the birds in terms of 2L was c. 135 metres and c. 170 metres for the Great and the Long-tailed Tits respectively. These values exceeded 2R, e.g. 50 metres, so that formula (II) was used in the calculation of the densities.

Table III The comparison of the densities of the Great Tit (Parus major) and the Long-tailed Tit (Aegithalos caudatus) estimated by sample counts and calculation, with the densities determined by complete censuses.

<table>
<thead>
<tr>
<th>Data (in 1956)</th>
<th>Great Tit (number of pairs per 100 ha)</th>
<th>Long-tailed Tit (number of pairs per 100 ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Apr. 10-14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 2-5</td>
<td>44.0</td>
<td>100.0</td>
</tr>
<tr>
<td>May 22-27</td>
<td>31.5</td>
<td>100.0</td>
</tr>
<tr>
<td>June 14-17</td>
<td>38.9</td>
<td>92.3</td>
</tr>
<tr>
<td>July 3-7</td>
<td>22.2</td>
<td>92.3</td>
</tr>
<tr>
<td>July 24-27</td>
<td>21.3</td>
<td>69.2</td>
</tr>
</tbody>
</table>

Note: D=the density calculated by formula (II); N=the density determined by complete census.

The densities of both species at various periods which were obtained by calculation were compared with those which were determined by the complete census conducted at the same time in the same place (see Table III). With both species the calculated values do not fit the actual densities obtained by the complete census. The faster the average speed of the birds, the greater is the departure of the calculated from the observed values. The calculated values are always considerably smaller than the corresponding observed values. But when the ratio of the average number per hour per density determined by census, i.e. z/N, is calculated for each period, it is found that the ratio is fairly constant irrespective of the average speed of the birds. This tendency, as might be expected from the theoretical point of view mentioned already, cannot be compared to the situation represented by curve B but can rather be compared to curve C in Fig. 2.
This tendency was observed not only in the Great and the Long-tailed Tits but also in other miscellaneous species counted at the same time in the same place; $z/N$ was found to be constant throughout the period that these species were kept under observation (see Table IV). The remaining species which were also observed at the sample plot were omitted from the present discussion because they were so rare that the number per hour was affected greatly by chance variation. It is not plausible to assume that the average speed of these seven species shown in Table IV did not vary from one breeding stage to another, but it is quite likely that they moved faster when they were engaged in foraging for the young in their nests.

Table IV  The number of birds recorded per hour, the absolute number of pairs per ha. and their ratio in miscellaneous species (including the Great and the Long-tailed Tits).

