



The Theory of Line Transects

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THE THEORY OF LINE TRANSECTS

by

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SUMMARY

A line transect may be used to determine the density of animals or plants by means of the formula

$$D = \frac{z}{2R(\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}}$$

where D is the number of organisms per unit area, z is the number of encounters between observer and organism in unit time, R is the effective radius of the organism, \bar{u} is the average speed of the organism, and \bar{w} that of the observer. Some of the terms in this equation are difficult to determine, but transects may be used for comparative purposes when the terms are unknown but may be assumed to be constant. Under certain conditions this assumption is probably justified.

INTRODUCTION

Line transects were invented by botanists, but a modified form of them has been widely used for sampling populations of birds. The observer walks on a straight line, and records the birds which he sees or hears. It has been generally assumed that the results of such transects can be used to give information about the relative frequency of different species of birds, and about the relative frequency of the same species in different habitats, but so far as I am aware no proper theoretical analysis has ever been made. Nordberg (1948) in Finland made empirical tests to compare the results of line transects with censuses, but it is clear that any conclusions reached in this way could apply only in a particular habitat and under particular conditions. Colquhoun (1940) tried to compare transects for different species of birds by introducing a factor which he called the 'Index of Conspicuousness', which he determined by observation. It was really, in the form in which he calculated it, an index of inconspicuousness, for it increased the more difficult the bird was to see or hear, and being empirical it was valid only for the habitat in which it was determined. Lack and Venables (1939) in the co-operative survey of woodland birds which they organised for the British Trust for Ornithology, used line transects, and made elaborate deductions about the relative frequency in different types of wood of a number of species. Although their observers were asked to record the size of the wood, the distance walked and the time taken, no use was made of this information in the calculations, nor is it recorded in the paper. Their conclusions about relative densities in different types of woodland are therefore of little value, for clearly, other things being equal, the larger woods will give the higher frequencies.

There must be some theoretical relationship between the results of these moving line transects and the density of the animals encountered, and what follows is an attempt to express it in mathematical terms. If the method is valid, it should be useful for estimating not only birds, but other animals such as insects in the field, and small animals such as Protozoa in cultures. Botanists have not, so far as I know, used line transects as a means of estimating plant density, but McIntyre (1953) has recently suggested that this might be possible. As will be seen later, my results are of rather more general application than his, and, especially where high accuracy is not required, would be quicker in their application.

The problem of encounters between moving particles is in its essence the same whatever the nature of the particles, and the frequency of collisions depends on three things only—the size and speed of the particles, and their density in space. In a line transect there is one particle of one sort (the observer) and many of another (the birds, or whatever they may be). It is simplest to give all the size to the one type of particle (it does not matter which) and to regard the other as a mere point. What has sometimes been called the ‘recognition distance’ is either regarded as the radius of the bird, or as the radius of the observer, his sense-tentacles, as it were, stretching out to that distance from his body. Since this radius is different for different species, it is less offensive to common sense to make the first of these simplifications, and it can then be shown that

$$D = \frac{z}{2R(\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}}$$

where D is the number of organisms per unit area;

z is the number of encounters between observer and organism in unit time;

R is the effective radius of the organism;

\bar{u} is the average speed of the organism;

\bar{w} is the average speed of the observer.

A proof of this is given in the Appendix. It is possible to make a correction for cases where the shape of the particle is not a circle, but the error introduced by neglecting this is not great.

DISCUSSION OF THE EQUATION

To determine how far this theoretical relationship can be applied in the field, we must consider each term of the equation in turn.

1. It is clear that if D , the number of organisms per unit area, is not constant during the period of the count, no estimate of it can be made by any method which is not instantaneous, unless the immigration and emigration rates are known or can be calculated. This difficulty has been recognised by Beven (1951) who points out that counts of winter tit-flocks in a wood are of little value because the edge of the wood is not necessarily a boundary which confines the birds, and numbers may be seen entering after the count is completed. Under these conditions a large sample, or many small samples, must be used, and this in its turn introduces the difficulty

that the time which one observer must spend on the counts is extended beyond one day, so that there may be additional seasonal fluctuations (or, more probably, trends) in *D*. This would suggest that the line transect is likely to give better results in summer, when numbers are relatively stable, than in winter.

