AN ATTEMPT TO DETERMINE THE ABSOLUTE NUMBER OF RATS ON A GIVEN AREA

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(*With* 3 *Figures in the Text*)

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1. INTRODUCTION

ONE of the most interesting problems for the ecologist is the estimation of the density of a particular animal species and in an attempt to determine this a system of trapping is among the devices most commonly employed. The reaction between a number of traps and a population of animals is essentially a special case of the predator-prey relationship; and perhaps it would not be too much to say that the experimental study of this trap-animal reaction is fundamental to the development of quantitative ecology in the field. The proper procedure would be to formulate a theory of trapping in the simplest terms possible and then to experiment with a given number of animals under known conditions. On the comparison of the results with the equations deduced from theory would depend whether the hypothesis be accepted or recast. The observations discussed in this paper were made in order to see whether any consistent results could be obtained by means of a standardized trapping method: they are not experiments in the sense we have outlined since the number of animals at risk was unknown. But, although a number of details will be noticed in which, from this point of view, an improvement or economy of design might have been achieved, the design as a whole fulfilled certain essential conditions of such an experiment. It is interesting to observe that the arithmetical analysis of this data has not revealed any result which

is inconsistent with the fundamental hypothesis. Logically this does not mean that its truth is to be accepted; indeed it would be surprising if such an elementary theory should prove a sufficient explanation of what must necessarily be a most complex relationship. The most that can be said of these results is that they appear promising, and it is in the hope of stimulating further work on the lines we have indicated that they are discussed in some detail.

2. Field observations

The field observations were carried out in Freetown, Sierra Leone, during the dry season in February and March 1937. An area of 22·5 acres, defined by the ordinates of the survey map, was chosen as being a typical block of houses occupied by natives. It contained, as will be seen from the map (Fig. 1), no open spaces such as, for example, parks, railway sidings or foreshore, and was inhabited for the most part by a more intelligent type of native than other possible quarters of the town. This is an important point, since the success of an extensive trapping experiment will depend on the intelligent co-operation between assistants and inhabitants. Although the possibility of interference with the traps by the natives cannot be wholly eliminated, we consider that in the present instance this disturbing factor was reduced to a minimum.

The experiment was carried out in the following way. A plan was made and the area then divided into two roughly by the line Lewis Street—George Street West. Scattered over the half-area below the division line 35 houses were chosen from the plan, and on the first evening three traps were set in each house, left for the twelve hours of darkness and collected in the morning. The next night 35 houses in the other half were similarly treated. On the third night a return was made to the bottom half of the plan; on the fourth to the top half and so on alternately up to the sixth night. 35 new houses were trapped on each occasion and these were chosen so far as was possible adjacent to those trapped on the night when the half-area was previously visited. The buildings varied in size, ranging up to three stories, and the three traps were distributed among the various floors. There was then a pause for one night and on the eighth day the rotation of sites was restarted, wherever possible using the same houses as were trapped during the first week. If for any reason a particular house could not be revisited, an alternative one was substituted in its stead. The whole experiment lasted for a period of six weeks, and during each week 630 traps were set in 210 houses.

The traps were of the "breakback" variety, which is generally considered to be the most efficient, and only one animal could be taken in each. They were made by the French firm, "Manufactures des armes et des cycles", Loire, and consisted of two semicircles of stout wire joined across the diameter by a spring. When set a circle is formed with the bait on a trigger in the centre and the two semicircles spring together when the trigger is released. Slices of

