DEPARTMENT OF APPLIED MATHEMATICS,
UNIVERSITY COLLEGE, UNIVERSITY OF LONDON

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BIOMETRIC SERIES. III.

MATHEMATICAL CONTRIBUTIONS TO THE THEORY OF EVOLUTION.—XV. A MATHEMATICAL THEORY OF RANDOM MIGRATION.

BY
KARL PEARSON, F.R.S.
WITH THE ASSISTANCE OF
JOHN BLAKEMAN, M.Sc.

[With Seven Diagrams.]

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Mathematical Contributions to the Theory of Evolution.

XV. A MATHEMATICAL THEORY OF RANDOM MIGRATION. By

KARL PEARSON, F.R.S., with the assistance of JOHN BLAKEMAN, M.Sc.

(1) *Introductory.* In dealing with any natural phenomenon,—especially one of a vital nature, with all the complexity of living organisms in type and habit,—the mathematician has to simplify the conditions until they reach the attenuated character which lies within the power of his analysis*. The problem of migration is one which is largely statistical, but it involves at the same time a close study of geographical and geological conditions, and of food and shelter supply peculiar to each species. Some years ago the late Professor Weldon started an extensive study as to the distribution of various species and local races of land snails, but he was struck by the absence in several cases of any definite change of environment at the boundaries of the distribution of a definite race. It occurred to me in thinking over the matter that such boundaries, where they exist, may possibly not be permanent. To take a purely hypothetical illustration: A species is pushed back to a certain limit by a change of environmental conditions—say, an ice age. Does it follow that if the environment again becomes favourable, that it will *rapidly* occupy possible country? What is the rate of infiltration of a species into a possible habitat? It depends, of course, on a whole series of most complex conditions, the rate of locomotion, the channels of communication, the distribution of food areas and breeding grounds in the new country, and the connecting links between all these. Every detail must be studied by the field naturalist in relation to each species. All the mathematician can do is to make an idealised system, which may be dangerous, if applied dogmatically to any particular case, but which can hardly fail to be suggestive, if it be treated within the limits of reasonable application. The idealised system which I proposed to myself was of the following kind:

(i) Breeding grounds and food supply are supposed to have an average uniform distribution over the district under consideration. There is to be no special following of river beds or forest tracks.

* This is of course a perfectly familiar process to every mathematical physicist, but its unfamiliarity leads the biologist to suspect or even discard mathematical reasoning, instead of testing the result as the physicist does by experiment and observation.

(ii) The species scattering from a centre is supposed to distribute itself uniformly in all directions. The average distance through which an individual of the species moves from habitat to habitat will be spoken of as a "flight," and there may be n such "flights" from locus of origin to breeding ground, or again from breeding ground to breeding ground, if the species reproduces more than once. A flight is to be distinguished from a "flitter," a mere two and fro motion associated with the quest for food or mate in the neighbourhood of the habitat.

(iii) Now taking a centre, reduced in the idealised system to a point, what would be the distribution after n random flights of N individuals departing from this centre? This is the *first* problem. I will call it the *Fundamental Problem of Random Migration.*

(iv) Supposing the first problem solved, we have now to distribute such points over an area bounded by any contour, and mark the distribution on both sides of the contour after any number of breeding seasons. The shape of the contour and the number of seasons dealt with provide a series of problems which may be spoken of as *Secondary Problems of Migration.*

A little consideration of the Fundamental Problem showed me that it presented considerable analytical difficulties, and I was by no means clear that the series of hypotheses adopted would be sufficiently close to the natural conditions of any species to repay the labour involved in the investigation. At this stage the matter rested, until last year Major Ross put before me the same problem as being of essential importance for the infiltration of mosquitoes into cleared areas, and asked me if I could not provide the statistical solution of it. He considered that we might treat a district as approximately "equi-swampous," and thus my conditions (i), (ii) above could be applied to obtain at any rate a first approximation to the solution.

Starting on the problem again I obtained the solution for the distribution after two flights, an integral expressing the distribution after three flights, which I carelessly failed to see could be at once reduced to an elliptic integral, and the general functional relation between the distribution after successive flights. At this point I failed to make further progress, and under the heading of "The Problem of the Random Walk" asked for the aid of fellow-mathematicians in *Nature**. The reply to my appeal was threefold. Mr Geoffrey T. Bennett sent me in terms of elliptic integrals the solution for three flights. Lord Rayleigh drew my attention to the fact that the "problem of the random walk" where the number of flights is very great becomes identical with a problem in the combination of sound amplitudes in the case of notes of the same period, which he has dealt with in several papers†. Lastly Professor J. C. Kluyver presented a paper to the Royal Academy

* July 27th, 1905.

† *Phil. Mag.*, August, 1880, p. 75; February, 1899, p. 246.

of Sciences of Amsterdam, entitled "A local probability problem."* Professor Kluyver obtains the general solution in terms of the integral of a product of Bessel's functions of the zero and first orders. He deduces Rayleigh's solution for n large, he shows that the Bessel function integral represents a series of different analytic functions in different intervals, and proves a number of special problems of very considerable interest. Referring to his general solution, he writes, however:

"From this result we infer that the probability sought for is of a rather intricate character. The $n+1$ functions J are oscillating functions, and have their signs altering in an irregular manner as the variable u increases. Hence even an approximation of the integral is not easily found, and as a solution of Pearson's problem it is little apt to meet the requirements of the proposer."†

Kluyver's solution is of extreme suggestiveness for the analytical theory of discontinuous functions. In the endeavour to express it in a form suited to my special purposes I have come across a long series of Bessel function properties, some at least of which seem to me novel, but have unfortunately no bearing on the problem of migration. If we turn to Rayleigh's solution for n large, I must confess at once to being unconvinced of the adequacy of the proofs used to deduce it, especially that in the *Theory of Sound*‡. Kluyver's proof of Rayleigh's solution§ appears to me to also require much strengthening, and in neither case do we have any practical measure of what the number of flights must be before we have in practice a reasonable accordance between the discontinuous Bessel's function integral expression and the Rayleigh solution of Gaussian frequency type.

After a good many failures I have succeeded in obtaining a solution in series of the Bessel function integral, but this not of a character to be of service for *frequent* arithmetical calculations. It serves, however, to test the approximation of the Rayleigh solution and the accuracy of the solutions for few flights obtained by other processes. At this stage I realised that the functional equation between the distributions for n and $n+1$ flights could be solved graphically, and that starting with the known distributions for $n=2$ or $n=3$, we could by very great labour, but absolutely straightforward graphical work and the use of mechanical integrators, build up in succession the solutions for $n=4$, 5, 6, 7, etc. I proposed that this process should be continued until the graphically found distribution coincided with the plotted values obtained from the above solution in series. This was achieved for $n=7$. For $n=6$ and $n=7$, the solution in series approaches to the Rayleigh solution, with which for all practical purposes it may be asserted to coincide for $n=10$. We have thus reached a continuous graphical illustration of the transition of a series of discontinuous and, in many respects, remarkable analytical functions, step by step with the increase of n into a normal curve of errors. The relation-

* *Koninklijke Akademie van Vetenschappen te Amsterdam.* Proceedings, Oct. 25, 1905, pp. 341—50.

† *loc. cit.* p. 343.

‡ 2nd Edition, § 42 a.

§ Kluyver, *loc. cit.* p. 345.

ship is a noteworthy one, and not without suggestion for other branches of investigation.

The exact method of graphical solution will be described later; the whole labour of it, involving many weeks' work, was due to my assistant, Mr John Blakeman, M.Sc.

(2) *General Analytical Solution of the Fundamental Problem.* Let the origin be taken at the centre of dispersion and r be the distance of any small elementary area a from the centre of dispersion. Let $\phi_n(r^2) \cdot a$ be the frequency of individuals on a after the nth flight, and $\phi_{n+1}(r^2)\, a$ their frequency on the same element after the $(n+1)$th flight. Let l be the length of the flight. Then only those individuals who were on a circle of radius l round the centre of a after the nth flight can reach a with the $(n+1)$th flight, and only those individuals of these who take their flight in one definite direction. Let O be the centre of dispersion, C the centre of a, P a point on the circle of radius l round C, $\angle PCO = \theta$, then the frequency per unit area at P is $\phi_n(r^2 + l^2 - 2rl\cos\theta)$, and the amount which goes in directions between θ and $\theta + \delta\theta$ is $d\theta/2\pi$. Hence the frequency per unit area at C after the $(n+1)$th flight is given by:

$$\phi_{n+1}(r^2) = \frac{1}{2\pi}\int_0^{2\pi} \phi_n(r^2 + l^2 - 2rl\cos\theta)\, d\theta \quad \text{.....................(i).}$$

This is the equation, which I shall speak of as the general functional relation between the densities at successive flights. Now assume: $\phi_n(r^2) = C_n J_0(ur)$, where C_n is any undetermined function of n, l and u, and u is at present an undetermined variable.

Then by Neumann's Theorem*:

$$J_0(u\sqrt{r^2 + l^2 - 2rl\cos\theta}) = J_0(ur)\, J_0(ul) + 2\sum_1^\infty J_t(ur)\, J_t(ul)\cos t\theta.$$

Hence:
$$\begin{aligned}\frac{1}{2\pi}\int_0^{2\pi} C_n J_0(u\sqrt{r^2 + l^2 - 2rl\cos\theta})\, d\theta &= C_n J_0(ur)\, J_0(ul)\\ &= C_{n+1} J_0(ur), \text{ by (i).}\end{aligned}$$

Therefore
$$C_{n+1} = J_0(ul)\, C_n.$$

It follows that $C_n = D\{J_0(ul)\}^n$, where D may be any function of l, but not of n.

Thus we have:
$$\phi_n(r^2) = D\, J_0(ur)\, \{J_0(ul)\}^n,$$

where we may sum for any or all values of u.

Now when $n = 1$, $\phi_1(r^2)$ must be zero, for all values of r except $r = l$ to $l + \tau$, and it then equals $N/(2\pi l\tau)$, τ being very small and N the total number issuing from the centre of dispersion. We know, however, that†:

$$\begin{aligned}\int_0^\infty du \int_q^p u\rho f(\rho)\, J_n(u\rho)\, J_n(ur)\, d\rho &= f(r), \text{ if } q < r < p;\\ &= 0, \quad \text{if } r > p \text{ or } < q.\end{aligned}$$

* C. Neumann, *Theorie der Besselschen Functionen*, S. 65.

† Gray and Mathews, *Treatise on Bessel's Functions*, p. 80.

Now take $n=0,\ q=l,\ p=l+\tau$ and $f(\rho)=\dfrac{N}{2\pi l\tau}$,

then we have: $$\int_0^\infty ul\,\frac{N}{2\pi l\tau}\,J_0(ul)\,J_0(ur)\,\tau du=\phi_1(r^2),$$

or, $$\phi_1(r^2)=\frac{N}{2\pi}\int_0^\infty u\,J_0(ul)\,J_0(ur)\,du \quad\text{.......................(ii).}$$

This determines the form of D and the summation of u; for, if we take

$$\phi_n(r^2)=\frac{N}{2\pi}\int_0^\infty u\,J_0(ur)\{J_0(ul)\}^n\,du \quad\text{.......................(iii),}$$

we satisfy the general functional relation (i) and further the initial equation (ii).

Let $P_n(r)$ be the probability that an individual after n flights will be a distance r or less from the centre of dispersion. Then clearly

$$P_n(r)=2\pi\int_0^r r\,dr\,\phi_{n+1}(r^2)$$

$$=N\int_0^r r\,dr\int_0^\infty u\,J_0(ur)\,\{J_0(ul)\}^n\,du.$$

But* $$ur\,J_0(ur)=\frac{d\{J_1(ur)\,ur\}}{d(ur)},$$

hence $$P_n(r)=N\int_0^\infty du\int_0^{ur} d(ur)\,\frac{d\{J_1(ur)\,ur\}}{d(ur)}\,\frac{\{J_0(ul)\}^n}{u}$$

$$=N\int_0^\infty r\,J_1(ur)\,\{J_0(ul)\}^n du,$$

or if $v=ur$: $$=N\int_0^\infty J_1(v)\,J_0\left(\frac{lv}{r}\right)^n dv \quad\text{..................................(iv).}$$

(iv) is Kluyver's fundamental solution, which he reaches by a very different and more general analysis. (iii) is the form of it which best suits my present investigation.

(3) *On an expansion in series of the expression for* $\phi_n(r^2)$. By straightforward but somewhat laborious multiplication it can be shown that:

$$\{J_0(2\sqrt{y})\,e^y\}^n=1-\tfrac{1}{4}ny^2-\tfrac{1}{9}ny^3+\frac{(6n-11)\,n}{192}\,y^4$$

$$+\frac{(50n-57)\,n}{1800}\,y^5-\frac{(1892-2125n+270n^2)\,n}{103{,}680}\,y^6,\ \text{etc.}$$

* Gray and Mathews, *loc. cit.* p. 13.

Hence putting $2\sqrt{y}=z$,

$$\{J_0(z)\}^n = e^{-\frac{1}{4}nz^2}\left\{1-\frac{n}{64}z^4-\frac{n}{576}z^6+\frac{(6n-11)\,n}{192}\frac{z^8}{256}\right.$$
$$\left.+\frac{(50n-57)\,n}{1800}\frac{z^{10}}{1024}-\frac{(1892-2125n+270n^2)\,n}{103{,}680}\frac{z^{12}}{4096}-\text{etc.}\right\}\ \ldots\ldots(\text{v})$$
$$= e^{-\frac{1}{4}nz^2}\{1-\alpha_4 z^4-\alpha_6 z^6-\alpha_8 z^8-\alpha_{10}z^{10}-\alpha_{12}z^{12}-\text{etc.}\},$$

let us write, for brevity. The α's are then known coefficients.

Now by (iii)

$$\phi_n(r^2)=\frac{1}{2\pi}\int_0^\infty u\,J_0(ur)\,\{J_0(ul)\}^n\,du.$$

But we know that*:

$$\int_0^\infty ue^{-\frac{1}{4}nu^2l^2}J_0(ur)\,du=\frac{2}{nl^2}e^{-r^2/nl^2}\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots(\text{vi}).$$

Write: $$\tfrac{1}{2}nl^2=\sigma^2\ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(\text{vii}).$$

Thus: $$\int_0^\infty ue^{-\frac{1}{2}u^2\sigma^2}J_0(ur)\,du=\frac{1}{\sigma^2}e^{-\frac{1}{2}r^2/\sigma^2}\ \ldots\ldots\ldots\ldots\ldots\ldots(\text{viii}).$$

Differentiate (viii) s times with regard to σ^2:

$$(-\tfrac{1}{2})^s\int_0^u u^{2s+1}e^{-\frac{1}{2}u^2\sigma^2}J_0(ur)\,du=\frac{d^s}{d(\sigma^2)^s}\left\{\frac{1}{\sigma^2}e^{-\frac{1}{2}r^2/\sigma^2}\right\}.$$

Hence, if $\beta=-2\sigma^2/r^2$, we have:

$$I_{2s}=\int_0^\infty u^{2s+1}e^{-\frac{1}{2}u^2\sigma^2}J_0(ur)\,du$$
$$=-\frac{2^{2s+1}}{r^{2s+2}}\frac{d^s}{d\beta^s}\left(\frac{1}{\beta}e^{1/\beta}\right)$$
$$=-\frac{2^{2s+1}}{r^{2s+2}}\dot{i}_{2s},\ \text{say}.$$

We have therefore:

$$\phi_n(r^2)=\frac{N}{2\pi\sigma^2}e^{-\frac{1}{2}r^2/\sigma^2}+\frac{N}{2\pi}\mathop{S}_{s=2}^{s=\infty}\frac{l^{2s}2^{2s+1}\alpha_{2s}\dot{i}_{2s}}{r^{2s+2}}\ \ldots\ldots\ldots\ldots\ldots\ldots(\text{ix}),$$

where it remains to evaluate $\dot{i}_{2s}=\dfrac{d^s}{d\beta^s}\left(\dfrac{1}{\beta}e^{1/\beta}\right)$.

We find:

$$\dot{i}_4=-\frac{1}{8}\left(\frac{r}{\sigma}\right)^6e^{-r^2/2\sigma^2}\left(2-2\frac{r^2}{\sigma^2}+\frac{1}{4}\frac{r^4}{\sigma^4}\right),$$
$$\dot{i}_6=-\frac{1}{16}\left(\frac{r}{\sigma}\right)^8e^{-r^2/2\sigma^2}\left(6-9\frac{r^2}{\sigma^2}+\frac{9}{4}\frac{r^4}{\sigma^4}-\frac{1}{8}\frac{r^6}{\sigma^6}\right),$$
$$\dot{i}_8=-\frac{1}{32}\left(\frac{r}{\sigma}\right)^{10}e^{-r^2/2\sigma^2}\left(24-48\frac{r^2}{\sigma^2}+18\frac{r^4}{\sigma^4}-2\frac{r^6}{\sigma^6}+\frac{1}{16}\frac{r^8}{\sigma^8}\right),$$

* Gray and Mathews, *loc. cit.* Eqn. (162), p. 78

$$i_{10} = -\frac{1}{64}\left(\frac{r}{\sigma}\right)^{12} e^{-r^2/2\sigma^2}\left(120 - 300\frac{r^2}{\sigma^2} + 150\frac{r^4}{\sigma^4} - 25\frac{r^6}{\sigma^6} + \frac{25}{16}\frac{r^8}{\sigma^8} - \frac{1}{32}\frac{r^{10}}{\sigma^{10}}\right),$$

$$i_{12} = -\frac{1}{128}\left(\frac{r}{\sigma}\right)^{14} e^{-r^2/2\sigma^2}\left(720 - 2160\frac{r^2}{\sigma^2} + 1350\frac{r^4}{\sigma^4} - 300\frac{r^6}{\sigma^6} + \frac{225}{8}\frac{r^8}{\sigma^8} - \frac{9}{8}\left(\frac{r}{\sigma}\right)^{10} + \frac{1}{64}\left(\frac{r}{\sigma}\right)^{12}\right).$$

Remembering that by (vii) $l^2 = 2\sigma^2/n$, we have from (ix)

$$\begin{aligned}\phi_n(r^2) = \frac{N}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2}\Bigg\{1 &- \frac{1}{4n}\left(2 - 2\frac{r^2}{\sigma^2} + \frac{1}{4}\frac{r^4}{\sigma^4}\right) - \frac{1}{9n^2}\left(6 - 9\frac{r^2}{\sigma^2} + \frac{9}{4}\frac{r^4}{\sigma^4} - \frac{1}{8}\frac{r^6}{\sigma^6}\right)\\ &+ \frac{6n-11}{192n^3}\left(24 - 48\frac{r^2}{\sigma^2} + 18\frac{r^4}{\sigma^4} - 2\frac{r^6}{\sigma^6} + \frac{1}{16}\frac{r^8}{\sigma^8}\right)\\ &+ \frac{50n-57}{1800n^4}\left(120 - 300\frac{r^2}{\sigma^2} + 150\frac{r^4}{\sigma^4} - 25\frac{r^6}{\sigma^6} + \frac{25}{16}\frac{r^8}{\sigma^8} - \frac{1}{32}\frac{r^{10}}{\sigma^{10}}\right)\\ &- \frac{1892 - 2125n + 270n^2}{103{,}680n^5}\left(720 - 2160\frac{r^2}{\sigma^2} + 1350\frac{r^4}{\sigma^4} - 300\frac{r^6}{\sigma^6} + \frac{225}{8}\frac{r^8}{\sigma^8} - \frac{9}{8}\frac{r^{10}}{\sigma^{10}} + \frac{1}{64}\frac{r^{12}}{\sigma^{12}}\right)\\ &- \text{etc.}\Bigg\} \quad\ldots\ldots\ldots\ldots\ldots\ldots(\text{x}).\end{aligned}$$

This is the general expansion for the distribution of the individuals emerging from a centre of dispersion after n random flights. Clearly if we want to go as far as $\frac{1}{n^q}$ we must retain terms up to $(r^2/\sigma^2)^{2q}$, and the convergence is small for n small. Thus for the first two or three flights, (x) as far as I have calculated the terms gives poor results, even if they are notwithstanding better than the Rayleigh solution. The arithmetical work required to calculate the ordinates is also severe. If we put $n = \infty$, we have

$$\phi_\infty(r^2) = \frac{N}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2} \quad\ldots\ldots\ldots\ldots(\text{xi}),$$

Lord Rayleigh's expression. Now $\sigma^2 = \frac{1}{2}nl^2$, hence unless l becomes indefinitely small as n becomes indefinitely large the population becomes widely scattered. If the single flight l be very small, but the total flight nl be finite, then $\frac{1}{2}nl^2$ tends to become vanishingly small, or the population remains close to the centre of dispersion. This is really the "flitter" as distinct from the flight.

Examining the solution found it is clear that it may be looked upon as the sum of products of two factors, one series of factors not involving r/σ but only n and the other not involving n but only r/σ. Thus we may write

$$\phi_n(r^2) = N(\nu_0\omega_0 + \nu_2\omega_2 + \nu_4\omega_4 + \nu_6\omega_6 + \ldots),$$

where

$$\omega_0 = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2}, \qquad \nu_0 = 1,$$

$$\omega_2 = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2}\left(1 - \frac{1}{2}\frac{r^2}{\sigma^2}\right), \qquad \nu_2 = 0,$$

$$\omega_4 = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2} \left(2 - 2\frac{r^2}{\sigma^2} + \frac{1}{4}\frac{r^4}{\sigma^4}\right), \qquad \nu_4 = -\frac{1}{4n},$$

$$\omega_6 = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2} \left(6 - 9\frac{r^2}{\sigma^2} + \frac{9}{4}\frac{r^4}{\sigma^4} - \frac{1}{8}\frac{r^6}{\sigma^6}\right), \qquad \nu_6 = -\frac{1}{9n^2},$$

etc. ....(xii).

The ω-functions form a series of such special interest that a few of their remarkable properties will be stated in the next section.

(4) *Properties of the ω-functions.*

Let us consider the pth moment round the origin of the $2s$th ω-function taken over all plane space. We will denote it by $m_{p,2s}$. Then

$$m_{p,2s} = \int_0^{2\pi} d\theta \int_0^\infty r\,dr\,\omega_{2s} r^p$$

$$= 2\pi \int_0^\infty \omega_{2s} r^{p+1} dr \quad \text{......................................(xiii).}$$

Now $$\omega_{2s} = -\frac{1}{2\pi\sigma^2}(-\beta)^{s+1} \frac{d^s}{d\beta^s}\left(\frac{1}{\beta}e^{1/\beta}\right) \quad \text{......................(xiv),}$$

and by $\beta = -2\sigma^2/r^2$ we have $\qquad d\beta = \dfrac{4\sigma^2}{r^3} dr.$

Hence writing $p = 2q$ we find

$$m_{2q,2s} = (-1)^{q+s-1}(2\sigma^2)^q \int_{-0}^{-\infty} \beta^{s-q-1} \frac{d^s}{d\beta^s}\left(\frac{1}{\beta}e^{1/\beta}\right) d\beta \quad \text{..............(xv).}$$

Integrate by parts and we have

$$m_{2q,2s} = (-1)^{q+s-1}(2\sigma^2)^q \left[\left\{\beta^{s-q-1}\frac{d^{s-1}}{d\beta^{s-1}}\left(\frac{1}{\beta}e^{1/\beta}\right)\right\}_{-0}^{-\infty} - (s-q-1)\int_{-0}^{-\infty} \beta^{s-q-2}\frac{d^{s-1}}{d\beta^{s-1}}\left(\frac{1}{\beta}e^{1/\beta}\right) d\beta\right].$$

The part in curled brackets vanishes at the limits and thus

$$m_{2q,2s} = (-1)^{q+s-2}(2\sigma^2)^q (s-q-1)\int_{-0}^{-\infty} \beta^{s-q-2}\frac{d^{s-1}}{d\beta^{s-1}}\left(\frac{1}{\beta}e^{1/\beta}\right) d\beta$$

$$= m_{2q,2s-2}(s-q-1).$$

Repeating this process we find

$$m_{2q,2s} = (s-1-q)(s-2-q)(s-3-q)\ldots(-q)$$

$$\times(-1)^{q-1}\times(2\sigma^2)^q \times \int_{-0}^{-\infty} \beta^{-q-2} e^{1/\beta} d\beta \quad \text{.....................(xvi).}$$

The integral is finite and known; hence if q be less than s we find for integer values

$$m_{2q,2s} = 0, \qquad q < s \quad \text{.............................(xvii).}$$

Now consider ω_{2s} as made up of two parts,

$$\omega_{2s} = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2} \times \chi_{2s} \quad \text{..........................(xviii).}$$

Then it is clear that χ_{2q}, if q be less than s, consists of powers of r^2 less than s, and therefore

$$\int_0^\infty \omega_{2s}\chi_{2q}rdr=0.$$

Accordingly a remarkable property holds for the χ-function part of the ω-function, namely, if χ_{2q} and $\chi_{2q'}$ be two such functions, then it follows that

$$\int_0^\infty e^{-\frac{1}{2}r^2/\sigma^2}\chi_{2q}\chi_{2q'}rdr=0, \text{ if } q \text{ and } q' \text{ be different}, \quad\text{(xix)}.$$

Returning to (xvi), let us put $q=s$, then

$$m_{2s,2s}=-(2\sigma^2)^s\,\underline{|s}\int_{-0}^{-\infty}\beta^{-s-2}e^{1/\beta}d\beta$$

$$=\frac{(2\sigma^2)^s\,\underline{|s}}{2^s}(-1)^s\int_0^\infty x^{2s+1}e^{-\frac{1}{2}x^2}dx,$$

or,

$$m_{2s,2s}=(-1)^s\sigma^{2s}2^s(\underline{|s})^2 \quad\text{(xx)}.$$

Let us now consider the integral over the plane

$$I=2\pi\int_0^\infty \omega_{2s}\chi_{2s}rdr.$$

Except for the last term in χ_{2s}, it will consist of a number of terms having for factors $m_{2s,2q}$ with $q<s$ and these all vanish. The last term in χ_{2s} is

$$(-1)^s\frac{1}{2^s}\left(\frac{r}{\sigma}\right)^{2s},$$

and accordingly

$$I=2\pi\int_0^\infty \omega_{2s}\chi_{2s}rdr=\frac{2\pi(-1)^s}{2^s}\frac{1}{\sigma^{2s}}\int_0^\infty \omega_{2s}r^{2s+1}dr,$$

or by (xx)

$$I=(\underline{|s})^2 \quad\text{(xxi)}.$$

Hence we have the following properties:

(*a*) The integral all over the plane of distribution of one product of a χ-function into an ω-function of a different order is zero.