Birds which are present chiefly or only in flocks, such as tits and Woodpigeons (*Columba palumbus*) in winter and Rooks (*Corvus frugilegus*) at all times of the year, present another difficulty. I try to make the best estimate of their numbers that I can, but there are certainly differences between the accuracy that can be obtained in a bare, open oakwood and a close plantation of spruce, to take two extremes. Sometimes a flock can be counted as it crosses a ride. Theoretically it would be possible to take the flock as a unit and multiply by factors for its average size and composition, but we do not know enough at present to do this. For winter tit flocks there would be differences for types of woods, times of year, and probably parts of England; for Woodpigeons there are such big variations from year to year (largely dependent on acorns and other crops) that no average is likely to be useful.

2. The number of observers is fixed at one, and his size arbitrarily at zero. His speed can be determined relatively easily. At less than 1 m.p.h. not enough ground is covered, and at more than 2 m.p.h. one cannot give attention to what one is doing, and the formula breaks down because one does not recognise birds with which one in fact makes contact. A fast and noisy approach may also affect recognition distance, positively for some species by making them fly earlier, negatively for others by making them slip away unnoticed. Subject to a qualification made below I would suggest that 2 m.p.h. should be aimed at as the standard. Few birds are missed through failure in recognition at this speed, and it can be maintained in most types of country for long periods. Exceptions are thick and boulder-strewn woods where not more than 1 m.p.h. is possible, but these are unsuitable for line transects of any sort, since too much attention has to be paid to one's own progress.

Momentary pauses to make records must be taken into one's time in calculating the average speed, but they should be reduced to the minimum by the use of some form of quick-opening notebook with the names of likely birds written in. All longer pauses, whether for rests or for the identification of a bird, should be deducted from the total time, and birds observed during them ignored.

3. The speed of the organism is difficult. There may be specific differences, and to use the formula for comparisons of densities from one species to another is only justifiable if their speeds are the same or known. The simplest case is that of birds such as owls (Strigidae) and the Woodcock (*Scolopax rusticola*), which roost by day and so have zero speed. Another relatively simple case is that of a male territorial bird in the breeding season, which hardly ever moves for distances greater than its own diameter, since its song is audible over the whole of its territory and beyond. For other birds, which move intermittently and at varying speeds over relatively large areas, we should need to know their mean

speed over the period of observation. This could with difficulty be obtained, but it would be subject to a large variance. I have timed feeding winter tit flocks, for instance, at speeds ranging from one-eighth to 2 m.p.h., and sometimes they remain stationary for periods of up to 25 minutes. Hinde (1952) has produced evidence that there is variation of the usual speeds both with time of day and with season of the year.

4. R , the effective radius of the organism, may be either auditory or visual.

In many ways auditory radius is much simpler than visual. Hearing is not a directional sense in the way in which sight is, nor is it affected so much by the type of environment or by its seasonal condition (days of high wind, or areas near falling water must generally be ruled out as useless for the work and can be avoided). There is no great difference in the maximum distance at which a given sound can be heard when it comes from different directions, and what little difference there is can be largely eliminated by scanning, which the practised naturalist habitually does by turning his head from side to side. There is, however, a large personal variation, and the maximum values of R will therefore be different for different observers. No doubt they could be determined, but it would be laborious to do so; only for the commonest species could it be done in reasonable time, and the values would change with changing experience of the observer, and with his age as hearing became less acute.

More important is the fact that only exceptionally is a bird calling or singing continuously, so that an observer may walk through a bird's territory without making contact. A usual size of territory for woodland passerine birds is about 2 acres (see, for example, Hinde (1952) and May (1949)) which, as a circle, gives a diameter of about 110 yards. The bird's song will be audible outside its territory to a varying degree, but it would seem to be on the safe side to say that the observer will hear the bird if it sings at any time while he is within a circle of twice the diameter of its territory, that is of 220 yards. Many birds can be heard over greater distances than this; Nicholson (1936) gives 200 yards for a number of species, and half a mile for the Blackbird and a mile for the Cuckoo.