cassava (*Manihot utilissima*) were employed as bait. The actual process of setting and collection had to be entrusted to native assistants and from D. H. S. D.'s. experience of them we are reasonably certain that the work was efficiently carried out. They also entered in a book the results from each house and there
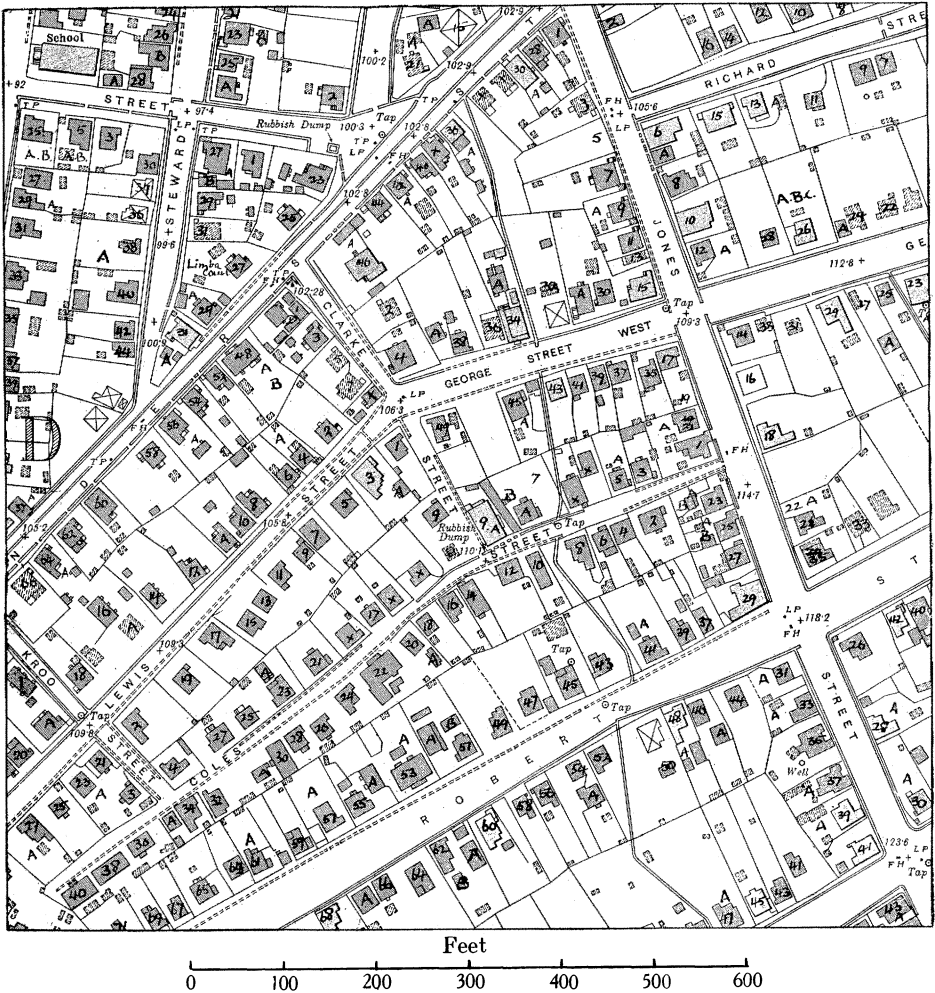
Fig. 1. Map of the area trapped. (Reproduced by permission of the Director of Surveys, Freetown.)

are a few indications of possible errors in bookkeeping, e.g. rats entered as being trapped at the wrong address. This is however a small matter, as we are not concerned with the results from the individual houses, but rather with the total catch. This was checked in the laboratory where the rats were typed, sexed and so on by D. H. S. D. There remains the question of those traps, either with or without bait, which were found sprung and containing no rat or other

animal. Undoubtedly the greater proportion of these were sprung either accidentally by members of the household, stray dogs, cats, hens, etc., or by the rats themselves who managed to avoid capture: but also a number may actually have trapped rats, which were afterwards either thrown away by the inhabitants or eaten, for example, by cats. Both of these latter alternatives were reported to have occurred on three occasions during this series, and it is always possible that further instances may have been overlooked by the assistants or concealed from them by the inhabitants concerned. But such sources of error are inherent in the conditions under which this experiment was done, and provided this accidental or purposeful sabotage—if one might so term it—remains on a relatively small scale, allowance can always be made for it in the final calculations. It is most unfortunate that we have no records for this series of the number of such negative-sprung traps and, as will be seen later, we have been compelled to adopt an average figure derived from a similar type of experiment on another area in Freetown. Possibly we have painted the picture blacker than it actually was: in our judgement the figures reported in this paper were the results of efficient trapping and such errors as may have occurred were relatively unimportant.

The sum of the first two nights' results from 210 traps set in 70 houses represents the first trapping of the whole area: the sum of the third and fourth nights' the second trapping: and so on. The results are given in Table 1. The most frequent type to be captured was *Rattus rattus*; but in addition a number

Table 1

Trapping no.	Number trapped						Weekly total of		Total no. R. rattus trapped
	R. rattus	Other species					R. rattus	Other species	
		RN	MM	C	M	Total			
1	49	7	3	.	.	10			
2	32	4	3	.	.	7			
3	31	5	7	.	.	12	112	29	112
4	34	5	4	.	.	9			
5	16	8	1	.	.	9			
6	33	7	2	.	.	9	83	27	195
7	22	5	1	.	.	6			
8	27	4	5	.	.	9			
9	17	5	11	.	.	16	66	31	261
10	19	1	3	1	.	5			
11	18	10	3	.	1	14			
12	16	3	3	1	.	7	53	26	314
13	18	2	2	.	.	4			
14	12	1	2	.	.	3			
15	14	1	5	.	.	6	44	13	358
16	12	3	2	1	.	6			
17	17	3	2	.	.	5			
18	7	2	5	.	.	7	36	18	394

210 traps were set on each occasion.