(*b*) The integral all over the plane of distribution of the product of a χ-function into an ω-function of the same order is, if $2s$ be the order, equal to $(\underline{|s})^2$.

These properties enable us—as in the case of Bessel's functions or Legendre's functions—to expand any function symmetrical round a centre and a function only of the square of the distance from that centre in ω-functions.

Thus let

$$F(r^2)=\sum_{s=0}^{s=\infty}(b_{2s}\omega_{2s}),$$

multiply by χ_{2s} and integrate all over the plane,

$$2\pi \int_0^\infty F(r^2)\, \chi_{2s}\, r dr = b_{2s}\, 2\pi \int_0^\infty \omega_{2s}\, \chi_{2s}\, r dr = b_{2s}\, \{\lfloor s\}^2.$$

Hence
$$b_{2s} = \frac{2\pi}{\{\lfloor s\}^2} \int_0^\infty F(r^2)\, \chi_{2s}\, r dr \quad \text{...........................(xxii).}$$

Now χ_{2s} consists of an algebraic series in $\left(\frac{r}{\sigma}\right)$. Thus the discovery of the value of the integral $\int_0^\infty F(r^2)\, \chi_{2s}\, r dr$ depends solely on the determination of the odd moments of $F(r^2)$ between 0 and ∞. We conclude therefore that an expansion in ω-functions involves merely the determination of moments, such as every statistician has been accustomed for years to calculate. This is not the proper occasion to deal fully with the properties of the ω-functions, nor to generalise them for odd powers of r, and to consider the convergency of expansions in terms of ω-functions. They will be discussed on another occasion, but the present writer believes that they will be found of not inconsiderable service, not only in statistical problems, but in certain physical problems where intensity round an axis diminishes with the distance.

(5) Two further problems are of service for the theory of dispersion. Suppose

$$F(r^2) = \mathop{S}_{s=0}^{s=\infty} (b_{2s}\, \omega_{2s}).$$

Integrate over the plane and remember that $\chi_0 = 1$,

$$2\pi \int_0^\infty F(r^2)\, r dr = \mathop{S}_{s=0}^{s=\infty} 2\pi \int_0^\infty b_{2s}\, \omega_{2s}\, \chi_0\, r dr$$
$$= b_0 \text{.......................................(xxiii).}$$

Thus the first coefficient is merely the total volume of the surface $z = F(r^2)$, taken over the plane.

Next consider the second moment

$$2\pi \int_0^\infty r^2 F(r^2)\, r dr = \mathop{S}_{s=0}^{s=\infty} 2\pi \int_0^\infty b_{2s}\, .\, \omega_{2s}\, .\, r^2.\, r dr.$$

Every term of the summation vanishes except for $s = 0$ and $s = 1$, and the left-hand side is the second moment of the function about the axis perpendicular to the plane through the centre = volume × (swing-radius)^2 = $b_0 \times K^2$, say. Thus:

$$b_0 \times K^2 = \frac{1}{\sigma^2} \int_0^\infty b_0 e^{-\frac{1}{2} r^2/\sigma^2} r^3 dr + \frac{1}{\sigma^2} \int_0^\infty b_2 e^{-\frac{1}{2} r^2/\sigma^2} \left(1 - \frac{1}{2} \frac{r^2}{\sigma^2}\right) r^3 dr$$
$$= 2 b_0 \sigma^2 + b_2 (2 - 4)\, \sigma^2 = 2\, (b_0 - b_2)\, \sigma^2,$$

or
$$b_2 = b_0 \{1 - \tfrac{1}{2} K^2/\sigma^2\} \text{...(xxiv).}$$

Thus far no choice has been made of σ^2. If we take $\sigma^2 = \frac{1}{2}K^2$, we have $b_2 = 0$, or if σ^2 be taken half the square of the swing-radius about the axis of the solid of revolution $z = F(r^2)$, that is if σ be the swing-radius of the solid about any plane through its axis, then the second term in the expansion of $F(r^2)$ in ω-functions disappears.

We are now able, I think, to grasp the relation of the Rayleigh solution to the complete solution of the random scatter round a centre of dispersion. If $\phi_n(r^2)$ be the function giving the distribution after n flights, then $\phi_n(r^2)$ can be expanded in a series of ω-functions, *i.e.*

$$\phi_n(r^2) = b_0\omega_0 + b_2\omega_2 + b_4\omega_4 + \ldots + b_{2s}\omega_{2s} + \ldots.$$

By choosing the σ^2 of the ω-functions $= \frac{1}{2}K^2$, this becomes, since b_0 the volume $= N$,

$$\phi_n(r^2) = \frac{N}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2} \{1 + b_4\chi_4 + \ldots + b_{2s}\chi_{2s} + \ldots\}.$$

Lord Rayleigh's solution provides the first term of this series, or is the correct solution to two terms in the expansion by ω-functions. It possesses the properties (a) that its volume is the same as that of the complete solution, and (b) the mean square deviation from the centre of dispersion is the same, *i.e.* $2\sigma^2$, as for the complete solution.

The latter depends upon the fundamental property of the ω-functions that $\int_0^\infty \omega_{2s} r^3 dr = 0$, if s be > 1.

The expansion in ω-functions shows us at once that, whatever be the magnitude of n, the mean square deviation from the centre of dispersion is $\sqrt{n}l$, and this gives us readily a *rough* measure of the range of habitat of any species for which n and l are approximately known.

Another point may be noted here as to the Rayleigh solution. That solution is the best fitting Gaussian error surface to the distribution, *i.e.* its volume and its standard deviation are the same as those of the actual distribution, whatever n may be. If we take the section, however, of the distribution through its axis the standard deviation of this according to the Rayleigh solution is $\sigma = \sqrt{\frac{1}{2}n}l$, but this is not the standard deviation of the section of the actual distribution, *i.e.* the Rayleigh solution does not give the best fitting normal curve to the section. It gives only the standard deviation corresponding to ω_0. It is of some value to note what are the standard deviations of other component ω_{2s} terms.

To obtain this we must determine the area and even moments corresponding to any ω_{2s} term. Let

$$A_{2s} = \int_0^\infty \omega_{2s} dr = \frac{1}{\pi\sigma} \frac{1}{2^{3/2}} (-1)^{s+\frac{1}{2}} \int_{-0}^{-\infty} \beta^{s-\frac{1}{2}} \frac{d^s}{d\beta^s}\left(\frac{1}{\beta} e^{1/\beta}\right) d\beta,$$

whence integrating by parts:

$$A_{2s}=\frac{1}{\pi\sigma}\frac{1}{2^{3/2}}(-1)^{\frac{1}{2}}\left(s-\frac{1}{2}\right)\left(s-\frac{3}{2}\right)\left(s-\frac{5}{2}\right)\cdots\frac{1}{2}\int_{-0}^{-\infty}\beta^{-3/2}e^{1/\beta}d\beta$$

$$=\frac{1}{2\pi\sigma}\left(s-\frac{1}{2}\right)\left(s-\frac{3}{2}\right)\left(s-\frac{5}{2}\right)\cdots\frac{1}{2}\int_0^{\infty}e^{-\frac{1}{2}x^2}dx$$

$$=\frac{1}{\sqrt{2\pi}\sigma}\frac{1}{2}\left(s-\frac{1}{2}\right)\left(s-\frac{3}{2}\right)\left(s-\frac{5}{2}\right)\cdots\frac{1}{2}\quad\text{.............................(xxv)},$$

$s=$ or >1.

If $s=0$, $$A_0=\frac{1}{\sqrt{2\pi}\sigma}\frac{1}{2}\quad\text{...............................(xxvi)}.$$

I now take: $$\mu_{2p,2s}=\int_0^{\infty}\omega_{2s}r^{2p}dr$$

$$=-\frac{1}{2\pi\sigma^2}\int_0 r^{2p}(-\beta)^{s+1}\frac{d^s}{d\beta^s}\left(\frac{1}{\beta}e^{1/\beta}\right)dr,$$

and find, reducing in the same manner,

$$\mu_{2p,2s}=\frac{1}{\sqrt{2\pi}\sigma}\frac{\sigma^{2p}}{2}\left(s-p-\frac{1}{2}\right)\left(s-p-\frac{3}{2}\right)\cdots\left(-p+\frac{1}{2}\right)\times 1.3.5\ldots(2p-1)\ldots\text{(xxvii)}.$$

Clearly: $$m_{2p-1,2s}=2\pi\int_0^{\infty}\omega_{2s}r^{2p}dr$$

by (xiii), hence: $$=2\pi\mu_{2p,2s}.$$

Or, $$m_{2p-1,2s}=\sqrt{2\pi}\sigma^{2p-1}\left(s-p-\frac{1}{2}\right)\left(s-p-\frac{3}{2}\right)\cdots\left(-p+\frac{1}{2}\right)$$

$$\times 1.3.5(2p-1)\quad\text{.......................(xxviii)}.$$

Thus the odd moments of the ω_{2s} functions are known*.

For the particular case when $p=1$:

$$\mu_{2,2s}=\frac{1}{\sqrt{2\pi}\sigma}\frac{\sigma^2}{2}\left(s-\frac{3}{2}\right)\left(s-\frac{5}{2}\right)\cdots\left(-\frac{1}{2}\right)\quad\text{..................(xxxii)},$$

if k_{2s} be the swing-radius round the axis of the function ω_{2s}. Hence by (xxv)

$$k_{2s}{}^2=\frac{\sigma^2(-\frac{1}{2})}{s-\frac{1}{2}}=-\frac{\sigma^2}{2s-1}\quad\text{.......................(xxxiii)}.$$

* If $x=r/\sigma$ the following finite difference and differential equations are fundamental in the theory of the ω-functions:

$$\omega_{2(s+2)}-(2s+3-\tfrac{1}{2}x^2)\,\omega_{2(s+1)}+(s+1)^2\,\omega_{2s}=0\quad\text{.............................(xxix)},$$

$$\omega_{2(s+1)}=(s+1)\,\omega_{2s}+\tfrac{1}{2}x\frac{d\omega_{2s}}{dx}\quad\text{.....................................(xxx)},$$

$$\frac{d^2\omega_{2s}}{dx^2}+\left(x+\frac{1}{x}\right)\frac{d\omega_{2s}}{dx}+2(s+1)\,\omega_{2s}=0\quad\text{............................(xxxi)}.$$

But the fuller treatment of the ω-functions must be deferred.

This is also true for $s=0$, as well as any integer value. It follows accordingly that while the total area of any ω-function from 0 to ∞ is positive, its k is negative for values of $s>1$. In other words the negative parts of ω are on the whole furthest from the axis. Again the absolute value of k_{2s} decreases as $\frac{1}{\sqrt{2s-1}}$ when s increases, or the higher the ω-function the less it contributes relative to its area to the total mean square deviation of the curve.

Applying these results to the curve of scatter given by (x), *i.e.*

$$\phi_n(r^2)=N\left(\omega_0-\frac{1}{4n}\omega_4-\frac{1}{9n^2}\omega_6+\frac{6n-11}{192n^3}\omega_8+\frac{50n-57}{1800n^4}\omega_{10}\right.$$
$$\left.-\frac{1892-2125n+270n^2}{103,680n^5}\omega_{12}-\text{etc.}\right) \quad\ldots\ldots\ldots\ldots\text{(xxxiv)},$$

we have if A be the whole area and k the radius,

$$A=\frac{N}{\sqrt{2\pi}\sigma}\frac{1}{2}\left\{1-\frac{3}{16}\frac{1}{n}-\frac{5}{24}\frac{1}{n^2}+\frac{35}{1024}\frac{6n-11}{n^3}+\frac{21}{1280}\frac{50n-57}{n^4}\right.$$
$$\left.-\frac{77}{49152}\frac{1892-2125n+270n^2}{n^5}-\text{etc.}\right\} \quad\ldots\ldots\ldots\text{(xxxv)},$$

$$Ak^2=\frac{N}{\sqrt{2\pi}\sigma}\frac{\sigma^2}{2}\left\{1+\frac{1}{16}\frac{1}{n}+\frac{1}{24}\frac{1}{n^2}-\frac{5}{1024}\frac{6n-11}{n^3}-\frac{7}{3840}\frac{50n-57}{n^4}\right.$$
$$\left.+\frac{7}{49152}\frac{1892-2125n+270n^2}{n^5}+\text{etc.}\right\} \quad\ldots\ldots\ldots\text{(xxxvi)}.$$

Hence if we even neglect terms of order $\frac{1}{n^2}$, we see that the Rayleigh solution gives too large an area for the curve of section and too small a swing-radius; these values are

$$\text{Rayleigh area, } \frac{1}{2}\frac{N}{\sqrt{2\pi}\sigma}, \qquad \text{Rayleigh swing-radius, } \sigma,$$

$$\text{True area to } \frac{1}{n},\quad \frac{1}{2}\frac{N}{\sqrt{2\pi}\sigma}\left(1-\frac{3}{16}\frac{1}{n}\right); \qquad \text{True swing-radius to } \frac{1}{n},\quad \sigma\left(1+\frac{1}{8n}\right).$$

Accordingly for n small the graph of the Rayleigh solution tends to exaggerate the concentration, *i.e.* using it as an approximation we shall somewhat reduce the extreme parts of the curve at the expense of exaggerating those near the centre of dispersion.

While there is no difficulty about determining the curve of distribution when n is large from (xxxiv), beyond the great labour of dealing with hitherto untabled functions, the investigation becomes very troublesome when n is small. The functions ω are suited in this case to represent the discontinuous functions which actually form the values of $\phi_n(r^2)$, but the extreme discontinuity of $\phi_n(r^2)$ for n

small, compels us to use a very great number of ω-functions, and the convergency of (xxxiv) is then small.

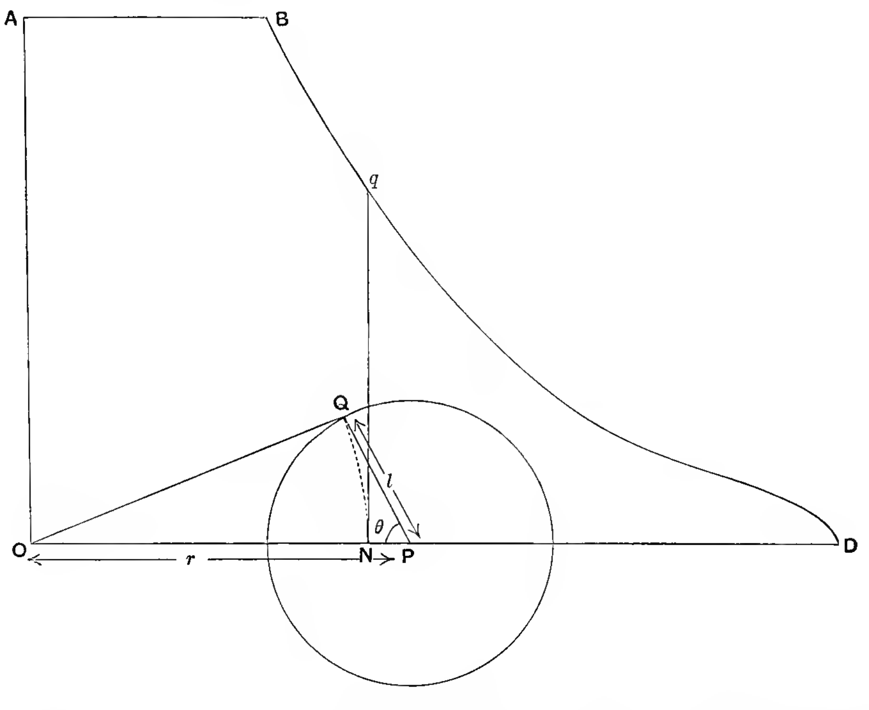
Another method of determining the distribution of the dispersed population has then to be applied to the case of n small.

(6) *Graphical Solution of the Fundamental Problem for n small.*

Let us consider the general functional relation (i)

$$\phi_{n+1}(r^2) = \frac{1}{2\pi}\int_0^{2\pi} \phi_n(r^2 + l^2 - 2rl\cos\theta)\, d\theta.$$

Suppose the graph of ϕ_n from 0 to nl known. This may be any discontinuous function. From nl to ∞, it will be zero. Let ABD be the graph of ϕ_n and OA the axis.



$OP = r$. Round P describe a circle of radius l, take the radius PQ, so that the angle $OPQ = \theta$; then clearly, $OQ^2 = r^2 + l^2 - 2rl\cos\theta$; rotate OQ round O down into line OD, as ON; draw the ordinate of the graph Nq, then we have

$$Nq = \phi_n(r^2 + l^2 - 2rl\cos\theta)$$

and $$\phi_{n+1}(OP^2) = \frac{1}{2\pi}\int_0^{2\pi} Nq\, d\theta.$$

Hence if we divide the circle up into a number of equal parts, and determine the ordinates Nq, corresponding to each of them, we can plot a curve to the base 2π, of which the mean ordinate will be $\phi_{n+1}(OP^2)$, or the ordinate at r of the new curve of dispersion for $\overline{n+1}$ flights. This can be done for a series of values of r from 0 to $\overline{n+1}\, l$ and thus $\phi_{n+1}(r^2)$ will be determined as a new graph. The area of the plotted curve which gives any new ordinate can be found mechanically. It will be seen that the process is theoretically straightforward, but very laborious. Thus for the dispersion curve after the fourth flight some 43 points had to be found, and this involved the construction of 43 subsidiary curves and their integration.

There were, of course, graphical difficulties in the construction of the subsidiary curves in the neighbourhood of the asymptotes and various devices had to be used, but at almost every point there were tests of the accuracy of the work. Some of these I shall now notice.

Case (i). The solution for two flights is:

$$\left.\begin{aligned}\phi_2(r^2) &= \frac{N}{\pi^2 r}\frac{1}{\sqrt{4l^2-r^2}} \quad r<2l\\ &= 0 \qquad\qquad\qquad r>2l\end{aligned}\right\}\text{....................(xxxvii).}$$

The reader will find no difficulty in deducing this directly from the case of $n=1$, which corresponds to a narrow zone of radius $r=l$, the rest of the plane being unoccupied. Thus:

$$\left.\begin{aligned}\phi_1 &= \frac{N}{2\pi l\epsilon}\text{ from } r=l-\tfrac{1}{2}\epsilon \text{ to } r=l+\tfrac{1}{2}\epsilon\\ &= 0 \text{ from } r=0 \text{ to } l-\tfrac{1}{2}\epsilon \text{ and } r=l+\tfrac{1}{2}\epsilon \text{ to } \infty\end{aligned}\right\}\text{...... (xxxvii } bis\text{)},$$

ϵ being taken indefinitely small.

By distributing each element of ϕ_1 on the zone round a circle of radius l we obtain (xxxvii).

The result may be obtained also from (iii) by putting $n=2$, *i.e.*

$$\begin{aligned}\phi_2(r^2) &= \frac{N}{2\pi}\int_0^\infty u\,J_0(ur)\,\{J_0(ul)\}^2\,du,\\ &= \frac{N}{2\pi}\frac{[(2l+r)\,r\,(2l-r)\,r]^{-\frac{1}{2}}}{\sqrt{\pi}\,2^{-1}\,\Pi(-\frac{1}{2})} \text{ from } r=0 \text{ to } 2l,\\ &= 0 \text{ from } r=2l \text{ to } \infty,\end{aligned}$$

from a theorem of de Sonin by putting $a=r$, $b=c=l$. Compare Gray and Mathews, p. 239, Ex. 52.

Case (ii). The solution for three flights may be obtained from that for two, by distributing analytically the density given by ϕ_2 round circles of radius l about each point. The resulting double integral is then expressible in elliptic integrals*. We find:

$$\left.\begin{aligned}\phi_3(r^2) &= \frac{N}{2\pi^3 l}\frac{1}{\sqrt{rl}}\,\kappa\,F\left(\frac{\pi}{2},\kappa\right),\\ &\qquad\text{where } \kappa^2=16l^3r/\{(r+l)^3(3l-r)\},\\ &\qquad\qquad\qquad r>0 \text{ and } <l;\\ &= \frac{N}{2\pi^3 l}\frac{1}{\sqrt{rl}}\,F\left(\frac{\pi}{2},\kappa\right),\\ &\qquad\text{where } \kappa^2=(r+l)^3(3l-r)/(16l^3r),\\ &\qquad\qquad\qquad r>l \text{ and } <3l;\\ &= 0 \qquad\qquad\quad r>3l \text{ to } r=\infty\end{aligned}\right\}\text{........... (xxxviii).}$$

* This solution, or its equivalent, was first sent me by Mr Geoffrey T. Bennett.

We have here at $r=l$ a typical instance of the discontinuity.

In Table I. columns (i) and (ii) the calculated ordinates of ϕ_2 and ϕ_3 are given, the latter having been determined by the use of Legendre's Tables of the Elliptic Integral F. In these cases, as in the later values of the ordinates of the dispersion curves, N is taken as unity. The dispersion curves are plotted in Diagrams I. and II. The Rayleigh solution is given in broken line; it will be noticed how very far it is from representing the facts at this early stage of the number of flights. One of the most interesting features of the investigation is to mark the gradual approximation of the discontinuous series of functions to the Gaussian normal curve of errors as the value of n increases.

The first test of the graphical method of dealing with the problem was to start from the curve for $n=2$ and construct the graph of ϕ_3. The result was found to be extremely close to the elliptic integral solution obtained by analysis and calculated from Legendre, and this gave us every confidence in the correctness within reasonable limits of the graphical solution, where no such direct verification was possible. After the ordinates of any graph had been found their differences were plotted, and these difference curves submitted to most careful inspection. Larger irregularities led to a reinvestigation of the points, smaller irregularities were smoothed with the spline, and from the final smoothed difference curve the ordinates were corrected.

Another test was now possible. In every case $2\pi\int_0^\infty \phi_n(r^2)\, r\, dr$ ought to be unity. Each ordinate was now multiplied by its r and a quadrature formula used to find the integral. The integral would usually differ very slightly from unity. Its reciprocal was then used as a factor to each ordinate and the ordinates so modified were the final corrected ordinates of the corresponding graph. The graphs were made on a large scale, and the accompanying Table I., columns (iii)—(vi), gives the ordinates of the dispersion curves from four to seven flights.