<table>
<thead>
<tr>
<th>Year</th>
<th>May 2-5</th>
<th>May 22-27</th>
<th>June 14-17</th>
<th>July 3-7</th>
<th>July 24-27</th>
<th>May 17-23</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total hour spent in the field (in mins.)</td>
<td>740</td>
<td>740</td>
<td>795</td>
<td>690</td>
<td>730</td>
<td>840</td>
</tr>
<tr>
<td>1. Emberiza spodocephala</td>
<td>5.84</td>
<td>5.68</td>
<td>6.49</td>
<td>5.48</td>
<td>4.85</td>
<td>6.50</td>
</tr>
<tr>
<td>(II)</td>
<td>1.85</td>
<td>2.08</td>
<td>2.38</td>
<td>2.08</td>
<td>1.69</td>
<td>2.31</td>
</tr>
<tr>
<td>(III)</td>
<td>3.16</td>
<td>2.73</td>
<td>2.73</td>
<td>2.63</td>
<td>2.87</td>
<td>2.81</td>
</tr>
<tr>
<td>2. Anthus hodgsoni</td>
<td>4.30</td>
<td>4.54</td>
<td>4.45</td>
<td>4.70</td>
<td>2.55</td>
<td>4.86</td>
</tr>
<tr>
<td>(II)</td>
<td>1.85</td>
<td>1.77</td>
<td>1.92</td>
<td>1.85</td>
<td>1.08</td>
<td>1.62</td>
</tr>
<tr>
<td>(III)</td>
<td>2.32</td>
<td>2.56</td>
<td>2.32</td>
<td>2.54</td>
<td>2.36</td>
<td>3.00</td>
</tr>
<tr>
<td>3. Zosterops palpebrosa</td>
<td>1.46</td>
<td>1.54</td>
<td>1.28</td>
<td>2.70</td>
<td>2.22</td>
<td></td>
</tr>
<tr>
<td>(II)</td>
<td>0.77</td>
<td>0.77</td>
<td>0.69</td>
<td>0.85</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td>(III)</td>
<td>1.90</td>
<td>2.00</td>
<td>1.86</td>
<td>3.18</td>
<td>2.41</td>
<td></td>
</tr>
<tr>
<td>4. Parus major</td>
<td>2.02</td>
<td>2.20</td>
<td>1.74</td>
<td>1.64</td>
<td>1.20</td>
<td></td>
</tr>
<tr>
<td>(II)</td>
<td>1.00</td>
<td>1.00</td>
<td>0.92</td>
<td>0.92</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>(III)</td>
<td>2.02</td>
<td>2.20</td>
<td>1.89</td>
<td>1.78</td>
<td>1.74</td>
<td></td>
</tr>
<tr>
<td>5. Parus ater</td>
<td>0.57</td>
<td>0.65</td>
<td>0.60</td>
<td>0.52</td>
<td>0.49</td>
<td></td>
</tr>
<tr>
<td>(II)</td>
<td>0.38</td>
<td>0.31</td>
<td>0.46</td>
<td>0.23</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>(III)</td>
<td>1.50</td>
<td>2.10</td>
<td>1.30</td>
<td>2.26</td>
<td>2.13</td>
<td></td>
</tr>
<tr>
<td>6. Aegithalos caydatus</td>
<td>0.87</td>
<td>0.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(II)</td>
<td>0.31</td>
<td>0.31</td>
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<tr>
<td>(III)</td>
<td>2.81</td>
<td>3.00</td>
<td></td>
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<tr>
<td>7. Muscicapa latirostris</td>
<td>1.05</td>
<td>0.81</td>
<td>0.91</td>
<td>0.87</td>
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<tr>
<td>(II)</td>
<td>0.53</td>
<td>0.38</td>
<td>0.46</td>
<td>0.46</td>
<td></td>
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</tr>
<tr>
<td>(III)</td>
<td>1.98</td>
<td>2.13</td>
<td>1.98</td>
<td>1.89</td>
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<tr>
<td>8. Muscicapa narcissina</td>
<td>0.89</td>
<td>0.41</td>
<td>1.13</td>
<td>0.70</td>
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<td>(II)</td>
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<td>0.15</td>
<td>0.46</td>
<td>0.31</td>
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<tr>
<td>(III)</td>
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<td>2.73</td>
<td>2.46</td>
<td>2.26</td>
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<tr>
<td>9. Turdus chrysolaus</td>
<td>1.54</td>
<td>1.46</td>
<td>0.83</td>
<td>2.43</td>
<td>1.73</td>
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<tr>
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<td>0.53</td>
<td>0.38</td>
<td>0.92</td>
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<tr>
<td>(III)</td>
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<td>2.75</td>
<td>2.18</td>
<td>2.64</td>
<td>2.79</td>
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Note: (I)=the average number of birds recorded per hour; (II)=the absolute number of pairs per ha. determined by censuses; (III)=the ratio (I)/(II).

The recorded/absolute-number ratio (III) does not differ significantly from time to time and from species to species.
Discussion

There are four possible explanations for the discrepancy between the calculated and the observed densities:

1) the spatial movement of the birds was not satisfactorily represented by the model from which the mathematical formulae were derived;

2) the average speed of the birds measured in the field and used in the calculation of density did not represent the average speed at the moment when the count were being conducted;

3) the actual densities were not sufficiently accurately determined by the complete census; and

4) a certain factor which was not taken into account in our mathematical model entered into the situation.