RN = *Rattus norvegicus*   C = *Crocidura*
MM = *Mus musculus*   M = *Mastomys*

of traps were occupied by other species, by far the greater part being *R. nor-vegicus* and *Mus musculus*. From the weekly totals it is seen that these are relatively much less numerous than *Rattus rattus* and this latter type may be regarded as the principal rodent infesting this block of property. In order to avoid any misconceptions it might be as well to point out that they are not confined to the houses. A fortnight after this series was ended the area was treated with the same rotation of sites, only the traps were set in the compounds instead of in the houses. The number of traps set was 630 and 32 *rattus* were captured; a figure which agrees very well with the last weekly total for the
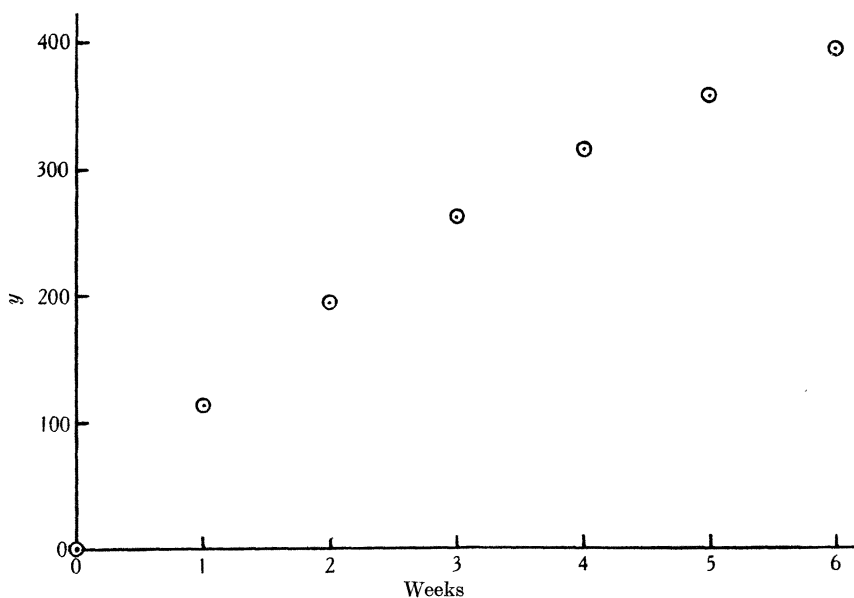

Fig. 2. The total number of *R. rattus* (y) which were trapped plotted as a function of time.

house-trapping, namely 36. The last column of Table 1 gives the total number of *rattus* trapped up to the end of each week, and when these figures are plotted as a function of time, it will be seen from Fig. 2 that they form an extraordinarily smooth curve. It was this suggestion of an underlying law and order that prompted a more detailed analysis.

3. General conceptions

Reduced to essentials, a number of animals is imagined to start their search for food at different points over an area. Supposing that in the type of animal society we are considering each individual searches independently from the others, the movements of the population may be said to be unorganized or in other words at random. During their search a certain number of traps

are encountered. This conception of a number of individuals moving over a topographic field and suffering a number of random collisions with other animals or objects in their environment, has the merits of simplicity and has been employed by many authors, e.g. Lotka (1925) and Volterra (1931), in the mathematical treatment of population questions. As Lotka (1925, p. 358) has pointed out: "we might seek to develop, for such a system, a discipline of statistical mechanics similar to that which the physicist has developed to deal with the kinetic theory of gases and allied problems."

In the type of system dealt with here, there are in reality two separate areas to consider: the area bounded by the extreme limits of the individual paths of search, within which the population may be said to be moving at random, and the area within which all the traps lie. In the case of an island, for instance, it is easy to see that the two areas can be made to coincide and the total population will then be exposed to risk. But where there are no topographical features to form a barrier to the movements of the individuals and when the same trap-boundaries are used repeatedly, the relation between the two areas becomes of some importance. The area of search for food over a period of time will depend on the habit of the species; whether it be migrant or having some fixed point such as a nest or lair to which it returns. In the case of the rat when the population is in a settled condition—neglecting, that is to say, the migratory movements which are reported to occur from time to time—the individuals leave their holes and return again to the same point or at any rate a point very close to where they started. By making the dimensions of the trap area large relative to the average radius of movement of a rat, it is thus possible to include within its bounds, as in an imaginary island, an unknown number of individuals. The overlap, which must always occur with surrounding areas, can now be considered negligible. The experience of Petrie & Todd (1923) in Egypt, where R. rattus were trapped alive, marked and then released, was that the movements of recaptured animals over a period of three months were limited, consisting for the most part of oscillations between two or three adjacent houses. They noted also that intensive trapping did not apparently disturb the population and that the broader streets appeared to act as a natural barrier to their movements. Although we can produce no definite measurements in support of the statement, there is no reason to suppose that the movements of R. rattus in Freetown were any different from those of their brethren in Egypt. This point will be returned to later in the section devoted to the arithmetical analysis of the results: for the moment it will be assumed that the furthest distance reached by any one rat during its search for food was small compared to the dimensions of the trapping area.