The mean length of the chords of a circle ranges from $r \times \frac{4}{\pi}$, when

they radiate from a point on the circumference, to $r \times \frac{\pi}{2}$ when they radiate from a point at infinity, i.e. are parallel, and unless the territory is of the same order of size as the area under investigation, the true value will always be very close to the second of these. On average the observer will be within this area for the time that it takes him to walk this distance. For a circle of 220 yards diameter the mean chord is about 165 yards, and at 2 m.p.h. this will take 2.8 minutes, which in this approximate calculation we may round off to 3. The observer will, therefore, make satisfactory contact with tit flocks in winter, which are rarely silent, and with many males in the breeding season under good weather conditions and in

the morning. There is little published information on song-output, and almost none in a form which is of use here. Most woodland bird songs are given in stanzas, each of which takes from 2 seconds up to 10 or more according to the species, and the number of stanzas per minute when the bird is singing ranges usually between 4 and 8 per minute. (For detailed information see Nicholson (1936); I can confirm many of his figures.) Under these conditions no birds will be missed. There may be, however, longer periods when the bird does not sing at all, but general experience suggests that in good weather at the height of the singing season pauses of more than 3 minutes are for many species rare, and that they are often interrupted by calls other than the song. There are, however, exceptions. Buxton (1950) for instance has confirmed that during the period of nest building, which occupies about a week, the Redstart (*Phoenicurus phoenicurus*) is almost songless. This does not mean that it is silent, or that it cannot be observed; there will be some compensation in an increased visual conspicuousness, since the collecting of nest-material is necessarily an active process in which contact with an observer is likely.

The effect of long periods of silence is to reduce the mean effective diameter of the bird. Since these periods vary from hour to hour and day to day, it will clearly have a large standard deviation, which would be difficult to determine, but which can be reduced by careful choosing of the conditions. As far as possible counts to be compared should be made at the same time of day. The use of a large sample, and a slower observer's speed, will also help. If, for example, the observer took an hour to walk the mean chord of the bird's territory, it is almost certain that the bird would produce some audible sound during this time, so that a contact would be scored. In practice this advantage must be balanced against the reduction in the number of contacts which follows from the simple formula. On these grounds it might be better in woodland to take 1 m.p.h. as the best speed instead of the 2 m.p.h. which I have suggested above.

In woodland, visual contacts are much less important than auditory, as is proved by Table I, which shows for seven of the

TABLE I
FIRST CONTACTS OF SEVEN OF THE CHARACTERISTIC SPECIES IN A SERIES OF COUNTS IN
DURMAST OAKWOOD DURING MAY

	Visual	Auditory	Visual as % auditory
Tree Pipit (<i>Anthus trivialis</i>)	3	24	12
Chaffinch (<i>Fringilla coelebs</i>)	17	92	18
Pied Flycatcher (<i>Muscicapa hypoleuca</i>)	16	49	32
Coal Tit (<i>Parus ater</i>)	6	20	30
Redstart (<i>Phoenicurus phoenicurus</i>)	8	16	50
Wood Warbler (<i>Phylloscopus sibilatrix</i>)	3	62	4.8
Willow Warbler (<i>Phylloscopus trochilus</i>)	1	30	3.3

commoner species the number of first contacts of the two kinds in a series of counts in rather open oakwood (*Quercetum petraeae*). In

close plantations, or in woods with a shrub layer, the proportion of visual contacts will be even less. The interspecific variation is great; it was to be expected that the proportion of visual contacts would be lower for dull-coloured birds such as the warblers (*Phylloscopus*) than for the Chaffinch (*Fringilla coelebs*), but the difference between the Chaffinch and the Redstart is more likely to be due to the different proportions of the day which the two species spend in singing, or to the different carrying powers of their songs. It may well be that better results would be got by taking either auditory or visual contacts in any series of counts, instead of combining the two as is usually done.

Some workers have endeavoured to get over the interspecific variation in the carrying power of songs by recording only birds heard within some fixed distance, such as 40 yards. This appears attractive, but introduces new difficulties. It does not deal with variations in song-output, and it puts a great deal of responsibility on the judgement of the observer. Since this cannot be measured, and is likely to have a large personal error, I do not recommend the method. I find it quite impossible to apply myself in the breeding season, and with many observers there would be a tendency to deviate towards an unfamiliar or interesting bird heard in the distance.

In open country visual contacts may be the more important. I have made relatively few counts in such places, but a recent short series in May in newly-planted heather moor, with the young conifers barely visible, gave for the Skylark (*Alauda arvensis*) 15 visual first contacts and 16 auditory, and for the Meadow Pipit (*Anthus pratensis*) 16 visual and 17 auditory. In open country, more than in woodland, there is a distinction between two types of visual contacts, those which follow spontaneous movement of the bird, and those which follow flushing of the bird by the observer. In the second type the bird's speed is zero, and it would be possible to determine a mean flushing distance, which would be half the effective diameter, for each species. It would be advantageous, and might be feasible, to distinguish between the two.