Naturally the model situation was not identical with the actual situation because, as mentioned already, it was much simplified for the derivation of the mathematical formulae. But this cannot explain the fact that \( z/N \) was constant from one period to another because, however great the departure of the actual moving pattern of the birds from that assumed in our model, the chance of recording more birds increases as the average speed of the birds increases.

It can be seen that as many male birds sing almost persistently early in the morning or late in the evening, their speed may be well assumed to be slower during these periods than those values shown in Table II which were obtained from data which included measurements made in the middle of the day. But such a conjecture is not plausible because the Great Tits engaged in foraging for their young at the nest are most active during these periods (see Kluijver, 1950; Hinde, 1952; Royama, 1959). Therefore, the values of \( û \) shown in the table do not seem to be too high. Moreover, their magnitudes are in the right order as compared with those obtained by Odum (1941/2), Hinde (1952) and Yapp (1955) for American and European tits.

The absolute densities of the tits in the sample plot were determined very easily. Most of the Great Tits that utilized nest-boxes and natural holes were easily detected, for in the sample plot there was a very small number of natural holes and almost all of them had been previously known and checked. The nests of the Long-tailed Tits were also easily found because, as the birds were seldom afraid of a human observer, it was not difficult for him to follow them to their nests. Besides, the results of the nest counts coincided well with the results obtained by territory mapping.

Therefore explanations (1), (2) and (3) do not seem to explain the differences between the calculated and the observed densities and, therefore, only the fourth explanation is plausible.

In our model situation it was assumed that all the organisms were equally likely to be conspicuous. But this appears not to be the case. First of all a bird becomes less conspicuous as the distance between the observer and a bird increases. Second, as many ornithologists know, a male bird is most conspicuous when he is singing at his own singing post (his speed is virtually zero) but he is far less conspicuous when he is moving about quickly but silently searching for food. A pair of Great Tits before incubation period usually patrol their own territory uttering feeble but distinct call notes to each other, so that they are comparatively conspicuous (personal obser-
vation). At this period territorial disputes occur frequently and these add to their conspicuousness. When the young hatch, however, the moving speed increases markedly because of the necessity of foraging for their young, but they usually move in silence and the territorial disputes become less frequent. Thus at this period the birds are least conspicuous. When the young leave the nest the moving speed of the family party becomes slower again, but the young utter their begging notes almost continuously and this adds to their conspicuousness again. From the above statement one may reasonably assume that the conspicuousness of a bird in terms of the easiness of seeing or hearing for the observer is reciprocally proportional to the speed of movement of the birds.

Colquhoun (1940b) referred to the conspicuousness of birds in terms of the maximum distance of effective recognition. He pointed out that the more conspicuous a bird the greater the distance at which it can be recognized and vice versa. If this idea is introduced in our mathematical formulae, it can be seen that the right side of formula (1) or (II) would almost become a constant. But still some degree of discrepancy between the calculated and the observed values remains in such a correction, i.e., the actual number of birds recorded per unit time was still smaller than the minimum number of birds recorded per unit time which would be expected by the present theory when \( u \) is zero. This seems to imply that the distance of recognition which was determined arbitrarily by the observer in the present study might actually be smaller. Skellam (1958) stated that \( R \) can be determined arbitrarily by the observer. But if the conspicuousness is to reflect upon the distance of recognition, \( R \) should be a variable which may not be determined arbitrarily. If \( R \) is to be determined arbitrarily, it should be sufficiently small to make all the birds within that range around the observer fully, or equally likely to be, conspicuous to him. But if this is done, it is quite probable that the behaviour of the birds may be affected by the presence of the observer, and it may result in a biased estimation of the density.

The above conjecture was made on a rather speculative level and not a conclusive one. However, it can be noted that conspicuousness of organisms is a very important factor which affects the estimation of the density by a visual and auditory sample count. Therefore it is necessary for us to know more precisely the true nature of conspicuousness.