Additional tests were as follows:

Since $$\phi_{n+1}(r^2) = \frac{1}{2\pi}\int_{2\pi}^{\pi} \phi_n(r^2 + l^2 - 2lr\cos\theta)\, d\theta,$$

it follows that $$\phi_{n+1}(0) = \frac{1}{2\pi}\int_0^{2\pi} \phi_n(l^2)\, d\theta = \phi_n(l^2),$$

or: The axial ordinate of the $\overline{n+1}$th dispersion curve is the ordinate at a distance l, or a flight, from the centre of the nth dispersion curve. Table IV. illustrates the degree of accuracy reached here.

The ordinate at $r=l$ of the seventh curve given by the expansion in ω-functions is ·0375, and this is precisely the value of the central ordinate of the eighth curve given by the same expansion. Thus the graphical method runs with surprising accuracy into the analytical. The Rayleigh solution gives ·0398 for the central ordinate of the eighth curve as against the ·0375 of the ω-expansion, or the ·0378 of the

TABLE I. *Ordinates of the Dispersal Curves.*

(i) Two Flights ($n=2$)*		(ii) Three Flights ($n=3$)†		(iii) Four Flights ($n=4$)‡		(iv) Five Flights ($n=5$)‡		(v) Six Flights ($n=6$)‡		(vi) Seven Flights ($n=7$)§			
r/l	zl^2/N	r/l	zl^2/N	r/l	zl^2/N	r/l	zl^2/N	r/l	zl^2/N	r/l	zl^2/N	r/l	zl^2/N
0·00	∞	0·0	·0585	0·0	∞	0·0	·0537	0·0	·0538	0·0	·0420	0·0	·0425
·05	1·0139	·2	·0593	·1	·1074	·2	·0537	·2	·0513	·2	·0419		(·0455)
·07	·7246	·4	·0619	·2	·0891	·4	·0537	·4	·0489	·4	·0415		
·08	·6342	·6	·0674	·3	·0809	·6	·0537	·6	·0464	·6	·0407	0·7	·0399
·09	·5635	·8	·0794	·4	·0746	·8	·0537	·8	·0439	·8	·0394		(·0424)
·1	·5072	·9	·0933	·5	·0695	1·0	·0537	1·0	·0415	1·0	·0378		
·2	·2546	·94	·1045	·6	·0652	1·2	·0474	1·2	·0390	1·2	·0358		
·3	·1708	·98	·1285 (?)	·7	·0615	1·4	·0413	1·4	·0364	1·4	·0335	1·4	·0331
·4	·1293	1·00	∞	·8	·0585	1·6	·0363	1·6	·0338	1·6	·0310		(·0344)
·5	·1046	1·02	·1265 (?)	·9	·0560	1·8	·0322	1·8	·0309	1·8	·0283		
·6	·0885	1·06	·0990	1·0	·0537	2·0	·0285	2·0	·0277	2·0	·0256		
·7	·0773	1·1	·0856	1·1	·0516	2·2	·0250	2·2	·0240	2·2	·0229	2·1	·0242
·8	·0691	1·2	·0672	1·2	·0496	2·4	·0217	2·4	·0206	2·4	·0202		(·0242)
·9	·0630	1·4	·0488	1·3	·0477	2·6	·0185	2·6	·0177	2·6	·0177		
1·0	·0585	1·6	·0386	1·4	·0459	2·8	·0153	2·8	·0150	2·8	·0153	2·8	·0155
1·1	·0551	1·8	·0319	1·5	·0442	3·0	·0121	3·0	·0126	3·0	·0130		(·0148)
1·2	·0528	2·0	·0270	1·6	·0426	3·2	·0093	3·2	·0106	3·2	·0110		
1·3	·0513	2·2	·0233	1·7	·0410	3·4	·0070	3·4	·0087	3·4	·0092	3·5	·0085
1·4	·0507	2·4	·0205	1·8	·0396	3·6	·0053	3·6	·0070	3·6	·0076		(·0079)
1·5	·0511	2·6	·0181	1·9	·0382	3·8	·0039	3·8	·0055	3·8	·0062		
1·6	·0528	2·8	·0162	2·0	·0369	4·0	·0029	4·0	·0042	4·0	·0050		
1·7	·0566	3·0	·0146	2·02	·0348	4·2	·0021	4·2	·0032	4·2	·0039	4·2	·0039
1·8	·0646			2·06	·0308	4·4	·0013	4·4	·0023	4·4	·0031		(·0037)
1·9	·0854			2·1	·0284	4·6	·0007	4·6	·0016	4·6	·0024		
1·94	·1074			2·2	·0242	4·8	·0002	4·8	·0011	4·8	·0018	4·9	·0015
1·96	·1299			2·3	·0210	5·0	·0000	5·0	·0007	5·0	·0013		(·0015)
1·98	·1815			2·4	·0185			5·2	·0004	5·2	·0009		
1·99	·2552			2·5	·0165			5·4	·0002	5·4	·0006		
2·00	∞			2·6	·0148			5·6	·0001	5·6	·0004	5·6	·0004
				2·7	·0133			5·8	·0000	5·8	·0003		(·0005)
				2·8	·0120			6·0	·0000	6·0	·0001		
				2·9	·0106					6·2	·0000	6·3	·00008
				3·0	·0095					6·4	·0000		(·0002)
				3·2	·0076					6·6	·0000		
				3·4	·0059					6·8	·0000		
				3·6	·0043					7·0	·0000	7·0	·00000
				3·8	·0027								(·00004)
				3·9	·0019								
				3·92	·0017								
				3·94	·0015								
				3·96	·0012								
				3·98	·0008								
				4·00	·0000								

* Calculated from formula. † Calculated from Tables of Elliptic Integrals. ‡ Calculated graphically.

§ Values to the left calculated graphically, values to the right found from the ω-function expansion for comparison, the values in brackets are those given by the Rayleigh solution.

TABLE II. *Values of the ω-functions.*

r/σ	$\sigma^2\omega_0$	$\sigma^2\omega_2$	$\sigma^2\omega_4$	$\sigma^2\omega_6$	$\sigma^2\omega_8$	$\sigma^2\omega_{10}$	$\sigma^2\omega_{12}$
0	+ ·159,1550	+ ·159,1550	+ ·318,3100	+ ·954,9300	+ 3·819,7200	+ 19·098,6000	+ 114·591,6000
·1	+ ·158,3611	+ ·157,5693	+ ·313,5589	+ ·935,9497	+ 3·724,9378	+ 18·530,6202	+ 110·620,7235
·2	+ ·156,0035	+ ·152,8834	+ ·299,5891	+ ·880,4201	+ 3·449,0302	+ 16·885,5699	+ 99·177,8011
·3	+ ·152,1517	+ ·145,3049	+ ·277,2242	+ ·792,4264	+ 3·016,3079	+ 14·332,2150	+ 81·601,7164
·4	+ ·146,9185	+ ·135,1650	+ ·247,7634	+ ·678,3356	+ 2·464,2124	+ 11·127,4046	+ 59·905,9470
·5	+ ·140,4537	+ ·122,8970	+ ·212,8751	+ ·546,1784	+ 1·839,0999	+ 7·583,1582	+ 36·489,3471
·6	+ ·132,9374	+ ·109,0087	+ ·174,4670	+ ·404,8965	+ 1·191,1906	+ 4·027,9574	+ 13·802,7339
·7	+ ·124,5713	+ ·094,0513	+ ·134,5401	+ ·263,5330	+ ·569,3039	+ ·767,7288	− 5·975,6743
·8	+ ·115,5702	+ ·078,5877	+ ·095,0449	+ ·130,4593	+ ·016,0640	− 1·947,9139	− 21·205,3207
·9	+ ·106,1526	+ ·063,1608	+ ·057,7497	+ ·012,7166	− ·435,8815	− 3·949,8656	− 30·951,7904
1·0	+ ·096,5323	+ ·048,2662	+ ·024,1331	− ·084,4658	− ·766,2251	− 5·161,4614	− 35·039,7166
1·2	+ ·077,4690	+ ·021,6913	− ·028,0128	− ·206,6600	− 1·045,7098	− 5·351,9170	− 28·874,9613
1·4	+ ·059,7326	+ ·001,1947	− ·057,3194	− ·235,2026	− ·900,0451	− 3·455,1198	− 12·119,1731
1·6	+ ·044,2510	− ·012,3903	− ·065,5623	− ·194,3306	− ·521,5103	− ·916,7705	+ 4·126,7483
1·8	+ ·031,4966	− ·019,5279	− ·058,4451	− ·119,4328	− ·116,5429	+ 1·050,8391	+ 12·770,4428
2·0	+ ·021,5393	− ·021,5393	− ·043,0786	− ·043,0786	+ ·172,3144	+ 1·895,4584	+ 12·751,2656
2·2	+ ·014,1523	− ·020,0963	− ·025,8081	+ ·013,8001	+ ·295,4776	+ 1·723,4411	+ 7·400,1858
2·4	+ ·008,9341	− ·016,7961	− ·010,9496	+ ·043,9712	+ ·279,7081	+ 1·008,2741	+ 1·194,4811
2·6	+ ·005,4188	− ·012,8967	− ·000,5180	+ ·050,7478	+ ·188,3692	+ ·246,6709	− 2·829,6050
2·8	+ ·003,1578	− ·009,2208	+ ·005,3253	+ ·042,6344	+ ·083,3863	− ·258,5489	− 3·915,1831
3·0	+ ·001,7680	− ·006,1880	+ ·007,5140	+ ·028,5090	+ ·003,6465	− ·439,7348	− 2·949,4384
3·2	+ ·000,9511	− ·003,9185	+ ·007,3562	+ ·014,7914	− ·038,3979	− ·385,6461	− 1·308,1481
3·4	+ ·000,4916	− ·002,3498	+ ·006,0410	+ ·004,6874	− ·048,6501	− ·231,6523	+ ·007,0283

I owe this preliminary table of ω-functions to the kindness of Dr Alice Lee. Much more elaborate tables will have to be calculated, if as I anticipate the ω-functions are found valuable for other purposes. The present table suffices to indicate their general numerical character, and enables one to calculate some of the quantities needed in the present memoir.

graphical construction. The fact that the central ordinate of the sixth curve is almost identical with the ordinate of the fourth curve at $r = l$, seems conclusive as to the general accuracy of the process.

The above test of the general accuracy of Mr Blakeman's graphical work is only a part of the still more sufficient test that in the seventh curve the graph and the ω-expansion practically coincide. See Diagram VI. After $r = 5l$ the two curves cannot be distinguished, and between $r = 0$ and $3l$ the deviation is probably as much due to the neglect of higher ω-functions as to errors in the graphical treatment.

Another method adopted by Mr Blakeman for testing the accuracy of his graphical work, especially at the end of the range, was to obtain expansions to $\phi_n(r^2)$, when r does not differ much from nl, $= nl - \xi$, say, where ξ is supposed small. If $f_n(\xi) = \phi_n((nl-\xi)^2)$, then generally for ξ small:

$$f_n(\xi) = \frac{N}{l^2(\sqrt{2})^{n+3}\,\pi^{n-1}\sqrt{n}}\left(\frac{\xi}{l}\right)^{(n-3)/2} I_1 I_2 I_3 \dots I_{n-3} \quad \text{..........(xxxix)},$$

where $$I_q = \int_0^{\pi/2} \cos^q\theta\, d\theta = \Gamma\left(\tfrac{1}{2}(n+1)\right)\Gamma\left(\tfrac{3}{2}\right)/\Gamma\left(\tfrac{1}{2}(n+2)\right).$$

TABLE III. *Table of the ν constants.*

$m=1$	$n=6$	$n=7$	$n=8$
ν_4	$-\cdot041,666,667$	$-\cdot035,714,286$	$-\cdot031,250,000$
ν_6	$-\cdot003,086,420$	$-\cdot002,267,574$	$-\cdot001,736,111$
ν_8	$\cdot000,602,816$	$\cdot000,470,724$	$\cdot000,376,383$
ν_{10}	$\cdot000,104,167$	$\cdot000,067,796$	$\cdot000,046,522$
ν_{12}	$+\cdot000,001,412$	$-\cdot000,000,142$	$-\cdot000,000,639$

Table of the N constants.

$m=5$	$n=6$	$n=7$	$n=8$
N_4	$-\cdot008,333,333$	$-\cdot007,142,857$	$-\cdot006,250,000$
N_6	$-\cdot000,123,457$	$-\cdot000,090,703$	$-\cdot000,069,444$
N_8	$\cdot000,032,600$	$\cdot000,024,174$	$\cdot000,018,636$
N_{10}	$\cdot000,000,990$	$\cdot000,000,627$	$\cdot000,000,422$
N_{12}	$-\cdot000,000,078$	$-\cdot000,000,047$	$-\cdot000,000,033$
$m=10$	$n=6$	$n=7$	$n=8$
N_4	$-\cdot004,166,667$	$-\cdot003,571,429$	$-\cdot003,125,000$
N_6	$-\cdot000,030,864$	$-\cdot000,022,676$	$-\cdot000,017,361$
N_8	$\cdot000,008,415$	$\cdot000,006,211$	$\cdot000,004,771$
N_{10}	$\cdot000,000,126$	$\cdot000,000,082$	$\cdot000,000,053$
N_{12}	$-\cdot000,000,011$	$-\cdot000,000,007$	$-\cdot000,000,006$
$m=20$	$n=6$	$n=7$	$n=8$
N_4	$-\cdot002,083,333$	$-\cdot001,785,714$	$-\cdot001,562,500$
N_6	$-\cdot000,007,716$	$-\cdot000,005,669$	$-\cdot000,004,340$
N_8	$\cdot000,002,137$	$\cdot000,001,574$	$\cdot000,001,207$
N_{10}	$\cdot000,000,016$	$\cdot000,000,010$	$\cdot000,000,007$
N_{12}	$-\cdot000,000,0014$	$-\cdot000,000,0009$	$-\cdot000,000,0006$

TABLE IV. *Central ordinates and ordinates at $r=l$.*

No. of Flights	Central ordinate	Ordinate at $r=l$
First	0	∞
Second	∞	·0585
Third.........	·0585	∞
Fourth	∞	·0537
Fifth	·0537	·0537
Sixth.........	·0538	·0415
Seventh......	·0415	·0378

Hence: $$f_n(\xi) = \frac{N(\xi/l)^{\frac{1}{2}(n-3)}}{(\sqrt{2\pi})^{n+1} l^2 \sqrt{n}\, 2^{n-2}\, \Gamma(\frac{1}{2}(n-1))} \quad \text{(xxxix } bis\text{)}.$$

This can be proved by induction.

For most of the cases more approximate formulae still were deduced. Thus:

$$f_3(\xi) = \frac{1}{8\sqrt{3}l^2\pi^2}\left(1 + \frac{1}{2}\frac{\xi}{l} + \frac{5}{24}\frac{\xi^2}{l^2}\right) \quad \text{(xl)},$$

$$f_4(\xi) = \frac{1}{16\sqrt{2}l^2\pi^3}\sqrt{\frac{\xi}{l}}\left(1 + \frac{21}{48}\frac{\xi}{l} + \frac{557}{1536}\frac{\xi^2}{l^2}\right) \quad \text{(xli)},$$

$$f_5(\xi) = \frac{1}{64\sqrt{5}l^2\pi^3}\left(\frac{\xi}{l}\right)\left(1 + \frac{2}{5}\frac{\xi}{l} + \frac{507}{2560}\frac{\xi^2}{l^2}\right) \quad \text{(xlii)},$$

$$f_6(\xi) = \frac{1}{96\sqrt{12}l^2\pi^4}\left(\frac{\xi}{l}\right)^{3/2}\left(1 + \frac{9}{24}\frac{\xi}{l} + \dots\right) \quad \text{(xliii)},$$

after which the first term only as given by (xxxix) is sufficient. It will be observed that after $\phi_5(r^2)$, the curve touches at $r = nl$ or $\xi = 0$, and the contact becomes higher and higher as n increases. Thus, although short of $n = \infty$, there is no real asymptoting to the axis, still $\phi_n(r^2)$ for $n > 5$ not only vanishes for $r = nl$, but has increasingly higher contact as n increases. This explains how the Gaussian curve can fairly well represent the state of affairs towards the end of the dispersal range, if n is > 5.

Mr Blakeman found that the ends of the range for the various cases ran closely into the curves (xl) to (xliii), and they were tested and, if needful, corrected by these formulae.

Thus the whole graphical work was kept in check, and, I think, we may be confident that the true forms of the dispersal curves for $n = 4$ to 7 are really given by our diagrams and tables.

(7) We may note a few features of these curves.

Dispersal Curve for Two Flights (Diagram I.).

There is no discontinuity in the solution from $r = 0$ to $2l$, the range within which all individuals fall. The curve asymptotes to the vertical at the axis and at $r = 2l$. Of course, while the density becomes infinite, the number on any small area near $r = 0$ or $r = 2l$, is finite. Thus the number between the circles of radii r_1 and r_2 is

$$\frac{2N}{\pi}\left(\sin^{-1}\frac{r_2}{2l} - \sin^{-1}\frac{r_1}{2l}\right).$$

If $r_1 = 0$ and $r_2 = \epsilon_1$, where ϵ_1 is small, the number ν_1 within the small circle of radius ϵ_1 at the centre of dispersion $= N\epsilon_1/(\pi l)$. If $r_2 = r_1 + \epsilon_2$, the number lying on the zone of breadth ϵ_2 is $\dfrac{N\epsilon_2}{\pi l}\left(1 - \dfrac{r_1^2}{4l^2}\right)^{-\frac{1}{2}}$, and this if $r_1 = 2l - \epsilon_2$, is $\nu_2 = \dfrac{N}{\pi}\sqrt{\dfrac{\epsilon_2}{l}}$. At the position of minimum density $r_1 = \sqrt{2}l$, and the number on the zone r_1 to $r_1 + \epsilon_3$ is $\nu_3 = N\epsilon_3/(\pi l\sqrt{1/2})$. Hence it follows that the numbers on narrow zones ϵ_1, ϵ_2, ϵ_3 in breadth, of equal areas $\pi\epsilon_1^2 = \pi 4l\epsilon_2 = \pi 2\sqrt{2}l\epsilon_3$, are given by

$$N\epsilon_1/(\pi l), \quad N\sqrt{\epsilon_2}/(\pi\sqrt{l}), \quad \text{and} \quad N\epsilon_3\sqrt{2}/(\pi l),$$

or in the ratio

$$N\epsilon_1/(\pi l) : \tfrac{1}{2}N\epsilon_1/(\pi l), \quad \tfrac{1}{2}N\epsilon_1/(\pi l) \times \frac{\epsilon_1}{l}.$$

Thus the total population on a small area at the centre of dispersion is twice that on an equal area at the periphery of the distribution, and at both indefinitely greater than on an equal belt at the distance of minimum density. The same point can be indicated in another way. From $r=0$ to $r=\frac{1}{2}l$ is $\frac{1}{16}$ of the total area occupied after dispersion, it contains $\cdot 16N$ or about $\frac{1}{6}$ of the total population; from $r=\frac{3}{2}l$ to $r=2l$ is $\frac{7}{16}$ of the total area, it contains $\cdot 54\,N$. In other words the half of the area nearest and farthest from the centre of dispersion contains $\frac{7}{10}$ of the dispersed population; the "middle" half of the area contains only $\frac{3}{10}$ of the population. The nature of the distribution is thus extremely different from that given by the rotation of the Gaussian curve about its axis for this small number of flights. For in the Gaussian case if the central area $\pi\epsilon_1^2 = 2\pi r_1\epsilon_2$, the area of the zone at distance r_1, the population on the centre patch is $\frac{1}{2}N\epsilon_1^2/\sigma^2$ and on the zone is

$$\tfrac{1}{2}N\epsilon_1^2/\sigma^2 \times \epsilon^{-\frac{1}{2}r_1^2/\sigma^2},$$

which is always less and diminishes *continuously* with increase of r_1. Thus the Rayleigh solution fails in this, as in the next three cases, not only to give the form of the curve at dispersion, but to indicate that the dispersed populations on zones of equal area round the centre do not decrease uniformly in number.

Dispersal Curve for Three Flights (Diagram II.).

The solution is discontinuous at $r=l$. The density is here infinite, but has become finite at the origin. There is no discontinuity at $r=2l$, but at the end of the range the density drops suddenly from a finite value to zero. Thus the integral of the Bessel function product (see Eqn. (iii)) is discontinuous at two points. The Rayleigh solution is still widely divergent from the true curve of dispersal.

Dispersal Curve for Four Flights (Diagram III.).

By the rule already referred to (p. 18) the infinite density has returned to the origin. There are only two points of discontinuity, *i.e.*, at $r=l$ and $r=4l$ the end of the range, at both of which there is an abrupt change in the slope of the curve. The density at the end of the range is now zero and will remain so, but the dispersal curve rises at right angles to the axis. The true dispersal curve is bending round somewhat to the Rayleigh curve, but the latter is not even yet a rough approximation to the facts.

Dispersal Curve for Five Flights (Diagram IV.).

All infinite densities have now finally disappeared. The density vanishes at the end of the range, but the dispersal curve makes a finite angle with the horizontal axis. There is a marked discontinuity of slope at $r=l$; a still more noteworthy feature is that from $r=0$ to $r=l$ the graphical construction, however carefully reinvestigated, did not permit of our considering the curve to be anything but a *straight* line. If this could be verified from the analytical expression

$$\phi_4(r^2)=\frac{N}{2\pi}\int_0^\infty u\, J_0(ur)\{J_0(ul)\}^4\,du$$

by showing that the integral is independent of r from 0 to l it would be of much interest. Even if it be not absolutely true, it exemplifies the extraordinary power of such integrals of J products to give extremely close approximations to such simple forms as horizontal lines.

The approach of the Rayleigh curve to the result is now more noticeable.

Dispersal Curve for Six Flights (Diagram V.).

There is contact now of the first order at the end of the range. From $r=0$ to $r=l$ the curve of dispersal appears to be a sloping straight line tangential to the continuous curve from $r=l$ to $r=6l$. No other discontinuity of a low order is now visible. The curve, except for the finite slope at $r=0$, is becoming much more of the Gaussian form. It runs fairly closely to the solution in ω-functions up to ω_{12}, in fact is not separable at the extreme part of the range, where the Rayleigh curve still gives finite ordinates beyond the possible range.

Dispersal Curve for Seven Flights (Diagram VI.).

All sign of discontinuity has gone, the curve is horizontal at the centre of dispersion and might be easily mistaken for a normal curve of errors. The expansion in ω-functions represents the result within the limits almost of constructional error. It was not thought necessary to continue the graphical work beyond this stage. We may conclude that:

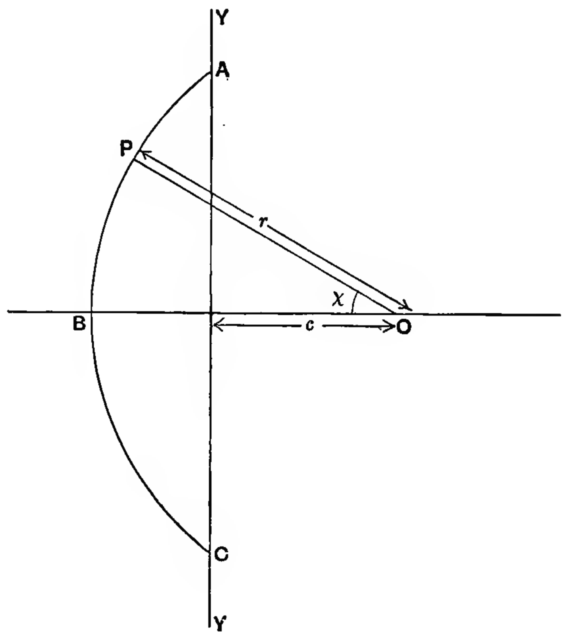
The deviation of the Rayleigh solution for seven and more flights from the true dispersal curve is practically the same as its deviation from the solution in ω-functions when five terms of that series are retained.

This I think completes the full solution of the fundamental problem. The dispersal curves for the cases of 2 to 7 flights are given in the Table I. of ordinates and the Diagrams I. to VI. For higher values the ω-function series gives the solution. This solution could be applied to calculate the ordinates of the dispersal curve for fewer flights than 6 or 7, but several more ω-functions would have to be used and the arithmetical work—especially while these functions are as yet untabled*—then becomes somewhat severe.

* Table II. provides a preliminary series of values of the ω-functions.

