Contributions to the Mathematical Theory of Epidemics. II. The Problem of Endemicity

W. O. Kermack and A. G. McKendrick

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Summary.

It is shown that where we have no previous knowledge of the probable degree of precision of a set of observations, the correct procedure is to assume that the probability of a value of h in the range dh is proportional to dh/h.

The result is applied to the theory of least squares, with definite results. It is found that where the number of observations is small, the probability of error is more widely distributed than is given by the usual formula. In the extreme case of two observations and one unknown, the probable error of the mean is equal to the standard deviation.

Contributions to the Mathematical Theory of Epidemics.
II.—*The Problem of Endemicity.*

By W. O. Kermack and A. G. McKendrick.

Introduction.

In a previous communication* an attempt was made to investigate mathematically the course of an epidemic in a closed population of susceptible individuals. In order to simplify the problem certain definite assumptions were made, namely, that all individuals were equally susceptible, and that death resulted, or complete immunity was conferred, as the result of an attack. The infectivity of the individual and his chances of death or recovery were represented by arbitrary functions, and the chance of a new infection occurring was assumed to be proportional to the product of the infected and susceptible members of the population. In spite of the introduction of the arbitrary functions, it was shown that in general a critical density of population existed, such that if the actual density was less than this, no epidemic could occur, but if it exceeded this by n an epidemic would appear on the introduction of a focus of infection, and further that if n was small relative to the population density, the size of the epidemic would be $2n$ per unit area. It was shown that these

* 'Proc. Roy, Soc.,' A, vol. 115, p. 700 (1927).

conclusions could be readily extended to the case of a metaxenous disease, that is, one in which transmission takes place through an intermediate host.

It is the purpose of the present paper to consider the effect of the continuous introduction of fresh susceptible individuals into the population. It appeared desirable to investigate this point, since it might make it possible to interpret certain aspects of the incidence of disease not only in human communities where there is usually an influx of fresh susceptible individuals either by immigration or by birth, but also in the animal experiments carried out by Topley and others—where fresh animals were introduced at a constant rate into the cages in which cases of disease were already present—from which certain definite results were obtained.

In order to make the present enquiry more general an attempt has also been made to include the effect of the partial immunity which may follow an attack of disease. The susceptibility of the individual who has recovered from an attack is assumed to be a function of the time which has elapsed since his complete recovery. In general this function will either remain constant or will increase with the time. This point is rather important as it will be shown that it enables us to reach certain conclusions even when the function character-ising the susceptibility is otherwise quite arbitrary.

It will be seen therefore that in the most general system which is under investigation there will be four classes of individuals : Those which have never experienced an attack of the disease in question, these for convenience we shall call " virgin " ($\bar{x}$); those who have experienced one or more attacks of the disease but have recovered (x); those who at the moment in question are actually suffering from the disease (y); and, finally, there are the dead (z). All those who enter in to the community first of all pass into the virgin group. In order to make the results as general as possible we shall in the first instance assume that the number so entering this group has a constant component m which may be regarded as representing immigration, and a second component of the form $\bar{\mu}\bar{x} + \mu x + \nu y$, which may be regarded as representing births, the birth-rate of the virgins being $\bar{\mu}$, of the recovered μ, and of the sick ν. By choosing suitable values of m, $\bar{\mu}$, μ and ν the results for various special cases are readily found. Thus taking $\bar{\mu} = \mu = \nu = 0$, we have the case where immigration alone is operative, whilst taking $m = \nu = 0$ and $\bar{\mu} = \mu$, we have the case where there is no immigration, but where all the healthy individuals multiply at the rate μ.

In the mathematical sections which follow, the general case is worked out first of all for constant recovery, death and infectivity rates. Five selected

special cases are then considered, and the results are shown in Table I. The same problem is then worked out for the case in which the recovery, death and infectivity rates are represented by arbitrary general functions instead of by constants. The results obtained are then checked by replacing the arbitrary general functions by the constant coefficients. From the general results the equations for the five selected special cases, this time with arbitrary general functions, are worked out and discussed, and a summary of the findings is given in Table II. Some of the more interesting points which emerge are noted in the general discussion in the final section.

In dealing with the equations referring to constant coefficients the problem of the stability of the steady state is worked out. In the general case with arbitrary general functions, the equations representing the result of the introduction of a small disturbance introduced at a particular time have been formulated, but the detailed discussion of these equations and the stability of the steady state is reserved for a future communication.

The results arrived at in this paper refer to the case where only one disease is operative. It should be emphasised that this implies that the one disease under consideration is thus the only cause of death, and is consequently the only means of balancing in a steady state the increase of population due to immigration and birth. But it is obviously desirable to allow for deaths which may occur from other causes. The methods which are developed in the

Table I.

	$\bar{X}.$	$X.$	$Y.$	$\bar{U}.$	$U.$
General Case	$\dfrac{d}{\bar{k}}$	$\dfrac{l}{k}$	$\dfrac{m + \bar{\mu}\dfrac{d}{\bar{k}} + \mu\dfrac{l}{k}}{d - \nu}$	$\dfrac{d\left(m + \bar{\mu}\dfrac{d}{\bar{k}} + \mu\dfrac{l}{k}\right)}{d - \nu}$	$\dfrac{l\left(m + \bar{\mu}\dfrac{d}{\bar{k}} + \mu\dfrac{l}{k}\right)}{d - \nu}$
(1) $m = 0, \bar{\mu} = \mu, \nu = 0$	$\dfrac{d}{\bar{k}}$	$\dfrac{l}{k}$	$\dfrac{\mu}{d}\left(\dfrac{d}{\bar{k}} + \dfrac{l}{k}\right)$	$\mu\left(\dfrac{d}{\bar{k}} + \dfrac{l}{k}\right)$	$\dfrac{l\mu}{d}\left(\dfrac{d}{\bar{k}} + \dfrac{l}{k}\right)$
(2) $m = 0, \bar{\mu} = \mu, \nu = 0, l = 0$	$\dfrac{d}{\bar{k}}$	0	$\dfrac{\mu}{\bar{k}}$	$\mu\dfrac{d}{\bar{k}}$	0
(3) $\bar{\mu} = \mu = \nu = 0$	$\dfrac{d}{\bar{k}}$	$\dfrac{l}{k}$	$\dfrac{m}{d}$	m	$m\dfrac{l}{d}$
(4) $\bar{\mu} = \mu = \nu = l = 0$	$\dfrac{d}{\bar{k}}$	0	$\dfrac{m}{d}$	m	0
(5) $\bar{\mu} = \mu = \nu = d = 0$	0	$\dfrac{l}{k}$	$n - \dfrac{l}{k}$	0	0

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Table I—(continued).

	V.	Ṽ.	V̄.
General Case	$\dfrac{(d+l)\left(m+\bar{\mu}\dfrac{d}{\bar{k}}+\mu\dfrac{l}{k}\right)}{d-\nu}$	$\dfrac{l\left(m+\bar{\mu}\dfrac{d}{\bar{k}}+\mu\dfrac{l}{k}\right)}{d-\nu}$	$\dfrac{d\left(m+\bar{\mu}\dfrac{d}{\bar{k}}+\mu\dfrac{l}{k}\right)}{d-\nu}$
(1) $m=0,\ \bar{\mu}=\mu,\ \nu=0$	$\dfrac{\mu(d+l)}{d}\left(\dfrac{d}{\bar{k}}+\dfrac{l}{k}\right)$	$\dfrac{\mu l}{d}\left(\dfrac{d}{\bar{k}}+\dfrac{l}{k}\right)$	$\mu\left(\dfrac{d}{\bar{k}}+\dfrac{l}{k}\right)$
(2) $m=0,\ \bar{\mu}=\mu,\ \nu=0,\ l=0$	$\mu\dfrac{d}{\bar{k}}$	0	$\mu\dfrac{d}{\bar{k}}$
(3) $\bar{\mu}=\mu=\nu=0$	$\dfrac{m(d+l)}{d}$	$\dfrac{ml}{d}$	m
(4) $\bar{\mu}=\mu=\nu=l=0$	m	0	m
(5) $\bar{\mu}=\mu=\nu=d=0$	$l\left(n-\dfrac{l}{k}\right)$	$l\left(n-\dfrac{l}{k}\right)$	0

	W	Equation for α.
General Case	$\dfrac{d\left(m+\bar{\mu}\dfrac{d}{\bar{k}}+\mu\dfrac{l}{k}\right)}{d-\nu}$	$\begin{cases}\alpha^2+\left\{\dfrac{\bar{k}\left(m+\bar{\mu}\dfrac{d}{\bar{k}}+\mu\dfrac{l}{k}\right)-\bar{\mu}}{d-\nu}\right\}\alpha+\bar{k}\left(m+\bar{\mu}\dfrac{d}{\bar{k}}+\mu\dfrac{l}{k}\right)=0\\ \alpha=-k\mathrm{Y}\end{cases}$
(1) $m=0,\ \bar{\mu}=\mu,\ \nu=0$	$\mu\left(\dfrac{d}{\bar{k}}+\dfrac{l}{k}\right)$	$\begin{cases}\alpha^2+\dfrac{\bar{k}\mu l}{dk}\alpha+\dfrac{\bar{k}\mu l}{k}+\mu d=0\\ \alpha=-k\mathrm{Y}\end{cases}$
(2) $m=0,\ \bar{\mu}=\mu,\ \nu=0,\ l=0$	$\mu\dfrac{d}{\bar{k}}$	$\begin{cases}\alpha^2+\mu d=0\\ [\alpha=-k\mathrm{Y}]\end{cases}$
(3) $\bar{\mu}=\mu=\nu=0$	m	$\begin{cases}\alpha^2+\dfrac{\bar{k}m}{d}\alpha+\bar{k}m=0\\ \alpha=-k\mathrm{Y}\end{cases}$
(4) $\bar{\mu}=\mu=\nu=l=0$	m	$\begin{cases}\alpha^2=\dfrac{\bar{k}m}{d}\alpha+\bar{k}m=0\\ [\alpha=-k\mathrm{Y}]\end{cases}$
(5) $\bar{\mu}=\mu=\nu=d=0$	$9\cdot$	$\begin{cases}\alpha\left\{\alpha+\bar{k}\left(n-\dfrac{l}{k}\right)\right\}=0\\ \alpha=-k\mathrm{Y}\end{cases}$

Table II.