An interesting special case of visual recording is the line transect made from a railway train. This can be used only for the larger birds, from Magpie size upwards, but for them it should be very accurate. The observer should ride near the front of the train, and it is here probably easy, and so a good thing, to count only birds seen within an arbitrary radius, say of 50 yards. Average speeds of the train can be obtained with a watch and the published distances on the line, and the period of observation is reduced by the time spent in tunnels and cuttings and between trees. Most of the birds to be seen will be feeding on the ground, and their speeds will be negligible in comparison with that of the train. If there is only one observer he can only watch from one side of the train, so that his total contacts must be doubled before they are used in the equation. A transect made in this way in February 1950 between Leamington and a point south of Bicester scored 110 contacts for Rooks and gave a density of 122/sq. mile. The next week a longer count

between Coventry and Leighton Buzzard gave 187 contacts, which worked out at 78/sq. mile. There are no figures available for the nesting Rook population of this part of England, but the 1944 census of a large area in Oxfordshire and Berkshire gave 38 nests/sq. mile (Fisher, unpublished). As the winter population must in general be larger than the breeding population, the train transects at least give results of the right order of magnitude, and fit in with the greater density as one goes to the south. Results of train transects for comparing densities of species of similar degrees of conspicuousness can be very striking. See, for example, Southern (1944) on the Woodpigeon (*Columba palumbus*) and Stock Dove (*C. oenas*).

5. z , the number of contacts in unit time, is, by the formula, a function of all the properties which we have been considering. Even in cases where D (the number of organisms per unit area) remains constant throughout the observations, and \bar{w} (the average speed of the observer) is controlled, there will be wide variations in R (the effective radius of the organism) and \bar{u} (the average speed of the organism). These variations are of two sorts: those from time to time and place to place within one species, and those between the means for different species. Unless we know the mean values for each species, and their standard deviation, we cannot use the formula for calculating the absolute value of D , but if it can be shown, or assumed with some probability, that these means and deviations remain constant for each species, we can, without knowing what they are, use the formula for comparing populations at different times and places. On general grounds the assumption is probably safe under certain restricted conditions. (1) The observations to be compared must be made in the same phase of the birds' seasonal cycle, e.g. in the nest-building phase, or the incubating phase, or during winter flocking. (2) The time of day, weather conditions and so on must be reasonably uniform. This condition can be satisfied by avoiding extremes, such as the time of the dawn chorus, sunset, days of high wind or unseasonable temperature. (3) Those features of the environment which affect contact-making must be uniform. It is unlikely that the ecological nature of a woodland affects auditory recognition to any very great extent, but this should be determined. It might or might not have an effect on the bird's speed. (My observations on winter tit-flocks suggest that, if such an effect exists, it is small.) Visual recognition is obviously greatly affected by the density of the trees, and it is therefore probably best to use only auditory contacts for woodland comparisons. On open country the nature of the vegetational substrate might or might not have an effect on flushing distance; this could be determined by observation.

CONCLUSIONS

The line transect can be used for determining absolute densities only when all the terms of the equation are known. At present we have not such knowledge, but there seems no reason why it should not be accumulated in time. When conditions are carefully chosen

there seems no reason why the method should not work reasonably well as a means of comparison, and it is in this way that it has generally been used. Comparisons may be of two main sorts—between species and between habitats.

In the first of these, the relative frequency of contacts is used as a measure of the relative density of species in one area or in one type of habitat. There is not an exact correspondence, since a bird of conspicuous song or behaviour will appear higher in the list than it ought to do and an inconspicuous bird will be lower. In spite of this, since on the whole the conspicuous passerine birds are, in their appropriate habitats, common, and the inconspicuous birds uncommon, a list of contacts per hour with the species in order does give a recognisable and reproducible picture of the fauna of a habitat, even if it is a slightly distorted one. When a large number of samples of one habitat is available the percentage frequency technique, as used for plants by Raunkiaer (1934), affords a valuable check on the order of merit determined by the contacts per hour. The theory of the percentage frequency technique is that the proportion of a large number of samples in which a species occurs will bear some sort of relation to its absolute density. The ornithologist can seldom lay out standard quadrats as a botanist can, but where a number of similar samples of a habitat of approximately equal size can be visited, they can be used in this way. Table II shows the percentage frequency and the order of merit for birds