Colquhoun (op. cit.) calculated a ratio of the number of birds observed per unit time per actual absolute abundance and called this ratio the \( "\text{index of conspicuousness}" \); this is the ratio already referred to as \( z/N \) in the present paper. This ratio, however, is not a true index of conspicuousness because it may vary even when all the birds are fully conspicuous. True conspicuousness should be the ease of seeing or hearing a bird (or ease of recognition) for the observer, and this might be determined by characteristics of the birds, e.g. songs, call notes, colour patterns, or movements. It is reasonable to assume that these characteristics can vary with the speed of movement which in turn affects the distance of recognition, rather than to assume that they are constant irrespective of the speed. The ease of recognition, i.e. the true conspicuousness, can be determined numerically if the ratio of recognition to total actual encounters is calculated. Therefore, if the discrepancy between the density calculated by our mathematical formulae and the actual density is related only to the conspicuousness, the ratio \( D/N \) could be used as the absolute measure of
Though Colquhoun's maximum distance of recognition can be a relative measure of conspicuousness, if we can determine the distance at which the birds are recognisable to the observer at a given ratio of recognition to total actual encounters, then such distance is in more strict sense a relative measure of conspicuousness.

Conclusion

In the above discussion it was shown that the discrepancy between the actual density and the calculated density of birds was probably due to variation of the conspicuousness of the birds which had not been taken into account in the derivation of our mathematical formulae. The conspicuousness is assumed to vary not only with the species, with the observer and with the habitat, as has frequently been pointed out by many ornithologists and ecologists (see Dice, 1952), but also with the speed of the birds. Therefore it should be born in mind that if no account is made of the complicated nature of conspicuousness, considerable errors may be introduced into the results obtained by visual or auditory sample counts. At present there is no general mathematical theory which, by taking this factor into account, can be widely applicable to divergent situations in the field. But it is possible to check the errors to some extent by making use of our knowledge of field experiences. To accomplish this, the method can be classified into three categories according to the kinds of animals that are to be sampled and what factors should be considered in estimating density:

1) When visual sample counts are applied to animals in open spaces, e.g. sea birds, grass- or pastureland, flying dragonflies, or water-striders.

These animals are those whose conspicuousness is not likely to vary with the species, with the observer, with the habitat, with the distance, or with the speed of movement. Probably our mathematical theory can be directly applied to these animals. Care should be taken, however, when the density is to be determined by Yapp's formula to count the animals every time they come into the observer's field of perception. When my formulae are used to calculate the density, the same individual must not be counted more than once.

2) When visual or auditory sample counts are applied to birds of woodlands in breeding season, e.g. woodland small passerines.

These animals are those whose conspicuousness seems to vary with their speed of movement. It may be said that the conspicuousness of many of such species in breeding season varies inversely to the speed, as was the case observed in the Great Tits. In this case the number recorded per unit time can be used as an index of relative abundance without taking into account the speed of the animals. But care should be taken not to count the same individual more than once. It must be remembered, however, that their conspicuousness may also vary with the species, with the observer and with the habitat. Therefore the use of the index (the number per unit time) for comparative purpose is limited. If wide application of this index is to be made, the ratio z/N has to be determined for the species, for the observer and for the habitat before the investigation begins.

3) When visual sample counts are applied to animals, such as rabbits, whose conspicuousness may increase as they become more active.
Newmann (1959) conducted winter roadside counts of cottontails in the United States and compared the results obtained under various conditions. He found that the more active the animals, the greater the number recorded per unit time. In this case, if the density is estimated from sample counts by using our mathematical theory, it may be expected that the less active the animals the more is underestimated the density but the more active the animals the closer becomes the calculated density to the actual density. At present there is no good method to correct the results obtained under divergent field conditions. Therefore the number per unit time obtained under a given standard condition can only be used for comparative purpose.

Finally it may be noted that if a very accurate result needs not to be required line transects are useful because they are very convenient and widely applicable to the field investigations under various conditions, but if too much labour is required to obtain a correct result, then the method will become less useful.

**Summary**

1) The present paper dealt with the problems of line transects in animal ecology. Several methods of the use of line transects were compared with one another and criticised both from the theoretical and practical point of view.