	$\overline{\text{X}}$.	X.	Y.	$\overline{\text{U}}$.	U.	Equation for V.	$\widetilde{\text{V}}$.	$\overline{\text{V}}$.	W.
General Case	$\dfrac{D}{\overline{K}}$	LVF(V)	NV	DV	LV	$DV = m + \bar{\mu}\dfrac{D}{\overline{K}} + \mu LVF(V) + \nu NV$	LV	DV	DV
(1) $m=0, \bar{\mu}=\mu, \nu=0$	$\dfrac{D}{\overline{K}}$	LVF(V)	NV	DV	LV	$F(V) = \dfrac{D}{L}\left(\dfrac{1}{\mu} - \dfrac{1}{\overline{K}V}\right)$	LV	DV	DV
(2) $m=0, \bar{\mu}=\mu, \nu=0$ $l_\theta=0$	$\dfrac{1}{\overline{K}}$	0	$\dfrac{N\mu}{\overline{K}}$	$\dfrac{\mu}{\overline{K}}$	0	$V = \dfrac{\mu}{\overline{K}}$	0	$\dfrac{\mu}{\overline{K}}$	$\dfrac{\mu}{\overline{K}}$
(3) $\bar{\mu}=\mu=\nu=0$	$\dfrac{D}{\overline{K}}$	$L\dfrac{m}{D}F(V)$	$\dfrac{mN}{D}$	m	$L\dfrac{m}{D}$	$V = \dfrac{m}{D}$	$L\dfrac{m}{D}$	m	m
(4) $\bar{\mu}=\mu=\nu=0$ $l_\theta=0$	$\dfrac{1}{\overline{K}}$	0	mN	m	0	$V = m$	0	m	m
(5) $m=\bar{\mu}=\mu=\nu=0$ $d_\theta=0$	0	VF(V)	NV	0	V	$n = V(F(V) + N)$	V	0	0

following pages can also be applied to the problem as modified by this factor, and it is hoped to deal with this more complicated case later.

1. *Constant Rates.*

Let us consider a population comprising four classes of individuals :—

(1) $\overline{x}$ individuals who have never been infected—" virgin " ;

(2) x partially immune individuals who have recovered from at least one infection ;

(3) y individuals who are sick, and capable of transmitting the disease ;

(4) z individuals who have died of the disease.

These numbers will be taken as referring to unit area, so that they really represent population densities. This holds throughout the present paper.

The relationship between the different classes is shown in fig. 1.
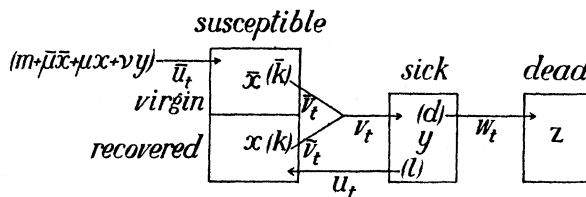

Fig. 1.

In the present section we shall consider the case where the chances of death d, and of recovery l, are independent of the stage of illness, and where the chance

of infection of a particular virgin is proportional to the number of contacts made with individuals already infected, that is to say, it is equal to $\bar{k}y$, whilst the chance of infection of a recovered person is similarly equal to ky. In order to accommodate an immigration of fresh individuals from without at a constant rate, and also reproduction at a constant rate by the three groups— virgin $\bar{x}$, recovered x, and sick y—the rate at which new individuals accrue is taken to be $\bar{u} = m + \bar{\mu}\bar{x} + \mu x + \nu y$. In particular cases, suitable values of m, $\bar{\mu}$, μ and ν may be taken. Clearly u, the rate at which individuals pass into the recovered group, is equal to ly, and $\bar{v}$ the rate at which virgins turn ill is $\bar{x}\bar{k}y$, because, as explained above, the chance of any particular virgin becoming infected is $\bar{k}y$. Similarly $\tilde{v}$, the rate at which the recovered turn ill is equal to kxy. Also $v = \bar{v} + \tilde{v}$, measures the incidence of the disease, and $w = dy$ measures the incidence of deaths.

We have then the following equations :—

$$\frac{d\bar{x}}{dt} = \bar{u} - \bar{v} = m + \bar{\mu}\bar{x} + \mu x + \nu y - \bar{k}\bar{x}y, \tag{1}$$

$$\frac{dx}{dt} = u - \tilde{v} = ly - kxy, \tag{2}$$

$$\frac{dy}{dt} = v - w - u = \bar{k}\bar{x}y + kxy - dy - ly. \tag{3}$$

We shall now find the conditions for a steady state, that is such that

$$\frac{d\bar{x}}{dt} = \frac{dx}{dt} = \frac{dy}{dt} = 0.$$

Clearly if $\bar{X}$, X, Y, U, etc., are the values of $\bar{x}$, x, y, u, etc., consistent with a steady state, then

$$\bar{X} = \frac{d}{\bar{k}}, \quad X = \frac{l}{k}, \quad \text{and} \quad Y = \frac{1}{d - \nu}\left(m + \frac{\bar{\mu}d}{\bar{k}} + \mu\,\frac{l}{k}\right),$$

whence it follows that

$$\bar{U} = \bar{V} = W = \frac{d}{d - \nu}\left(m + \frac{\bar{\mu}d}{\bar{k}} + \mu\,\frac{l}{k}\right)$$

and

$$U = \tilde{V} = \frac{l}{d - \nu}\left(m + \frac{\bar{\mu}d}{\bar{k}} + \mu\,\frac{l}{k}\right) \tag{4}$$

We shall now consider a system in which the values of $\bar{x}$, x, y, u, etc., differ only very slightly from $\bar{X}$, X, Y, U, etc. Such a system may be considered

as the result of an arbitrary disturbance introduced when the system was in a steady state. The behaviour of this system will clearly indicate whether the steady state is stable or unstable.

Let $\bar{x} = \bar{X} + \bar{x}'$, $x = X + x'$, and so on. We substitute these values of $\bar{x}$, x and y in equations (1), (2) and (3), and we shall neglect any terms in which products of $\bar{x}'$, x' and y' occur. After reduction we obtain the set of linear differential equations :—

$$\frac{d\bar{x}'}{dt} = \bar{\mu}\bar{x}' + \mu x' + \nu y' - \bar{k}Y\bar{x}' - \bar{k}\bar{X}y', \tag{5}$$

$$\frac{dx'}{dt} = ly' - kXy' - kYx', \tag{6}$$

$$\frac{dy'}{dt} = \bar{k}\bar{X}y' + \bar{k}Y\bar{x}' + kXy' + kYx' - dy' - ly'. \tag{7}$$

Putting $\bar{X} = \dfrac{d}{\bar{k}}$, $X = \dfrac{l}{k}$ as found in (4), these equations reduce to :—

$$\frac{d\bar{x}'}{dt} = \bar{\mu}\bar{x}' + \mu x' + \nu y' - dy' - \bar{k}Y\bar{x}', \tag{8}$$

$$\frac{dx'}{dt} = -kYx', \tag{9}$$

$$\frac{dy'}{dt} = \bar{k}Y\bar{x}' + kYx'. \tag{10}$$

The solution of equation (9) is

$$x' = re^{-kYt}.$$

The values of $\bar{x}'$ and y' will then be given by

$$\bar{x}' = \bar{r}_1 e^{a_1 t} + \bar{r}_2 e^{a_2 t} + \bar{r}_3 e^{-kYt}$$

and

$$y' = s_1 e^{a_1 t} + s_2 e^{a_2 t} + s_3 e^{-kYt}, \tag{11}$$

where α_1 and α_2 are the roots of

$$\begin{vmatrix} \bar{\mu} - \bar{k}Y - \alpha, & \nu - d \\ \bar{k}Y, & -\alpha \end{vmatrix} = 0. \tag{12}$$

$\overline{r}_3$ and s_3 are given in terms of r by the equations

$$(\overline{\mu} + k\mathrm{Y} - \overline{k}\mathrm{Y})\,\overline{r}_3 + \mu r + (\nu - d)\,s_3 = 0 \left.\vphantom{\begin{array}{c}a\\b\end{array}}\right\} ,\qquad (13)$$
$$\overline{k}\mathrm{Y}\overline{r}_3 + k\mathrm{Y}r + k\mathrm{Y}s_3 = 0$$

and $\overline{r}_1$, $\overline{r}_2$, s_1 and s_2 are suitably adjusted in accordance with the initial conditions, and with equations (8) and (10). The determinant (12) reduces to

$$\alpha^2 + \left\{\frac{\overline{k}}{d-\nu}\left(m + \frac{\overline{\mu}d}{\overline{k}} + \mu\,\frac{l}{k}\right) - \overline{\mu}\right\}\alpha + \overline{k}\left(m + \frac{\overline{\mu}d}{\overline{k}} + \mu\,\frac{l}{k}\right) = 0. \quad (14)$$

We shall now examine the nature of the roots α_1 and α_2. Since

$$\mathrm{Y} = \frac{1}{d-\nu}\left(m + \frac{\overline{\mu}d}{\overline{k}} + \mu\,\frac{l}{k}\right)$$

must be positive, a necessary condition for a steady state to exist is $d > \nu$. The coefficient of α in (14) may be written

$$\frac{\overline{k}}{d-\nu}\left(m + \mu\,\frac{l}{k}\right) + \overline{\mu}\left(\frac{d}{d-\nu} - 1\right)$$

$$= \frac{\overline{k}\left(m + \mu\,\dfrac{l}{k}\right) + \overline{\mu}\nu}{d-\nu}$$

and is therefore positive.