(8) *Secondary Migration Problems.*

Problem I. *On one side of a straight line there is supposed to be a uniform distribution of habitats; on the other at starting no habitats. To investigate the distribution in the unoccupied area after one migration. Each individual is supposed to take n-flights to the new habitat.*



Let YY be the straight line and O a point at distance c from it on the unoccupied side of it. Let N be the average density per unit of area on the occupied side. Then after an n-flight migration, the contribution from P (co-ordinates r, χ) at O will be $Nr\delta\chi\delta r\,\phi_n(r^2)$, and integrating this all round a circle of radius r from A to C within the occupied area, we have for the quantity $F_n(c)$ at O

$$F_n(c) = 2N\int_c^\infty \int_0^{\cos^{-1}c/r} \phi_n(r^2)\, r\, d\chi dr$$

$$= 2N\int_c^\infty \cos^{-1} c/r\, \phi_n(r^2)\, r\, dr.$$

Hence $$\frac{dF_n(c)}{dc} = -2N\int_c^\infty \frac{\phi_n(r^2)\, r\, dr}{\sqrt{r^2-c^2}} = -2N\int_0^\infty \phi_n(c^2+y^2)\, dy \quad \text{......(xliv)}.$$

The evaluation of this integral needs a further consideration of the ω-functions. By (xiv)

$$\omega_{2s} = -\frac{1}{2\pi\sigma^2}(-\beta)^{s+1}\frac{d^s}{d\beta^s}\left(\frac{1}{\beta}e^{1/\beta}\right), \text{ where } \beta = -2\sigma^2/r^2.$$

Transfer the differentiations from β to σ^2 and we have:

$$\omega_{2s} = \frac{(-1)^s}{2\pi} (\sigma^2)^s \frac{d^s}{d(\sigma^2)^s} \left(\frac{1}{\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2}\right)$$

$$= (-1)^s (\sigma^2)^s \frac{d^s \omega_0}{d(\sigma^2)^s} \quad \text{.................................(xlv)},$$

or, all the ω-functions can be found by differentiating the first ω-function with regard to the standard-deviation squared. Then by (xii) we have

$$\phi_n(r^2) = \left\{1 + \nu_4 (\sigma^2)^2 \frac{d^2}{d(\sigma^2)^2} - \nu_6 (\sigma^2)^3 \frac{d^3}{d(\sigma^2)^3} + \ldots + (-1)^s \nu_{2s} (\sigma^2)^s \frac{d^s}{d(\sigma^2)^s} + \right\} \omega_0 \quad \text{......(xlvi)}.$$

Thus, if we put $\sigma^2 = t$:

$$\frac{dF_n(c)}{dc} = -2N\left(1 + \nu_4 t^2 \frac{d^2}{dt^2} - \nu_6 t^3 \frac{d^3}{dt^3} + \ldots + (-1)^s \nu_{2s} t^s \frac{d^s}{dt^s} + \ldots\right) \times \int_0^\infty \omega_0 (c^2 + y^2)\, dy.$$

But: $$\int_0^\infty \omega_0 (c^2+y^2)\, dy = \frac{1}{2\pi\sigma^2} \int_0^\infty e^{-(c^2+y^2)/2\sigma^2} dy = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}c^2/\sigma^2} \tfrac{1}{2}\sqrt{2\pi}\,\sigma$$

$$= \tfrac{1}{2} \frac{1}{\sqrt{2\pi}\,\sigma} e^{-\frac{1}{2}c^2/\sigma^2}.$$

Now $\int_\infty^c e^{-\frac{1}{2}c^2/\sigma^2} dc = \sigma \int_\infty^{c/\sigma} e^{-\frac{1}{2}x^2} dx$, and this integral vanishes when $c = \infty$. Hence

$$F_n(c) = \frac{N}{\sqrt{2\pi}} \left(1 + \nu_4 t^2 \frac{d^2}{dt^2} - \nu_6 t^3 \frac{d^3}{dt^3} + \ldots + (-1)^s \nu_{2s} t^s \frac{d^s}{dt^s} + \right) \int_{c/\sigma}^\infty e^{-\frac{1}{2}x^2} dx \quad \text{......(xlvii)}.$$

Since $F_n(c)$ clearly vanishes for c infinite, it is not needful to introduce a constant.

It remains accordingly to determine the successive differentials of the integral with regard to t. Call the integral i; then, if $\eta = c/\sigma = c/\sqrt{t}$,

$$\frac{di}{dt} = -e^{-\frac{1}{2}\eta^2} \frac{d\eta}{dt} = \frac{1}{2} \frac{c}{t^{\frac{3}{2}}} e^{-c^2/2t} = \pi \frac{c}{\sigma} \omega_0 = \pi c \omega_0/\sqrt{t}.$$

By (xlv) we know that $d^s\omega_0/dt^s = (-1)^s \omega_{2s}/t^s$. Hence differentiating $s-1$ times we have:

$$\frac{d^s i}{dt^s} = \frac{\pi c}{\sqrt{t}} \left(\frac{d^{s-1}\omega_0}{dt^{s-1}} - (s-1)\frac{d^{s-2}\omega_0}{dt^{s-2}} \frac{1}{2t} + \frac{(s-1)(s-2)}{2!} \frac{d^{s-3}\omega_0}{dt^{s-3}} \frac{1.3}{2.2} \frac{1}{t^2} - \text{etc.}\right)$$

$$= \frac{(-1)^{s-1}\pi c}{t^{s-\frac{1}{2}}} \left(\omega_{2(s-1)} + (s-1)\, \omega_{2(s-2)} \tfrac{1}{2} + \frac{(s-1)(s-2)}{1.2} \omega_{2(s-3)} \frac{1.3}{2.2} + \frac{(s-1)(s-2)(s-3)}{1.2.3} \omega_{2(s-4)} \frac{1.3.5}{2^3} + \ldots \text{etc.}\right).$$

Thus $t^s \frac{d^s i}{dt^s} = (-1)^{s-1}\pi\frac{c}{\sigma}\left(\sigma^2\omega_{2(s-1)} + \frac{(s-1)}{1!\,2}\sigma^2\omega_{2(s-2)} + \frac{(s-1)(s-2)}{2!\,2^2}1.3.\sigma^2\omega_{2(s-3)}\right.$

$$\left. + \frac{(s-1)(s-2)(s-3)}{3!\,2^3}1.3.5\,\sigma^2\omega_{2(s-4)} + \text{etc.}\right) \text{........ (xlviii).}$$

Substituting in (xlvii) we have, if $\overline{\psi}(\eta) = \frac{1}{\sqrt{2\pi}}\int_\eta^\infty e^{-\frac{1}{2}x^2}dx$ ....(xlix),

$$F_n(c) = N\left[\overline{\psi}\left(\frac{c}{\sigma}\right) - \sqrt{\frac{\pi}{2}}\frac{c}{\sigma}\{\sigma^2\omega_0(\tfrac{1}{2}\nu_4 + \tfrac{3}{4}\nu_6 + \tfrac{15}{8}\nu_8 + \tfrac{105}{16}\nu_{10} + \tfrac{945}{64}\nu_{12})\right.$$

$$+ \sigma^2\omega_2(\nu_4 + \nu_6 + \tfrac{9}{4}\nu_8 + \tfrac{15}{2}\nu_{10} + \tfrac{525}{16}\nu_{12})$$

$$+ \sigma^2\omega_4(\nu_6 + \tfrac{3}{2}\nu_8 + \tfrac{9}{2}\nu_{10} + \tfrac{75}{4}\nu_{12})$$

$$+ \sigma^2\omega_6(\nu_8 + 2\nu_{10} + \tfrac{15}{2}\nu_{12})$$

$$\left. + \sigma^2\omega_8(\nu_{10} + \tfrac{5}{2}\nu_{12}) + \sigma^2\omega_{10}\nu_{12} + \ldots\}\right] \text{.......................(l),}$$

as far as coefficients of the order ν_{12} and functions of order ω_{10}.

This is the solution in ω-functions. Table III., p. 21, gives the values of the ν's for certain values of n, and Table II., p. 20, is a preliminary table of the ω-functions. These will enable us to readily find the values of $F_n(c)$. I have done this for the case of $n = 6$ and $n = 7$, which will suffice to illustrate the character of these curves. $\overline{\psi}(c/\sigma)$ can be found at once from Tables of the probability integral. It is drawn with a broken line in Diagram VII. and is the Rayleigh solution for this case. I term $F_n(c)$ an "infiltration curve" of the first order.

Substituting the values of the ν's from Table III., we have for $n = 6$:

$$F_6(c)/N = \overline{\psi}\left(\frac{c}{\sigma}\right) + \frac{c}{\sigma}\{\cdot026{,}712{,}414\,(\sigma^2\omega_0) + \cdot053{,}325{,}539\,(\sigma^2\omega_2)$$

$$+ \cdot002{,}114{,}303\,(\sigma^2\omega_4) - \cdot001{,}029{,}898\,(\sigma^2\omega_6)$$

$$- \cdot000{,}134{,}978\,(\sigma^2\omega_8) - \cdot000{,}001{,}770\,(\sigma^2\omega_{10}) + \ldots\},$$

and for $n = 7$:

$$F_7(c)/N = \overline{\psi}\left(\frac{c}{\sigma}\right) + \frac{c}{\sigma}\{\cdot022{,}850{,}925\,(\sigma^2\omega_0) + \cdot045{,}644{,}347\,(\sigma^2\omega_2)$$

$$+ \cdot001{,}578{,}008\,(\sigma^2\omega_4) - \cdot000{,}758{,}570\,(\sigma^2\omega_6)$$

$$- \cdot000{,}084{,}525\,(\sigma^2\omega_8) + \cdot000{,}000{,}178\,(\sigma^2\omega_{10}) + \ldots\}.$$

The first term $\overline{\psi}\left(\frac{c}{\sigma}\right)$ is the ogive curve already drawn corresponding to the Rayleigh solution. We see at once that the term $\sigma^2\omega_{10}$ will not affect the fourth place of decimals.

TABLE V. *Ordinates of Infiltration Curve over straight Boundary.*

$+c/\sigma$	$n=6$	$n=7$	$n=\infty$	$-c/\sigma$	$n=6$	$n=7$	$n=\infty$
0	·5000	·5000	·5000	—	—	—	—
·1	·4614	·4612	·4602	– ·1	·5386	·5388	·5398
·2	·4231	·4228	·4207	– ·2	·5769	·5772	·5793
·3	·3854	·3850	·3821	– ·3	·6146	·6150	·6179
·4	·3488	·3483	·3446	– ·4	·6512	·6517	·6554
·5	·3135	·3128	·3085	– ·5	·6865	·6872	·6915
·6	·2797	·2790	·2743	– ·6	·7203	·7210	·7257
·7	·2478	·2469	·2420	– ·7	·7522	·7531	·7580
·8	·2177	·2169	·2119	– ·8	·7823	·7831	·7881
·9	·1898	·1889	·1841	– ·9	·8102	·8111	·8159
1·0	·1640	·1632	·1587	– 1·0	·8360	·8368	·8413
1·2	·1193	·1186	·1151	– 1·2	·8807	·8814	·8849
1·4	·0834	·0830	·0808	– 1·4	·9166	·9170	·9192
1·6	·0558	·0557	·0548	– 1·6	·9442	·9443	·9452
1·8	·0356	·0356	·0359	– 1·8	·9644	·9644	·9641
2·0	·0215	·0214	·0228	– 2·0	·9785	·9786	·9772
2·2	·0121	·0124	·0139	– 2·2	·9879	·9876	·9861
2·4	·0064	·0066	·0082	– 2·4	·9936	·9934	·9918
2·6	·0030	·0033	·0047	– 2·6	·9970	·9967	·9953
2·8	·0015	·0013	·0026	– 2·8	·9985	·9987	·9974
3·0	·00046	·00060	·00135	– 3·0	·99954	·99940	·99865
3·2	·00012	·00020	·00069	– 3·2	·99988	·99980	·99931
3·4	·00000	·00004	·00034	– 3·4	1·00000	·99996	·99966

$n=\infty$ is used to denote the Rayleigh solution.

This table suggests some interesting points. The curves for $n=6$ and $n=7$ are fairly close together, but differ sensibly from the Rayleigh solution, perhaps 4 or 5 per cent., where the density is at all material. For many practical purposes this might be close enough, and we see that for infiltration as distinct from dispersal curves, the Rayleigh solution—owing to integration over an area—gives fairly close results. The greatest percentage deviations from the Rayleigh solution are to be found in the tail. Now no individual can be found beyond the range nl from the boundary, and $\sigma=\sqrt{\tfrac{1}{2}n}\,l$; thus the maximum range is $\sqrt{2n}\,\sigma$, or, for $n=6$ and 7, the maximum range is $3{\cdot}46\sigma$ and $3{\cdot}74\sigma$ respectively. The ω-function expansion brings this out well. For $n=6$ at $3{\cdot}4\sigma$ there is not one in 100,000 individuals, while the Rayleigh solution gives 34. For $n=7$ there are still 4 in the 100,000, because we are a little distance still from the limit of the range. The Rayleigh solution continues to give sensible densities beyond the range, although they may be sufficiently small to be neglected in practice.

For rough purposes a first approximation to the infiltration curves may be found from the Rayleigh solution, they will err on the side of safety if we are considering the effect of a clearance at a considerable distance from the boundary. But with the aid of the tables of the ω-functions and the ν-coefficients, it is not difficult to obtain the actual form of the infiltration curves as I have done in the present case. Diagram VII. compares the Rayleigh approximation and the infiltration curve for $n=7$.

It will be seen that an infiltration curve of the first order gives not only the density of the population after a first migration into cleared or unoccupied area across a straight boundary, but also the diminution of density on the populated side of the area, when we put c negative, *i.e.* it gives both the 'depopulation' and 'repopulation.' The reduced density at the boundary is $\frac{1}{2}N$, and if we take the point where the infiltration curve cuts the vertical through the boundary as origin, we see that it is centrally symmetrical; or the loss of population at a given distance from the boundary is exactly equal to the gain at the same distance on the opposite side of the boundary.

If we require an infiltration curve of the second order, we must now multiply the ordinates of the curve of the first order by (i) the average fertility of the species, say μ, and (ii) the survival rate Δ. If the environment be the same on either side of the boundary, and neither μ nor Δ affected by the density of the population, then $\mu\Delta$ may be treated as a constant and the infiltration curves of higher orders can be found with moderate ease for simple cases. We thus have the distributions after two, three or more migrations accompanied by reproduction and death. On the other hand both μ and Δ may be functions of the density of the population, and in this case the ordinates of the infiltration curves of the second and higher orders can only be determined when the nature of μ and Δ is known. On the whole it is probable that the average fertility depending on the mating frequency will be highest where the density is greatest, as mating opportunities will then be most frequent, but in such cases the survival rate Δ may be lower, as more enemies are likely to be present and the food supply is also likely to be less, where the population is densest. Thus $\mu\Delta$ as a whole may not be very different on the depopulated and repopulated sides of the boundary. We shall only consider in this memoir cases in which this product is (i) supposed constant throughout, or (ii) constant for each migration season; but supposing uniform environment on both sides of the boundary, it is conceivable that $\mu\Delta$ will be correlated with the population density and this will modify the basis of the distribution from which the second and later migrations start.

(9) Problem II. *To investigate the distribution after m migrations from uniformly densely occupied space across a straight boundary into unoccupied space.*

Let the axis of x be taken perpendicular to the boundary and the axis of y be the boundary. Let us consider the density at $x = c$, on the originally unoccupied side of the boundary. Then the density at a distance x from the boundary is given by (xlvii), or if we write the operator as Q_t, we have

$$F_n(x) = NQ_t \frac{1}{\sqrt{2\pi}} \int_{x/\sigma}^{\infty} e^{-\frac{1}{2}x^2} dx = u_1, \text{ say,} \qquad \text{(li).}$$

Here Q_t involves only n and σ and not x.

Now the distance r from the point x, y to the point c, 0 at which we want the density after the next migration is given by:

$$r^2 = y^2 + (x-c)^2,$$

and $\mu\Delta$ being the fertility-survival factor, we have for the density at c,

$$u_2 = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \mu\Delta u_1 \phi_n(r^2)\, dx\, dy.$$

Now
$$\phi_n(r^2) = Q_t\omega_0 = Q_t \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}r^2/\sigma^2}.$$

To mark that this Q_t operates only on this part of the expression, write it Q_t' and suppose it to operate on σ' written for σ. After the operations are complete we can put σ' again $=\sigma$. Let

$$v_1 = \frac{1}{\sqrt{2\pi}} \int_{x/\sigma}^{+\infty} e^{-\frac{1}{2}x^2} dx.$$

Then if $\mu\Delta$ be constant (see p. 29):

$$u_2 = \frac{\mu\Delta N}{2\pi} Q_t Q_t' \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} v_1 \frac{1}{\sigma'^2} e^{-\frac{1}{2}\{(x-c)^2 + y^2\}/\sigma'^2} dx\, dy.$$

Completing the integration with regard to y we have:

$$u_2 = \frac{\mu\Delta N}{\sqrt{2\pi}} Q_t Q_t' \int_{-\infty}^{+\infty} v_1 \frac{1}{\sigma'} e^{-\frac{1}{2}(x-c)^2/\sigma'^2} dx.$$

Differentiate with regard to c:

$$\frac{du_2}{dc} = \frac{\mu\Delta N}{\sqrt{2\pi}} Q_t Q_t' \int_{-\infty}^{+\infty} v_1 \frac{1}{\sigma'} \frac{d}{dx} \left(-e^{-\frac{1}{2}(x-c)^2/\sigma'^2}\right) dx.$$

Integrate by parts, and notice that the part between limits vanishes at both of them and we have:

$$\frac{du_2}{dc} = \frac{\mu\Delta N}{\sqrt{2\pi}} Q_t Q_t' \int_{-\infty}^{+\infty} \frac{dv_1}{dx} \frac{1}{\sigma'} e^{-\frac{1}{2}(x-c)^2/\sigma'^2} dx.$$

But
$$\frac{dv_1}{dx} = -\frac{1}{\sqrt{2\pi}} \frac{1}{\sigma} e^{-\frac{1}{2}(x/\sigma)^2};$$

hence:
$$\frac{du_2}{dc} = -\frac{\mu\Delta N}{2\pi} Q_t Q_t' \frac{1}{\sigma\sigma'} \int_{-\infty}^{+\infty} e^{-\frac{1}{2}\left(\frac{x^2}{\sigma^2} + \frac{(x-c)^2}{\sigma'^2}\right)} dx.$$

This is integrable and gives:

$$\frac{du_2}{dc} = -\mu\Delta N Q_t Q_t' \frac{1}{\sqrt{2\pi}\sqrt{\sigma^2+\sigma'^2}} e^{-\frac{1}{2}c^2/(\sigma^2+\sigma'^2)}.$$

Integrate with regard to c, and remember that $u_2 = 0$ if $c = \infty$; thus:

$$u_2 = \mu\Delta N Q_t Q_t' \frac{1}{\sqrt{2\pi}} \int_c^\infty \frac{1}{\sqrt{\sigma^2+\sigma'^2}} e^{-\frac{1}{2}x^2/(\sigma^2+\sigma'^2)}\, dx$$

$$= \mu\Delta N Q_t Q_t' \frac{1}{\sqrt{2\pi}} \int_{c/\sqrt{\sigma^2+\sigma'^2}}^\infty e^{-\frac{1}{2}x'^2}\, dx' \quad \text{......(lii)}.$$

Comparing this with (li) we see that u_2 differs from u_1 by (a) the introduction of the factors Q_t' and $\mu\Delta$ and (b) the replacement of σ in the lower limit by $\sqrt{\sigma^2+\sigma'^2}$. The process can therefore be repeated as often as we please, and we have for u_m the value:

$$u_m = (\mu\Delta)^{m-1} N Q_t Q_t' Q_t'' \dots \text{ to } m \text{ terms } \frac{1}{\sqrt{2\pi}} \int_{c/\Sigma}^\infty e^{-\frac{1}{2}x'^2}\, dx',$$

where $\Sigma^2 = \sigma + \sigma'^2 + \sigma''^2 + \dots$ to m terms.

After the operations indicated by the Q's are completed, we are to put

$$\sigma' = \sigma'' = \sigma''' = \dots = \sigma.$$

Now it is clear that a differentiation with regard to any σ^2 is precisely the same as one with regard to Σ^2. We can therefore write for all the Q's the simple expression

$$1 + \nu_4 (\sigma^2)^2 \frac{d^2}{d(\Sigma^2)} - \nu_6 (\sigma^2)^3 \frac{d^3}{d(\Sigma^2)^3} + \dots + (-1)^s (\sigma^2)^s \frac{d^s}{d(\Sigma^2)^s} + \dots$$

understanding that $d/d(\Sigma^2)$ operates only on Σ and that after the operation is completed we can put $\Sigma = \sqrt{m}\sigma$. Thus the complete solution is:

$$u_m = N(\mu\Delta)^{m-1} \left(1 + \nu_4 (\sigma^2)^2 \frac{d^2}{d(\Sigma^2)^2} - \nu_6 (\sigma^2)^3 \frac{d^3}{d(\Sigma^2)^3} + \dots + (-1)^s \nu_{2s} \frac{d^s}{d(\Sigma^2)^s} + \dots\right)^m$$

$$\frac{1}{\sqrt{2\pi}} \int_{c/\Sigma}^\infty e^{-\frac{1}{2}x^2}\, dx \quad \text{......(liii)}.$$

This is true for c positive or negative, *i.e.* whether the density be considered at a point on the originally occupied or originally unoccupied side of the boundary.

Up to terms of order $1/n^3$ we have for the operator the value

$$1 + m(\nu_4 q^2 - \nu_6 q^3 + \nu_8 q^4 - \nu_{10} q^5 + \nu_{12} q^6)$$

$$+ \frac{m(m-1)}{1.2} (\nu_4^2 q^4 - 2\nu_4\nu_6 q^5 + 2\nu_4\nu_8 q^6)$$

$$+ \frac{m(m-1)(m-2)}{1.2.3} \nu_4^3 q^6, \text{ where } q \text{ stands for } \sigma^2 d/d(\Sigma^2).$$

Now exactly as on p. 26 we may show that:

$$q^s \frac{1}{\sqrt{2\pi}} \int_{c/\Sigma}^{\infty} e^{-\frac{1}{2}x^2} dx = \left(\frac{\sigma}{\Sigma}\right)^{2s} \frac{1}{\sqrt{2\pi}} \frac{c(-1)^{s-1}}{2\Sigma} e^{-\frac{1}{2}c^2/\Sigma^2} \psi_{2(s-1)}(c/\Sigma)$$

$$= \frac{1}{\sqrt{2\pi}} \frac{(-1)^{s-1}}{2m^s} \eta_m e^{-\frac{1}{2}\eta_m^2} \psi_{2(s-1)}(\eta_m),$$

where: $$\psi_{2(s-1)}(\eta_m) = \chi_{2(s-1)}(\eta_m) + \frac{(s-1)}{1!\,2} \cdot \chi_{2(s-2)}(\eta_m) + \frac{(s-1)(s-2)}{2!\,2^2} 1 \cdot 3 \cdot \chi_{2(s-3)}(\eta_m)$$
$$+ \frac{(s-1)(s-2)(s-3)}{3!\,2^3} 1 \cdot 3 \cdot 5 \cdot \chi_{2(s-4)}(\eta_m) + \dots,$$

$\eta_m = c/(\sqrt{m}\,\sigma)$, and χ_{2s} is defined on p. 10, Equation (xviii).

Thus

$$u_m = N(\mu\Delta)^{m-1} \left\{ \overline{\psi}(\eta_m) - \frac{1}{2} \frac{1}{\sqrt{2\pi}} \eta_m e^{-\frac{1}{2}\eta_m^2} \left(\frac{m}{m^2} \nu_4 \psi_2(\eta_m) + \frac{m}{m^3} \nu_6 \psi_4(\eta_m) \right.\right.$$
$$+ \frac{\{m\nu_8 + \frac{1}{2}m(m-1)\nu_4^2\}}{m^4} \psi_6(\eta_m) + \frac{m\nu_{10} + m(m-1)\nu_4\nu_6}{m^5} \psi_8(\eta_m)$$
$$\left.\left. + \frac{m\nu_{12} + m(m-1)\nu_4\nu_8 + \frac{1}{6}m(m-1)(m-2)\nu_4^3}{m^6} \psi_{10}(\eta_m) \right) \right\} \quad \dots\dots\text{(liv)}.$$

We see that this expression converges much more rapidly than that for $\phi_n(r^2)$, if m be at all large.

