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THE MATHEMATICAL FOUNDATIONS UNDERLYING THE USE OF LINE TRANSECTS IN ANIMAL ECOLOGY

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INTRODUCTION

Transect methods have been known and employed for many years in plant ecology and are particularly simple because of the stationary character of the objects studied. The estimation of populations of large animals such as birds by transects is, however, an extremely difficult and complex problem primarily because of their locomotion. There are two aspects to be considered: (1) the purely mathematical problems arising in abstract or ideal situations, and (2) the practical and technical difficulties encountered in standardizing the field procedure in order that a mathematical model be applicable. Though we are here concerned essentially with the mathematical aspects, it is nevertheless important to bear in mind the nature and magnitude of the various types of error arising from practical considerations, and it is emphasized that the biology and behaviour of the individuals of the population being estimated require thorough study before even a rough assessment can be made of the applicability of any census method in any particular instance. The ornithologist is particularly fortunate in this respect for the distribution, movements, and habits of many birds can and have been studied sufficiently to permit him to judge beforehand whether to count them on their breeding territory, at the roost, or on their feeding area, and to select the time when movements into, out, and within the study area are most nearly "frozen." Even in favourable cases where the assumptions underlying a particular method seem well satisfied, a decision to employ that method is a judgment which bitter experience indicates should be made with reserve, and alternative ways of confirming the answer looked for. Moreover, results require careful scrutiny in relation to established ecological knowledge. A rough first check, for example, is possible in the case of birds, where the normal, upper, and lower ranges of density in the main 'habitat' types (e.g., woodland, moorland) are fairly well known, so that any freak figure is immediately suspect.

The question of conspicuousness [Colquhoun, 1940] is indeed an important practical one which could render almost any direct census method inapplicable. Otters, for example, though larger than almost all British birds, so far defy census entirely, though certain insects such as dragonflies [Moore, 1953] appear to be suitable material for population studies. Awareness of the presence of an organism may arise through auditory rather than visual channels. But even with song birds, the period of song may be limited to certain phases of the breeding cycle, [Buxton, 1950] and may only approximate to continuity at certain times of the day. No experienced ornithologist, however, would consider taking a count without first obtaining a clear knowledge of seasonal, diurnal, and other patterns likely to affect the results, or without guarding against the potential errors arising through the inconspicuousness of certain species.

At high densities the counting of moving organisms becomes humanly impossible by reason of the failure of the observer to distinguish between those organisms which have already been counted and those which have not, and to note the presence of the latter before they have moved on. Only because birds are so high in the ecological pyramid that their densities related to the available foraging area are relatively so low, is it normally possible to count them at all, and then not in all circumstances. Special methods have been devised for enumerating large aggregations, one of the best of which is by use of enlarged aerial or other photographs taken simultaneously with direct counts.

Conversely, it has also to be borne in mind at the present stage of development of statistical ecology that the framing of a methodological basis for animal transect censuses must inevitably start with simple ideal situations, where the organisms are perfectly conspicuous and do not behave abnormally in the neighbourhood of the observer, and that apart from temporary expedients, the modifications and adjustments which must be made to simple models before they can be employed in circumstances where complicating factors cannot be ignored, are matters for future research.

An important point which has to be borne in mind in this as in many other fields is the assessment of acceptable margins of error in relation to the use to be made of the material, either scientifically or practically. For certain purposes very high accuracy is essential or the data are valueless, but in other cases even errors of the order of 50% or higher may be acceptable provided the existence of such a degree of error is plainly understood.

HISTORICAL

Interest in census problems has been stimulated greatly by the

efforts made by ornithologists during the last half century, and the principal methods devised and difficulties encountered have been discussed by Palmgren [1930], Nicholson [1931], Lack [1937], Nordberg [1947], and many others. Without doubt, wild bird populations exhibit a quite exceptional inherent suitability for the study of direct methods of enumeration, for not only is a considerable body of field knowledge already acquired, but large enough numbers of observers active in the field make it possible to build up a large body of census results.