The term independent of α is also positive. The quadratic has therefore either two real negative roots, or two complex roots, the real parts of which are negative. The only exception is when the coefficient of α or the constant term is zero. This can only happen in particular cases which will be considered later. It follows that, in general, the steady states found above correspond to stable states; any disturbance results in either damped vibrations, or in an aperiodic return towards the steady state.

We shall now consider certain special cases, each of which may be worked out separately.

(1) $m = 0$, $\overline{\mu} = \mu$, $\nu = 0$. This means that there is no immigration, and that all healthy persons reproduce at a constant rate.

(2) $m = 0$, $\overline{\mu} = \mu$, $\nu = 0$ and $l = 0$. The conditions are as in case (1), but in addition the disease is fatal. [It is to be noted that in this case the recovered play no part, so that equation (9) disappears, and with it the solution $x = re^{-k\mathrm{Y}t}$.]

(3) $\bar{\mu} = \mu = \nu = 0$. That is to say, immigration is operative but there is no reproduction.

(4) $\bar{\mu} = \mu = \nu = 0$ and $l = 0$. The conditions are as in case (3) but in addition the disease is fatal. [As in case (2) there is no solution $x = re^{-k\mathrm{Y}t}$.]

(5) $m = \bar{\mu} = \mu = \nu = 0$ and $d = 0$. That is to say, there are no deaths, births or immigrations. Here we are dealing with a closed population, and with a disease which is never fatal, and may be recovered from. In this case the total population n is fixed and $n = \mathrm{X} + \mathrm{Y}$ since $\bar{\mathrm{X}}$ is zero. It follows that

$$ n = \frac{d}{\bar{k}} + \frac{l}{k} + \frac{1}{d - \nu}\left(m + \frac{\bar{\mu}d}{\bar{k}} + \mu\,\frac{l}{k}\right), $$

whence as m, $\bar{\mu}$, μ, ν and d tend to zero

$$ \frac{1}{d - \nu}\left(m + \frac{\bar{\mu}d}{\bar{k}} + \mu\,\frac{l}{k}\right) $$

must tend to $n - \dfrac{l}{k}$, that is, to Y.

The possible values of α in this case are there found to be $\alpha = -k\mathrm{Y}$, $\alpha = -\bar{k}\mathrm{Y}$, and $\alpha = 0$. The root $\alpha = 0$ accommodates the circumstance that the disturbance may result in a change in the total number in the closed population by the introduction of new individuals. Of the other two roots, $\alpha = -\bar{k}\mathrm{Y}$ appears only when virgins are introduced; if the disturbance consists entirely in changes in the numbers of sick and recovered the only significant root is $\alpha = -k\mathrm{Y}$. This may readily be verified by treating the case separately.

The results in these special cases are summarised in Table I.

2. *Variable Rates.*

We shall now consider the more general case when the recovery rate l_θ and the death rate d_θ are no longer independent of the duration of the illness θ. Likewise the chance of a virgin being infected by an infected individual who has been ill for a time θ will now be taken as $\bar{k}_\theta$, whilst a recovered individual
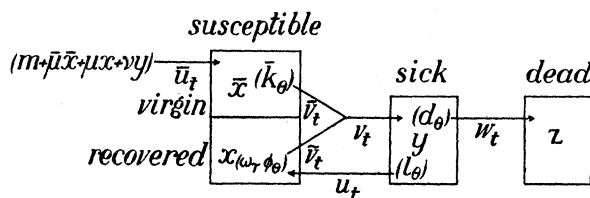

FIG. 2.

who has been recovered for a time τ is assumed to have the chance $k(\tau, \theta)$ of being infected by a person who has been ill for a time θ. We shall assume that $k(\tau, \theta)$ is of the form $\omega_\tau \phi_\theta$, where ω_τ and ϕ_θ are functions of τ and θ respectively. Fig. 2 will make the meanings of these symbols clear. The immigration and the birth-rates remain constant as before. We shall consider that the system is a closed one which has been in existence for an infinite period of time.

The following equations are readily obtained :—

$$\frac{d\overline{x}}{dt} = \overline{u}_t - \overline{v}_t \tag{15}$$

$$\frac{dx}{dt} = u_t - \tilde{v}_t, \tag{16}$$

$$\frac{dy}{dt} = v_t - w_t - u_t, \tag{17}$$

$$\frac{dz}{dt} = w_t. \tag{18}$$

Also

$$\overline{x} = \int_0^\infty \overline{u}_{t\lambda}\, d\lambda, \tag{19}$$

where $\overline{u}_{t\lambda}\, d\lambda$ denotes the number of individuals at the time t, who have been born for a period between λ and $\lambda + d\lambda$.

$$x = \int_0^\infty u_{t\tau}\, d\tau, \tag{20}$$

where $u_{t\tau}\, d\tau$ denotes the number of susceptibles at a time t who have been recovered for a period between τ and $\tau + d\tau$.

$$y = \int_0^\infty v_{t\theta}\, d\theta, \tag{21}$$

where $v_{t\theta}$ denotes the number of individuals at a time t who have been sick for a period between θ and $\theta + d\theta$. (Clearly v_{0t} is identical with v_t.)

$$\overline{u}_t = m + \overline{\mu}.\overline{x} + \mu x + \nu y, \tag{22}$$

$$u_t = \int_0^\infty l_\theta v_{t\theta}\, d\theta, \tag{23}$$

$$v_t = \tilde{v}_t + \overline{v}_t, \tag{24}$$

$$\tilde{v}_t = \int_0^\infty \int_0^\infty k(\tau, \theta)\, v_{t\theta} u_{t\tau}\, d\theta\, d\tau, \tag{25}$$

$$\overline{v}_t = \overline{x} \int_0^\infty \overline{k}_\theta v_{t\theta}\, d\theta, \tag{26}$$

$$w_t = \int_0^\infty d_\theta v_{t\theta}\, d\theta. \tag{27}$$

It is now necessary to express $\bar{u}_{t\lambda}$, u_{tr}, etc., in terms of $\bar{u}_t$, u_t, etc. The rate of infection with time of the group of individuals, the parameters of which, at the moment, lie between t and $t + \delta t$, and λ and $\delta\lambda$, is by definition equal to

$$- \delta t \, \delta\lambda \int_0^\infty \bar{u}_{t\lambda} \bar{k}_\theta v_{t\vartheta} \, d\theta,$$

but it is also given by

$$\delta t \, \delta\lambda \left(\frac{\partial \bar{u}_{t\lambda}}{\partial t} + \frac{\partial \bar{u}_{t\lambda}}{\partial \lambda} \right).{}^*$$

Hence we have the equation

$$\frac{\partial \bar{u}_{t\lambda}}{\partial t} + \frac{\partial \bar{u}_{t\lambda}}{\partial \lambda} = - \int_0^\infty \bar{u}_{t\lambda} \, \bar{k}_\theta v_{t\theta} \, d\theta,$$

$$= - \bar{u}_{t\lambda} \int_0^\infty \bar{k}_\theta v_{t\theta} \, d\theta,$$

$$= - \bar{u}_{t\lambda} \bar{f}(t), \qquad (28)$$

where $\bar{f}(t)$ is written for $\displaystyle\int_0^\infty \bar{k}_\theta v_{t\vartheta} \, d\theta$.

Now

$$\frac{\partial v_{t\theta}}{\partial t} + \frac{\partial v_{t\vartheta}}{\partial \theta} = - (l_\theta + d_\theta) \, v_{t\theta}$$

whence

$$v_{t\theta} = v_{t-\theta} \, e^{-\int_0^\theta (l_{\theta'} + d_{\theta'}) \, d\theta'}, \qquad (29)$$

the lower limit of integration being taken as zero, since $v_{t\theta} = v_t$.