The result (liv) might have been reached in a different manner. We might have supposed the $(\mu\Delta)^{m-1}N\alpha$ individuals to have started from any element α on the populated side of the boundary and taken mn flights without multiplying to their final resting-place. The effect of this would be that $\sigma^2 = \frac{1}{2}mnl^2$, and that in the values of the ν's we must write mn for n. But doing this gives us precisely the coefficients of the ψ's in (liv). Thus (liv) is deduced directly from (xlix). The proof becomes then much shorter, but it is more artificial; the fact that we may suppose all the unborn individuals to scatter from the original centre is not so easily realised, and further it does not in the process picture what takes place until the final arrangement after the mth breeding cycle is attained. In the method I have adopted we see the exact process of each breeding multiplication, its increase of the operating factor by an additional Q_t, and its increase of the square of the standard deviation by an additional σ^2. Lastly the final form (liv) enables us, without recalculating the ν's for each breeding cycle, to see very easily the effect in the case of any n-flight species, of taking any number of breeding cycles.

So long as we keep $\mu\Delta$ constant of course our result for m breeding cycles with n flights will be the same as for a simple scattering for mn flights of a larger number of individuals. If $\mu\Delta$ varies, however, we must adopt the method indicated in the above proof, and work out each migration successively. The same method must be adopted if a patch be rendered permanently sterile, because

TABLE VI. *Distances of given Densities from the Boundary measured into the Immigration area in terms of Boundary Density.*

Number of migrations	Percentage Density	Number of Flights					Percentage Density	Number of Flights				
		6	7	8	9	10		6	7	8	9	10
1	50	1·17	1·26	1·35	1·43	1·51	5	3·39	3·67	3·92	4·16	4·38
	30	1·99	2·15	2·30	2·44	2·57	1	4·46	4·82	5·15	5·46	5·76
	10	2·85	3·08	3·29	3·49	3·68	·1	5·70	6·16	6·58	6·98	7·36
2	50	1·65	1·78	1·91	2·02	2·13	5	4·80	5·19	5·54	5·88	6·20
	30	2·82	3·04	3·25	3·45	3·64	1	6·31	6·82	7·29	7·73	8·15
	10	4·03	4·35	4·65	4·93	5·20	·1	8·06	8·71	9·31	9·87	10·41
3	50	2·02	2·19	2·34	2·48	2·61	5	5·88	6·35	6·79	7·20	7·59
	30	3·45	3·73	3·98	4·23	4·46	1	7·73	8·35	8·92	9·46	9·98
	10	4·93	5·33	5·70	6·04	6·37	·1	9·87	10·66	11·40	12·09	12·74
4	50	2·34	2·52	2·70	2·86	3·02	5	6·79	7·33	7·84	8·32	8·77
	30	3·98	4·30	4·60	4·88	5·14	1	8·92	9·64	10·30	10·93	11·52
	10	5·70	6·16	6·58	6·98	7·36	·1	11·40	12·31	13·16	13·96	14·72
5	50	2·61	2·82	3·02	3·20	3·37	5	7·59	8·20	8·77	9·30	9·80
	30	4·46	4·81	5·14	5·46	5·75	1	9·98	10·78	11·52	12·22	12·88
	10	6·37	6·88	7·36	7·80	8·23	·1	12·74	13·77	14·72	15·61	16·45
10	50	3·69	3·99	4·27	4·52	4·77	5	10·74	11·60	12·40	13·15	13·86
	30	6·30	6·81	7·28	7·72	8·13	1	14·11	15·24	16·29	17·28	18·21
	10	9·01	9·73	10·40	11·03	11·63	·1	18·02	19·47	20·81	22·07	23·27
50	50	8·26	8·92	9·54	10·11	10·66	5	24·00	25·93	27·72	29·40	30·99
	30	14·09	15·22	16·27	17·26	18·19	1	31·55	34·08	36·43	38·64	40·73
	10	20·15	21·76	23·26	24·67	26·01	·1	40·30	43·53	46·53	49·36	52·03
100	50	11·68	12·62	13·49	14·31	15·08	5	33·95	36·67	39·20	41·58	43·83
	30	19·92	21·52	23·01	24·40	25·72	1	44·62	48·19	51·52	54·64	57·60
	10	28·49	30·78	32·90	34·90	36·78	·1	56·99	61·56	65·81	69·80	73·58

in such a case μ is not constant for all parts of the integrated area, and we cannot suppose the whole final population to scatter from the original centres.

If we neglect the $\psi_2, \psi_4 \ldots$ terms in (liv) we have the value which would follow from the Rayleigh solution of the fundamental problem, and this can be very readily expressed in geometrical terms. For we mark at once that u_1 and u_m are in type identical curves. Take u_1 and stretch it vertically in the uniform ratio of $\mu\Delta^{m-1}$ to 1, and horizontally in the ratio of $\sqrt{m}$ to 1, and it becomes u_m. In other words the broken line on Diagram VII. represents the approximate solution in this case after m migrations provided we read $N(\mu\Delta)^{m-1}$ for N on the vertical scale and $\Sigma = \sqrt{m}\,\sigma$ for σ on the horizontal scale. The Table on p. 33 gives the chief results.

The unit of this table is the length l of "flight." It will be desirable to illustrate its application. Any such application can be of course only a suggestion, and on this account the above Table has been calculated to only a few places of decimals. But such suggestions may not be without value. They will become more than suggestions when our knowledge is greater of the migratory habits of different species. At present only rough approximations can be made as to the values of n and l, and these admittedly are of small weight.

Illustration I. In captivity I have noted that *H. aspersa* will live for five years. For two years it does not usually lay eggs, and then it will generally, but not invariably, reproduce twice in the year. This is of course subject to claustral conditions, and while these seem in some cases unfavourable, in others they may be advantageous both in matter of longevity and—owing to the constant food supply—in number of broods. This snail, as far as my observation goes, appears to return to the same shelter after seeking its food. Leaving such "flitters" on one side, I think we might look upon thirty to forty yards as a maximum "flight" for such a snail and regard seven or eight such flights between its egg layings as on the average an exaggeration.

We might therefore take $l = 40$ yards, $n = 8$, and an average during life of one brood a year as being quite possible approximations in the case of some snails.

This indicates that the progress across a boundary into unoccupied country would be such that 1 per cent. of the density at the boundary and, therefore, possibly $\frac{1}{2}$ per cent. of the density in the fully-occupied country, would only be reached at 2061 yards from the boundary after 100 migrations. In other words, such a species would only progress a mile or two at most in a century. Such progress would hardly be noted in any studies hitherto made of distribution; the limits of a species a hundred years ago were certainly not closely defined to a mile or two, even if they have been recently. Of course there are many other ways in which a slow moving species can be transported than by its own "flights," and further no special stress is laid on the above case, but a study of Table VI. shows that the advance of a slow scattering species* may be comparatively small. The inference can accordingly be made that the existing boundaries of the geographical distribution of certain forms of animal and plant life which are not marked by natural barriers, and which do not correspond to obviously changing environmental conditions, need not after all be associated with subtle physical differences which have escaped the observation of the naturalist. The species may be progressing into an unoccupied area, but at a rate hardly observable in the time during which accurate distribution observations are available. If this view be correct we should expect such boundaries with no apparent environmental change in the case of species for which we might reasonably predict a small n and l.

Illustration II. I have endeavoured to apply the above theory to the immigration of mosquitoes into a cleared area. We will suppose in the present treatment that the area bounded by a straight line (some attempt to allow for curvature of the boundary will be considered later) has been cleared but is not kept sterile to the species. I shall speak of a district as rendered sterile to a species when it is made impossible for it to breed there, and kept sterile when the breeding possibilities are persistently destroyed. The distinction is an important one, especially in the mosquito case. For in the latter case all mosquitoes are immigrants, and in the former case we have not only immigrants, but their produce.

Major Ronald Ross, who has most kindly provided me with information as to mosquito habits, makes the following remarks:

(*a*) That the number of mosquitoes produced varies roughly (*ceteris paribus*) as the extent of surface breeding area.

(*b*) That the breeding area can be taken as consisting of numerous isolated small pools or vessels of water scattered fairly uniformly over the country.

(*c*) That the feeding places (houses, stables, birds, etc.) may be taken as scattered pretty uniformly between the breeding pools.

(*d*) That abundance or scarcity of food can scarcely influence the question much. A single man or bird will yield enough food for many mosquitoes, and if they starve it is not because the food is not there, but because they cannot reach it. They are therefore not likely to be drawn in general by special abundance of food in any special direction. Wind tends to make mosquitoes "sit tight," rather than allow themselves to be scattered.

It would thus appear that on the average an "equi-swampous" condition of the environment and random "flights" of the mosquito will not be very wide of the truth. The difficulty is to form some estimate of n and l. On these points again Major Ross came to my help, but naturally the statements he made were with great reservation.

* Of course any more quickly moving species that depends on this for food would have the same boundary, but in its case the boundary would be environmentally defined.

(α) From egg to egg (*i.e.* from laying of eggs, hatching, larval and pupal stages, to laying of eggs again) takes roughly about a fortnight in hot countries with most mosquitoes. In England, gnats may have only one generation or two in a summer, but in the tropics they may go on breeding throughout the year. In cool countries the egg to egg cycle may be prolonged to a month or two. In certain very hot and dry countries, breeding may be checked entirely except during the rainy season. I have accordingly taken 20, 10 and 5 breedings to the year to represent roughly these conditions.

(β) Major Ross distinguishes between "minor vicissitudes," which an insect makes when it hovers round its victim or mate, and "major vicissitudes" which it makes when it passes from feeding place to pool for egg laying. These correspond to my "flitters" and "flights." He considers that they go back to water every four or five days, so that a "major vicissitude" occurs every two days or so. We might therefore take, excluding flitters, the average number of flights to be six or seven. Of course this is the roughest approximation, but still not an unreasonable estimate of what probably takes place in the mosquito's life.

(γ) As to the magnitude of l we have less definite data. Mosquitoes of a rare kind have been said to have been found two or three miles from their breeding place. Major Ross thinks that Anopheles will exceptionally, when no houses are near, probably travel $\frac{1}{2}$ mile for their food, or perhaps further, but he supposes the average distance scarcely to exceed $\frac{1}{4}$ mile, and it may, as houses and suitable pools often abound not more than 50 yards apart, be not greater, perhaps, than 100 yards.

I have accordingly taken 100 yards and 500 yards as likely values for l, and considering 1 per cent. of the boundary value of the mosquitoes' density as a limit to their existence and 5 per cent. as objectionable, we have the following table:

TABLE VII. *Distances from the Boundary of a cleared but not sterile area at which 1 per cent. and 5 per cent. of the boundary density of Mosquitoes will be found in the course of a Year.*

		Supposed number of Breeding Cycles in Year					
		5		10		20	
Number of Flights............		6	7	6	7	6	7
Density 1 per cent.	$l = 100$	998	1078	1411	1524	1995	2155
,, ,, ,,	$= 500$	4990	5390	7055	7620	9975	10775
Density 5 per cent.	$= 100$	759	820	1074	1160	1518	1640
,, ,, ,,	$= 500$	3745	4100	5370	5800	7590	8200

The distances are all given in yards.

Thus we see that the least of these distances for 1 per cent. is greater than half a mile, or, if an area be cleared but not rendered sterile, we might expect within a year the mosquitoes to reappear within half a mile of the boundary, and to reach an objectionable frequency even at this distance for most of the cases considered.

As far then as these rough numbers can be taken to indicate the state of affairs, it is needful not only to clear an area but to maintain it sterile. The clearance radius may be only $\frac{1}{2}$ mile and is hardly likely to exceed a mile, and the above results only mark the progress of immigration in the course of one year after the clearance. Further the results would be accentuated if the boundary were curved or an approximately circular clearance made.

It does not appear to me that any substantial difference would be made in the main result by reducing n to 3 or 4, although some difference would occur if l were reduced to 20 or 30 yards.

(10) Problem III. *To determine the distribution after m n-flight migrations starting with a centre of population $N\alpha$.*

The previous two problems indicate the nature of the general solutions to which I now proceed. I shall adopt the longer process of proof in this first case as being the more suggestive.

By (xii) and (xlvi), calling the operator as before Q_t, we have for the distribution at X, Y due to a centre at the origin:

$$ {}_1\phi_n(X, Y) = \frac{N\alpha}{2\pi} Q_t \left(\frac{1}{\sigma^2} e^{-\frac{1}{2}(X^2+Y^2)/\sigma^2}\right) \quad \text{.....................(lv).}$$

Hence the distribution at (h, k) after a second migration of n flights is

$$ {}_2\phi_n(h, k) = \mu\Delta \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} {}_1\phi_n(X, Y)\, \frac{Q_t}{2\pi} \frac{e^{-\frac{1}{2}\{(X-h)^2+(Y-k)^2\}/\sigma^2}}{\sigma^2}\, dX dY.$$

Call the Q_t in this Q_{t_2} and write the σ^2 on which it operates σ_2^2; call the Q_t in ${}_1\phi_n(X, Y)$, Q_{t_1} and the σ^2 on which it operates σ_1^2, we have:

$$ {}_2\phi_n(h, k) = \frac{\mu\Delta N\alpha}{(2\pi)^2} Q_{t_1} Q_{t_2} \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} \frac{1}{\sigma_1^2\sigma_2^2} e^{-\frac{1}{2}\left\{\frac{(X-h)^2+(Y-k)^2}{\sigma_2^2}+\frac{X^2+Y^2}{\sigma_1^2}\right\}} dX dY.$$

The integrations can be performed and give us

$$ {}_2\phi_n(h, k) = \frac{\mu\Delta N\alpha}{2\pi} Q_{t_1} Q_{t_2} \frac{1}{\sigma_1^2+\sigma_2^2} e^{-\frac{1}{2}\{(h^2+k^2)/(\sigma_1^2+\sigma_2^2)\}} \quad \text{.............(lvi).}$$

This only differs from ${}_1\phi_n(X, Y)$ by the introduction of $\sigma_1^2+\sigma_2^2$ for σ^2 and of the factor $\mu\Delta Q_{t_2}$.

We can accordingly repeat the process as often as we like and we have:

$$ {}_m\phi_n(h, k) = \frac{(\mu\Delta)^{m-1} N\alpha}{2\pi} Q_{t_1} Q_{t_2} \ldots Q_{t_m} \frac{1}{\Sigma^2} e^{-\frac{1}{2}(h^2+k^2)/\Sigma^2} \quad \text{............(lvii)}, $$

where
$$ \Sigma^2 = \sigma_1^2 + \sigma_2^2 + \sigma_3^2 + \ldots + \sigma_m^2, $$

and after the operations have been performed we are to put all the σ's equal to σ or $\Sigma^2 = m\sigma^2$. But no operator Q_t affects any σ^2 in any other operator, and $\frac{d}{d\sigma_t^2} = \frac{d}{d\Sigma^2}$. Thus $(\sigma_t^2)^s \frac{d^s}{d(\sigma_t^2)^s}$ may be put $= (\sigma^2)^s \frac{d^s}{d(\Sigma^2)^s}$, and this makes all the operators identical in form and we may write

$$ \begin{aligned} Q_{t_1} Q_{t_2} \ldots Q_{t_m} &= \Big\{1 + \nu_4(\sigma^2)^2 \frac{d^2}{d(\Sigma^2)^2} - \nu_6(\sigma^2)^3 \frac{d^3}{d(\Sigma^2)^3} + \nu_8(\sigma^2)^4 \frac{d^4}{d(\Sigma^2)^4} \\ &\qquad + \ldots + (-1)^s \nu_{2s} (\sigma^2)^s \frac{d^s}{d(\Sigma^2)^s} + \ldots \Big\}^m \\ &= 1 + N_4(\sigma^2)^2 \frac{d^2}{d(\Sigma^2)^2} - N_6(\sigma^2)^3 \frac{d^3}{d(\Sigma^2)^3} + N_8(\sigma^2)^4 \frac{d^4}{d(\Sigma^2)^4} \\ &\qquad + \ldots + (-1)^s N_{2s}(\sigma^2)^s \frac{d^s}{d(\Sigma^2)^s} + \ldots . \end{aligned} $$

In this form of the operator we can now write at once $\sigma^2 = \frac{1}{m}\Sigma^2$ and call the expression Q_t^m.

Thus
$$ \begin{aligned} Q_t^m &= 1 + N_4(\Sigma^2)^2 \frac{d^2}{d(\Sigma^2)^2} - N_6(\Sigma^2)^3 \frac{d^3}{d(\Sigma^2)^3} + N_8(\Sigma^2)^4 \frac{d^4}{d(\Sigma^2)^4} \\ &\qquad + \ldots + (-1)^s N_{2s}(\Sigma^2)^s \frac{d^s}{d(\Sigma^2)^s} + \ldots \quad \text{......(lviii)}, \end{aligned} $$

where
$$ N_4 = \frac{m}{m^2}\nu_4, \qquad N_6 = \frac{m}{m^3}\nu_6, $$
$$ N_8 = \frac{m\nu_8 + \frac{1}{2}m(m-1)\nu_4^2}{m^4}, \qquad N_{10} = \frac{m\nu_{10} + m(m-1)\nu_4\nu_6}{m^5}, $$
$$ N_{12} = \frac{m\nu_{12} + m(m-1)\nu_4\nu_8 + \frac{1}{6}m(m-1)(m-2)\nu_4^3}{m^6}, \text{ etc. } \quad \text{.........(lix)}. $$

These values of the N's rapidly converge and their values are given in Table III. on p. 21 of this paper with those of the ν's for a few values of n and m. As we have seen on p. 32, they are the ν's obtained by using values of nm for n.

We now have the general solution of distribution from a centre:

$$ \begin{aligned} {}_m\phi_n(h, k) &= (\mu\Delta)^{m-1} \frac{N\alpha}{2\pi} Q_t^m \frac{1}{\Sigma^2} e^{-\frac{1}{2}(h^2+k^2)/\Sigma^2} \ldots \\ &= (\mu\Delta)^{m-1} N\alpha (\Omega_0 + N_4\Omega_4 + N_6\Omega_6 + \ldots + N_{2s}\Omega_{2s} + \ldots) \quad \text{...(lx)}. \end{aligned} $$

This is absolutely identical with (xii), except that the constants ν are replaced by other constants N of known value, and in every ω-function we are to replace σ^2 by $m\sigma^2$ or Σ^2, that is to say a uniform stretch in the ratio of $\sqrt{m}$ to l is given to any surface $z=\omega_{2s}$ parallel to the axes of x and y. This is denoted by writing Ω_{2s} for ω_{2s}.

If we confine our attention to the Rayleigh part of the solution—which will be more and more nearly exact as m increases, for the N's rapidly decrease in value—then we have

$$_m\bar{\phi}_n\,(h,\,k)=(\mu\Delta)^{m-1}N\alpha\Omega_0 \quad\text{..............................(lxi)},$$

and we see that every density gradient curve for the successive migrations is to be obtained by a stretch from the first migration density curve.

In general, however, this result is not absolutely true because the different components of the true solution are mixed in different proportions, the N's being functions of m. We see, however, that the stretching rule becomes more and more accurate, as we increase either the number of flights or the number of migrations.

(11) Problem IV. *To find the form of the general solution for the distribution into surrounding space after m migrations of any population initially spread uniformly over any given patch with density N.*

The density at h, k, after m migrations due to a centre $Ndxdy$, is by (lvii) above

$$=(\mu\Delta)^{m-1}\frac{Ndxdy}{2\pi}Q_t^m\frac{1}{\Sigma^2}e^{-\frac{1}{2}\{(x-h)^2+(y-k)^2\}/\Sigma^2}.$$

To give the patch let x be integrated from v_1 to v_2, where v_1 and v_2 will usually be functions of y, and then let y be integrated from u_1 to u_2. We find:

$$_m\mathcal{F}_n\,(h,\,k)=(\mu\Delta)^{m-1}\frac{NQ_t^m}{2\pi}\int_{u_1}^{u_2}\int_{v_1}^{v_2}\frac{1}{\Sigma^2}e^{-\frac{1}{2}\{(x-h)^2+(y-k)^2\}/\Sigma^2}dxdy \quad\text{......(lxii)}.$$

This is the general form of the solution when the population spreads from a uniform patch into non-sterile surrounding country.

If on the other hand we want the distribution after m migrations starting with a cleared patch, which is not kept sterile, we have

$$_mF_n\,(h,\,k)=(\mu\Delta)^{m-1}N-{}_m\mathcal{F}_n\,(h,\,k) \quad\text{.....................(lxiii)},$$

for the whole district would have had a uniform density of $(\mu\Delta)^{m-1}N$ had there been no clearance. Hence

$$_mF_n\,(h,\,k)=(\mu\Delta)^{m-1}NQ_t^m\left(1-\frac{1}{2\pi}\int_{u_1}^{u_2}\int_{v_1}^{v_2}\frac{1}{\Sigma^2}e^{-\frac{1}{2}\{(x-h)^2+(y-k)^2\}/\Sigma^2}dxdy\right)\text{...(lxiv)}.$$

Now $$_1F_n\,(h,\,k)=NQ_t'\left(1-\frac{1}{2\pi}\int_{u_1}^{u_2}\int_{v_1}^{v_2}\frac{1}{\sigma^2}e^{-\frac{1}{2}\{(x-h)^2+(y-k)^2\}/\sigma^2}dxdy\right).$$

Hence the rule: If the solution can be found for a single migration, replace σ^2 by $m\sigma^2$, and each ν by the proper N, multiply by the factor $(\mu\Delta)^{m-1}$, and the solution for m migrations is deduced.

It will thus be clear that, if the solution can in any case be found for one migration fully, we can at once extend it to the case of any number of migrations, with constant fertility-survival factor.

(12) Problem V. *To determine the distribution after a first migration into a cleared rectangular area.*

Let the area be the rectangle $2a \times 2b$, and the origin be taken at its centre and axes of x and y parallel respectively to the sides $2a$ and $2b$. Then the density at any point h, k, after a single migration $F_n(h, k)$ is given by the principle of the last problem by

$$\mathcal{F}_n(h, k) = N - F_n(h, k) \quad \text{.........................(lxv)},$$

where $F_n(h, k)$ is the distribution from a uniformly occupied rectangular area into surrounding unoccupied space.

But
$$F_n(h, k) = N \int_{-a}^{+a} \int_{-b}^{+b} \phi_n \{(x-h)^2 + (y-k)^2\} \, dx dy$$
$$= \frac{1}{2\pi} NQ_t \frac{1}{\sigma^2} \int_{-a}^{+a} \int_{-b}^{+b} e^{-\frac{1}{2}\left\{\frac{(x-h)^2}{\sigma^2} + \frac{(y-k)^2}{\sigma^2}\right\}} dx dy$$
$$= \frac{1}{2\pi} NQ_t \frac{1}{\sigma^2} \int_{-a}^{+a} e^{-\frac{1}{2}(x-h)^2/\sigma^2} dx \times \int_{-b}^{+b} e^{-\frac{1}{2}(y-k)^2/\sigma^2} dy.$$

Let $P_0(\epsilon)$ stand for the probability integral

$$\frac{1}{\sqrt{2\pi}} \int_0^{\epsilon} e^{-\frac{1}{2}x^2} dx.$$

Then:
$$\frac{1}{\sqrt{2\pi}\sigma} \int_{-a}^{+a} e^{-\frac{1}{2}(x-h)^2/\sigma^2} dx = \frac{1}{\sqrt{2\pi}} \int_{-(a+h)/\sigma}^{(a-h)/\sigma} e^{-\frac{1}{2}x^2} dx$$
$$= \frac{1}{\sqrt{2\pi}} \left(\int_0^{(a-h)/\sigma} + \int_0^{(a+h)/\sigma} \right) e^{-\frac{1}{2}x^2} dx$$
$$= P_0\left(\frac{a-h}{\sigma}\right) + P_0\left(\frac{a+h}{\sigma}\right).$$

Thus:
$$F_n(h, k) = NQ_t P_0 \left\{\left(\frac{a-h}{\sigma}\right) + P_0\left(\frac{a+h}{\sigma}\right)\right\} \left\{P_0\left(\frac{b-k}{\sigma}\right) + P_0\left(\frac{b+k}{\sigma}\right)\right\} \text{...(lxvi)}.$$

Now consider the differentiation of $P_0\left(\frac{u}{\sigma}\right)$ with regard to σ^2.

$$\frac{d}{d\sigma^2}\left\{P_0\left(\frac{u}{\sigma}\right)\right\} = \frac{d}{2\sigma d\sigma} \frac{1}{\sqrt{2\pi}} \int_0^{u/\sigma} e^{-\frac{1}{2}x^2} dx = -\frac{1}{2} \frac{u}{\sigma} \frac{1}{\sqrt{2\pi}} \frac{1}{\sigma^2} e^{-\frac{1}{2}(u^2/\sigma^2)}.$$

Writing $\sigma^2 = t$ as before, we find

$$\frac{d}{dt}\left\{P_0\left(\frac{u}{\sigma}\right)\right\} = -\frac{1}{2}\sqrt{2\pi}u\,\frac{\omega_0}{\sqrt{t}} \quad \text{.......................(lxvii).}$$

Hence

$$\frac{d^s}{dt^s}\left\{P_0\left(\frac{u}{\sigma}\right)\right\} = -\frac{1}{2}\sqrt{2\pi}u\,\frac{d^{s-1}}{dt^{s-1}}\left(\frac{\omega_0}{\sqrt{t}}\right)$$

$$= \frac{1}{2}\frac{\sqrt{2\pi}(-1)^s u}{t^{s-\frac{1}{2}}}\left(\omega_{2(s-1)} + (s-1)\,\omega_{2(s-2)}\frac{1}{2} + \frac{(s-1)(s-2)}{1\,.\,2}\,\omega_{2(s-3)}\frac{1\,.\,3}{2\,.\,2}\right.$$

$$\left. + \frac{(s-1)(s-2)(s-3)}{1\,.\,2\,.\,3}\,\omega_{2(s-4)}\frac{1\,.\,3\,.\,5}{2\,.\,2\,.\,2} + \text{etc.}\right),$$

$$t^s\frac{d^s}{dt^s}\left\{P_0\left(\frac{u}{\sigma}\right)\right\} = \frac{1}{2}\frac{1}{\sqrt{2\pi}}\frac{u}{\sigma}(-1)^s e^{-\frac{1}{2}u^2/\sigma^2}\psi_{2(s-1)}(u/\sigma) \quad \text{.............................(lxviii),}$$

the expression being the same as that on p. 32.