There is in addition another important point to be considered; whether the population at risk was distributed at random over the area. During a week 210 houses were trapped and up to three rats could be captured in each. If H = the number of houses and R = the number of *rattus* trapped during any

one week, the mean number of rats per house $= R/H = m$. Then under the hypothesis of a random distribution, the number of houses which should have 0, 1, 2 and 3 rats can be calculated by means of the successive terms

$$He^{-m}\left(1, m, \frac{m^2}{2!}, \frac{m^3}{3!}\right).$$

In Table 2 are given the number expected from this Poisson series, together with the numbers observed. The first two weeks' results are tabulated separately; while the remaining weeks have been added together in order to obtain

Table 2

No. rattus per house	Week 1 112 *rattus*		Week 2 83 *rattus*		Weeks 3, 4, 5 and 6 199 *rattus*	
	Obs. no. houses	Exp. no. houses	Obs. no. houses	Exp. no. houses	Obs. no. houses	Exp. no. houses
0	129	122·3	136	140·5	656	661·8
1	54	65·5	65	55·8	169	157·0
2	20	17·6	6	11·1	12	18·6
3	6	3·1	2	1·5	2	1·5
Total	209	208·5	209	208·9	839	838·9

$$\chi^2 = 3\cdot743 \qquad \chi^2 = 3\cdot340 \qquad \chi^2 = 2\cdot819$$
$$n = 1 \qquad\qquad n = 1 \qquad\qquad n = 1$$
$$P = <0\cdot10, >0\cdot05 \quad P = <0\cdot10, >0\cdot05 \quad P = <0\cdot10, >0\cdot05$$

Total $\chi^2 = 9\cdot902$; $n = 3$; $P = <0\cdot02, >0\cdot01$

In calculating χ^2 the 2- and 3-*rattus* houses were added together.

figures of a convenient magnitude in the 2-3-rat classes. Three houses were reported as having "rats" thrown away by the householders or eaten by cats, and since it is impossible to know whether these referred to *rattus* or *norvegicus*, they were left out of the calculations. The agreement between the expected and observed numbers is fairly close and the values of χ^2 fall just below the conventional level of $P = 0\cdot05$ in each of the three distributions. However when the three values are added together giving $\chi^2 = 9\cdot902$ and $n = 3$, $P =$ just $< 0\cdot02$; so that there is a suggestion of some slight disturbing influence on the random distribution. Possibly this may be due to errors of book-keeping or to the negative-sprung traps which have been previously mentioned; since for the purposes of this test we have assumed the complete efficiency of all the traps. Whatever the reason, the degree of departure from randomness is not sufficient to cause us to abandon any further application of the theory to these figures.

Lastly, there is the question of the relationship between the minimum number of hours during which every individual member of the population will have been exposed to risk and the time during which the area was trapped each night. Obviously in the design of any experiment it is desirable to have a conformity between these two times similar to that between the two areas discussed previously. Very little seems to be known about the activity of

the rat in the wild state. It has been shown by Richter (1927) that white rats in the laboratory have approximately a four-hourly rhythm of activity when food is present in the cages; when it is absent this period becomes shorter and Richter suggests that this restlessness and activity is associated with spasmodic contractions of the empty stomach. Supposing that the same conditions hold good in the field; and taking into consideration that the wild rat must search for food: then it appears a fair assumption to make that during a night every individual—apart from the young in the nests—will pass some period of time on the surface and therefore at the risk of being trapped. We are well aware that this is rather a sweeping assumption, to which a number of objections can easily be raised: but in the present state of our knowledge we submit that, for the purposes of this argument, it is good enough as a first approximation to the truth.

To summarize this section: the conception has been formed of an area being searched in a random fashion by a population which remained circumscribed over the period of the experiment owing to its habit of life. Moreover it is assumed that during any one night every individual rat inhabiting the half-area trapped will have been exposed to the risk of capture.

4. Theoretical

The area defined by the map ordinates, to which strictly speaking should be added the floor area of the second and third stories, will be regarded as a unit area and the number of hours of darkness elapsing between setting and lifting the traps as a unit of time.

Let a quantity p be defined as the probable value of the path an animal can traverse without colliding with a trap, i.e. the mean free path. Then, by the well-known theorem, the probability P that a single animal moving among a number of traps at rest will traverse a distance x without a collision, is

$$P = e^{-x/p}. \qquad\qquad ......(1)$$

Suppose that on the unit area there are T traps. Let the area be divided into T small squares, each of which on the average contains one trap. Let x be the length of the side of each of these squares; then one trap is contained in an area of x^2 and x is also the average distance between adjacent traps. It follows that $Tx^2 = 1$. Let r be the radius of the field of influence surrounding each baited trap and suppose that any animal which is within this imaginary circle will respond to the stimulus received through its senses by moving towards the centre. Then an animal may be said to have discovered or collided with any trap lying within a distance r from itself. If it moves over a distance x, which for the sake of simplicity is taken to be a straight line, it will search an area $2rx$ and will collide with any trap lying within this parallelogram. Since one trap is contained in the area x^2, the probability that there is a trap

on the area $2rx$ is $2rx/x^2$ and therefore the probability of there being no trap, i.e. no collision, is $1 - 2rx/x^2$. From (1)

$$e^{-x/p} = 1 - \frac{2r}{x},$$

or, expanding $\log_e \left(1 - \dfrac{2r}{x} \right)$ in series,

$$\frac{x}{p} = \frac{2r}{x} + \frac{1}{2} \left(\frac{2r}{x} \right)^2 + \frac{1}{3} \left(\frac{2r}{x} \right)^3 + \text{etc.}$$