Hence

$$\bar{f}(t) = \int_0^\infty \bar{k}_\theta v_{t-\theta} \, e^{-\int_0^\theta (l_{\theta'} + d_{\theta'}) \, d\theta'} \, d\theta,$$

$$= \int_0^\infty \bar{k}_\theta v_{t-\theta} \, N_\theta \, d\theta, \quad \text{where } N_\theta = e^{-\int_0^\theta (l_{\theta'} + d_{\theta'}) \, d\theta'} \qquad (30)$$

or

$$\bar{f}(t) = \int_0^\infty \overline{K}_\theta v_{t-\theta} \, d\theta, \quad \text{where } \overline{K}_\theta \text{ is written for } k_\theta N_\theta. \qquad (31)$$

The solution of equation (28) is then

$$\bar{u}_{t\lambda} = \bar{u}_{t-\lambda} \, e^{-\int_0^\lambda \bar{f}(t-\lambda+\xi) \, d\xi} .$$

Substituting $\xi' = t - \lambda + \xi$, this may be written in the form

$$\bar{u}_{t\lambda} = \bar{u}_{t-\lambda} \, e^{-\int_{t-\lambda}^t \bar{f}(\xi') \, d\xi'}$$

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* *cf.* Kermack and McKendrick (*loc. cit.*), and McKendrick, 'Proc. Edin. Math. Soc.,' vol. 44, p. 122 (1926).

which with the substitution $\lambda' = t - \xi'$ becomes

$$\overline{u}_{t\lambda} = \overline{u}_{t-\lambda} \, e^{- \int_0^\lambda \bar{f}(t-\lambda') \, d\lambda'} \tag{32}$$

Thus finally equation (19) becomes

$$\overline{x} = \int_0^\infty \overline{u}_{t-\lambda} \, e^{- \int_0^\lambda \bar{f}(t-\lambda') \, d\lambda'} \, d\lambda. \tag{33}$$

Again,

$$\frac{\partial u_{t\tau}}{\partial t} + \frac{\partial u_{t\tau}}{\partial \tau} = - \int_0^\infty k\,(\theta, \, \tau) \, u_{t\tau} \, v_{t\vartheta} \, d\theta,$$

$$= - u_{t\tau} \, \omega_\tau \int_0^\infty \phi_\theta \, v_{t\vartheta} \, d\theta,$$

since $k\,(\theta, \, \tau) = \phi_\theta \, \omega_\tau$ by hypothesis,

$$= - u_{t\tau} \, \omega_\tau \int_0^\infty \phi_\theta \, v_{t-\theta} \, N_\theta \, d\theta,$$

$$= - u_{t\tau} \, \omega_\tau \int_0^\infty \Phi_\theta \, v_{t-\theta} \, d\theta, \quad \text{where } \Phi_\theta \text{ is written for } \phi_\theta \, N_\theta \tag{34}$$

$$= - u_{t\tau} \, \omega_\tau \, f\,(t), \tag{35}$$

where

$$f\,(t) = \int_0^\infty \Phi_\theta \, v_{t-\theta} \, d\theta. \tag{36}$$

Solving equation (35) we have

$$u_{t\tau} = u_{t-\tau} \, e^{- \int_0^\tau f(t-\tau+\xi) \, \omega_\xi \, d\xi}, \tag{37}$$

where it must be remembered that $f\,(t)$ is a function of $v_{t-\theta}$.

Writing $\mathrm{F}\,(t - \tau, \, \tau)$ for $e^{- \int_0^\tau f(t-\tau+\xi) \omega_\xi \, d\xi}$, since it depends on the two variables $t - \tau$ and τ, we have

$$u_{t\tau} = u_{t-\tau} \, \mathrm{F}\,(t - \tau, \, \tau). \tag{38}$$

Thus equation (20) becomes

$$x = \int_0^\infty \mathrm{F}\,(t - \tau, \, \tau) \, u_{t-\tau} \, d\tau. \tag{39}$$

Also by equations (21), (29) and (30),

$$y = \int_0^\infty \mathrm{N}_\theta \, v_{t-\theta} \, d\theta, \tag{40}$$

and by equation (23)

$$u_t = \int_0^\infty l_\theta \, v_{t-\theta} \, N_\theta \, d\theta,$$

$$= \int_0^\infty L_\theta \, v_{t-\theta} \, d\theta, \quad \text{where } L_\theta \text{ is written for } l_\theta \, N_\theta. \tag{41}$$

By equation (25)

$$\tilde{v}_t = \int_0^\infty \phi_\theta \, v_{t\theta} \, d\theta \int_0^\infty \omega_\tau \, u_{t\tau} \, d\tau,$$

$$= \int_0^\infty \Phi_\theta \, v_{t-\theta} \, d\theta \int_0^\infty \omega_\tau \, F(t-\tau, \tau) \, u_{t-\tau} \, d\tau \quad \text{(by (34) and (38))},$$

$$= \int_0^\infty \Phi_\theta \, v_{t-\theta} \, d\theta \int_0^\infty G(t-\tau, \tau) \, u_{t-\tau} \, d\tau, \quad \text{where } G(t-\tau, \tau) = \omega_\tau \, F(t-\tau, \tau). \tag{42}$$

By equations (26), (29) and (30)

$$\bar{v}_t = \bar{x} \int_0^\infty \bar{k}_\theta v_{t-\theta} N_\theta \, d\theta,$$

$$= \bar{x} \int_0^\infty \overline{K}_\theta v_{t-\theta} \, d\theta, \quad \text{by (31)}$$

$$= \bar{x}\,\overline{f}(t), \quad \text{by (31).} \tag{43}$$

Finally by equation (27)

$$w_t = \int_0^\infty d_\theta v_{t-\theta} N_\theta \, d\theta,$$

$$= \int_0^\infty D_\theta v_{t-\theta} \, d\theta, \quad \text{where } D_\theta = d_\theta N_\theta. \tag{44}$$

We shall now find the conditions for a steady state. We shall assume that in this condition

$$\bar{x} = \overline{X}, \; x = X, \; y = Y, \; \bar{u}_t = \overline{U}, \; u_t = U, \; v_t = V, \; \tilde{v}_t = \widetilde{V}, \; \bar{v}_t = \overline{V} \text{ and } w_t = W.$$

We shall also adopt the notation

$$L = \int_0^\infty L_\theta \, d\theta, \qquad D = \int_0^\infty D_\theta \, d\theta, \qquad \overline{K} = \int_0^\infty \overline{K}_\theta \, d\theta, \qquad \text{etc.} \tag{45}$$

We shall in general assume that L_θ, D_θ, $\overline{K}_\theta$, etc., which are, of course, never negative, are zero for all values of θ greater than θ_0, where θ_0 is some finite

quantity. This ensures the convergency of the integrals denoted by L, D, $\overline{\text{K}}$, etc.

Clearly

$$\text{L} + \text{D} = \int_0^\infty (l_\theta + d_\theta)\, e^{-\int_0^\theta (l_{\theta'} + d_{\theta'})\, d\theta'}\, d\theta = 1, \tag{46}$$

since by assumption $\text{L}_\theta = \text{D}_\theta = 0$, when $\theta = \infty$.

By equations (15) and (22),

$$\overline{\text{U}} = \overline{\text{V}} = m + \overline{\mu}\overline{\text{X}} + \mu\text{X} + \nu\text{Y} \tag{47}$$

$$\text{U} = \tilde{\text{V}}, \text{ by equation (16),} \tag{48}$$

$$\text{V} = \text{W} + \text{U}, \text{ by equation (17).} \tag{49}$$

By equation (33)

$$\overline{\text{X}} = \overline{\text{U}} \int_0^\infty e^{-\int_0^\lambda \bar{f}(t - \lambda')\, d\lambda'}\, d\lambda,$$

but by (31)

$$\bar{f}(t) = \int_0^\infty \overline{\text{K}}_\theta v_{t-\theta}\, d\theta$$

$$= \text{V} \int_0^\infty \overline{\text{K}}_\theta\, d\theta$$

$$= \overline{\text{K}}\text{V}, \text{ by (45),} \tag{50}$$

hence

$$\overline{\text{X}} = \overline{\text{U}} \int_0^\infty e^{-\overline{\text{K}}\text{V}\lambda}\, d\lambda,$$

$$= \frac{\overline{\text{U}}}{\overline{\text{K}}\text{V}}. \tag{51}$$

Similarly by equation (39)

$$\text{X} = \text{U} \int_0^\infty \text{F}(t - \tau, \tau)\, d\tau,$$

but

$$\text{F}(t - \tau, \tau) = e^{-\int_0^\tau f(t - \tau + \xi)\, \omega_\xi\, d\xi},$$

and

$$f(t) = \int_0^\infty \Phi_\theta v_{t-\theta}\, d\theta, \text{ by (36),}$$

$$= \text{V}\Phi, \tag{52}$$

hence

$$\int_0^\infty \text{F}(t - \tau, \tau)\, d\tau = \int_0^\infty e^{-\text{V}\Phi \int_0^\tau \omega_\xi\, d\xi}\, d\tau = \text{F}(\text{V}). \tag{53}$$

[It is to be noted that Φ is independent of V.]

Thus finally
$$X = UF(V).\tag{54}$$

By equation (40)
$$Y = NV;\tag{55}$$

by equation (41)
$$U = LV,\tag{56}$$

hence
$$X = LVF(V).\tag{57}$$

By equations (42) and (48)
$$\widetilde{V} = \Phi VUG(V) = U,\tag{58}$$

since

$$G(V) = \int_0^\infty G(t - \tau, \tau)\,d\tau$$

$$= \int_0^\infty \omega_\tau F(t - \tau, \tau)\,d\tau, \text{ by } (42),$$

$$= \int_0^\infty \omega_\tau e^{-V\Phi \int_0^\tau \omega_\xi \, d\xi}\,d\tau,$$

$$= \frac{1}{\Phi V}.\tag{59}$$

Also by equation (26)
$$\overline{V} = \overline{X}\overline{K}V,\tag{60}$$

and by equation (27)
$$W = DV.\tag{61}$$

From these relations it follows that

$$\left.\begin{aligned}
U &= \widetilde{V} = LV \\
\overline{U} &= \overline{V} = W = DV \\
\overline{X} &= \frac{D}{\overline{K}} \\
X &= LVF(V) \\
Y &= NV
\end{aligned}\right\}.\tag{62}$$

and

Hence, making the necessary substitutions in equation (47), viz.,

$$\overline{U} = m + \overline{\mu}\overline{X} + \mu X + \nu Y,$$

we have

$$DV = m + \overline{\mu}\frac{D}{\overline{K}} + \mu LVF(V) + \nu NV,\tag{63}$$

an equation which determines V.