Now let us write the following for brevity where $\eta = u/\sigma$:

$$L_1(\eta) = \frac{1}{2}\frac{1}{\sqrt{2\pi}}\eta e^{-\frac{1}{2}\eta^2}(\nu_4\psi_2(\eta) + \nu_6\psi_4(\eta) + \ldots + \nu_{2s}\psi_{2(s-1)}(\eta) + \ldots),$$

$$L_2(\eta) = \frac{1}{2}\frac{1}{\sqrt{2\pi}}\eta e^{-\frac{1}{2}\eta^2}(2\nu_4 + 3\nu_6\psi_2(\eta) + \ldots + s\nu_{2s}\psi_{2(s-2)}(\eta) + \ldots),$$

$$L_3(\eta) = \frac{1}{2}\frac{1}{\sqrt{2\pi}}\eta e^{-\frac{1}{2}\eta^2}\left(3\nu_6 + 6\nu_8\psi_2(\eta) + \ldots + \frac{s(s-1)}{1\,.\,2}\nu_{2s}\psi_{2(s-3)}(\eta) + \ldots\right),$$

$$L_4(\eta) = \frac{1}{2}\frac{1}{\sqrt{2\pi}}\eta e^{-\frac{1}{2}\eta^2}\left(4\nu_8 + 10\nu_{10}\psi_2(\eta) + \ldots + \frac{s(s-1)(s-2)}{1\,.\,2\,.\,3}\nu_{2s}\psi_{2(s-4)}(\eta) + \ldots\right) \ldots \text{(lxix),}$$

and so on. All these functions are directly expressible in ω-functions as on p. 27.

Further let $$P_s(\eta) = (-1)^s t^s\frac{d^s}{dt^s}P_0(\eta) = \frac{1}{2}\frac{1}{\sqrt{2\pi}}\eta e^{-\frac{1}{2}\eta^2}\psi_{2(s-1)}(\eta) \quad \text{...........(lxx).}$$

Then we have, if

$$\eta_1 = (a-h)/\sigma,\quad \eta_2 = (a+h)/\sigma,\quad \epsilon_1 = (a-h)/\sigma,\quad \epsilon_2 = (a+h)/\sigma,$$

$$F_n(h, k) = N[\{P_0(\eta_1) + P_0(\eta_2)\}\{P_0(\epsilon_1) + P_0(\epsilon_2)\} + \{L_1(\eta_1) + L_1(\eta_2)\}\{P_0(\epsilon_1) + P_0(\epsilon_2)\}$$

$$+ \{P_0(\eta_1) + P_0(\eta_2)\}\{L_1(\epsilon_1) + L_1(\epsilon_2)\} + \{P_1(\epsilon_1) + P_1(\epsilon_2)\}\{L_2(\eta_1) + L_2(\eta_2)\}$$

$$+ \ldots + \{P_s(\epsilon_1) + P_s(\epsilon_2)\}\{L_{s+1}(\eta_1) + L_{s+1}(\eta_2)\} + \ldots] \quad \text{...........(lxxi).}$$

The L-functions involve the rapidly converging ν-coefficients, and the first few terms will suffice to get an idea of the distribution. If we retain only the Rayleigh terms we find:

$$F_n(h, k) = N[1 - \{P_0(\eta_1) + P_0(\eta_2)\}\{P_0(\epsilon_1) + P_0(\epsilon_2)\}] \quad \text{........(lxxii),}$$

which can be ascertained for given values of a, b, h, k and σ from the ordinary tables of the probability integral.

If we make b infinite, then $P_s(\epsilon_1)$ and $P_s(\epsilon_2)=0$ for $s>0$, and $L_1(\epsilon_1)$ and $L_1(\epsilon_2)=0$, $P_0(\epsilon_1)=P_0(\epsilon_2)=\frac{1}{2}$, and

$$F_n(h,k)=N\{1-P_0(\eta_1)-P_0(\eta_2)-L_1(\eta_1)-L_2(\eta_2)\} \quad \text{.........(lxxiii).}$$

This could be deduced directly from (xlix) and it represents the first migration distribution into an indefinitely long cleared strip or belt. This is a result of some interest as it might approximately apply to the migration into a zone cleared by a flood or a fire of certain types of animal or vegetable life.

(13) Problem VI. *To determine the distribution after m migrations into a cleared but not sterile rectangular area.*

By the general proposition on p. 39 we have only to write $\Sigma=m\sigma$ for σ, and the N's for the ν's in the L's. Let us put

$$\eta_1'=(a-h)/\Sigma=\eta_1/\sqrt{m},\quad \eta_2'=\eta_2/\sqrt{m},\quad \epsilon_1'=\epsilon_1/\sqrt{m},\quad \epsilon_2'=\epsilon_2/\sqrt{m}.$$

Let

$$L_1'(\eta_1')=\frac{1}{2}\frac{1}{\sqrt{2\pi}}\eta_1'e^{-\frac{1}{2}\eta_1'^2}\{N_4\psi_2(\eta_1')+N_6\psi_4(\eta_1')+\dots+N_{2s}\psi_{2(s-1)}(\eta_1')+\dots\},$$

and so forth, then we have for the full solution:

$$\begin{aligned} {}_mF_n(h,k)=(\mu\Delta)^{m-1}N[&\{P_0(\eta_1')+P_0(\eta_2')\}\{P_0(\epsilon_1')+P_0(\epsilon_2')\} \\ &+\{L_1'(\eta_1')+L_1'(\eta_2')\}\{P_0(\epsilon_1')+P_0(\epsilon_2')\}+\{P_0(\eta_1')+P_0(\eta_2')\}\{L_1'(\epsilon_1')+L_1'(\epsilon_2')\} \\ &+\{P_1(\epsilon_1')+P_1(\epsilon_2')\}\{L_2'(\eta_1')+L_2'(\eta_2')\} \\ &+\dots+\{P_s(\epsilon_1')+P_s(\epsilon_2')\}\{L'_{s+1}(\eta_1')+L'_{s+1}(\eta_2')\}+\dots] \quad \text{...............(lxxiv).} \end{aligned}$$

The terms here will very rapidly converge for any fairly large value of m, so that for many purposes we may write the solution:

$${}_mF_n(h,k)=(\mu\Delta)^{m-1}N\{P_0(\eta_1')+P_0(\eta_2')\}\{P_0(\epsilon_1')+P_0(\epsilon_2')\} \quad \text{......(lxxv),}$$

which can be found at once from the usual tables of the probability integral.

Illustration I. A rectangular patch 2 miles long and 1 mile broad is cleared of mosquitoes, but not retained sterile. What would be the central density at the end of the year? Suppose 10 breeding cycles with their scatter migrations, each of 6 flights, to take place in the year. Then if we take 200 yards as a possible round value for the flight we have:

$$\begin{aligned} &m=10,\ n=6,\ l=200\text{ yds.}, && \sigma^2=\tfrac{1}{2}nl^2=120{,}000 \text{ or } && \sigma=346{\cdot}41\text{ yds.} \\ &a=880\text{ yds.},\ b=1760\text{ yds.}, && \eta_1=\eta_2=2{\cdot}540, && \epsilon_1=\epsilon_2=5{\cdot}081, \\ &\Sigma=\sqrt{10}\sigma=1095{\cdot}44\text{ yds.}, && \eta_1'=\eta_2'={\cdot}803, && \epsilon_1'=\epsilon_2'=1{\cdot}607. \end{aligned}$$

Hence $${}_{10}F_6(0,0)=(\mu\Delta)^9 4P_0({\cdot}803)\,P_0(1{\cdot}607)\,N,$$

or, using Sheppard's Tables:

$$\begin{aligned} {}_{10}F_6(0,0)&=(\mu\Delta)^9 4\times{\cdot}2890\times{\cdot}4460N, \\ &=(\mu\Delta)^9\times{\cdot}5156N. \end{aligned}$$

Thus
$$ {}_{10}F_6(0,\,0) = (\mu\Delta)^9 (1 - \cdot 5156) N $$
$$ = (\mu\Delta)^9 \cdot 48N. $$

We see accordingly that if the fertility and the death-rate were the same in the clearance and in the populated district outside, the density at the centre of the cleared patch would at the end of the year be almost 50 per cent. of that in uncleared country. It is thus obvious that clearance can be of small use, unless it is followed by permanent preservation of sterility. Even if one *annual* clearance were made it is very unlikely—if the actual values of the constants are at all near those assumed—that the mosquitoes would not by the 9th or 10th breeding cycle within the year before the annual clearance was repeated have reached a very substantial density even at the centre of the patch. We have thus an additional argument in favour of rendering a district not only sterile, but keeping it so. In such a case since ν_4 and ν_6, ψ_2, ψ_4 are negative we shall have a density somewhat less than:

$$ {}_1F_6(0,\,0) = N\{1 - 4P_0(2\cdot 540)\, P_0(5\cdot 081)\} = N(1 - \cdot 9889) \text{ about.} $$

Thus:
$$ {}_1F_6(0,\,0) = \cdot 01N \text{ approximately.} $$

It follows that in the centre of such a rectangular patch, there would roughly be only about 1 mosquito for every 100 in uncleared country.

But while this shows that such a sterile patch would be a great improvement for a denizen at the centre it is well to enquire what happens in such patches some way from the centre. I accordingly add the following illustration.

Illustration II. A square area of one mile side is cleared and kept permanently sterile. What will be the density at the centre and a quarter of a mile from the centre on the same assumption as before?

Here
$$ a = b = 880 \text{ yds.} $$

At the centre $\eta_1 = \eta_2 = \epsilon_1 = \epsilon_2 = 2\cdot 54$ and:

$$ {}_1F_6(0,\,0) = N[1 - 4\{P_0(2\cdot 54)\}^2] = N\{1 - (\cdot 9889)^2\} = \cdot 022N; $$

or, we find one mosquito for every fifty in uncleared country. Taking our quarter of a mile directly towards one of the boundaries, we have $h = 440$, $k = 0$, and:

$$ \eta_1 = 1\cdot 27, \quad \eta_2 = 3\cdot 81, \quad \epsilon_1 = \epsilon_2 = 2\cdot 54. $$

Thus:
$$ {}_1F_6(440,\,0) = N[1 - \{P_0(1\cdot 27) + P_0(3\cdot 81)\}\{2P_0(2\cdot 54)\}] $$
$$ = N\{1 - (\cdot 3980 + \cdot 4999)(\cdot 9889)\} = \cdot 112N. $$

Thus at $\frac{1}{4}$ mile from the centre (or from the edge) of the clearance, the density is 11 per cent. of that in uncleared country. It may be doubted whether this is a sufficient reduction, and, supposing the above assumptions to be anything like roughly correct, it may be needful to render more than a square mile permanently sterile to protect a patch of one square half-mile.

On the other hand a cleared but not permanently sterile square mile would after a year have a density at the same point—$\frac{1}{4}$ mile from the centre—of:

$$ {}_{10}F_6(440,\ 0) = (\mu\Delta)^9 N[1 - \{P_0(\cdot 402) + P_0(1\cdot 205)\}\{2P_0(\cdot 803)\}] = (\mu\Delta)^9 \cdot 69N, $$

or of 69 per cent. of that in uncleared country.

Another point seems of some interest. What is the density at the boundary after the first migration?

At the middle point of the edge it is

$$ \begin{aligned} {}_1F_6(880,\ 0) &= N[1 - \{P_0(0) + P_0(5\cdot 08)\}\{2P_0(2\cdot 54)\}] \\ &= N(1 - \cdot 5000 \times \cdot 9889) \\ &= \cdot 506N. \end{aligned} $$

This is almost the $\frac{1}{2}N$ of an indefinitely long straight boundary.

At the corner it is

$$ {}_1F_6(880,\ 880) = N[1 - \{P_0(0) + P_0(5\cdot 08)\}^2] = \cdot 75N \text{ nearly}, $$

or, as we should expect, has risen much beyond the $\frac{1}{2}N$ value.

There is no difficulty in tracing the contour lines of the population density in this case.

If we consider a cycle of 10 breedings in a non-sterile patch we have:

$$ \begin{aligned} {}_{10}F_6(880,\ 0) &= (\mu\Delta)^9 N[1 - \{P_0(0) + P_0(1\cdot 607)\}\{2P_0(\cdot 808)\}] \\ &= \cdot 742N(\mu\Delta)^9, \end{aligned} $$

and

$$ \begin{aligned} {}_{10}F_6(880,\ 880) &= (\mu\Delta)^9 N[1 - \{P_0(0) + P_0(1\cdot 607)\}^2] \\ &= \cdot 801N(\mu\Delta)^9. \end{aligned} $$

Thus if the patch were not sterile, the effect of the clearance would at the boundary after the lapse of a year be marked by a 20 to 25 per cent. reduction. The illustrations I have given are of course dependent on the values of the constants selected. Such constants have at present been little studied, and accordingly small weight can be laid on the actual numerical results. But the theory appears to indicate useful lines of inquiry, even if its results will of course need to be controlled everywhere by local facts. In a general way there can be little doubt that a theory like the present will not only lead to a more systematic classification of local facts and to fuller observation of the habits of local species, but that this knowledge itself will in its turn test the applicability of the theory, or suggest the directions in which it may need modification.

(14) Problem VII. *To determine the distribution after a first migration into a cleared circular area.*

Let the radius of the cleared area be a. Then at distance c from the centre, inside or outside the circle of radius a, the distribution $F_n(c)$ is given by:

$$F_n(c) = N\int_a^\infty \int_0^{2\pi} \phi_n(c^2 + r^2 - 2rc\cos\theta)\, r\,d\theta\,dr \quad\text{.................(lxxvi)}$$

$$= \frac{N}{2\pi} Q_t \int_a^\infty \int_0^{2\pi} \frac{1}{\sigma^2} e^{-\frac{1}{2}(c^2+r^2)/\sigma^2} e^{-(rc\cos\theta)/\sigma^2} r\,d\theta\,dr$$

$$= \frac{N}{2\pi} Q_t \frac{e^{-\frac{1}{2}c^2/\sigma^2}}{\sigma^2} \int_a^\infty \int_0^{2\pi} e^{-\frac{1}{2}r^2/\sigma^2} r \mathop{S}_0^\infty \frac{1}{m!}\left(\frac{r}{\sigma}\right)^m \left(\frac{c}{\sigma}\right)^m \cos^m\theta\, d\theta\, dr.$$

Now $\int_0^{2\pi} \cos^m\theta\, d\theta = 0$, if m be odd, and $= 4\int_0^{\pi/2} \cos^{2s}\theta\, d\theta$

$$= 4\frac{(2s-1)(2s-3)\dots 1}{2s(2s-2)\dots 2}\frac{\pi}{2} = 2\pi\frac{2s!}{(2^s s!)^2},$$

if m be even and $=2s$.

Hence:

$$F_n(c) = NQ_t \frac{e^{-\frac{1}{2}c^2/\sigma^2}}{\sigma^2} \int_a^\infty e^{-\frac{1}{2}r^2/\sigma^2} r \mathop{S}_0^\infty \left\{\left(\frac{r^2}{\sigma^2}\right)^s \left(\frac{c^2}{\sigma^2}\right)^s \frac{1}{(2^s s!)^2}\right\} dr \quad\text{.........(lxxvii).}$$

Now
$$\int_a^\infty e^{-\frac{1}{2}r^2/\sigma^2} \frac{r^{2s+1}}{\sigma^{2s+1}}\, d\left(\frac{r}{\sigma}\right) = \int_{a/\sigma}^\infty e^{-\frac{1}{2}z^2} z^{2s+1} dz$$

$$= M_{2s+1}(a/\sigma) \quad\text{.....................(lxxviii).}$$

$M_{2s+1}(a/\sigma)$ is thus the $\overline{2s+1}$th moment of the 'tail' of a normal or Gaussian curve of errors (multiplied by $\sqrt{2\pi}$) about its axis. Its values have been tabled for $s = 1$, 2, 3 and 4.

Thus we have:

$$F_n(c) = NQ_t e^{-\frac{1}{2}c^2/\sigma^2} \mathop{S}_0^\infty \left(\frac{c^2}{\sigma^2}\right)^s \frac{M_{2s+1}(a/\sigma)}{(2^s s!)^2} \quad\text{..................(lxxix).}$$

But it is easy to see that:

$$M_{2s+1}(a/\sigma) = 2^s s!\, e^{-\frac{1}{2}a^2/\sigma^2}\left\{1 + \frac{1}{2}\frac{a^2}{\sigma^2} + \frac{1}{2.4}\left(\frac{a^2}{\sigma^2}\right)^2 + \dots + \frac{1}{2^s s!}\left(\frac{a^2}{\sigma^2}\right)^s\right\}.$$

Accordingly:

$$F_n(c) = NQ_t e^{-\frac{1}{2}(c^2+a^2)/\sigma^2} \mathop{S}_0^\infty \left(\frac{c^2}{\sigma^2}\right)^s \left\{1 + \frac{1}{2}\frac{a^2}{\sigma^2} + \frac{1}{2.4}\left(\frac{a^2}{\sigma^2}\right)^2 + \dots + \frac{1}{2^s s!}\left(\frac{a^2}{\sigma^2}\right)^s\right\}\frac{1}{2^s s!} \quad\dots\text{(lxxx).}$$

The successive differentiations of this expression with regard to $t = \sigma^2$, involved in the operator Q_t, which are needful if we wish to give the corrections to the Rayleigh solution, are straightforward but extremely laborious. We can throw the solution into other forms.

Write:
$$\epsilon_1 = \tfrac{1}{2}c^2/\sigma^2, \quad \epsilon_2 = \tfrac{1}{2}a^2/\sigma^2,$$

then we have:

$$F_n(c) = NQ_t e^{-(\epsilon_1+\epsilon_2)} \mathop{S}_0^\infty \frac{\epsilon_1^s}{s!}\left(1 + \epsilon_2 + \frac{\epsilon_2^2}{2!} + \dots + \frac{\epsilon_2^s}{s!}\right)$$

$$= NQ_t e^{-\epsilon_1} \mathop{S}_0^\infty \frac{\epsilon_1^s}{(s!)^2}\int_{\epsilon_2}^\infty x^s e^{-x} dx \quad\text{.........................(lxxxi).}$$

Here $\int_{\epsilon_2}^{\infty} x^s e^{-x} dx$ is the incomplete Γ-function for an integer value of s. This can be found fairly easily from the above series, or may be determined from tables of the incomplete Γ-function which it is hoped may be shortly published.

Again:
$$J_0(2i\sqrt{z}) = \overset{\infty}{\underset{0}{S}} \frac{z^s}{(s!)^2},$$
hence we have:
$$F_n(c) = NQ_t e^{-\epsilon_1} \int_{\epsilon_2}^{\infty} J_0(2i\sqrt{\epsilon_1 x})\, e^{-x} dx \ldots\ldots\ldots\ldots\ldots\ldots \text{(lxxxii)},$$
a very concise form, which does not, however, simplify the calculations. Integrate by parts and we have:
$$F_n(c) = NQ_t e^{-(\epsilon_1+\epsilon_2)} \overset{\infty}{\underset{0}{S}} \frac{d^s}{d\epsilon_2{}^s} \{J_0(2i\sqrt{\epsilon_1\epsilon_2})\}$$
$$= NQ_t e^{-(\epsilon_1+\epsilon_2)} \overset{\infty}{\underset{0}{S}} \epsilon_1{}^s \frac{d^s}{d(\epsilon_1\epsilon_2)^s} \{J_0(2i\sqrt{\epsilon_1\epsilon_2})\}.$$

But
$$\frac{d^s}{dz^s} J_0(2i\sqrt{2}) = \overset{\infty}{\underset{0}{S}} \frac{z^q}{q!\,(q+s)!} = \frac{J_s(2i\sqrt{z})}{(i\sqrt{z})^s},$$
or:
$$F_n(c) = NQ_t e^{-(\epsilon_1+\epsilon_2)} \overset{\infty}{\underset{0}{S}} \left\{\epsilon_1{}^s \frac{J_s(2i\sqrt{\epsilon_1\epsilon_2})}{(i\sqrt{\epsilon_1\epsilon_2})^s}\right\}$$
$$= NQ_t e^{-(\epsilon_1+\epsilon_2)} \overset{\infty}{\underset{0}{S}} \left(\sqrt{\frac{-\epsilon_1}{\epsilon_2}}\right)^s J_s(2i\sqrt{\epsilon_1\epsilon_2}) \;\ldots\ldots\ldots\ldots \text{(lxxxiii)}.$$

This is the solution in Bessel's functions, and inside the cleared area, where ϵ_2 is greater than ϵ_1, would give fairly good results if tables of the higher Bessel's functions for imaginary values of the argument were available.

We can also express the solution in terms of ω-functions as follows:

Write
$$I_s(a) = \int_0^{\infty} \left(\frac{1}{2}\frac{r^2}{\sigma^2}\right)^s e^{-\frac{1}{2}r^2/\sigma^2} \frac{rdr}{\sigma^2},$$
$$E_s(c) = \frac{1}{s!} e^{-\frac{1}{2}c^2/\sigma^2} \left(\frac{1}{2}\frac{c^2}{\sigma^2}\right)^s.$$

Then
$$F_n(c) = NQ_t \overset{\infty}{\underset{0}{S}} \frac{1}{s!} I_s(a)\, E_s(c).$$

Now
$$E_s(r) = \frac{1}{s!} e^{-\frac{1}{2}r^2/\sigma^2} \left(\frac{1}{2}\frac{r^2}{\sigma^2}\right)^s = 2\pi\sigma^2 \overset{\infty}{\underset{0}{S}} b_{2p}\omega_{2p},$$
the b's being undetermined constants, for dividing by the exponential factor we have an integer algebraic expression in r^2/σ^2 on both sides. Multiply both sides by $\chi_{2p} rdr$ and integrate between 0 and ∞, p being = or $< s$. Then:
$$\frac{1}{s!}\int_0^{\infty} e^{-\frac{1}{2}r^2/\sigma^2} \chi_{2p} \left(\frac{1}{2}\frac{r^2}{\sigma^2}\right)^s rdr = 2\pi\sigma^2 b_{2p} \int_0^{\infty} \chi_{2p}\omega_{2p} rdr,$$
$$\frac{2\pi\sigma^2}{s!}\int_0^{\infty} \omega_{2p} \frac{r^{2s+1}dr}{(2\sigma^2)^s} = 2\pi\sigma^2 b_{2p}(p!)^2, \text{ by (xix) and (xxi).}$$

Therefore by (xvi):

$$b_{2p}=\frac{1}{s!\,(p!)^2}(p-1-s)(p-2-s)\ldots(-s)(-1)^{s-1}\int_{-0}^{-\infty}\beta^{-s-2}e^{1/\beta}\,d\beta$$

$$=(-1)^p\frac{s(s-1)\ldots(s-p+1)}{s!\,(p!)^2}\int_0^\infty x^s e^{-x}\,dx, \text{ if } x=-1/\beta,$$

$$=(-1)^p\frac{s(s-1)\ldots(s-p+1)}{(p!)^2}.$$

Thus
$$E_s(r)=2\pi\sigma^2\left\{\omega_0-s\omega_2+\frac{s(s-1)}{(2!)^2}\omega_4-\frac{s(s-1)(s-2)}{(3!)^2}\omega_6+\ldots\right\}\ldots\text{(lxxxiv)}$$
$$=2\pi\sigma^2 U_s(r)^*, \text{ say.}$$

Now consider:

$$\int_r^\infty \omega_{2s}\frac{rdr}{\sigma^2}=(-1)^s(\sigma^2)^{s-1}\frac{d^s}{d(\sigma^2)^s}\int_r^\infty\omega_0 rdr$$

$$=(-1)^s(\sigma^2)^{s-1}\frac{d^s}{d(\sigma^2)^s}\left[-\frac{1}{2\pi}e^{-\frac{1}{2}r^2/\sigma^2}\right]_r^\infty$$

$$=(-1)^s(\sigma^2)^{s-1}\frac{d^s}{d(\sigma^2)^s}(\omega_0\sigma^2)$$

$$=\omega_{2s}-s\omega_{2s-2}\ldots\ldots\text{(lxxxv)}.$$

We can now express $I_s(r)$ in terms of ω-functions.