2) The densities of certain woodland bird populations were estimated by census and sample counts at the same time and in the same place. When the results were compared a serious discrepancy was observed between the density determined by complete census and the density determined by sample counts and mathematical calculation.

3) It was concluded that the discrepancy was probably due to the variablity of conspicuousness of the birds. The influence of conspicuousness of the animals on the results obtained by sample counts was discussed under the assumption that conspicuousness may vary not only with the species, with the observer, with the habitat, and with the distance, but also with the speed of the animals.

4) The methods of line transects were classified from a practical stand point according to what kinds of animals are to be sampled. The precautions to be taken in the application of each method was also suggested.

**References**


Following is a proof made in a somewhat different way from that of Yapp (1955), Masuyama (1957) and Skellam (1958). I recommend readers to refer the original papers by these authors. It is assumed here that the behaviour of the organisms (such as birds) and the observer can be reduced to that of two kinds of particles.

Suppose there is a number of particles of a kind p (the organisms), each of which is moving with an average speed $\bar{u}$ and with a definite range of movement of an equal size. Suppose there is another kind of particles $P_0$ (the observer) moving independent of p. When $P_0$ moves with an average speed of $w$, having a circle 0 of radius R around it (the observer’s field of perception) and when the ranges of movement (or the areas) of p (at least a part of one of them) are covered by 0, there may be contacts or recontacts between p and 0. If all the particles of p move at random the locations of encounters between p and 0 may be assumed to be random, in other words, the probability density of the locations of encounters may be taken to be uniform for all parts of the range of p covered by moving 0. Supposing that there is a number of points of a kind $p'$ (not moving) and distributed at random within each range of p, and that the locations of encounters between p and 0 are represented by the locations of $p'$ which come into contact with 0 as 0 moves, then the number of encounters per unit time is the number of points of $p'$ laying within a transect belt covered by per unit time. When the average speed of p relative to $P_0$ changes, the number of encounters between p and 0 per unit time changes.

It is assumed here that the number of encounters per unit time is proportional to the average relative speed of p. Let the number of points of $p'$ contained in each area of p be $n$, and when the total mount of the areas of the particles of p covered by the transect belt of 0 is equivalent to the average size of the area of a single particle of p, then $n$ points of $p'$ will be found within the transect, in other words, there will be $n$ encounters between p and 0. Therefore by the above assumption, $n$ is proportional to the average relative speed of p. Thus

$$n = kV$$

where V stands for the average relative speed of p and k a proportional factor which is constant for a given value of $\bar{w}$. It is plausible to assume that only one encounter will be made between p and 0 when all the particles of p are at rest and when the total area of p covered by 0 is equivalent to the average area of a single particle of p. In other words, when $V = \bar{w}$ (see Yapp’s second formula), only one point of $p'$ will be contained in each area of p, i.e., $n = 1$. Thus

$$k = \frac{1}{\bar{w}}$$

Therefore by (1) and (2)

$$n = \frac{V}{\bar{w}}$$

When there are N organisms over the plane region of area A, there are equivalently N particles of p, each containing on the average n points of $p'$ in each range of movement. Therefore there are $nN$ points of $p'$ over area A, their density being given by $nN/A$. If all the areas of p are
distributed at random over \( A \), the total number of points of \( p' \) found within the transect belt covered by \( 0 \) in unit time (its size being \( 2Rw \)) is given by the formula

\[
z = 2Rw \times nN/A
\]  

where \( z \) stand for the total number of points of \( p' \) found within the transect belt, i.e. the total number of encounters between the observer and the organisms per unit time. Then from formula (3)

\[
z = 2Rw \times VN/Aw
\]  

As \( N/A \) is the density of the organisms, formula (5) can be written as

\[
z = 2RV
\]  

or

\[
D = z/2RV
\]  

where \( D \) stands for the density of the organisms.

Formula (6) is same as Yapp’s first formula and the present model from which formula (6) was derived is not essentially different from Yapp’s model. Therefore, it is plausible to assume that the number of encounters per unit time between the organisms and the observer is proportional to the average relative speed of the organisms.