TABLE II
FREQUENCY AND TOTAL CONTACTS OF BIRDS IN ROSS AND SUTHERLAND BIRCHWOODS, JUNE
1952 AND 1953
TWENTY-FIVE WOODS, 970 MINUTES MOVING TIME

					Woods	Contacts
Willow Warbler (<i>Phylloscopus trochilus</i>)	25	c. 280
Chaffinch (<i>Fringilla coelebs</i>)	22	83
Tree Pipit (<i>Anthus trivialis</i>)	20	64
Robin (<i>Erithacus rubecula</i>)	17	46
Wren (<i>Troglodytes troglodytes</i>)	16	35
Coal Tit (<i>Parus ater</i>)	12	24
Song Thrush (<i>Turdus ericetorum</i>)	11	25
Redstart (<i>Phoenicurus phoenicurus</i>)	11	18
Great Tit (<i>Parus major</i>)	9	15
Spotted Flycatcher (<i>Muscicapa striata</i>)	6	12
Hooded Crow (<i>Corvus cornix</i>)	6	10
Cuckoo (<i>Cuculus canorus</i>)	5	18
Redpoll (<i>Carduelis flammea</i>)	5	c. 20
Blue Tit (<i>Parus caeruleus</i>)	5	12
Wood Warbler (<i>Phylloscopus sibilatrix</i>)	5	10
Creeper (<i>Certhia familiaris</i>)	2	2
Blackbird (<i>Turdus merula</i>)	1	1

in a group of 25 birchwoods in Ross and Sutherland, one of the biggest series of ecologically similar habitats for which this information is available. The agreement between the two methods is very close. A more accurate version of the percentage frequency

might be given by the time quadrat; that is, a record of the species heard in as many time-periods of standard length as possible, but I have not used this method. Half an hour would probably be suitable for woodland birds.

Orders of merit determined in this way should not differ greatly with different observers, since most types of personal error will apply equally to all species. Men with poor hearing may miss many of the more silent birds, so depressing them still further in the list.

When the order of merit and the contacts per hour have been produced for a series of habitats, they can be compared. The conditions of observation which must be satisfied for the comparison to be valid have been discussed above. When they are satisfied, and there is one observer, the comparison should introduce no greater errors than are present in the separate habitat lists. With more than one observer there will be personal errors, which should not be important if the observations are mixed, that is, if each observer is not responsible for a single habitat.

The contacts per hour for each species at a stated speed give one the fullest information, but the pattern of the community is more strikingly shown by expressing the contacts for each species as a percentage of the total. This however obscures the overall density and breaks down as a method when large flocks appear transiently in the habitat, as do Woodpigeons (*Columba palumbus*) in oakwoods in autumn. This method should never be used unless the total number of contacts per hour is also given.

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APPENDIX

DERIVATION OF THE EQUATION

The following argument is based on the kinetic theory of gases, as it is expounded in textbooks of physical chemistry. It is assumed, as in that theory, that the particles travel in straight lines and do not interact on each other.

The simplest case is that where all the particles are of the same kind and all but one are at rest.

Let L' = the mean free path, i.e. the average distance which the moving particle travels before it comes in contact with another.

R = the effective radius of a particle.

Then in a rectangle of length L' and side $4R$ there can, on the average, be only one particle, i.e. each particle inhabits an area of $4RL'$.

If the total number of particles in area A is N , the area per particle is A/N , and

$$4RL' = A/N$$

$$L' = \frac{A}{4NR} \quad \dots\dots\dots (1)$$

Now consider two kinds of particle, and suppose as before that all except one particle, of the first type, which we may call p , are fixed; the average distance which this travels before it meets a particle of the second type, q , is

$$L'_{p,q} = \frac{A}{2N_q(R_p + R_q)} \quad \dots\dots\dots (2)$$

If all the particles are in motion the mean free path differs from this value by a term which relates the relative velocity of the particles to their absolute velocity. It was shown by Maxwell (1860) that, for a mixture of two kinds of particle, an approximate result is given by

$$V^2 = \bar{u}^2 + \bar{w}^2 \quad \dots\dots\dots (3)$$

where \bar{u} = the average velocity of one kind of particle, \bar{w} = that of the other, and V is their relative velocity.