We have:

$$I_s(r)=\int_r^\infty s!\,E_s(r)\frac{rdr}{\sigma^2}$$

$$=s!\,2\pi\sigma^2\int_r^\infty\left\{\omega_0-s\omega_2+\frac{s(s-1)}{(2!)^2}\omega_4-\frac{s(s-1)(s-2)}{(3!)^2}\omega_6+\ldots\right\}\frac{rdr}{\sigma^2}$$

$$=s!\,2\pi\sigma^2(s+1)\left\{\omega_0-\frac{s\omega_2}{1!\,2!}+\frac{s(s-1)}{2!\,3!}\omega_4-\frac{s(s-1)(s-2)}{3!\,4!}\omega_6+\ldots\right\}$$

$$=s!\,2\pi\sigma^2(s+1)V_s(r).$$

Thus
$$F_n(c)=NQ_t4\pi^2\sigma^4\mathop{S}_0^\infty((s+1)U_s(c)V_s(a))\ldots\ldots\text{(lxxxvi)},$$

where:
$$U_s(r)=\omega_0-\frac{s}{(1!)^2}\omega_2+\frac{s(s-1)}{(2!)^2}\omega_4-\frac{s(s-1)(s-2)}{(3!)^2}\omega_6+\ldots,$$

$$V_s(r)=\omega_0-\frac{s}{1!\,2!}\omega_2+\frac{s(s-1)}{2!\,3!}\omega_4-\frac{s(s-1)(s-2)}{3!\,4!}\omega_6+\ldots,$$

a result which allows of fairly rapid determination from tables of $\sigma^2\omega_{2s}$.

There is, perhaps, less difficulty in this form in allowing for the first term or two of the operator Q_t, for $U_s(r)$ and $V_s(r)$ can be at once differentiated with regard to σ^2, but even then the final result has considerable complexity.

* This result involves the expression of any power of r^2 in χ-functions.

The Rayleigh solution value is easily found by putting $Q_t = 1$ in any of the forms of (lxxix), (lxxx), (lxxxi), (lxxxiii) or (lxxxvi).

A case of peculiar interest arises when $c=0$, or we take the density at the centre of the clearance. In this instance we have:

$$\mathsf{F}_n(0) = NQ_t e^{-\frac{1}{2}a^2/\sigma^2}.$$

Now

$$Q_t = 1 + \nu_4 (\sigma^2)^2 \frac{d^2}{d(\sigma^2)^2} - \nu_6 (\sigma^2)^3 \frac{d^3}{d(\sigma^2)^3} + \ldots + (-1)^s \nu_{2s} (\sigma^2)^s \frac{d^s}{d(\sigma^2)^s} + \ldots$$

and $$e^{-\frac{1}{2}a^2/\sigma^2} = 2\pi\sigma^2 \omega_0,$$

therefore
$$\begin{aligned}(\sigma^2)^s \frac{d^s}{d(\sigma^2)^s}(e^{-\frac{1}{2}a^2/\sigma^2}) &= 2\pi\sigma^2 \left\{\frac{d^s \omega_0}{d(\sigma^2)^s} + s\frac{d^{s-1}\omega_0}{d(\sigma^2)^{s-1}}\right\}(\sigma^2)^s \\ &= 2\pi\sigma^2\{(-1)^s \omega_{2s} + s(-1)^{s-1}\omega_{2(s-1)}\} \\ &= e^{-\frac{1}{2}a^2/\sigma^2}(-1)^s\{\chi_{2s} - s\chi_{2(s-1)}\}.\end{aligned}$$

Thus

$$\begin{aligned}\mathsf{F}_n(0) &= Ne^{-\frac{1}{2}a^2/\sigma^2}\{1 - 2\nu_4\chi_2 + (\nu_4 - 3\nu_6)\chi_4 + (\nu_6 - 4\nu_8)\chi_6 + (\nu_8 - 5\nu_{10})\chi_8 + \ldots\} \\ &= 2\pi\sigma^2 N(\omega_0 - 2\nu_4\omega_2 + (\nu_4 - 3\nu_6)\omega_4 + (\nu_6 - 4\nu_8)\omega_6 + (\nu_8 - 5\nu_{10})\omega_8 + \ldots) \ldots \text{(lxxxvii)}.\end{aligned}$$

We are also able to consider the secondary problem:

What is the distribution into unoccupied space surrounding a uniformly occupied circular area due to a first migration?

Let the radius of the area be a and let the density at any distance c be $F_n(c)$ after the first migration. Then clearly, if all space were uniformly filled, we should have uniformity after the first migration, or:

$$F_n(c) + \mathsf{F}_n(c) = N,$$

hence: $$F_n(c) = N - \mathsf{F}_n(c) \ldots\ldots\ldots\ldots \text{(lxxxviii)}.$$

The solution is thus thrown back on the solution obtained for the previous problem. In particular at the centre of the populated area we have:

$$F_n(0) = N - \mathsf{F}_n(0) \ \ldots\ldots\ldots\ldots \text{(lxxxix)}.$$

We are thus able to calculate the reduced central density due to a migration from the area to the surrounding unoccupied district, *i.e.* the effect on population of the spread outwards of a colony.

(15) Problem VIII. *Indirect solution of the General Problem of the Random Walk.*

It may not be without interest to put on record the distribution density after n flights in the case of a cleared circular area, if it be expressed in Kluyver's manner by the integral of a Bessel's function product.

We have:

$$F_n(c) = N \int_0^a \int_0^{2\pi} \phi_n(c^2 + r^2 - 2rc\cos\theta)\, r\,d\theta\,dr,$$

and

$$\mathcal{F}_n(c) = N - F_n(c)$$

$$= N\left\{1 - \frac{1}{2\pi}\int_0^a \int_0^{2\pi} \int_0^\infty u J_0(u\sqrt{c^2+r^2-2cr\cos\theta})\, J_0(ul)^n\, du\,r\,d\theta\,dr\right\},$$

by (iii),

$$= N\left[1 - \int_0^a \int_0^\infty u J_0(ur)\, J_0(uc)\, \{J_0(ul)\}^n\, du\,r\,dr\right],$$

by Neumann's Theorem (see p. 6)

$$= N\left[1 - \int_0^\infty \frac{\{J_0(ul)\}^n}{u} \left\{\int_0^a J_0(ur)\, ur\,d(ur)\right\} J_0(uc)\,du\right]$$

$$= N\left[1 - \int_0^\infty \frac{\{J_0(ul)\}^n}{u} \int_0^a d\{J_1(ur)\,ur\}\, J_0(uc)\,du\right],$$

by the theorem cited on p. 7,

$$= N\left[1 - \int_0^\infty \frac{\{J_0(ul)\}^n}{u} \Big\{urJ_1(ur)\Big\}_0^a J_0(uc)\,du\right]$$

$$= N\left[1 - \int_0^\infty \{J_0(ul)\}^n\, aJ_1(ua)\, J_0(uc)\,du\right].$$

Or, writing $v = au$, we have:

$$\mathcal{F}_n(c) = N\left[1 - \int_0^\infty J_1(v)\, J_0\left(v\,\frac{c}{a}\right)\left\{J_0\left(v\,\frac{l}{a}\right)\right\}^n dv\right] \quad\text{..............(xc).}$$

This expression is concise. The integral expresses the probability that if an individual start from the origin and take $(n+1)$ flights, the first of magnitude c and the remaining n of magnitude l, at random, he will find himself within a distance a of his starting point. But there does not seem any convenient method of evaluating the integral. Comparing with (lxxxiii) we have the curious identity:

$$\int_0^\infty J_1(v)\, J_0\left(v\,\frac{c}{a}\right)\left\{J_0\left(v\,\frac{l}{a}\right)\right\}^n dv = 1 - Q_t e^{-(a^2+c^2)/nl^2} \mathop{S}_0^\infty \left(i\,\frac{c}{a}\right)^s J_s\left(2i\,\frac{ac}{nl^2}\right) \text{...(xci).}$$

Write $c = l$, $a = r$ and $n-1$ for n, then

$$\int_0^\infty J_1(v)\left\{J_0\left(v\,\frac{l}{r}\right)\right\}^n dv = 1 - Q_{n-1} e^{-(r^2+l^2)/\{(n-1)l^2\}} \mathop{S}_0^\infty \left(i\,\frac{l}{r}\right)^s J_s\left(2i\,\frac{r}{(n-1)\,l}\right),$$

where Q_{n-1} is the operator,

$$1 + \nu_4(n-1)^2\frac{d^2}{dn^2} - \nu_6(n-1)^3\frac{d^3}{dn^3} + \dots + (-1)^s \nu_{2s}(n-1)^s \frac{d^s}{dn^s} + \dots,$$

or, by (iv), $P_n(r)$, the chance that an individual taking n flights from a centre should be found within a distance r from that centre, is:

$$P_n(r) = N\left\{1 - Q_{n-1}e^{-(r^2+l^2)/\{(n-1)l^2\}} \overset{\infty}{\underset{0}{S}} \left(i\frac{l}{r}\right)^s J_s\left(2i\frac{r}{(n-1)l}\right)\right\} \text{......(xcii).}$$

Since
$$\phi_n(r^2) = \frac{1}{2\pi r}\frac{d}{dr}\{P_n(r)\},$$

we have here the complete analytical solution in known functions—*i.e.* the Bessel's functions with imaginary arguments—of my original problem of the random walk. But this formal solution provides no better method for shortly determining the dispersal curves than that already indicated in these pages.

(16) Problem IX. *To find the distribution after m migrations each of n flights, there being originally a circular clearance which is not kept sterile.*

The solution is found by writing $m\sigma^2$ for σ^2, putting the N's for the ν's in Q_t which becomes Q_t^m, and multiplying by the factor $(\mu\Delta)^{m-1}$ assumed to be constant. This can be done to any of the forms (lxxix)—(lxxxiii), or (lxxxvi). If we write:

$$\bar{\epsilon}_1 = \epsilon_1/m \quad \text{and} \quad \bar{\epsilon}_2 = \epsilon_2/m$$

we find:

$${}_mF_n(c) = N(\mu\Delta)^{m-1}Q_t^m e^{-\bar{\epsilon}_1} \overset{\infty}{\underset{0}{S}} \left(\frac{\bar{\epsilon}_1^{\,s}}{(s!)^2}\int_{\bar{\epsilon}_2}^{\infty} x^s e^{-x}dx\right) \text{...........(xciii),}$$

or:

$${}_mF_n(c) = N(\mu\Delta)^{m-1}Q_t^m e^{-\bar{\epsilon}_1}\int_{\bar{\epsilon}_2}^{\infty} J_0(2i\sqrt{\bar{\epsilon}_1 x})\,e^{-x}dx \text{...........(xciv).}$$

Or again:

$${}_mF_n(c) = N(\mu\Delta)^{m-1}Q_t^m e^{-(\bar{\epsilon}_1+\bar{\epsilon}_2)} \overset{\infty}{\underset{0}{S}} \left(\sqrt{-\frac{\bar{\epsilon}_1}{\bar{\epsilon}_2}}\right)^s J_s(2i\sqrt{\bar{\epsilon}_1\bar{\epsilon}_2}) \text{..............(xcv),}$$

$${}_mF_n(c) = N(\mu\Delta)^{m-1}Q_t^m 4\pi^2 m^2\sigma^4 \overset{\infty}{\underset{0}{S}} \left(U_s\left(\frac{c}{\sqrt{m}}\right)V_s\left(\frac{a}{\sqrt{m}}\right)(s+1)\right) \text{......(xcvi).}$$

Of these, I have found the first quite as convenient as any other to obtain numerical results from. I shall now illustrate the circular patch formulae.

Illustration I. A circular patch $\frac{1}{2}$ mile radius is cleared of mosquitoes but not kept sterile. To find the density at the centre, at $\frac{1}{4}$ mile from the centre, and at the margin after ten breeding cycles.

We shall suppose as before $l = 200$ yards, $n = 6$, and therefore

$$\sigma^2 = 120{,}000 \text{ square yards.} \qquad \epsilon_2 = \frac{1}{2}\frac{a^2}{m\sigma^2} = \cdot 3227.$$

The second term in Q_t^m will be of the order $\frac{1}{240}$ of the first and I shall neglect it. Accordingly the solution may be taken

$$ {}_m\mathcal{F}_n(c) = e^{-(\bar\epsilon_1+\bar\epsilon_2)}(\mu\Delta)^{m-1}N\left(1+\bar\epsilon_1(1+\bar\epsilon_2)+\frac{\bar\epsilon_1^2}{2!}\left(1+\bar\epsilon_2+\frac{\bar\epsilon_2^2}{2!}\right)\right. $$
$$ \left.+\frac{\bar\epsilon_1^3}{3!}\left(1+\bar\epsilon_2+\frac{\bar\epsilon_2^2}{2!}+\frac{\bar\epsilon_2^3}{3!}\right)+\ldots\right). $$

The successive bracketted terms in $\bar\epsilon_2$ are

1·3227, 1·3748, 1·3804, 1·3809 and 1·3809,

which is equal to $e^{+\bar\epsilon_2}$ to our number of decimal places. Hence we may put

$$ {}_{10}\mathcal{F}_6(c) = (\mu\Delta)^9 N e^{-(\bar\epsilon_1+\bar\epsilon_2)}\left\{1+\bar\epsilon_1(e^{\bar\epsilon_2}-\cdot0582)+\frac{\bar\epsilon_1^2}{2!}(e^{\bar\epsilon_2}-\cdot0061)\right. $$
$$ \left.+\frac{\bar\epsilon_1^3}{3!}(e^{\bar\epsilon_2}-\cdot0005)+\overset{\infty}{\underset{4}{S}}\frac{\bar\epsilon_1^s}{s!}e^{\bar\epsilon_2}\right\} $$
$$ =(\mu\Delta)^9 N e^{-(\bar\epsilon_1+\bar\epsilon_2)}(1-e^{\bar\epsilon_2}+e^{(\bar\epsilon_1+\bar\epsilon_2)}-\cdot0582\bar\epsilon_1-\cdot0030\bar\epsilon_1^2-\cdot0001\bar\epsilon_1^3) $$
$$ =(\mu\Delta)^9 N\{1-e^{-\bar\epsilon_1}+e^{-(\bar\epsilon_1+\bar\epsilon_2)}(1-\cdot0582\bar\epsilon_1-\cdot0030\bar\epsilon_1^2-\cdot0001\bar\epsilon_1^3)\}. $$

At centre

$$ {}_{10}\mathcal{F}_6(0) = (\mu\Delta)^9 N\{e^{-\cdot3227}(1)\} = (\mu\Delta)^9 N\cdot724. $$

We can test the accuracy of this result by using Equation (lxxvii) which, if we put $\nu_4 = N_4$, gives:

$$ {}_{10}\mathcal{F}_6(0) = (\mu\Delta)^9 N e^{-\bar\epsilon_2}(1-2N_4\chi_2+\ldots) $$

and

$$ \chi_2 = 1-\bar\epsilon_2 = (\mu\Delta)^9 N e^{-\cdot3227}\left(1+\frac{\cdot6773}{120}+\ldots\right) $$
$$ =(\mu\Delta)^9 N\cdot730. $$

The agreement is accordingly good enough for practical purposes, and we may say that within a year the mosquitoes would at the centre of the patch have a density 73 per cent. of what they would have in uncleared country.

I now consider the density at a quarter of a mile from the centre, $\bar\epsilon_1 = \cdot0807$, and using the above formula we find:

$$ {}_{10}\mathcal{F}_6(440) = (\mu\Delta)^9 N(1-e^{-\cdot0807}+e^{-\cdot4034}\times\cdot9953) $$
$$ =(\mu\Delta)^9 N\cdot75, $$

or, we see that at a quarter mile, midway between centre and boundary of the patch, the density is only 2 per cent. more than at the centre.

Finally, at the boundary itself, $\bar\epsilon_1 = \cdot3227 = \epsilon_2$,

$$ {}_{10}\mathcal{F}_6(880) = (\mu\Delta)^9 N(1-e^{-\cdot3227}+e^{-\cdot6454}\times\cdot9809) $$
$$ =(\mu\Delta)^9 N\cdot79. $$

Thus the cleared patch would within the year have filled up with a population of mosquitoes varying in density from 73 per cent. at the centre to about 80 per cent. at the boundary, or the clearance without permanent sterility would have been quite ineffectual with the assumed values of the constants.

Illustration II. Let us assume precisely the same conditions as in the previous illustration, except that the area shall be supposed sterile, and we will consider what happens at the end of the first migration.

At the centre we have by Equation (lxxxvii):

$$ {}_1F_6(0) = Ne^{-\epsilon_2}\{1 - 2\nu_4\chi_2 + (\nu_4 - 3\nu_6)\chi_4 + (\nu_6 - 4\nu_8)\chi_6 + \ldots\}.$$

But

$$\begin{aligned} -2\nu_4 &= \cdot 083{,}333, & \chi_2(\epsilon_2) &= 1 - \epsilon_2 = -2\cdot 227{,}000, \\ \nu_4 - 3\nu_6 &= -\cdot 032{,}407, & \chi_4(\epsilon_2) &= 2 - 4\epsilon_2 + \epsilon_2^2 = -\cdot 494{,}471, \\ \nu_6 - 4\nu_8 &= -\cdot 005{,}498, & \chi_6(\epsilon_2) &= 6 - 18\epsilon_2 + 9\epsilon_2^2 - \epsilon_2^3 = 8\cdot 031{,}303, \\ \nu_8 - 5\nu_{10} &= \cdot 000{,}082, & \chi_8(\epsilon_2) &= 24 - 96\epsilon_2 + 72\epsilon_2^2 - 16\epsilon_2^3 + \epsilon_2^4, \\ \epsilon_2 &= 3\cdot 227, & &= 34\cdot 752{,}347. \end{aligned}$$

Hence:

$$ {}_1F_6(0) = Ne^{-3\cdot 227}(1 - \cdot 185{,}583 + \cdot 016{,}024 - \cdot 044{,}156 + \cdot 002{,}850)$$
$$= \cdot 031N.$$

This three per cent. of the density in uncleared area might possibly prove a trouble and on our assumptions it may be doubted whether the half-mile radius is sufficient. If we take the first term only, we find $\cdot 040N$, or four per cent., not an important practical difference.

The introduction of even the first modifying term when c is not zero appears to lead to such complexity that I content myself with calculating the approximate value given by the Rayleigh solution for distances of $\frac{1}{4}$ and $\frac{1}{2}$ mile from the centre of the clearance. In this case $\epsilon_2 = 3\cdot 227$, $\epsilon_1 = \cdot 807$ and $3\cdot 227$ respectively half-way to and at the boundary. I proceed just as before and deduce the following approximate value for ${}_1F_6(c)$, *i.e.*

$$ {}_1F_6(c) = (\mu\Delta)^9 N\{1 - e^{-\epsilon_1} + e^{-(\epsilon_1+\epsilon_2)}(1 - 20\cdot 9769\epsilon_1 - 7\cdot 8851\epsilon_1^2 - \cdot 2355\epsilon_1^3 - \cdot 0228\epsilon_1^4 - \cdot 0016\epsilon_1^5 - \cdot 0001\epsilon_1^6)\}.$$

Hence

$$ {}_1F_6(440) = \cdot 179\,(\mu\Delta)^9 N, \text{ corresponding to } \epsilon_1 = \cdot 807$$

and

$$ {}_1F_6(880) = \cdot 709\,(\mu\Delta)^9 N, \text{ corresponding to } \epsilon_1 = 3\cdot 227.$$

Thus the density at $\frac{1}{4}$ of a mile from the centre of the cleared patch would be some 18 per cent. of the density in uncleared country. In other words on our assumptions a clearance of one mile diameter, if kept sterile, would hardly suffice to keep an area of $\frac{1}{2}$ mile diameter free of mosquitoes.

Compared with a straight boundary, where the density falls to about one half that of uncleared country at the boundary, we see that the bending of the boundary has a most marked effect in its neighbourhood, the curvature raising the boundary density from about 50 to 71 per cent. of the uncleared density. In fact the density is almost equal to the 75 per cent. in the boundary angle of a square clearance.

The differences between a square and a circular patch inscribed in it are noteworthy, indicating the marked influence of the area at the angles. Thus at the centre we have only 2 per cent. as against 3 per cent., and at $\frac{1}{4}$ mile from the centre 11 per cent. as against 18 per cent.

As far as the above numerical investigations are to be looked upon as anything but illustrations of the nature of the calculations requisite to apply the theory of random migration to the mosquito clearance problem, they must be taken:

(i) As merely an incentive to further study of the manner in which mosquitoes scatter from the breeding ponds. It would seem possible, if difficult, to experimentally test this by in some way marking a large number of insects, and determining the nature and extent of the flight.

(ii) As indicating that permanent sterility of the protection belt is almost certainly needful. The $\frac{1}{2}$ to 3 per cent. of mosquitoes at the centre of the clearance amounting to 6 to 18 per cent. at $\frac{1}{4}$ mile distance may or may not be serious, but they certainly would very soon be if they were able to breed.

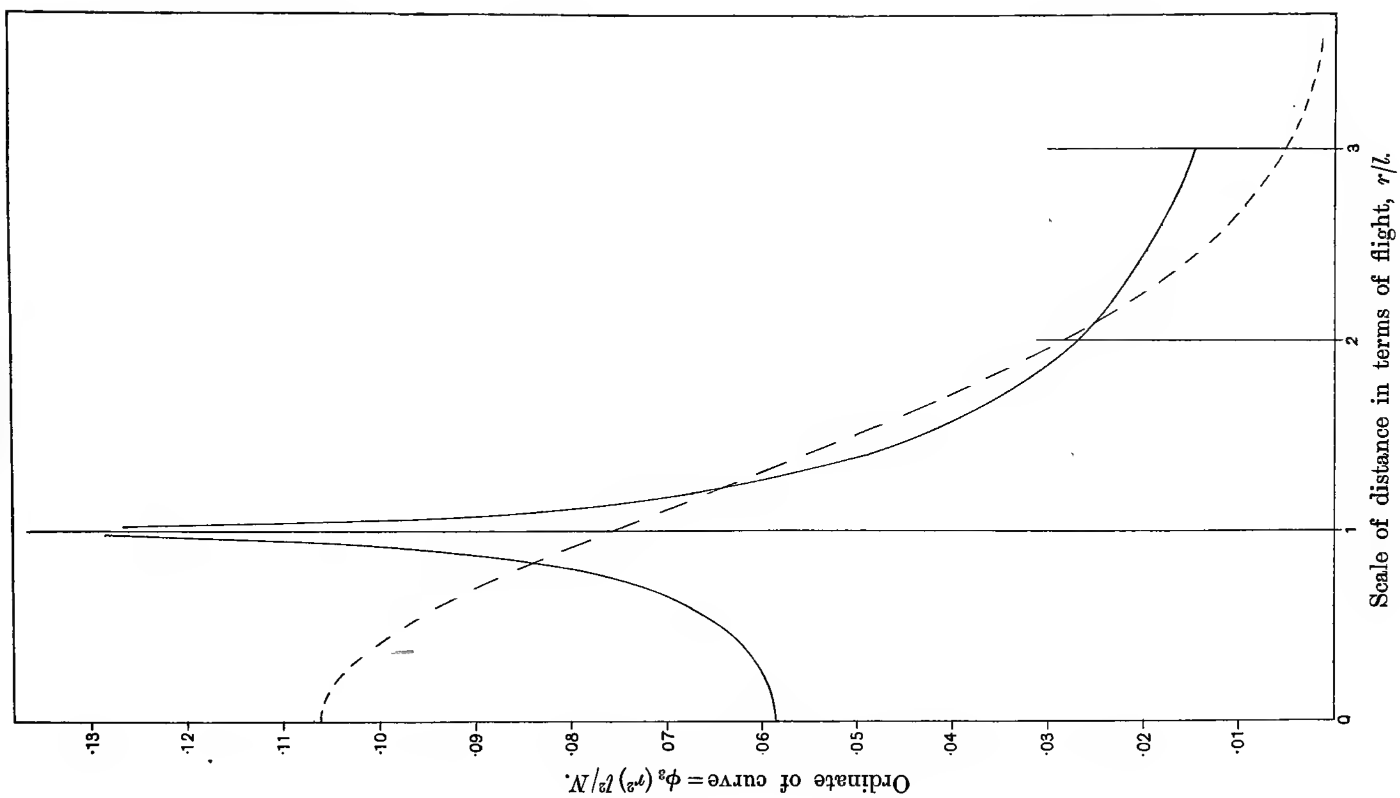
(iii) As showing that on the rough numbers taken, that a clearance belt of probably $\frac{1}{2}$ mile round a settlement would be the minimum desirable sterile zone. But it is quite possible that, when the requisite constants are better known, it will be found that smaller belts will suffice. It is possibly rather an exaggerated view to suppose a mosquito to make six random flights of 200 yards between breeding spot and breeding spot. But certainly many insects I have noted will fly with great rapidity in one flight 50, 100 or 200 yards, and these flights are quite distinct from "flitters."