Also the total number of individuals is

$$n = \overline{X} + X + Y$$

$$= V \left(\frac{D}{\overline{\overline{K}}} + LF(V) + N \right). \tag{64}$$

We shall now consider the nature of the real positive roots of equation (63). Let

$$\Theta(V) = \mu LF(V) + \nu N - D + \frac{m}{V} + \frac{\overline{\mu}D}{\overline{K}V}, \tag{65}$$

and let us write $F(V)$ in the form $\int_0^\infty e^{-\Phi V \overline{\Omega}_\tau} \, d\tau$, where $\overline{\Omega}_\tau$ is written for $\int_0^\tau \omega_\xi \, d\xi$. In general $\overline{\Omega}_\tau$ will have the following characteristics. It may be zero when $\tau = 0$ and $\tau = \varepsilon$, as ω_ξ may be zero for small values of ε, that is to say, immediately after recovery there may be complete immunity. It will then increase monotonically as ω_ξ is always positive. In general for large values of ξ, say $\xi > \eta$, ω_ξ will become sensibly constant and equal to ω. For large values of τ then,

$$\overline{\Omega}_\tau = \int_0^\tau \omega_\xi d\xi = \int_0^\eta \omega_\xi d\xi + \int_\eta^\tau \omega_\xi d\xi,$$

$$= \overline{\Omega}_\eta + \omega(\tau - \eta). \tag{66}$$

It may easily be shown that for finite positive values of V, $F(V)$ is always finite, and that as V increases $F(V)$ always decreases; also as V increases $\nu N - D + \frac{m}{V} + \frac{\overline{\mu}D}{\overline{K}V}$ always decreases, so that $\Theta(V)$ always decreases as V increases. Further, for small values of V, $\Theta(V)$ is very large and positive. Therefore there may be either one positive real root, or no positive real roots according as $\Theta(V = \infty)$ is negative or positive.

Now

$$F(V) = \int_0^\varepsilon e^{-\Phi V \overline{\Omega}_\tau} d\tau + \int_\varepsilon^\eta e^{-\Phi V \overline{\Omega}_\tau} d\tau + \int_\eta^\infty e^{-\Phi V \overline{\Omega}_\tau} d\tau. \tag{67}$$

The first integral is simply equal to ε. The second integral is equal to $(\eta - \varepsilon) e^{-\Phi V \overline{\Omega}_\pi}$, where $\overline{\Omega}_\pi$ is some value of $\overline{\Omega}_\tau$ between zero and $\overline{\Omega}_\eta$ and is therefore finite. The third integral becomes $\int_\eta^\infty e^{-\Phi V [\overline{\Omega}_\eta + \omega(\tau - \eta)]} \, d\tau$, by

equation (66). When V is very great the second integral vanishes since $\overline{\Omega}_\pi$ is finite ; and the third integral becomes

$$e^{-\Phi V \overline{\Omega}_\eta + \Phi V \omega_\eta} \times \int_\eta^\infty e^{-\Phi V \omega_\tau} \, d\tau,$$

$$= e^{-\Phi V \overline{\Omega}_\eta + \Omega V \omega_\eta} \times \frac{e^{-\Phi V \omega_\eta}}{\Phi V \omega},$$

$$= \frac{e^{-\Phi V \overline{\Omega}_\eta}}{\Phi V \omega}$$

which tends to zero as V tends to infinity.

Thus $F(V)_{v \to \infty} \to \varepsilon$, and $\Theta(V)$ tends to

$$\mu L \varepsilon + \nu N - D. \tag{68}$$

Consequently $\Theta(V) = 0$ has no real root if $D - \nu N - \mu L \varepsilon$ is negative, and has one real root if this expression is positive. It follows that no steady state exists if $D - \nu N - \mu L \varepsilon$ is negative, and that a unique steady state exists if it is positive. It is to be noted that ε is equal to the time during which immunity is absolute.

Let us now consider the effect of varying the immigration rate m, or the birth-rates $\overline{\mu}$, μ and ν, upon the number turning ill V. Equation (65) may be regarded as an equation giving V in terms of m, $\overline{\mu}$, μ and ν, hence

$$\frac{\partial \Theta}{\partial V} \delta V + \frac{\partial \Theta}{\partial m} \delta m + \frac{\partial \Theta}{\partial \overline{\mu}} \delta \overline{\mu} + \frac{\partial \Theta}{\partial \mu} \delta \mu + \frac{\partial \Theta}{\partial \nu} \delta \nu = 0,$$

or

$$\frac{\partial \Theta}{\partial V} \delta V + \frac{\delta m}{V} + \frac{D}{KV} \delta \overline{\mu} + LF \delta \mu + N \delta \nu = 0.$$

Consequently

$$\frac{\partial V}{\partial m} = -\frac{1}{V \Theta'}, \quad \frac{\partial V}{\partial \overline{\mu}} = -\frac{D}{KV \Theta'}, \quad \frac{\partial V}{\partial \mu} = -\frac{LF}{\Theta'} \text{ and } \frac{\partial V}{\partial \nu} = -\frac{N}{\Theta'}. \tag{69}$$

It has been shown above that Θ' is always negative, hence

$$\frac{\partial V}{\partial m}, \quad \frac{\partial V}{\partial \overline{\mu}}, \quad \frac{\partial V}{\partial \mu} \text{ and } \frac{\partial V}{\partial \nu}$$

are each positive. It follows that an increase of the immigration or birth-rates results in an increase in the number turning ill and *vice versa*.

Further, let us write $T = V/n$, so that $100T$ is the percentage rate of incidence of fresh cases of the disease.   Then

$$\frac{1}{T} = \frac{n}{V} = \frac{X}{V} + \frac{\overline{X}}{V} + \frac{Y}{V},$$

$$= LF + \frac{D}{KV} + N.$$

Hence

$$-\frac{1}{T^2}\frac{\partial T}{\partial V} = L\frac{dF}{dV} - \frac{D}{\overline{K}V^2}.$$

But

$$F = \int_0^\infty e^{-\Phi V \int_0^\tau \omega_\xi\, d\xi}\, d\tau.$$

Therefore

$$\frac{\partial F}{\partial V} = -\Phi \int_0^\infty \int_0^\tau \omega_\xi\, d\xi e^{-\Phi V \int_0^\tau \omega_\xi\, d\xi}\, d\tau = -\Phi I\, \Gamma,$$

where

$$\Gamma = \int_0^\infty \int_0^\tau \omega_\xi\, d\xi\, e^{-\Phi V \int_0^\tau \omega_\xi\, d\xi}\, d\tau,$$

which is always positive.   Thus

$$\frac{\partial T}{\partial V} = T^2\left(L\,\Phi\,\Gamma + \frac{D}{\overline{K}V^2}\right). \tag{70}$$

Hence $\dfrac{\partial T}{\partial V}$ is positive, and as

$$\frac{\partial V}{\partial m},\ \frac{\partial V}{\partial \overline{\mu}},\ \frac{\partial V}{\partial \mu}\ \text{and}\ \frac{\partial V}{\partial \nu}$$

are each positive, it follows that

$$\frac{\partial T}{\partial m},\ \frac{\partial T}{\partial \overline{\mu}},\ \frac{\partial T}{\partial \mu}\ \text{and}\ \frac{\partial T}{\partial \nu}$$

are each positive.   Since T is proportional to the percentage rate of incidence of fresh cases of the disease, it follows from the above, that if a condition of equilibrium exists, the percentage rate of incidence increases as the immigration or birth-rates increase.

In the previous section dealing with constant rates, the question of the stability of the steady states has been treated.   In the more general problem, now under consideration, the question of the stability of the steady states is much more difficult.   We shall at present confine ourselves to the formulation

of the equations which describe the behaviour of the system after the intro-
duction of a small disturbance at a particular time $-T$. Considerable progress
has been made with the investigation of these equations, and it is hoped to
present the results in a later communication. It is meanwhile convenient
to formulate the equations here in order to avoid repetition in the future of
the details of the epidemiological problem under consideration.

We shall consider, then, a system in which a steady state has existed for all
time, but into which, at a time $-T$ a small disturbance was introduced in
the form of a number of virgins $_0\overline{u}_\lambda \, d\lambda_1$ of age between λ_1 and $\lambda_1 + d\lambda_1$,
together with a number of recovered persons of whom $_0u_{\lambda_1}d\lambda_1$ had recovered
for a period between λ_1 and $\lambda_1 + d\lambda_1$, and a number of infected individuals
of whom $_0v_{\theta_1} \, d\theta_1$ had been infected for a period between θ_1 and $\theta_1 + d\theta_1$.

We shall first of all write down the exact equations which define the system.
To prevent confusion we shall, in what follows, limit $\overline{u}$, u and v so that they
refer solely to new virgins, recovered persons, or infected cases occurring as the
result of the working of the postulated processes within the system, and do not
include individuals introduced from without. The values $\overline{x}$, x and y, on the
other hand, include all the virgins, recovered persons, and infected individuals
independently of how they originated.

It follows that the equations (22), (41), (42) and (43) for $\overline{u}_t$, u_t, and v_t hold
without modification, whilst to the equations for $\overline{x}$, x and y (33), (39) and (40)
an extra term must be added to accommodate the introduction of the extra
individuals.