Fundamentally, there have been two main procedures. In the first, defined areas (or more conveniently, representative samples of them) are submitted to a thorough direct enumeration (*Probeflächenmethode*), and the density estimated in accordance with the definition by computing the ratio between the number of separate organisms (or sometimes pairs) observed and the area examined. The birds appear to be treated in principle almost as if they were stationary, and on discovery the usually recommended practice is to record them on a map of the area. Knowledge and field experience of bird biology and behaviour are brought to bear to avoid multiple recording of the same individual or pair. For example, most passerine birds at the onset of the breeding season establish more or less well defined territories or preferred areas [Hinde, 1952] and in these build their nests. The recognition that two appearances of cock birds in the same region might have to be attributed to a single individual helps considerably in enhancing accuracy. By repeated recording, carried out compartment by compartment, and by adopting the convention whereby any observed figure is regarded as a lower bound (*Minimizahl*), ornithologists usually consider it possible to assess very roughly the number of birds escaping notice in a single attempt at enumeration, and to arrive at a more reliable final estimate [Palmgren, 1930].

The second procedure (the *Transect* or *Linientaxierungsmethode*) may be regarded as a development of the first, brought about by choosing the sampling area in the form of a long, narrow belt, lying on one or both sides of the path taken by the observer, as he walks [Yapp, 1956] or rides [Nicholson, 1931; Southern, 1944] through the region being studied. Though this method is often adopted for ease and convenience (the first method, for example, being impracticable at sea) and the results used primarily for comparative purposes rather than the assessment of absolute numbers, transect procedures have a special merit in that they embrace a wider range of diversity in the habitat under general consideration than does a set of compact sample areas of comparable total extent, a result which is usually reflected by the greater number of species observed. But as Nordberg [1947] has pointed out, it is not permissible to estimate the true population from repeated

recordings of the same transect by the arguments and numerical devices usually employed in the case of compact areas. The transect belt is in fact so narrow that chance variation plays an important role, and a source of error arises from accidental encounters with birds nesting outside the strip. By dividing the transect into short segments, and adopting the largest recorded figure for each, it is by no means certain, in the case at least of fully conspicuous organisms, that the density might not be seriously over-estimated.

Though the procedures outlined above do not appear, for understandable reasons, to have been at all rigidly defined, the underlying mathematical argument tacitly omits the movement of the organisms, this being looked on as a troublesome complication, to be overcome, often apparently with considerable success, by sound judgment and field experience. The first attempt to remodel the methodological basis of transect censuses, so as to take the movements of the organisms into account in the calculations, is due to Yapp who early in 1953 in a personal communication to the author suggested that the encounters between a moving observer and the individuals of a mobile species could be likened to the collisions between a molecule of one kind and molecules of another, and he proposed making use of the analogy to estimate bird populations by applying a formula given by the immediate application of the classical kinetic theory of gases. His argument on these lines appears as an appendix in Yapp [1955]. On analysis his result can be resolved into two formulae, which it is here proposed to call Yapp's first and second formulae:

$$(i) \quad \mathfrak{D} = z/(2RV), \quad (1)$$

where \mathfrak{D} = density of population studied,
 z = number of encounters per unit time,
 V = average velocity of the organisms *relative to*
the moving observer,
 R = range or radial distance within which an or-
ganism must approach the observer to effect
an encounter.

$$(ii) \quad V^2 = \bar{u}^2 + \bar{w}^2, \quad (2)$$

where \bar{u} = average velocity of the organisms,
 \bar{w} = average velocity of the observer.

In deriving these results Yapp assumed the motion of the organisms, like that of molecules, to be rectilinear between encounters. Since to many biologists this condition might appear unacceptable in natural ecological situations, I examined the model on less restrictive assumptions, allowing the organisms to move in any way whatsoever provided

that their paths were rectifiable, that is, could be represented to any arbitrary preassigned degree of approximation (no matter how close) by a chain of minute straight links. The result was that Yapp's first formula was also valid under this general and acceptable condition.

The second formula, however, is true in the physical 3-dimensional analogue, not because of the shape of the paths, but because of the peculiar form of the distribution of velocities which molecules enjoy. It would also be valid in the biological 2-dimensional case if the organisms and the observer both satisfied a distribution of velocities which is the 2-dimensional analogue of Maxwell's distribution of molecular velocities [1860]. Since this can hardly be expected, Yapp's second formula will not be in general strictly true, though it would appear (see later sections) to be adequate in a large number of practical situations in which it might be employed.