(17) *Conclusions.* The present memoir suffers of course from all the defects which must accompany a first attempt to develop a mathematical theory of phenomena which have hitherto not been studied with this development in view. The theory itself suggests hypotheses and constants which have never yet been considered. How far with a broad average of environment in relation to food supply, breeding places, shelter, foes, etc. is the spread of a species random? Are any of the geographical limits to plant or insect or animal life non-environmental and in course of change? If so, statistical studies of the density gradients of such species for a few miles either side of the supposed boundary would form most interesting work for biometricians. But, apart from this observational work, a good deal of experimental inquiry might be usefully attempted with regard to the constants of random scatter or flight in the cases of both seeds and insects.

On the theoretical side there are many problems left untouched. The present memoir has only opened up the outskirts of a very big field. It would be of value to investigate the number of terms in the expansion in ω-functions requisite to practically reproduce the graphically constructed density distributions for migrations of 3, 4 or 5 flights. Our expansion to 6 terms is hardly close enough for practical work until $n=6$ or 7. Many other shapes of populated or of cleared areas would provide problems of some interest, especially when the spread of the colony was limited in one or more directions by environmental barriers, such as sea, river or mountain range. The problem of sterile areas has been by no means exhausted, for in such cases I have only dealt with a result of the first migration, but actually there will be a second and later migrations in which not only new immigrants will appear but a portion of the first immigrants will be emigrants and again able to breed when they reach uncleared country. Our solution thus gives only a minimum limit to the percentages if the immigrants do not die at the end of the first breeding cycle. Much interest attaches also to cases in which the fertility and the death-rate are correlated with the density, *i.e.* $\mu\Delta$ is not to be considered a constant. But in these as in other problems which suggest themselves, a further preliminary knowledge of some of the ecological constants suggested by the present enquiry would be an extremely valuable guide to the direction that research should take.

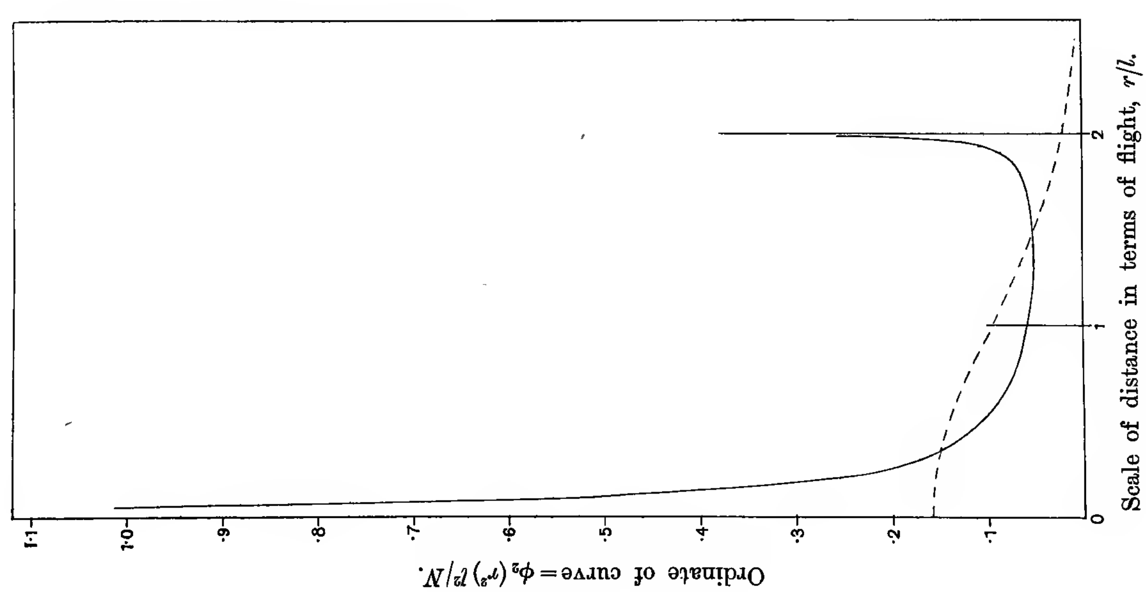
On the purely mathematical side the problem of the "random walk" may now be considered as fairly completely solved. The distribution curves have been determined until they pass into an analytical solution expressed by a new type of function. The expansion in these functions shows the limits to the accuracy of Lord Rayleigh's solution of a certain allied problem in the theory of sound. But the ω-functions which have arisen in the enquiry have most interesting properties, and have led me to a whole series of allied functions of one and two variables which I propose to discuss on another occasion. The expansion in ω-functions will I venture to think be found ultimately to have considerable importance for mathematical physics, especially in the evaluation of certain definite integrals which arise there. The possibility of practically carrying out such expansions depends on the determination of the successive moments (and products) of the original function, a process with which every statistician is now fairly familiar. But applied to definite mathematical functions it loses the disadvantage with which it is burdened in statistical practice—the high relative probable error of very high moments—and becomes closely allied to the process of determining the integral of the product of any function and a Legendre's coefficient (or solid harmonic). Should the generalised ω-functions prove, as I anticipate, of some mathematical interest, it will be another illustration of how the need of the applied mathematician has thrust him, almost unawares, into the path of a novel functional development.

DIAGRAM II.



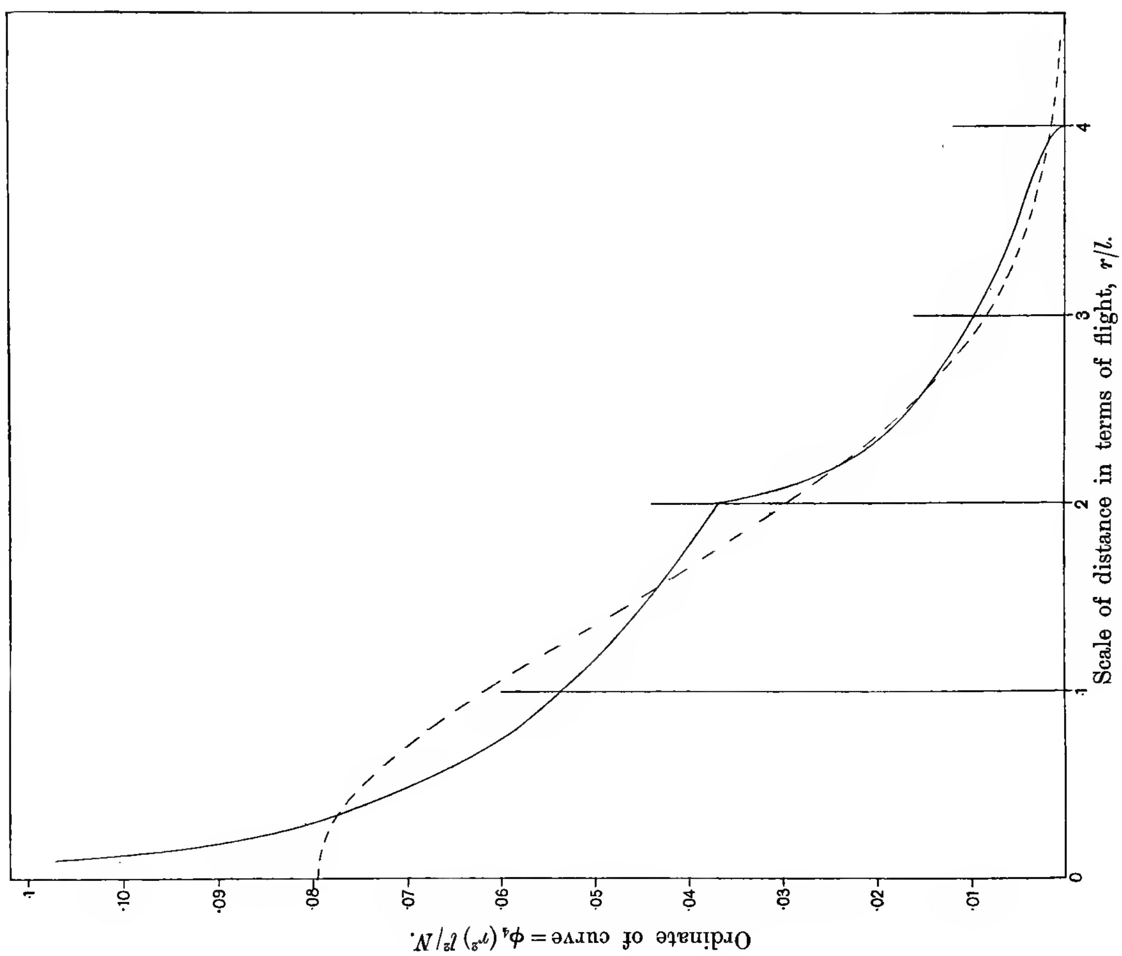
Third Dispersal Curve.

DIAGRAM I.



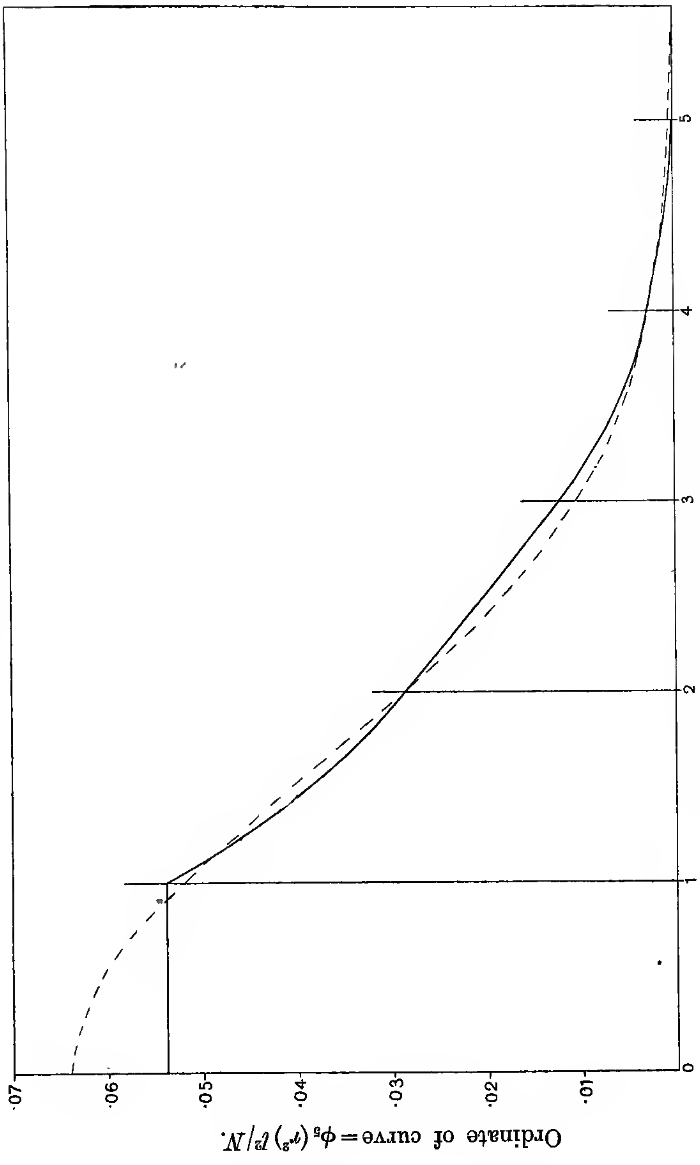
Second Dispersal Curve.

DIAGRAM III.



Fourth Dispersal Curve.

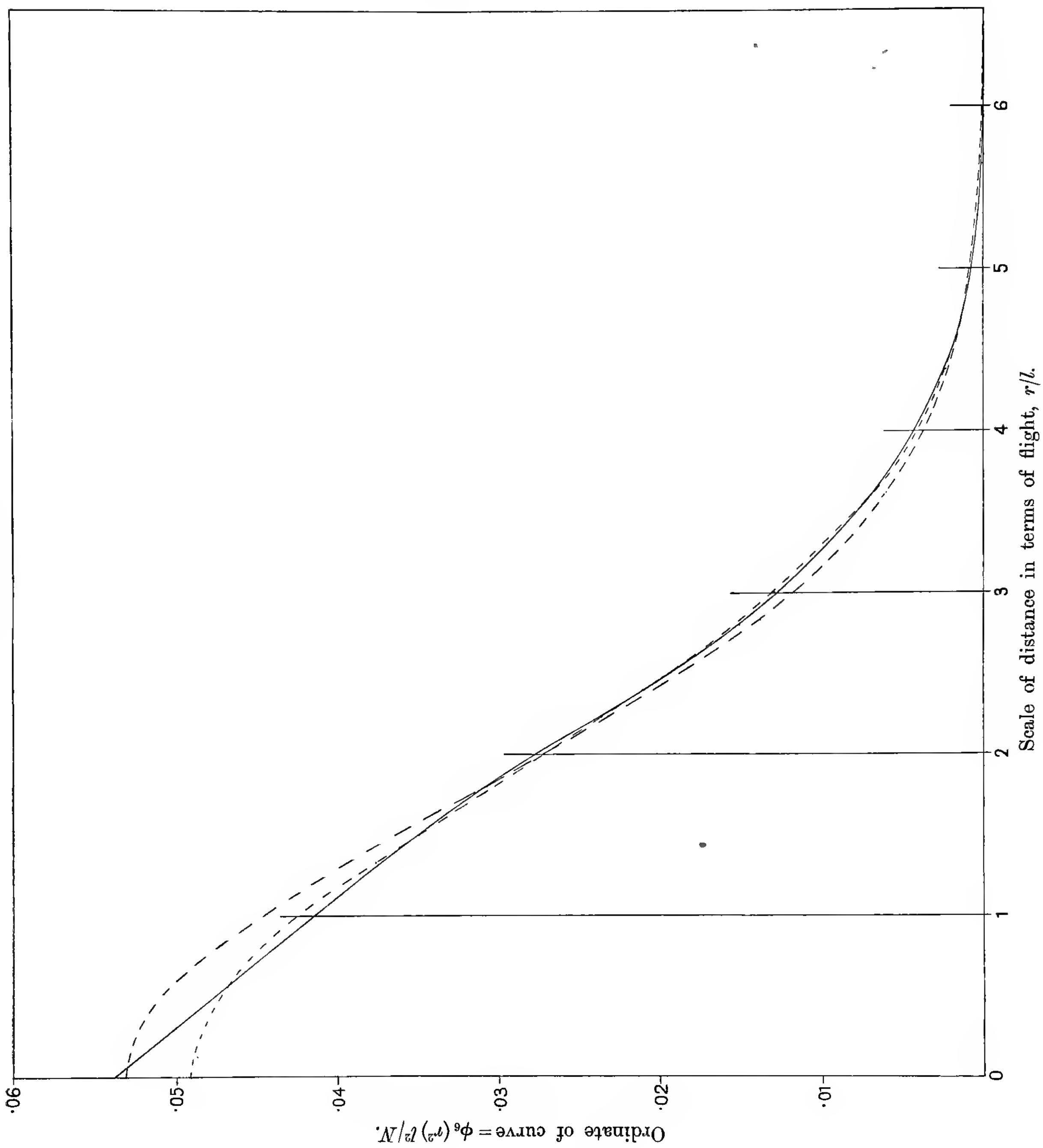
DIAGRAM IV.



Scale of distance in terms of flight, r/l.

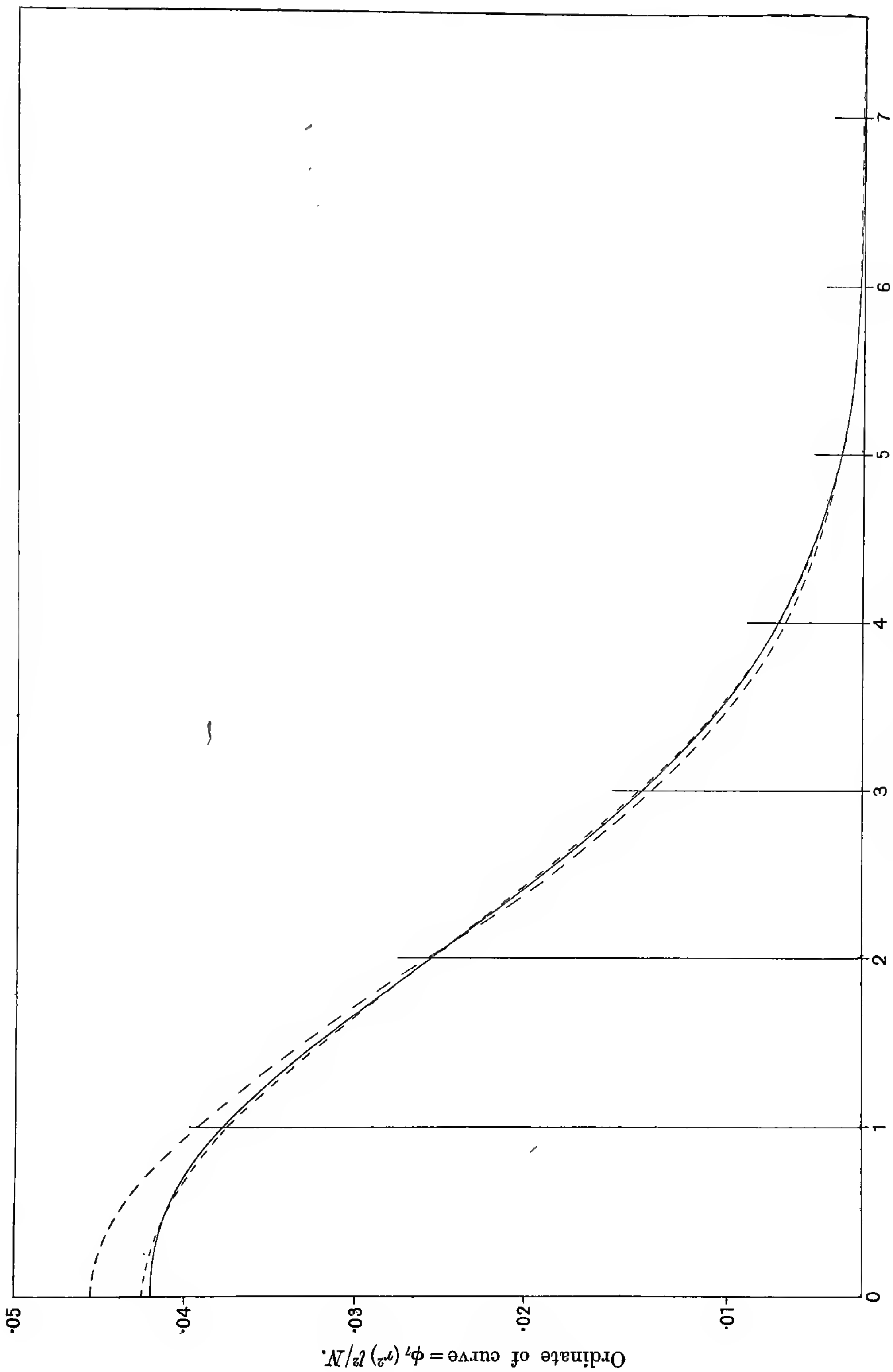
Fifth Dispersal Curve.

DIAGRAM V.

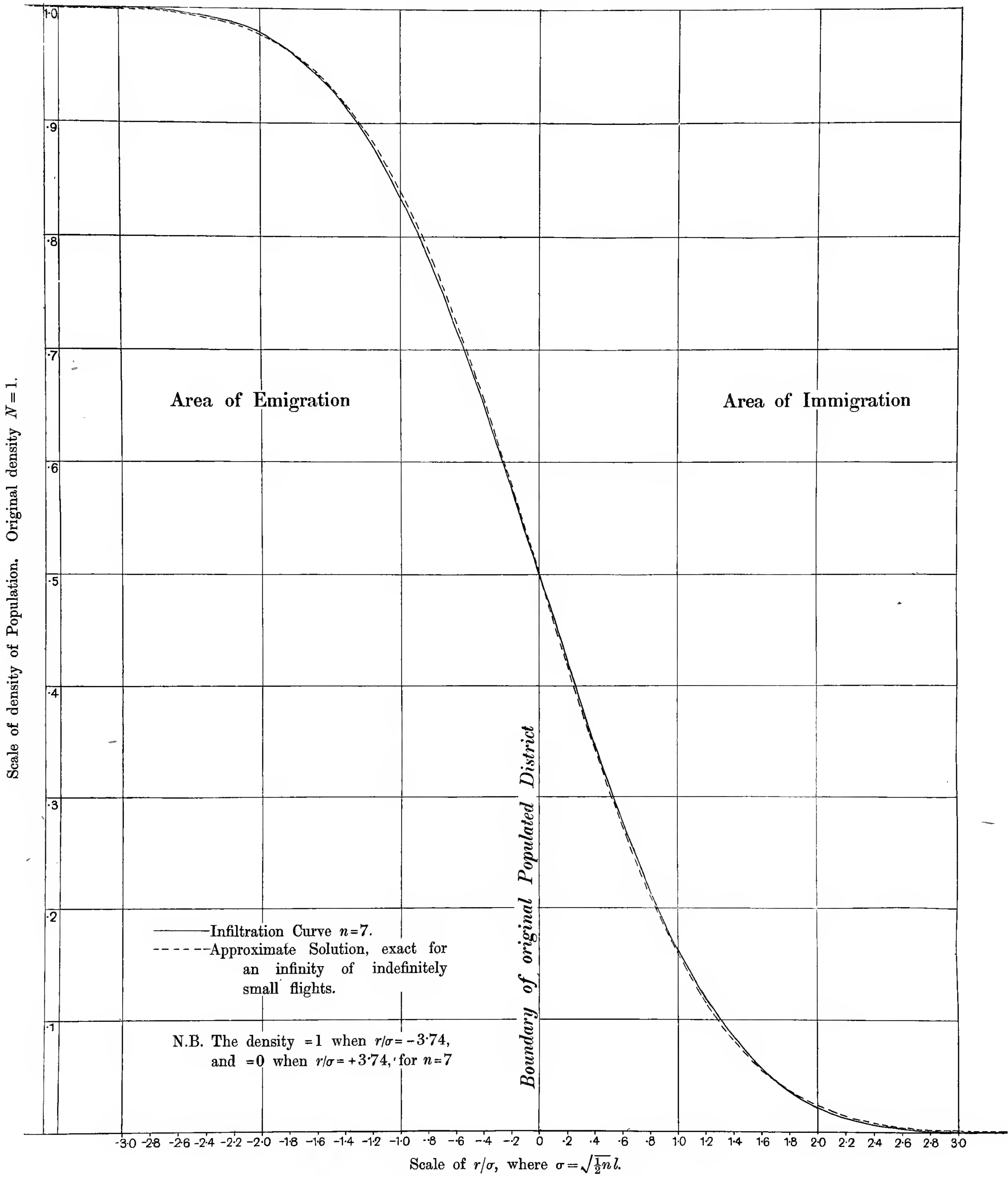


Sixth Dispersal Curve.

DIAGRAM VI.



Seventh Dispersal Curve.



First order infiltration curve across a straight boundary.

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