The above theory is applicable to the situation where every individual organism, which comes into contact with the observer’s field of perception, is counted irrespective of whether it has been previously met or not. On the other hand if any individual which has been met before is thereafter ignored, formula (6) is not applicable.

If, then, we count the same individual only once irrespective of the number of encounters, the number recorded per unit time will be the number of organisms which make contact with the observer’s field of perception at least once. In this case, the number recorded will be obtained by subtracting the number of organisms which, though their areas overlap the transect belt, happen not to be encountered by the observer, from the number of all the organisms whose areas overlap the transect. Mathematically this is given by the following general formula

\[
z = S_1D - S_2Pr(x=0)D
\]  

where \( S_1 \) is the area where there are centres of the areas of \( p \) which at least partly overlap the transect belt;

\( S_2 \) is the area in which there are centres of the areas of \( p \) which only partly overlap the transect belt;

\( Pr(x=0) \) is the probability that no encounter is expected at the part of the areas of \( p \) which overlap the transect belt.

The above terms can be obtained if the following terms are known

- \( s \) : the size of the area of one particle of \( p \).
- \( s' \) : the size of the overlapping part of the area of one particle of \( p \) which only partly overlaps the transect belt.

Now we assume again that there is a number of points of \( p' \) distributed randomly within the area of each particle of \( p \) and that the number and the locations of encounters between \( 0 \) and \( p \) are represented by those of \( p' \) which happen to be included within the transect belt. Then the probability that no encounter is expected is the probability that no point is found in \( s' \), and is given by

\[
nC_0 \left( \frac{s-s'}{s} \right)^n = \left( \frac{s-s'}{s} \right)^n
\]  

where \( n \) is given by formula (3). The probability that the centre of the area of any one of \( p \) is located within a region \((x, x+dx), (y, y+dy)\), where \( 0 < x < X \) and \( 0 < y < Y \) in area \( S_2 \) is \((dx/X)(dy/Y)\). Thus

\[
Pr(x=0) = \int_0^X \int_0^Y \left( \frac{s-s'}{s} \right)^n \frac{dx}{X} \frac{dy}{Y}
\]  

(15)
Now we assume that the area of one particle of p is a square of a side $2L^*$, any one of the
four sides being parallel to the transect of $P_0$, and that all such squares are distributed randomly
over the plane region, each square containing n points. According to the relationship between
the size of the square and the width of the transect belt of $P_0$, the situation is divided into two, i.e. $L \leq R$
and $L > R$.

1) When $L \leq R$.

Every case that the squares came to overlap the transect belt are shown in Fig. 3 (see squares
a to d). Square b, (whose two extreme locations coindex with those of squares a and c) is the one
that partly overlaps the transect belt. It is clear that centre of such square will be found in the
area defined by the two broken lines in Fig. 3 which pass the centres of squares a and c. Therefore,
as x takes a value between 0 and $2L$, and y between 0 and $\overline{w}$, the probability that x takes a value
between x and x+dx, and y between y and y+dy is \( \frac{dx}{2L} \frac{dy}{w} \). So that the probability that
none of n points is found within area $s'$ is

\[
N_{0}(\frac{s-s'}{s})^{n} = \left( \frac{2Lx}{4L^2} \right)^{n}
\]

because $s$ is $4L^2$ and $(s-s')$ is $2Lx$ (see Fig. 3).

Then the probability that none of n points is found within the overlapping part of all the squares
is, by (9) and (10),

\[
Pr(x=0) = \frac{2\overline{w}}{2L} \int_{0}^{2L} x^n \frac{dx}{(2L)^n} \frac{dy}{2L} \overline{w} = 1/(n+1)
\]

All the squares that overlap the transect belt will be found only within the area of length $\overline{w}$ and
width $2(R+L)$ and those that partly overlap the transect will be found within the area of length $\overline{w}$
and width $4L$ along the transect, so that

\[
S_l = 2\overline{w}(R+L)
\]

and

\[
S_s = 4\overline{w}L
\]