Thus

$$y = \int_0^\infty N_\theta v_{t-\theta} \, d\theta + \int_0^\infty v_{t\theta_1} \, d\theta_1, \tag{71}$$

where $v_{t\theta_1} \, d\theta_1$ indicates the number surviving at the time t, of the $_0v_{\theta_1} \, d\theta_1$
introduced at the time $-T$, who at that time were of age between θ_1 and
$\theta_1 + d\theta_1$.

Similarly
$$\overline{x} = \int_0^\infty \overline{u}_{t-\lambda} \, e^{-\int_0^\lambda \overline{f}(t-\lambda') \, d\lambda'} \, d\lambda + \int_0^\infty \overline{u}_{t\lambda_1} \, d\lambda_1, \tag{72}$$

and

$$x = \int_0^\infty F(t - \tau, \tau) \, u_{t-\tau} \, d\tau + \int_0^\infty u_{t\tau_1} \, d\tau_1. \tag{73}$$

In these equations and in those for $\overline{u}$, u, v, etc., we write

$$\overline{x} = \overline{X} + \overline{x}', \quad x = X + x', \quad y = Y + y', \quad \overline{u}_t = \overline{U} + \overline{u}'_t, \quad u_t = U + u'_t,$$

$$v_t = V + v'_t, \quad \overline{v}_t = \overline{V} + \overline{v}_t, \quad \tilde{v}_t = \tilde{V} + \tilde{v}'_t, \quad \text{and} \quad w_t = W + w'_t,$$

where $\overline{X}$, X, Y, $\overline{U}$, etc., are the steady state values found above, and $\overline{x}'$, x', y', etc., are zero for all values of $t < -\mathrm{T}$. The values $\overline{x}'$, x', y', etc., are very small quantities, provided that

$$\int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1, \qquad \int_0^\infty u_{t\tau_1}\, d\tau_1, \qquad \text{and} \qquad \int_0^\infty v_{t\vartheta_1}\, d\theta_1$$

are small, for they necessarily tend to zero as the disturbance represented by these integrals tends to zero.

After simple reductions, and, where necessary, neglecting small quantities of higher order than the first, we have

$$\frac{d\overline{x}'}{dt} = \overline{u}'_t - \overline{v}'_t, \tag{74}$$

$$\frac{d'x}{dt} = u'_t - \tilde{v}'_t, \tag{75}$$

$$\frac{dy'}{dt} = v'_t - w'_t - u'_t, \tag{76}$$

$$\overline{u}'_t = \overline{u}\,\overline{x}' + \mu x' + \nu y', \tag{77}$$

$$u'_t = \int_0^\beta \mathrm{L}_\theta\, v'_{t-\theta}\, d\theta, \qquad (\beta = \infty) \tag{78}$$

$$v'_t = \tilde{v}' + \overline{v}', \tag{79}$$

$$\overline{v}'_t = \overline{x}'\mathrm{KV} + \overline{X}\int_0^\beta \overline{\mathrm{K}}_\theta\, v'_{t-\theta}\, d\theta, \text{ from (43) } (\beta = \infty) \tag{80}$$

$$w'_t = \int_0^\beta \mathrm{D}_\theta\, v'_{t-\theta}\, d\theta. \tag{81}$$

Also from (71)

$$y'_t = \int_0^\beta \mathrm{N}_\theta\, v'_{t-\theta}\, d\theta + \int_0^\infty v_{t\vartheta}\, d\theta_1 \quad (\beta = \infty). \tag{82}$$

The following reductions are more complicated.

By equation (72) we have

$$\overline{x} = \overline{X} + \overline{x}' = \int_0^\beta (\overline{U} + \overline{u}'_{t-\lambda})\, e^{-\int_0^\lambda \overline{f}(t-\lambda')\, d\lambda'}\, d\lambda + \int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1, \qquad (\beta = \infty),$$

but by (31)

$$\overline{f}(t-\lambda') = \int_0^\infty \overline{\mathrm{K}}_\theta\, v_{t-\lambda'-\theta}\, d\theta,$$

$$= \int_0^\infty \overline{\mathrm{K}}_\theta\, (\mathrm{V} + v'_{t-\lambda'-\theta})\, d\theta,$$

$$= \overline{\mathrm{K}}\mathrm{V} + \int_0^\infty \overline{\mathrm{K}}_\theta\, v'_{t-\lambda'-\theta}\, d\theta. \tag{83}$$

Hence

$$\overline{X} + \overline{x}' = \int_0^\infty (\overline{U} + \overline{u}'_{t-\lambda})\, e^{-\overline{K}V\lambda}\, e^{-\int_0^\lambda \int_0^\infty \overline{K}_\theta\, v'_{t-\lambda'-\theta}\, d\theta\, d\lambda'}\, d\lambda + \int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1,$$

$$= \int_0^\infty (\overline{U} + \overline{u}'_{t-\lambda})\, e^{-\overline{K}V\lambda} \left(1 - \int_0^\lambda \int_0^\infty \overline{K}_\theta\, v'_{t-\lambda'-\theta}\, d\theta\, d\lambda'\right) d\lambda + \int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1,$$

$$= \frac{\overline{U}}{\overline{K}V} + \int_0^\infty \overline{u}'_{t-\lambda}\, e^{-\overline{K}V\lambda} d\lambda - \overline{U} \int_0^\infty e^{-\overline{K}V\lambda} \int_0^\lambda \int_0^\infty \overline{K}_\theta\, v'_{t-\lambda'-\theta}\, d\theta\, d\lambda'\, d\lambda$$

$$+ \int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1,$$

whence

$$\overline{x}' = \int_0^\beta \overline{u}'_{t-\lambda}\, e^{-\overline{K}V\lambda}\, d\lambda - \overline{U} \int_0^\beta e^{-\overline{K}V\lambda} \int_0^\lambda \int_0^{\beta-\lambda^1} \overline{K}_\theta\, v'_{t-\lambda'-\theta}\, d\theta\, d\lambda'\, d\lambda + \int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1,$$

$$\tag{84}$$

where $\beta = \infty$.

Also by equation (42)

$$\tilde{v}_t = \int_0^\infty \Phi_\theta (V + v'_{t-\theta})\, d\theta \int_0^\infty G(t-\tau,\, \tau)(U + u'_{t-\tau})\, d\tau.$$

Writing

$$G(t-\tau,\, \tau) = \omega_\tau F(t-\tau,\, \tau)$$

$$= \omega_\tau F_\tau + \omega_\tau F'(t-\tau,\, \tau),$$

where $F'(t-\tau,\, \tau)$ contains only small quantities of the first order, small quantities of the second and higher orders being neglected, we have

$$\tilde{V} + \tilde{v}' = \int_0^\infty \Phi_\theta (V + v'_{t-\theta})\, d\theta \int_0^\infty (U + u'_{t-\tau})\{\omega_\tau F_\tau + \omega_\tau F'(t-\tau,\, \tau)\}\, d\tau$$

$$= \left[\Phi V + \int_0^\infty \Phi_\theta v'_{t-\theta}\, d\theta\right] \int_0^\infty \{U\omega_\tau F_\tau + U\omega_\tau F'(t-\tau,\, \tau) + \omega_\tau F_\tau u'_{t-\tau}\}\, d\tau.$$

Thus writing $G = \int_0^\infty \omega_\tau F_\tau\, d\tau$, and $G' = \int_0^\infty \omega_\tau F'(t-\tau,\, \tau)\, d\tau$, so that $G_t = G + G'_t$ to a first order of approximation; since $\tilde{V} = \Phi V U G$,

$$\tilde{v}' = \Phi V U \int_0^\beta \omega_\tau F'(t-\tau,\, \tau)\, d\tau + \Phi V \int_0^\beta \omega_\tau F_\tau\, d\tau + U G \int_0^\beta \Phi_\theta v'_{t-\theta}\, d\theta. \tag{85}$$

Again by equation (73)

$$X + x' = \int_0^\infty (U + u'_{t-\tau})\{F_\tau + F'(t-\tau,\, \tau)\}\, d\tau + \int_0^\infty u_{t\tau_1}\, d\tau_1,$$

$$= \int_0^\infty U F_\tau\, d\tau + \int_0^\infty U F'(t-\tau,\, \tau)\, d\tau + \int_0^\infty F_\tau u'_{t-\tau}\, d\tau + \int_0^\infty u_{t\tau_1}\, d\tau_1,$$

$$= U F + U \int_0^\infty F'(t-\tau,\, \tau)\, d\tau + \int_0^\infty F_\tau u'_{t-\tau}\, d\tau + \int_0^\infty u_{t\tau_1}\, d\tau_1.$$

Therefore since $X = UF$

$$x' = U \int_0^\beta F'(t - \tau, \tau)\, d\tau + \int_0^\beta F_\tau u'_{t-\tau}\, d\tau + \int_0^\infty u_{t\tau_1}\, d\tau_1 \qquad (\beta = \infty). \quad (86)$$

Thus $\overline{u}'$, $\overline{u}'$, v', $\overline{x}'$, x', etc., are determined by equations (77) to (86). As, however, all these functions are zero when $t < -T$, it is easily seen that the upper limit β of the integrals involving these unknown functions may be put equal to $t + T$ instead of infinity. It follows that these functions at any point, which have now been defined in terms of finite integrals of their values up to that point, must remain finite and single valued for all finite values of t, provided that the initial disturbance is defined unambiguously.