In the conditions of an experiment like the one we are considering, r must be small compared with the average distance between adjacent traps. It follows that $2r/x$ is a small quantity compared with unity and therefore its square, cube, etc. can be neglected. The expression above then reduces to

$$\frac{x}{p} = \frac{2r}{x},$$

and since $Tx^2 = 1$ $\qquad\qquad\qquad p = \dfrac{1}{2rT}.$ $\qquad\qquad\qquad$ ......(2)

Although its movement may be intermittent, an animal during a unit of time will cover a certain distance which can be termed its velocity v. The probable number of collisions which it will make is

$$\frac{v}{p} = v2rT.$$

Suppose that there are N animals on the area and that all these individuals are exposed to risk during some period of a unit of time. Now it will be very unlikely that the quantities $v_1, v_2, v_3, ..., v_N$ will all be the same, but it is convenient to make the simplifying assumption that they are. When in the molecular theory of gases the velocities of the individual molecules are assumed to be distributed according to the Maxwellian law, it is found that the equation defining the probable value of the mean free path differs only by a constant ($\sqrt{2}$) from that arrived at when the velocities are assumed to be the same. We can therefore say either that the N individuals move with the same velocity V; or, better, regard the quantity V as an average value defining some unknown distribution, equivalent to the Maxwellian,[1] which is assumed to be constant and independent of any factor such as the age distribution of the population. The N animals will therefore in a unit of time suffer $V2rTN$ collisions with traps.

[1] Working in two dimensions, the equivalent distribution to the Maxwellian would be that the number of animals having a velocity between v and $v + dv$ is assumed to be given by

$$dN = 2Nh^2v \, e^{-h^2v^2} \, dv.$$

As a matter of interest it might be mentioned in passing that we have recently observed this distribution to be realized very closely in a similar type of problem, namely the distances, measured in a straight line, between the points at which long-tailed field-mice (*Apodemus sylvaticus*) were trapped alive and subsequently recaptured.

In general it will not be true that every collision results in the capture of an animal. Even if the traps are mechanically efficient and properly set, it may still happen that owing to the design of the trap an animal, in order to spring it, must approach in a particular way. Let c be the fraction of collisions which result in capture; then c may be called a measure of the efficiency of the traps. In future we shall employ the word "collision" in the sense of "effective collision".

Suppose for the moment that trapping is a continuous process which is not terminated at the end of each unit of time by the removal of the traps. Let y be the total number of animals trapped up to the time t and N be the initial population on the area. In addition assume that the population does not increase through young leaving the nest and immigration, or decrease through normal deaths and emigration during the time of the experiment. Then at the time t there will be $N-y$ animals and $T-y$ traps left. In the interval of time $t+dt$ the $N-y$ animals will make $cV2r\,(T-y)\,(N-y)\,dt$ collisions with the remaining traps and this quantity must equal the dy animals captured. We have, therefore, putting the constant $cV2r=s$,

$$\frac{dy}{dt} = s\,(T-y)\,(N-y), \qquad\qquad \ldots\ldots(3)$$

which gives on integration

$$\frac{T-y}{N-y} = \frac{T}{N}\,e^{-s\,(N-T)\,t}. \qquad\qquad \ldots\ldots(4)$$

In the case of a planned experiment, where the initial number of animals is known, this equation should express the interaction between animals and traps, if the assumptions made as to the random nature of collisions and the constant mean velocity of the individuals hold good. But in the absence of any knowledge about the value of N and given only the value of y at the end of one unit of time, as in the present series of results, little use can be made of it and we must proceed somewhat differently.[1]

In the differential equation (3) instead of the variable $(T-y)$ put $T=$ the number of traps set and keep it constant. This is the same thing as assuming that the "breakback" traps, which can catch only one individual, have become

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[1] In the first part of this theory which is merely an adaptation in two dimensions of the elementary kinetic theory of gases, we have borrowed freely from various sources, e.g. Lotka (1925) and Mellor's *Higher Mathematics for Students of Physics and Chemistry*, and reference may be made to these or to any textbook of physical chemistry for further details. It should be noted that if rats be regarded as prey and traps as predators, both equations (4) and (5) can be derived immediately from the well-known Lotka-Volterra system of simultaneous equations, $dN_1/dt = (a_1 - b_1 N_2)\,N_1$, $dN_2/dt = (-a_2 + b_2 N_1)\,N_2$, where a_1, a_2, b_1, b_2 are constants and N_1 and N_2 are the number of prey and predators respectively: in the case of (4) by putting $a_1 = a_2 = 0$ and $b_2 = -b_1$; and in the case of (5) $a_1 = 0$, $dN_2/dt = 0$. But it seemed advisable to give the development of this special case of the predator-prey relationship in full for the sake of clarity, and in order that the biological significance which is attached to the various constants may be of assistance in the design of any future experiment.