YAPP'S FIRST FORMULA

The applicability of a mathematical model to a biological situation rests on the correspondence which can be set up between the simple abstract elements of the one and the real and highly complex elements of the other, and its value depends on the closeness with which the relations connecting the elements of the model hold also for the corresponding biological components. It is inevitable that the two things should be described in different language. However, in the present treatment, it may perhaps help to remember that the term particle corresponds to animal and the term contour to the boundary of the field of perception of the observer.

In a large plane region (see Fig. 1) let there be a large number of particles moving about in rectifiable paths not necessarily independently (e.g., in groups), and let the average density of the particles be \mathcal{D} . An observer O moves independently across the region in an equally arbitrary manner, his path being termed a transect. Associated with the observer is a frame of reference (such as a set of ordinary cartesian coordinates), and marked out on this frame is a closed contour. It is not assumed that the particles or the observer move with uniform velocity, but only that in an infinitesimally small interval of time the velocities may be regarded as such. It is also assumed that the behaviour of the particles is the same in the neighbourhood of the contour as elsewhere, irrespective of local variations in probability density. This condition restricts the applicability of the mathematical model to biological situations where the organism being counted is indifferent to the presence of the observer, and would probably not hold in the case of timid birds or attracted tsetse flies. For the present it is assumed that all parts of the area are

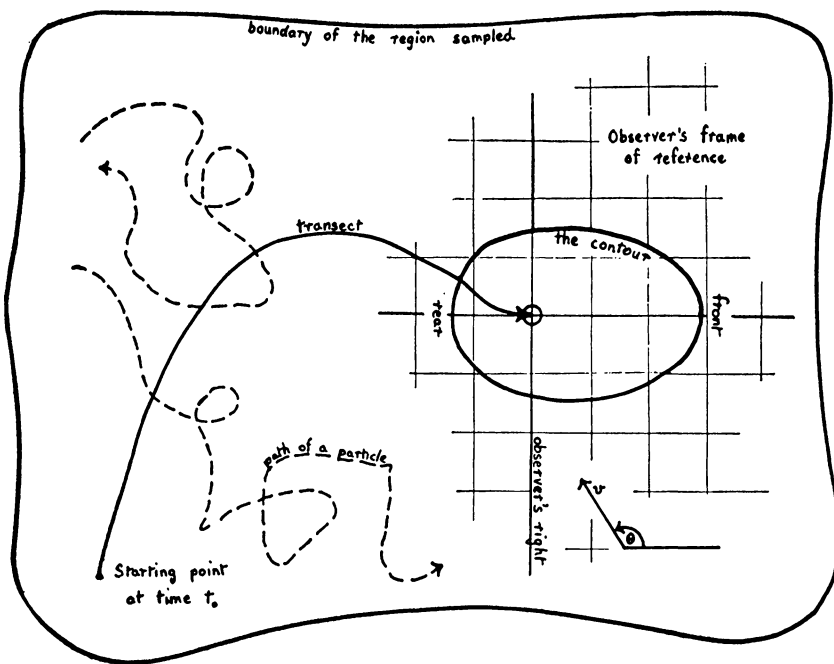


FIGURE 1.
AN OBSERVER'S SAMPLING REGION

equally likely either to contain particles *or* to be visited by the observer. More strictly stated, the probability density is taken to be uniform for all transects or segments of the same transect planned without prior knowledge of the spatial distribution of density in the area.

In this section of the paper the velocities of the particles, both in magnitude and direction, are measured relatively to the observer, that is, on the imaginary frame of reference which he carries about with him. It may be convenient for ecologists not accustomed to the idea of relative velocity to think of the framework of reference as a material surface on which the particles trace out a permanent record of their movements, and that we are concerned with the directions and rates at which these tracks are being added to. Thus at time t a particular particle may have a relative velocity with direction $\theta(t)$ and magnitude $v(t)$.

Let the particles be classified at time t on the basis of the magnitude of their relative velocities and on the relative direction of their motion, so that $f(v, \theta, t) dv d\theta$ represents the proportion at time t having speeds in the elementary interval $v \pm \frac{1}{2}dv$ and directions in $\theta \pm \frac{1}{2}d\theta$.