It is now necessary to express $v_{t\theta_1}$ in terms of $_0v_{\theta_1}$ the number actually introduced at the time $-T$. It can be shown that

$$v_{t\theta_1} = {}_0v_{\theta_1} e^{-\int_{\theta_1}^{t+T+\theta_1} (l_{\theta'} + d_{\theta'})\, d\theta'}. \quad (87)$$

Also

$$\overline{u}_{t\lambda_1} = {}_0\overline{u}_{\lambda_1} e^{-\int_{\lambda_1}^{t+T+\lambda_1} \overline{f}(t-\lambda')\, d\lambda'}. \quad (88)$$

Since $\overline{f}(t) = \int_0^\infty \overline{K}_\theta v_{t-\theta}\, d\theta$, therefore to a first approximation,

$$\overline{f}(t) = \int_0^\infty \overline{K}_\theta V\, d\theta = \overline{K}V,$$

hence

$$\overline{u}_{t\lambda_1} = {}_0\overline{u}_{\lambda_1} e^{-\overline{K}V(t+T)}. \quad (89)$$

It may also be shown that

$$u_{t\tau_1} = {}_0u_{\tau_1} \frac{F(-T - \tau_1,\, t + T + \tau_1)}{F(-T - \tau_1,\, \tau_1)}. \quad (90)$$

But $F(t - \tau, \tau) = e^{-\int_0^\tau f(t-\tau+\xi)\omega_\xi\, d\xi}$, and to a first approximation $f(t) = \Phi V$, therefore $F(t - \tau, \tau) = e^{-\Phi V}$, so that

$$\frac{F(-T - \tau_1,\, t + T + \tau_1)}{F(-T - \tau_1,\, \tau_1)} = e^{-\Phi V \int_{\tau_1}^{t+T+\tau_1} \omega_\xi\, d\xi}. \quad (91)$$

From the above we obtain finally the five equations :—

$$\overline{x}' = \int_0^{t+T} \overline{u}'_{t-\lambda} e^{-\overline{K}V\lambda}\, d\lambda - \overline{U} \int_0^{t+T} e^{-\overline{K}V\lambda} \int_0^\lambda \int_0^{t+T-\lambda^1} \overline{K}_\theta v'_{t-\lambda'-\theta}\, d\theta\, d\lambda'\, d\lambda$$

$$+ \int_0^\infty \overline{u}_{t\lambda_1}\, d\lambda_1, \quad (92)$$

$$x' = \mathrm{U} \int_0^{t+\mathrm{T}} \mathrm{F}'(t-\tau, \tau)\, d\tau + \int_0^{t+\mathrm{T}} \mathrm{F}_\tau u'_{t-\tau}\, d\tau + \int_0^\infty u_{t\tau_1}\, d\tau_1, \tag{93}$$

$$y' = \int_0^{t+\mathrm{T}} \mathrm{N}_\theta v'_{t-\theta}\, d\theta + \int_0^\infty v_{t\theta_1}\, d\theta_1, \tag{94}$$

$$u'_t = \int_0^{t+\mathrm{T}} \mathrm{L}_\theta v'_{t-\theta}\, d\theta, \tag{95}$$

$$v' = \tilde{v}' + \overline{v}', \tag{96}$$

where

$$\tilde{v}' = \Phi \mathrm{VU} \int_0^{t+\mathrm{T}} \omega_\tau \mathrm{F}'(t-\tau, \tau)\, d\tau + \Phi \mathrm{V} \int_0^{t+\mathrm{T}} \omega_\tau \mathrm{F}_\tau u'_{t-\tau}\, d\tau + \mathrm{UG} \int_0^{t+\mathrm{T}} \Phi_\theta v'_{t-\theta}\, d\theta,$$

and

$$\overline{v}' = \overline{x}' \overline{\mathrm{K}} \mathrm{V} + \overline{\mathrm{X}} \int_0^{t+\mathrm{T}} \overline{\mathrm{K}}_\theta v'_{t-\theta}\, d\theta.$$

These five equations contain five unknown functions and are sufficient to determine these functions for all values of $t > -\mathrm{T}$. It is often convenient to consider the disturbance as occurring at $t = 0$, in which case the necessary equations are obtained by putting $\mathrm{T} = 0$ in the above. It is hoped to discuss the nature of the solutions of these somewhat complicated equations in a future communication.

We shall now consider special examples of the general case corresponding to the five special cases treated on pp. 62 and 63. The results are summarised in Table II. The results in each special case may be verified by working it out *ab initio*, and also by substituting for the variables l_θ, d_θ, etc., the corresponding constant coefficients when the values detailed in Table I are obtained.

(1) $m = 0$, $\overline{\mu} = \mu$, $\nu = 0$. No immigration; all healthy persons reproduce at a constant rate.

(2) $m = 0$, $\overline{\mu} = \mu$, $\nu = 0$ and $l_\theta = 0$. As in case (1), but in addition the disease is fatal.

(3) $\overline{\mu} = \mu = \nu = 0$. Immigration operative but no birth-rate.

(4) $\overline{\mu} = \mu = \nu = 0$ and $l_\theta = 0$. As in case (3), but in addition the disease is fatal.

(5) $m = \overline{\mu} = \mu = \nu = 0$ and $d_\theta = 0$. No deaths, no births, no immigration, the total population $n = x + y$. Here we are dealing with a closed population, and with a disease which is never fatal, and which may be recovered from. The total population in the steady state is

$$n = \mathrm{X} + \mathrm{Y} = \mathrm{V}(\mathrm{F}(\mathrm{V}) + \mathrm{N}). \tag{97}$$

The fifth case requires fuller discussion. Let us consider the value of $\chi(V) = V(F(V) + N) - n$ as V tends to zero. Clearly

$$\chi(V)_{V \to 0} = \text{Limit } \{VF(V)\}_{V \to 0} - n.$$

We assume that $\bar{\Omega}_\tau \equiv \int_0^\tau \omega_\lambda \, d\lambda$ has the properties given on p. 70; that is, it is zero between $\tau = 0$ and $\tau = \varepsilon$, then it increases monotonically, and finally for large values of τ greater than η it becomes $\bar{\Omega}_\eta + \omega(\tau - \eta)$.

Thus

$$\{\chi(V)\}_{V \to 0} = \{VF(V)\}_{V \to 0} - n,$$

$$= \left\{ V \int_0^\varepsilon e^{-\Phi V \bar{\Omega}_\tau} \, d\tau + V \int_\varepsilon^\eta e^{-\Phi V \bar{\Omega}_\tau} \, d\tau + V \int_\eta^\infty e^{-\Phi V \bar{\Omega}_\tau} d\tau \right\}_{V \to 0} - n,$$

$$= \left\{ V\varepsilon + V(\eta - \varepsilon) e^{-\Phi V \bar{\Omega}_\pi} + V \int_\eta^\infty e^{-\Phi V [\bar{\Omega}_\eta + \omega(\tau - \eta)]} d\tau \right\}_{V \to 0} - n,$$

which, as before, if ε and η are finite

$$= \left\{ V \int_\eta^\infty e^{-\Phi V [\bar{\Omega}_\eta + \omega(\tau - \eta)]} \, d\tau \right\}_{V \to 0} - n,$$

$$= \left\{ e^{-\Phi V (\bar{\Omega}_\eta - \omega\eta)} V \int_\eta^\infty e^{-\Phi V \omega\tau} d\tau \right\}_{V \to 0} - n,$$

$$= \frac{1}{\Phi\omega} - n. \tag{98}$$

Further $\{\chi(V)\}_{V \to \infty} \to +\infty$, hence if, $\dfrac{1}{\Phi\omega} - n$ is negative, the equation $\chi(V) = 0$ has one real positive root, and may in general have an odd number of such roots, whilst if $\dfrac{1}{\Phi\omega} - n$ is positive, there are either no real positive roots, or an even number of such roots. We shall now assume that $d\omega/d\tau$ is never negative. This is the case which is most important in practice, since the condition implies that after an attack of the disease susceptibility remains constant or increases, but never decreases. We shall also assume in the first instance that ω_0 is not equal to zero. We shall now show that under these conditions $\chi(V)$ always increases with V.

$$VF(V) = V \int_0^\infty e^{-\Phi V \int_0^\tau \omega_\lambda \, d\lambda} \, d\tau,$$

$$= -\frac{1}{\Phi} \int_0^\infty \frac{1}{\omega_\tau} \, de^{-\Phi V \int_0^\tau \omega_\lambda \, d\lambda},$$

$$= \frac{1}{\Phi\omega_0} - \frac{1}{\Phi} \int_0^\infty e^{-\Phi V \int_0^\tau \omega_\lambda \, d\lambda} \frac{1}{\omega_\tau^2} \frac{d\omega}{d\tau} \, d\tau. \tag{99}$$

Thus

$$\chi(V) = \frac{1}{\Phi\omega_0} - \frac{1}{\Phi}\int_0^\infty \frac{1}{\omega_\tau^2}\frac{d\omega}{d\tau}\, e^{-\Phi V \int_0^\tau \omega_\lambda d\lambda}\, d\tau + NV - n. \qquad (100)$$