a type of cage-trap, catching any number, and that all the collisions which are made by chance with a trap already occupied result in capture. Putting $sT = k$

$$\frac{dy}{dt} = k\,(N-y),$$

whence
$$y = N\,(1-e^{-kt}). \qquad\qquad \ldots\ldots(5)$$

It follows from this equation that during one unit of time there would occur $N\,(1-e^{-k})$ collisions and this quantity would represent the number trapped if all the collisions were able to take place. Let

$$1-e^{-k} = k'.$$

The average number of collisions per trap is $k'N/T$ and, since it has been assumed that the collisions take place at random, it follows from the Poisson distribution that the proportion of traps which suffer 0, 1, 2, etc. collisions will be given by

$$e^{-k'N/T}, \quad \frac{k'N}{T}e^{-k'N/T}, \quad \frac{1}{2!}\left(\frac{k'N}{T}\right)^2 e^{-k'N/T}, \text{ etc.}$$

The first collision results in the trapping of an animal and any second or more collisions on that trap are ineffective. Those animals which might have been captured at this point are therefore free to collide with other unoccupied traps. But if $k'N < T$, the proportion of traps which would be expected to suffer two or more collisions is small compared with the proportion which suffer none or only one: therefore the number of animals which collides by chance with an occupied trap is small and the possibility that these animals manage to collide with unoccupied traps during the time left to them, might be considered negligible. An imaginary numerical example will perhaps make this point clear. If $k'N/T = 0.281$ and $T = 200$, the expected number of traps which will suffer no collision is 151·0; one collision, 42·4; two collisions, 6·0; and three collisions, 0·6. Had all these resulted in capture we should have expected 56 animals to have been trapped; actually only 49 could have been owing to the type of trap. There were therefore seven animals which during the course of the night collided with traps already occupied and were then free to make contact with the remaining unoccupied ones. If we assume, taking into account their velocity and the average distance between traps, that it is very unlikely that they will have managed to do so during the time left before the night's experiment was ended, then, putting $R =$ the number of *rattus* captured, the proportion of unoccupied traps,

$$\frac{T-R}{T} = e^{-k'N/T}. \qquad\qquad \ldots\ldots(6)$$

With regard to the present experiment there are two further complications which have to be taken into account: a certain number of traps were occupied

by other species and others were found sprung and containing no animal in the morning. Both these factors act in the same way by preventing *rattus* being caught by these particular traps. Apart from those which actually caught *rattus*, the initial number of traps (T) is being decreased throughout any one night by the action of these outside agencies. Let b equal the number of traps occupied by other species and found negatively sprung; then provided that b be relatively small compared with T, it will be sufficiently accurate for our purpose to assume that the number of traps set, which we have taken as constant in equation (5), can be described by a decreasing linear function of time, say $T - bt$. It follows that the average number of traps per unit time which are free to catch *rattus* is $T - b/2$. Let $b/2 = n$: then had there been only *rattus* present on the area and no negative sprung traps, we should have expected the n traps to have caught the same proportion as the $T - n$, i.e. $nR/T - n$. For instance on the first trapping of the area, $T = 210$, $n = 26$ and 49 *rattus* were trapped; $49/184 = 0\cdot2663$ and we should have expected $26 \times 0\cdot2663$, say approximately seven *rattus* to have been caught in the 26 traps. We can apply to these individuals the same arguments used in the case of those rats which collided with traps already occupied by their own species. The proportion of traps unoccupied by *rattus* is $T - n - R/T - n$ and from (6)

$$T \{\log_e (T-n) - \log_e (T-n-R)\} = k'N. \qquad \ldots\ldots(7)$$

It will be seen from the foregoing argument that this equation can hold good only in certain limited conditions. In the first place, the type of trap which is commonly employed as being the most efficient and which can only catch one individual, raises a number of grave difficulties. It might be suggested that it is only when $k'N/T$ is a relatively small quantity, e.g. $< 0\cdot4$ or $0\cdot5$, that it is justifiable to assume the improbability of the individuals who collided with occupied traps, being able to collide with other, unoccupied ones during their remaining search for food. These figures are equivalent to 67–60 % of traps remaining unoccupied and any experiment giving a lower percentage would be suspect. But it is impossible to be dogmatic on this point in the present state of our knowledge and these suggestions must be taken as merely tentative. Lastly the species trapped must be either the only or at least the preponderating type on the area. If the number of traps occupied by other species becomes relatively large, or several species are caught in approximately equal numbers, the conditions are changed and the problem becomes one of the competition for traps between two or more populations, each having different velocities.

5. ARITHMETICAL ANALYSIS

The highest value of $k'N/T$ which these results gave was 0·3097 and *R. rattus* was the preponderating type on the area: we shall conclude therefore that a quantity, which was proportional to the population each time the area was trapped, can be calculated by means of the expression

$$T\{\log_e(T-n)-\log_e(T-n-R)\}.$$

It follows that if a suitable function to describe the population can be found, it should be possible to calculate a value for k'. Apart from the loss due to trapping, the population will lose in numbers through the normal death-rate and emigration; and it will gain through immigration from sources outside the area and also the number of young leaving the nest to enter the population at risk. So far as our observations went, the rats of Freetown as a whole showed no violent fluctuations in numbers: it appeared a relatively stable population. Since this experiment lasted for only six weeks, the simplest assumption to make is that during this period immigration and young recruits balanced on the average the loss due to emigration and normal deaths. Then if N_0 be the original number of *rattus* on the area and y the total number trapped up to any particular time t

$$N_t = N_0 - y_t,$$

and therefore from (7), putting

$$T\{\log_e(T-n)-\log_e(T-n-R)\} = z, \qquad \ldots\ldots(8)$$
$$z = k'N_0 - k'y.$$