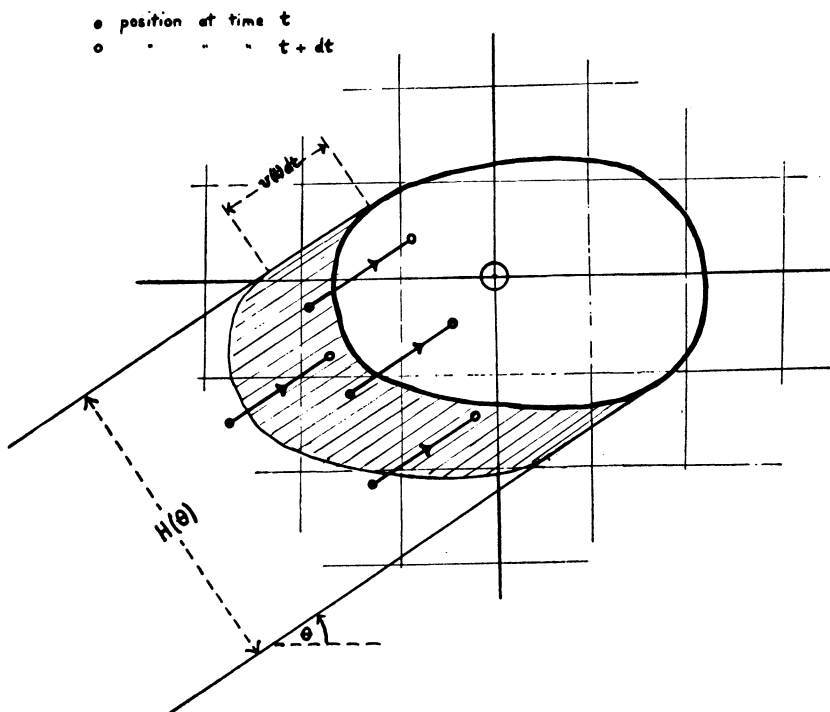


FIGURE 2.
THE MOTION OF PARTICLES

In the following treatment it is assumed that the contour encloses a convex figure, though the results with appropriate modifications can be extended to figures with concave indentations of the boundary.

Let two parallel tangents to the contour having direction θ be drawn (Fig. 2) and let the distance between them be $H(\theta)$. Let a border of width $v(t) dt$ be marked off and shaded as in the figure.

Then any particle of the class with speed $v \pm \frac{1}{2}dv$ and direction $\theta \pm \frac{1}{2}d\theta$ will cut the contour (from without) in the elementary interval of time from t to $t + dt$ if and only if it lies in the shaded border at time t . Since the area of this band is $H(\theta)v(t) dt$, the expected number of particles of the stated class lying in it will be $\mathfrak{D}f(v, \theta, t) dv d\theta H(\theta)v(t) dt$.

The expected total number cutting the contour from without in the minute interval of time dt is given by integrating all classes, that is over all values of v and θ ; and the expected total number $\mathcal{E}\{n\}$ doing so in the whole interval from T_0 to T_1 by integrating over t . Thus

$$\mathcal{E}\{n\}_{(T_0, T_1)} = \mathfrak{D} \int_0^{2\pi} \int_0^\infty \int_{T_0}^{T_1} f(v, \theta, t) v(t) H(\theta) d\theta dv dt. \quad (3)$$

The Parameter H

When the contour is not a circle and it is impracticable to evaluate the integral in (3), it is, nevertheless, possible to fix upper and lower bounds to it by employing the mean value theorem.

Because f , v are both positive, we may write

$$\varepsilon\{n\} = \mathfrak{D}H \int_0^{2\pi} \int_0^\infty \int_{T_0}^{T_1} f(v, \theta, t)v(t) d\theta dv dt,$$

where H is some value intermediate between the least and greatest possible values of $H(\theta)$.

Since the mean value of v for the period involved is by definition

$$V = \frac{1}{T_1 - T_0} \int_{T_0}^{T_1} \int_0^{2\pi} \int_0^\infty v(t)f(v, \theta, t) dt d\theta dv, \quad (4)$$

we obtain $\varepsilon\{n\} = \mathfrak{D}HTV$ where $T = T_1 - T_0$.

In the special case where the contour is a circle so that $H = 2R$, this reduces in form to Yapp's first formula $\mathfrak{D} = z/(2RV)$, where, however, $z = \varepsilon\{n\}/T$ may be interpreted as the expected value of n/T , the average rate of occurrence of encounters for the period concerned.