It is readily seen from the form of this expression that $\chi(V)$ increases with V, provided that $d\omega/d\tau$ is never negative. Let us now suppose that $\omega_\tau = 0$, between $\tau = 0$ and $\tau = \varepsilon$, and let $\omega_{\varepsilon+\delta\varepsilon} \equiv \omega'$, a small but finite quantity. Then

$$VF(V) = V\int_0^\varepsilon e^{-\Phi V\bar\Omega_\tau}\, d\tau + V\int_\varepsilon^{\varepsilon+\delta\varepsilon} e^{-\Phi V\bar\Omega_\tau}\, d\tau + V\int_{\varepsilon+\delta\varepsilon}^\infty e^{-\Phi V\bar\Omega_\tau}\, d\tau,$$

$$= V(\varepsilon + \delta\varepsilon) + \frac{1}{\Phi\omega'} - \frac{1}{\Phi}\int_{\varepsilon+\delta\varepsilon}^\infty \frac{1}{\omega_\tau^2}\frac{d\omega}{d\tau}\, e^{-\Phi V\bar\Omega_\tau}\, d\tau. \qquad (101)$$

It follows as above that $\chi(V)$ constantly increases as V increases, even though ω_τ for small values of τ is zero. Thus it appears that if $d\omega/d\tau$ is not negative, the equation $\chi(V) = 0$ has one and only one real root provided that $n > 1/\Phi\omega$, and has no real roots if $n < 1/\Phi\omega$. The value $n_0 = 1/\Phi\omega$ may be called the *threshold density* of population, as no endemic disease can exist when the density is less than $1/\Phi\omega$. Let us suppose that the actual density exceeds the threshold density by a small amount n', and further let

$$\left\{\frac{d}{dV}VF(V)\right\}_{V=0} = \lambda.$$

From what has been proved above λ must be positive if $d\omega/d\tau$ is never negative and not constantly zero. If $d\omega/d\tau$ is constantly zero, ω_τ is a constant, and it is then easy to show that λ is equal to zero. Apart from this special case λ is positive. The equation for V then becomes

$$n_0 + n' = \frac{1}{\Phi\omega} + \lambda V + NV + \text{higher powers of V.}$$

As $n_0 = 1/\Phi\omega$, the equation will have a solution V so small that squares and higher powers of V may be neglected. Hence to a first approximation

$$V = \frac{n'}{\lambda+N}, \quad \text{whence} \quad Y = \frac{n'N}{\lambda+N} \quad \text{and} \quad X = n_0 + \frac{n'\lambda}{\lambda+N}. \qquad (102)$$

As λ is in general positive, Y is less than n', and $X - n_0$ is positive. Hence when n' individuals are added to a population already at its threshold density, a certain amount of endemic disease will set in, the number who are ill being less than the actual excess of the population density over the threshold density.

In the equilibrium condition the density of the healthy population will in general exceed the threshold. In the special case where ω is a constant the number who are ill will actually equal the excess, and the number who are well will equal the threshold. The value of λ—apart from simple cases, such as $\omega = \text{constant}$—is related apparently in a complicated way to the function ω_τ, and so far we have been unable to find a simple expression for it.

Discussion.

The mathematical results which we have obtained above are very general in character, and a complete discussion of all the special conclusions which may be drawn would of necessity be unduly long. We shall, therefore, at present confine ourselves to pointing out some of the more important features of the system which is under investigation. Two important limitations of the above theory should in the first place be emphasised. The effect of the age of the individuals is not taken into account at all. Other things being equal, individuals are assumed to have the same susceptibility, the same infectivity and the same chance of dying or recovering whatever their age. In most cases this assumption will not be true. In diseases of comparatively short duration and especially those confined to particular age periods such as childhood, the effect of age may be of relatively little importance, but in diseases which last for periods comparable with the average age during life, the effect of age is likely to be very much more important. The second factor which has been neglected in the above treatment is the effect of death from causes other than the single disease which is assumed to be operative, or the removal of individuals from the population through some independent mechanism. For example, in the case of diseases limited to a particular age group the individual would automatically pass out of the population susceptible to the disease by becoming older. We hope in the future to extend the treatment which has been elaborated in the present paper so as to take into account the effect of a general death rate, and if possible the effect of age.

The results obtained above refer partly to the conditions for the existence of a steady state, and partly to the nature of the equilibrium so obtained. It is of considerable interest that in the general problem a particular system admits at the most of only one steady state provided that the susceptibility never decreases as time goes on. This follows from the fact that equation (63) has only one real positive solution. It may have no real positive solution at all, in which case no steady state can exist. Equation (68) gives the condition under

which this will occur. This limitation of the number of steady states to one at most, is not immediately obvious. One did not know for certain that a number of steady states might not exist, each being characterised by a different value of V.

In the problem dealt with in our previous paper we showed that a threshold population density existed which was such that no epidemic could occur if the population density was less than this threshold. In the present problem a threshold of an analogous type turns up only in case 5, that is, when the population is closed so that no individuals can leave or enter it. In the other cases the population level automatically adjusts itself in conformity with the values of the arbitrary functions. Naturally no such adjustment is possible with the closed population considered in case 5, and it has been shown that in this instance no disease can exist unless the total density of population exceeds a certain level. In the special case of constant coefficients this threshold density happens to be identical with the threshold density found in dealing with constant coefficients in the previous paper, being equal to l/k. Further, we have also shown that in the case of constant coefficients the number of healthy individuals remains at the threshold level when the number of the population exceeds this threshold, and that the excess are found in the diseased group. In the general case, however, this does not necessarily hold, the number who are ill may not, and in general will not, be equal to, but form only a fraction of the excess, so that the number of healthy individuals in the population will usually become greater as the total population increases beyond the threshold. The disease rate of the population will, to a first approximation, be proportional to the excess of the population over the threshold, when this excess is small.

Some interesting results follow from the present work in regard to the effect of the rate of influx of fresh individuals on the mortality rate, and the endemic level of a population. The mortality rate is equal to $W/n = DT$, the disease rate is denoted by $V/n = T$, whilst the endemic level of fraction of the population actually infected is $Y/n = NT$. We have shown that an increase in the immigration rate, or in the birth-rate either of the virgin, the recovered or the diseased, will result in an increase of T, and therefore in increases of the mortality rate, the disease rate and the endemic level. A fall in immigration rate or birth-rate will have the opposite effect. Although in obtaining this result the various assumptions mentioned at the beginning of the discussion have been made, yet it is to be expected that in general a fall in the birth-rate would be accompanied by a fall in the prevalence of all contagious diseases. We hope to deal with this problem more fully at a later date, when considering

a system in which allowance is made for deaths or removals from causes other than the single disease under discussion.

The equilibrium states which we have been discussing so far may be either stable or unstable. In the former case, when the population is almost, but not quite, in equilibrium, then as time goes on it will gradually approach the equilibrium condition. When the equilibrium is unstable one or two things may happen. The population may gradually move farther and farther away from the equilibrium condition, until the disease completely disappears, or the population is wiped out. On the other hand, the population may oscillate about its equilibrium state, but these oscillations may gradually increase in amplitude until they become very great. (As a border line case we have the special possibility of continuous oscillations of constant amplitude, but this will appear only under very special conditions.) We may define the first type of instability as aperiodic, and the second as periodic. The nature of the equilibrium in the case of constant coefficients will be determined by the nature of the roots of the equation (14) in α. If one of these roots corresponds to unstable equilibrium, then, although the others may correspond to stability, yet the state will be unstable. In the same way in an unstable system the instability might in general be mixed, that is, the equation in α might have roots corresponding to both types of instability. It is readily seen that the condition for stability is that the real roots of the equation should be negative and that the complex roots should have negative real parts. We have shown that in general this condition is always satisfied in the case of constant coefficients. The only exception occurs in the limiting case (3) in which the real part is zero, and pure harmonic vibrations result. The exceptional value $\alpha = 0$ obtained in case (5) accommodates a disturbance within a closed population resulting in a change in the total number.

The theory as elaborated in this paper only applies to oscillations of small amplitude about the equilibrium condition. When these amplitudes increase the theory will cease to hold. It does not give a complete account of what happens in a system possessing periodic or aperiodic instability. It only indicates the nature of the stability. As, however, there is at most only one equilibrium condition the system cannot change to any steady condition other than one in which there is no disease at all or one in which the whole population has been wiped out. Apart from these two possibilities, it seems that it is not possible from the above to indicate how a system exhibiting periodic instability may behave after the oscillations have reached a considerable amplitude.

Summary.

(1) A mathematical investigation has been made of the prevalence of a disease in a population from which certain individuals are being removed as the result of the disease, whilst fresh individuals are being introduced as the result of birth or immigration. Allowance is made for the effects of the immunity produced as the result of an attack of the disease, but the effect of deaths from other causes is not taken into account, and the action of the disease is supposed to be independent of the age of the individual.

(2) As a special case of the above, results have been obtained for a closed population in which no deaths occur and to which no fresh individuals are added, but in which the individuals after being infected acquire immunity, and then may be again infected. A threshold density of population exists analogous to that described in the previous paper, which is such that no disease can exist in a population, the density of which is below the threshold.

(3) In other special cases investigated when either immigration or birth is operative in the supply of fresh individuals, as well as in the general case, only one steady state of disease is possible. To reach this state the population must be of a certain density which will be determined by the functions characterising the infectivity, morbidity, etc., of the disease.

(4) Increase of the immigration rate or of the birth-rate results in an increase in the rate of infection of the healthy individuals and also in the percentage rate of infection, the percentage of sick, and in the percentage mortality from the disease. This result is, of course, a necessary consequence of our assumption that the disease is the only cause of death.

(5) More particular results have been obtained by substituting constants in the place of the undetermined functions assumed in the general theory. Further, under these conditions the nature of the steady states has been more fully investigated and it has been shown that in all cases, except one, the steady states are stable ones. In the exception, a disturbance would result in purely periodic oscillations about the steady state.