Thus by formula (7) the number of organisms recorded per unit time is

\[
z = 2\overline{w}D(R+L) - 4\overline{w}DL/(n+1)
\]

* On account of the facilitation of the solution of the integral in the right side of formula (9), a
square is taken instead of a circle.
In this simplified model no consideration is taken of those squares that could also overlap the transect belt, though their centres are located outside the range \((o, \bar{w})\). In other words, those that are located near the beginning and the end of the transect are not taken into consideration. Formula (14) will, however, give a close approximation if \(\bar{w}\) is so large that the effect of the presence of these squares upon the estimation of \(D\) is negligible.

2) When \(L > R\).

The squares which overlap the transect belt are divided here into two groups; one consists of those squares whose centres lay between distance \(L+R\) and \(L-R\) from the central line of the transect belt (see squares A, B and C in Fig. 3). The other group consists of the remainders which are shown as squares D and E in Fig. 3. Let the coordinate of the centre of one of the squares belonging to the former group be \((x, y)\), then \(x\) can take a value between \(o \) and \(L+R\) and \(y\) between \(o\) and \(\bar{w}\). Therefore the probability that \(x\) and \(y\) take a value between \(x\) and \(x+dx\), \(y\) and \(y+dy\) respectively is \(\frac{dx\ dy}{L+R \ \bar{w}}\). As \(s = 4L^2\) and \(s' = 2L(2R-x)\),

\[
nGo\left(\frac{s-s'}{s}\right) = \left(\frac{2L-2R+x}{2L}\right)^n \tag{15}
\]

Therefore

\[
Pr(x=o) = \frac{2R}{\bar{w}} \int_0^{2L} \int_0^{2L} \left(\frac{2L-2R+x}{2L}\right)^n \ dx \ dy
\]

\[
= \frac{1}{n+1} \int_0^L \int_0^{(L-R)^{n+1}} \left(\frac{L-R}{RL}\right)^n \ dx \ dy \tag{16}
\]

In the latter group of the squares \(s'\) is \(2L\cdot2R\), and \(x\) can take a value between \(o\) and \(L-R\), and \(y\) between \(o\) and \(\bar{w}\). Thus

\[
nGo\left(\frac{s-s'}{s}\right) = \left(\frac{L-R}{L}\right)^n \tag{17}
\]

and therefore

\[
Pr(x=o) = \left(\frac{L-R}{L}\right)^n \int_0^{L-R} \int_0^{(L-R)^{n+1}} \frac{dx \ dy}{\bar{w}} = \left(\frac{L-R}{L}\right)^n \int_0^{L-R} \int_0^{(L-R)^{n+1}} \frac{dx \ dy}{\bar{w}} \tag{18}
\]

In the former group, \(S_2\) is \(4R\bar{w}\) and in the latter group it is \(2(L-R)\bar{w}\). Therefore, as \(S_1\) is \(2(L+R)\bar{w}\), the total number of organisms recorded per unit time is given by

\[
z = 2(R+L)\bar{w}D - 4R\bar{w}D \int_0^{1} \left(\frac{L}{R} - \left(\frac{L-R}{RL}\right)^{n+1}\right) - 2(L-R)\bar{w}D \left(\frac{L-R}{L}\right)^n \int_0^{L-R} \int_0^{(L-R)^{n+1}} \frac{dx \ dy}{\bar{w}} \tag{19}
\]

where \(n\) is given by formula (3), i.e. \(n = \frac{V}{\bar{w}}\). In this case also \(\bar{w}\) should not be too small because the squares that are located near the beginning and the end of the transect are not taken into account.

In most cases \(R\) and \(\bar{w}\) can be measured in the field. The direct measurement of \(V\), however, is impossible so that it should be calculated by Yapp's second formula. The range of movement of the organism, such as home range or territory, is by no means square, and a circle as a more general shape may suit an actual situation better than a square. But it would make formulae (14) and (19) much more complicated. In actual calculation \(2L\) in the formulae may be substituted by the square root of the average size of the areas of the organisms.