In general, this result should be more than sufficient for normal ecological practice, when we consider the very considerable technical sources of error involved even in determining the shape and extent of the contour.

In the particular case where the observer is at rest and it is reasonable to rule out the existence of specially favoured directional movement on the part of the particles, $f(v, \theta, t)$ is independent of θ . Equation (3) then reduces to the product of two integrals and

$$H = \frac{1}{2\pi} \int_0^{2\pi} H(\theta) d\theta.$$

By a result due to Legendre (see Edwards I, p. 543 §532), it is known that the perimeter s of a closed oval of continuous curvature is given by $s = \int_0^{2\pi} p(\theta) d\theta$, where $p(\theta)$ is the length of the perpendicular from a fixed point within the figure to a tangent with direction θ , this angle taking on successive values from 0 to 2π as the tangent "rolls" round the figure back to its initial position. It follows immediately that $H = s/\pi$, a result which may also be derived from first principles, as an alternative to the method used above, by considering the flow of particles across an element ds of the contour.

When the observer moves sufficiently rapidly, the particles will almost invariably cut the contour at the observer's front, so that the

appropriate value of H for this limiting case is the distance H_0 between tangents drawn parallel to the direction of motion.

In general H lies between s/π and H_0 according to the relative magnitudes of the velocities of particle and observer.

The Effect of Rotation

When the observer turns round with his frame of reference, the relative velocity $v(t)$ of a particle is usually increased, especially if located at a considerable distance from the observer. For an observer rotating at a fixed spot, the relative motion of a fixed particle is in a circle. Particles, which otherwise would never be encountered, will, if sufficiently near to the observer, cut the contour one or more times in every complete rotation. The only exception arises when the contour is itself a circle with the observer at the centre, and then rotation has no effect whatsoever on increasing the number of encounters, for in this case we need not rotate the frame of reference associated with the observer but merely allow the contour conceived as a material hoop to rotate instead.

If the shape of the contour differs considerably from that of a circle with centre the observer, as would happen in purely visual studies where also rotation of the eyes and head would be inevitable, it would appear that an element of commonsense judgment is called for and assumed on the part of the observer in order that he can discount repeated encounters of the same particle due solely to repeated scanning of his immediate environment. If a commonsense continuity principle is adopted, the field of perception is not that given instantaneously but that synthesized over a short period of time from a rapid succession of observations covering a wide range of directions. It will in general have a more circular character than before, the possible deficiency in the rear being compensated for by the greater attention given ahead. Even so, the observer would not be at the centre of the field, and rapid changes in his direction of movement might be a serious source of complexity. Much of the error from this source could however be avoided fairly easily by suitable definition of the transect procedure so as to exclude marked changes in direction. This would certainly be better than attempting to incorporate the effects of rotation into the general formulation. Henceforth it will be assumed that rotation has been excluded.

Effect of Heterogeneity

Consider what happens in a heterogeneous region, and for simplicity but without loss of generality, suppose that the area can be subdivided

into a large number (N) of sub-areas in each of which the earlier stated conditions hold. Then

$$\varepsilon\{n\} = \sum_{i=1}^N \varepsilon\{n_i\} = \sum_{i=1}^N \mathfrak{D}_i H_i T_i V_i, \quad (5)$$

where T_i denotes the expected amount of time spent by the observer in the j th sub-area.

If the values of \mathfrak{D}_i , H_i , T_i , V_i vary from place to place in such a manner that their distributions are statistically independent, the mean value of their product is the product of their mean values, and (5) reduces to

$$\varepsilon_0\{n\} = \mathfrak{D}HTV, \text{ where } T = \sum T_i. \quad (6)$$

If, however, in regions in which the observer could only move slowly there were strong tendencies for the particles to be more dense and more active and for the contour to expand, formula (3) would give too small a value to the expected number of encounters.

The ratio between (5) and (6) is, of course, independent of the units in which the parameters \mathfrak{D}_i , H_i , T_i , V_i are measured and, though variable, these quantities cannot be negative. It is perhaps surprising, however, that even with considerable heterogeneity and marked correlation between them, the error involved is often not great, particularly if the correlations are not all of the same sign.