That is to say, the values of z should fall on a straight line when plotted against the values of y; $k'N_0$ being the value of z when $y=0$, and k' being the tangent of the angle which the line makes with the y axis. The next step is to fit a straight regression line to the data and to test its goodness of fit by the customary statistical methods. In doing so, we are testing not only whether the assumption of a balanced population is correct, but also the validity of the various assumptions made in section 3. If any one or all of these were to fail, we should expect either that the points of z would fall on a curve relative to the y axis or that no simple functional relationship between z and y could be established.

In calculating the values of z from the observed data by means of equation (8), it is unfortunate, as was mentioned in a previous section, that no figures are available for the number of negative-sprung traps. On another area in Freetown, which was trapped in a similar fashion to the present one, it was observed that in one week during which 630 traps were set overnight, 128 or 20·3 % were found in the morning sprung and containing no rat or other animal. We have assumed this to be an average figure which might be expected in a trapping experiment done under similar urban conditions. The estimate of n for each trapping is thus half the sum of 42 plus the number of traps

observed which were occupied by other species. The estimates of z being made from the proportion of unoccupied traps are subject to large sampling errors (Greenwood & Yule, 1917; Fisher, 1935) and therefore a considerable scatter of the observations will be expected in the graph (see Fig. 3). The sampling variance of an estimate of z is given by

$$\sigma_z^2 = \frac{T^2 R}{(T-n)(T-n-R)},$$

and the square root of this quantity is the standard error. In columns 4 and 5 of Table 3 are given the values of $z \pm$ s.e. derived from the data together with those calculated from the regression line, fitted by the Method of Least Squares,
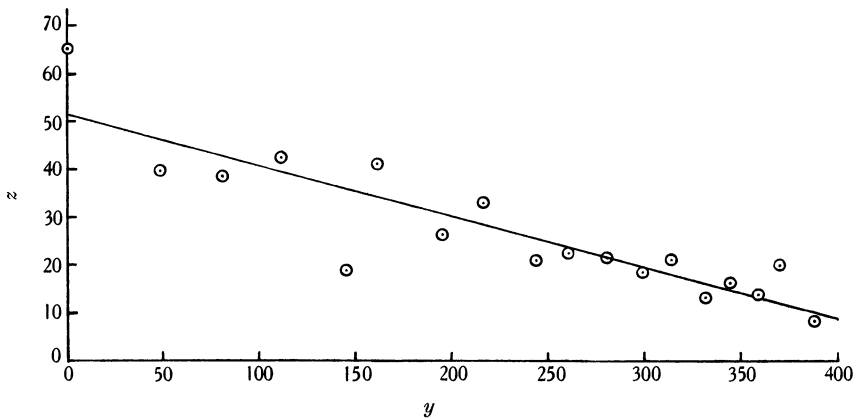
$$z = 51\cdot26737 - 0\cdot105642\ y.$$

Fig. 3. The observed values of z plotted against y. The equation for the straight line is $z = 51\cdot26737 - 0\cdot105642 y$.

The mean sampling variance of the values of z calculated from the observations can be used as a test for the goodness of fit of the regression line, by comparing it with the mean square deviation of the observed values from those calculated by means of the equation. For if the departure from linearity is at all marked, the mean square deviation from the regression line will be significantly greater than the mean variance expected from the errors of random sampling. The mean variance of the 18 values of z is 33·2269 and the sum of the squares of the deviations of the observed values from those calculated by means of the equation, is 735·47669. Since two constants have been calculated from the data, $18 - 2 = 16$ degrees of freedom are left and thus the mean square deviation from the regression line is 45·9673. If the estimate of the mean variance of the observed values of z were exact, we could test by means of