The corrected value for the mean free path is then

$$L_{p,q} = L'_{p,q} \frac{\bar{w}}{V}$$

$$= \frac{A}{2N_q(R_p + R_q)} \times \left(\frac{\bar{w}^2}{\bar{u}^2 + \bar{w}^2} \right)^{\frac{1}{2}} \quad \dots\dots\dots (4)$$

The number of encounters in unit time between one particle of p and all the particles of q is the distance which it travels in unit time divided by the mean free path, i.e. $\bar{w}/L_{p,q}$ and the total number of encounters in unit time between all the particles of p in unit area and all the particles of q is

$$z'_{p,q} = \frac{\bar{w}}{L_{p,q}} \times \frac{N_p}{A}$$

$$= \frac{2N_p N_q (R_p + R_q)}{A^2} \times \bar{w} \times \left(\frac{\bar{u}^2 + \bar{w}^2}{\bar{w}^2} \right)^{\frac{1}{2}}$$

$$= \frac{2N_p N_q (R_p + R_q)}{A^2} (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}} \quad \dots\dots\dots (5)$$

If there is a single observer in unit area counting birds it may be assumed that he has negligible radius, and (5) reduces to

$$z' = \frac{2N_q R_q}{A^2} (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}} \quad \dots\dots\dots (6)$$

or

$$N_q = \frac{z' A^2}{2R_q (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}} \quad \dots\dots\dots (7)$$

The number of encounters in unit time between all the particles of p in area A and the observer is

$$z = \frac{2N_q R_q}{A} (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}} \quad \dots\dots\dots (8)$$

and

$$N_q = \frac{z A}{2R_q (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}} \quad \dots\dots\dots (9)$$

For comparative purposes this may be written as

$$D = \frac{z}{2R_q (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}} \quad \dots\dots\dots (10)$$

where D is the number of birds per unit area, or their density.

The effective area of non-territorial solitary birds which are stationary or moving at random will be a circle, whether they are first recognised by sight or sound, unless there is a consistent bias which makes them easier to recognise in one direction than another. It is clear that where this is so the radius, R_q , must be multiplied by some factor to correct for the difference. McIntyre (1953) has dealt with a similar problem in determining the density of plants from line transects, and gives a number of formulae which he has shown to work well on an empirical model. One of them (his equation (4)) uses for any shape of plant, the longest chord parallel to the line of transect, multiplied by the mean value of the ratio of the maximum perpendicular distance between tangents parallel to the transect, to the longest chord parallel to the transect. Translated into the symbols which I have used in this paper, his equation (4) becomes

$$D = \frac{\Sigma (1/2R'_q)}{\bar{u} \times t \times h} \dots\dots\dots (11)$$

where $R' =$ half the longest chord, $h =$ the ratio defined above, and t the unit of time in the measurement of the velocity. (The term t is unity, but must come into the equation to make the dimensions the same on the two sides.) For a circle, h is obviously unity, and R' is the radius, which I have written as R_q . Under these conditions, since $\Sigma (1/R_q)/\bar{u}$ is, if the values of R_q do not vary greatly, approximately equal to $\frac{z}{R_q}$, McIntyre's equation is a special form of mine for particles q which are stationary.

McIntyre has worked out values of h for various shapes; for an ellipse of ratio $b/a = 0.8$ he finds it to be 1.025; for an ellipse of ratio $b/a = 0.4$ it is 1.450; and for various irregular shapes something between these two values. My equation (9) could be made more general by the introduction of this factor.

$$N_q = \frac{z'A}{2hR_q(\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}} \dots\dots\dots (12)$$

Botanists are able to measure both R_q and h fairly accurately, but ornithologists can only make an estimate of R_q and an even poorer one of h . In view of this, and of the fact that h appears to be always between unity and 1.5 and often very near the former, it will seldom be worth while to use equation (12) rather than equation (9).

Mr. J. G. Skellam will be considering the mathematics of the relationship in a paper shortly to be published, and he allows me to state the following conclusions from it. The Maxwellian formula for the relative velocities is true as a special case, and the value that it gives for V is equal to or greater than the true value, but not far from it. My formula holds even if the motion is not in straight lines, and the effect on it of moderate heterogeneity in the distribution of the particles is small. The precision of the estimate of D increases with R , provided that R can be determined accurately.