YAPP'S SECOND FORMULA

In this section we are concerned with the derivation of the mean relative velocity V , given information about the absolute velocities (u , w) of the particles and of the observer respectively and with the acceptable assumption that the directions of the particles are randomly and uniformly distributed with respect to the direction of motion of the observer.

A General Result

If we are given two fixed velocities of magnitude u and w , and if θ is the angle between them, the magnitude of the relative velocity is given by forming the triangle of velocities and applying the cosine rule.

$$v^2 = u^2 + w^2 - 2uw \cos \theta. \quad (7)$$

If now u , w , and θ are variable, and if the distribution of θ is independent of uw , we have, on taking expectations in (7),

$$\varepsilon\{v^2\} = \varepsilon\{u^2\} + \varepsilon\{w^2\},$$

since

$$\mathcal{E}\{uw \cos \theta\} = \mathcal{E}\{uw\}\mathcal{E}\{\cos \theta\},$$

and

$$\int_0^{2\pi} \cos \theta \, d\theta = 0.$$

Now for any random variable x , $\mathcal{E}\{x^2\} = \bar{x}^2 + \text{var } x$, so that we obtain

$$V^2 = \bar{u}^2 + \bar{w}^2 + \text{var } u + \text{var } w - \text{var } v, \quad (8)$$

in contrast to Yapp's formula

$$V_0^2 = \bar{u}^2 + \bar{w}^2. \quad (9)$$

If u and w are constant, it is clear that the second formula (9) gives a value in excess of the true value (8).

Case of Velocities of Fixed Magnitude

The mean value of the relative velocity for vectors u and w of fixed magnitude is

$$V = \frac{1}{2\pi} \int_0^{2\pi} v \, d\theta \quad \text{where} \quad v = (u^2 + w^2 - 2uw \cos \theta)^{1/2}.$$

By symmetry and the substitution $\cos \theta = 1 - 2 \sin^2 \frac{1}{2}\phi$, the integral readily reduces to

$$V = \frac{2}{\pi} (u + w) \int_0^{\pi/2} \left(1 - \frac{4uw}{(u + w)^2} \sin^2 \phi \right)^{1/2} d\phi. \quad (10)$$

This can be evaluated immediately using tables of the elliptic integral [Legendre, 1825],

$$E_{\pi/2}(\psi) = \int_0^{\pi/2} (1 - \sin^2 \psi \sin^2 \phi)^{1/2} d\phi,$$

by setting

$\psi = \arcsin [2(uw)^{1/2}/(u + w)]$. The values of this exact solution (V) and those of Yapp's formula (V_0) are tabulated below for a series of values of $\rho = u/w$. It is easily proved analytically that the greatest error occurs when $\rho = 1$ (and is then about 10%) and that the error progressively decreases to zero as ρ moves away from this value. It will be apparent from the table that, for values of ρ very small or very large compared with unity, the error involved is almost negligible when considered in relation to other sources of inaccuracy.

TABLE 1
THE RELATIVE SIZES OF $V = (1/2\pi) \int_0^{2\pi} (u^2 + w^2 - 2uw \cos \theta)^{1/2} d\theta$
AND $V_0 = (u^2 + w^2)^{1/2}$ FOR VARIOUS VALUES OF $\rho = u/w$

ρ	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
$1/\rho$	∞	10	5	3.3	2.5	2	1.7	1.4	1.2	1.1	1.0
V/V_0	1	1.00	.99	.98	.97	.95	.94	.92	.91	.90	.90

An Important Special Case

The analogue of Maxwell's distribution appropriate to the present 2-dimensional problem is $dF(u) = e^{-cu^2} 2cu \, du$, where $dF(u)$ denotes the probability that a particle picked at random has a speed in the elementary interval $u \pm \frac{1}{2}du$, and c is a parameter whose value depends on the nature of the particles and on the conditions. The mean velocity is

$$\mathcal{E}\{u\} = \int_0^\infty ue^{-cu^2} 2cu \, du.$$

The substitution $\beta = cu^2$ then gives

$$\mathcal{E}\{u\} = \frac{1}{\sqrt{c}} \int_0^\infty \beta^{1/2} e^{-\beta} d\beta = \frac{1}{2} \left(\frac{\pi}{c}\right)^{1/2}. \tag{11}$$

For comparison with a later result we need to know the form of the moment generating function of u^2 . By definition this is

$$\begin{aligned} \phi(t) = \mathcal{E}\{e^{tu^2}\} &= \int_0^\infty e^{-(c-t)u^2} 2cu \, du \\ &= \int_0^\infty e^{-(c-t)\alpha} c \, d\alpha = \left(1 - \frac{t}{c}\right)^{-1}. \end{aligned} \tag{12}$$

We now show that, if the observer's velocity w also varies in the above way but with a different parameter value (k), then the resultant velocity v has the same kind of distribution but with parameter $kc/(k + c)$. This result implies [using (11)] that \bar{u} , \bar{w} , V are proportional respectively to

$$\sqrt{\frac{1}{c}}, \sqrt{\frac{1}{k}}, \sqrt{\frac{k+c}{kc}},$$

from which it follows immediately that $V^2 = \bar{u}^2 + \bar{w}^2$, which is Yapp's second formula.

To prove the statement, we deduce the moment generating function of the distribution of $v^2 = u^2 + w^2 - 2uw \cos \theta$ and show that it has the same form as (12). This function is

$$\begin{aligned}\Phi(t) &= \mathcal{E}\{e^{t v^2}\} \\ &= \frac{1}{2\pi} \int_0^\infty \int_0^\infty \int_0^{2\pi} e^{t(u^2 + w^2 - 2uw \cos \theta) - c u^2 - k w^2} ck \, du^2 \, dw^2 \, d\theta.\end{aligned}\tag{13}$$

Now

$$\frac{1}{2\pi} \int_0^{2\pi} \exp(\pm \cos \theta) \, d\theta = I_0(q) = \sum_{n=0}^\infty \frac{(\frac{1}{2}q)^{2n}}{n!n!}.\tag{14}$$

Integrating (13) with respect to θ , using (14), now gives

$$\begin{aligned}\Phi(t) &= ck \sum_{n=0}^\infty t^{2n} \int_0^\infty e^{-u^2(c-t)} \frac{(u^2)^n}{n!} \, du^2 \int_0^\infty e^{-w^2(k-t)} \frac{(w^2)^n}{n!} \, dw^2 \\ &= ck \sum_{n=0}^\infty \{t^{2n}/[(c-t)(k-t)]^{n+1}\} = \left\{1 - \left(\frac{1}{c} + \frac{1}{k}\right)t\right\}^{-1},\end{aligned}\tag{15}$$

where in the first line we have twice used the result

$$\int_0^\infty e^{-px} x^n \, dx = n!/p^{n+1}$$

and in the second have simply summed the geometric series.

This remarkable result, that the relative velocity has a probability distribution with the same general mathematical form as that of the components, does not appear to be true in any other cases I have studied.

THE ESTIMATION OF DENSITY

Formula (4) provides us immediately with an unbiased estimator of \mathfrak{D} when V , H , T are given, namely: $\hat{\mathfrak{D}} = n/(HTV)$, where n denotes the actual number of encounters in the course of a transect. For every observed value of n , we can compute a corresponding value of $\hat{\mathfrak{D}}$, and it is clear that the variance of $\hat{\mathfrak{D}}$ is proportional to that of n . The basic question, therefore, is—"What is the variance of n ?", a question that can be approached both theoretically and practically.

The obvious practical course would be to repeat the experiment a number of times, or, if this were not permissible, to conduct the experiment so as to be able to split the transect up into a large number of separate pieces and then to apply the principle that the variance of the mean of ν independent values is $1/\nu$ times the variance of a single value. The latter can be estimated directly from the data in the usual way. Since it is based on $\nu - 1$ degrees of freedom, it will not be very reliable

if ν is small. But the important thing is not to know this variance with high accuracy but merely to use it to assess the order of reliability that can be attached to a particular estimate of density, a consideration which often has to be faced at the planning or preliminary stage of a census before the results of replicate transects are available.

A rigorous theoretical approach to the problem is not only difficult but appears to call for the development of new mathematical tools. Whereas the expected number of encounters does not appear to depend on the shapes of the paths, the variance of the number of encounters does. Nevertheless, by theoretical argument it is possible to conjecture the general character of the result. It seems that, if the particles sweep across the observer's space without any special tendency to double back on their tracks or to execute oscillatory movements, and as it were to become merged into the general picture, then the number of encounters for a fixed interval of time will be a Poisson variate. The variance and mean are then equal. If the particles are aggregated in groups, say of size g , then the variance will be g times the mean. Any complicated folding back of the particles on their tracks will have an effect on the variance equivalent to that of aggregation. Again, heterogeneity (local variations in probability density) will increase the magnitude of the sampling variance.

In order to provide concrete support for the theoretical formulae given earlier and the conjectures outlined above, it was thought desirable to set up laboratory experiments on Monte Carlo lines. It was necessary, of course, to represent the continuous motion of the particles and the observer by somewhat abrupt movements in discrete time. The scheme adopted was perhaps the simplest approximation possible. The particles were represented by coloured pins randomly distributed on a triangular lattice provided by large sheets of triangular graph paper. From any point on the lattice, six directions were possible, and the directions of movement of the particles were determined by the random procedure of throwing dice. By assigning fresh random directions to the particles individually after each move, the latter assumed the irregular paths required of them. The shape of the contour was chosen to be hexagonal and its size was such that the contour passed midway between the lattice points just inside it and those just outside. The path of the observer was determined arbitrarily in advance well within the confines of the whole field. In order to maintain a constant overall density of particles, the convention was adopted that any particle leaving the area automatically re-entered at a corresponding point on the opposite side. The magnitude of the velocity of the observer was taken as two units and that of the particles as one.

There were two ways of counting the number of encounters per unit

of time. In method I, after each completed move counts were made of the particles now inside but previously outside. Since in a continuous system it is possible for a particle to move in and out again in any finite interval of time, this method of counting apparently leads to underestimates. In method II, each completed move was considered in two parts: first the pins were moved and a count taken; then the observer moved and a second count taken. This method allows for the recording of encounters which in a continuous system need not necessarily occur, and therefore yields over-estimates. Though the purpose of the experiment was primarily to assess the order of magnitude of the variance, and could hardly be expected to yield more than a crude estimate of the density, it is of interest to note that whereas the true value of \mathfrak{D} was 0.08, the estimates obtained by the application of the appropriate formulae (already derived on the basis of a continuous model) to the observed results were for the two methods of counting 0.072 and 0.099 respectively, the standard errors of these figures being estimated from the data as approximately 0.007 and 0.010.

Several series of short transects were made and for each series the ratio of the observed value of the variance to the mean number of encounters was calculated. The results are summarized below. Statistical analysis confirms the conjectures, (1) that the variance and mean are of the same order of magnitude, and (2) that with moderately irregular paths, such as those occurring in these experiments (shape being considered in the space of the observer), the ratio actually exceeds unity.

TABLE 2
SUMMARY OF EXPERIMENTAL RESULTS

Duration of Transect	Number of Replicates	Ratio of Variance to Mean			
		Analogue I		Analogue II	
		Series A	Series B	Series A	Series B
3 moves	40	1.16	1.09	1.32	1.57
6 moves	20	1.59	0.93	1.98	1.42

It follows from the proportionality between $\hat{\mathfrak{D}}$ and n that

$$\frac{\text{s.d. of } \hat{\mathfrak{D}}}{\hat{\mathfrak{D}}} = \frac{\text{s.d. of } n}{\mathfrak{E}\{n\}} = \frac{Q}{\sqrt{\mathfrak{E}\{n\}}}, \quad \text{where } Q^2 = \frac{\text{var } n}{\mathfrak{E}\{n\}}. \quad (16)$$

In practice $\mathfrak{E}\{n\}$ can be replaced by the observed value n , and, from the

argument given above, Q can be regarded as a number in general somewhat greater than unity, its value depending on the degree of aggregation of the moving particles or the character of their paths or the heterogeneity of the area. Even where Q cannot be assessed precisely, it may nevertheless be possible to set some reasonable bounds to it and thereby set bounds to the estimates of density.

Mathematically speaking H (or $2R$) can be chosen arbitrarily. It is at the disposal of the observer to be used as he finds most convenient. Other considerations being equal, the larger H , the greater $\varepsilon\{n\}$ and the greater the precision of $\hat{\mathfrak{D}}$. The quantity V is here treated as a parameter regarded as calculable once adequate information about the velocities of the particles and the observer is given, though the actual estimation of these directly raises practical problems of considerable magnitude. The effects of errors in the use of the contour or in the estimation of V are not, of course, included in formula (13) above.

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