$$\frac{\chi^2}{16} = \frac{45\cdot9673}{33\cdot2269},$$

whence

$$\chi^2 = 22\cdot13.$$

Table 3

Trapping no.	$T - n$	y	Observed $z \pm$ S.E.	Calculated z	Expected no. *rattus* trapped	Observed no. *rattus* trapped $= R$
1	184	0	$65\cdot03 \pm 9\cdot33$	$51\cdot267$	$39\cdot9$	49
2	185	49	$39\cdot88 \pm 7\cdot06$	$46\cdot091$	$36\cdot5$	32
3	183	81	$38\cdot98 \pm 7\cdot01$	$42\cdot710$	$33\cdot7$	31
4	185	112	$42\cdot65 \pm 7\cdot33$	$39\cdot435$	$31\cdot7$	34
5	184	146	$19\cdot10 \pm 4\cdot78$	$35\cdot844$	$28\cdot9$	16
6	185	162	$41\cdot26 \pm 7\cdot19$	$34\cdot153$	$27\cdot8$	33
7	186	195	$26\cdot43 \pm 5\cdot64$	$30\cdot667$	$25\cdot3$	22
8	184	217	$33\cdot32 \pm 6\cdot42$	$28\cdot343$	$23\cdot2$	27
9	181	244	$20\cdot71 \pm 5\cdot03$	$25\cdot491$	$20\cdot7$	17
10	187	261	$22\cdot50 \pm 5\cdot16$	$23\cdot695$	$20\cdot0$	19
11	182	280	$21\cdot87 \pm 5\cdot16$	$21\cdot688$	$17\cdot9$	18
12	185	298	$19\cdot00 \pm 4\cdot75$	$19\cdot786$	$16\cdot6$	16
13	187	314	$21\cdot25 \pm 5\cdot01$	$18\cdot096$	$15\cdot4$	18
14	188	332	$13\cdot85 \pm 4\cdot00$	$16\cdot194$	$13\cdot9$	12
15	186	344	$16\cdot43 \pm 4\cdot39$	$14\cdot927$	$12\cdot8$	14
16	186	358	$14\cdot01 \pm 4\cdot04$	$13\cdot447$	$11\cdot5$	12
17	187	370	$20\cdot02 \pm 4\cdot86$	$12\cdot180$	$10\cdot5$	17
18	185	387	$8\cdot10 \pm 3\cdot06$	$10\cdot384$	$8\cdot9$	7
Total					$395\cdot2$	394

$y =$ Total number of *R. rattus* caught up to the time of each trapping.
$z = 210 \{\log_e (T - n) - \log_e (T - n - R)\}$

$\chi^2 = 16\cdot792$
$n = 16$
$P = \; < 0\cdot50, \; > 0\cdot30$

For 16 degrees of freedom, $P = \; < 0\cdot20, \; > 0\cdot10$ or in other words a value of χ^2 as large as $22\cdot13$ would be expected in about 10 % of such cases. Since the mean variance also has a sampling error, there is really nothing in it and the straight regression line gives a perfectly satisfactory fit to the data.

In columns 6 and 7 of Table 3 are given the observed number of *rattus* caught at each trapping of the area, together with the number expected from theory. These latter figures, allowing for the same number of traps occupied by other species and negatively sprung, are calculated from the values of z in column 5 by means of the expression

$$\text{Expected number of } rattus = (T - n)(1 - e^{-z/T}).$$

The agreement is very good indeed; $\chi^2 = 16\cdot792$ and for 16 degrees of freedom P lies between $0\cdot30$–$0\cdot50$. As judged by these statistical tests, there is nothing in this data which is inconsistent with the various assumptions made during the course of the argument. Whether they are sufficient remains to be seen from further work on the lines indicated in the introduction to this paper.

An estimate can now be made of the two unknown constants, N_0 and $s = cV2r$. The calculated value of $k' = 0\cdot105642$; $k'N_0 = 51\cdot26737$ and therefore the probable number of *rattus* on the area at the start of the experiment was

$$N_0 = 485.$$

Since $k' = 1 - e^{-k}$, $k = 0\cdot111649$; the number of traps set was 210 and since $k = sT$

$$s = 0\cdot00053166.$$

As a check on the number of *rattus* which should have been caught during each unit of time, it is now interesting to use equation (4) when $t = 1$, i.e.

$$\frac{T - y}{N - y} = \frac{T}{N} e^{-s(N-T)}.$$

The average number of traps which could catch *rattus* during any particular unit of time, namely $T - n$, is used in this equation instead of the actual number set (T). For the first trapping of the area, $T - n = 184$; inserting this together with the above values of N_0 and s, and solving for y, the expected number of *rattus* $= 40 \cdot 2$. Actually 49 were trapped; so that at the time of the second trapping $N = 485 - 49 = 436$; $T - n = 185$, whence $y = 36 \cdot 8$. The calculation can be carried out in a similar fashion for the remaining 16 trappings. As shown in Table 3, the expected numbers calculated by the previous method for the first and second trappings were 39·9 and 36·5 respectively, so the agreement is very close indeed.

The last step is to estimate the errors which must be attributed to the calculated values of N_0 and s. If Z be the value calculated by means of the regression line for any particular value of y and z be the observed value, then the mean square deviation from the regression line, n being the number of observations and S the symbol for summation, is

$$\sigma^2 = \frac{S(z - Z)^2}{n - 2} = 45 \cdot 967293. \qquad \ldots\ldots(9)$$

Then the variance (V) of k' is given by

$$V(k') = \frac{\sigma^2}{S(y - \bar{y})^2},$$

where $\bar{y}$ is the arithmetic mean of the values of y. The square root of this quantity is the standard error of k' and was found to be 0·014009. Then since

$$1 - k' = e^{-k},$$

it can be shown that $\qquad V(k) = \frac{1}{(1 - k')^2} V(k')$,

whence the standard error of $k = 0 \cdot 015664$. Since $k = sT$ and $T = 210$ is known exactly

$$s = 0 \cdot 00053166 \pm 0 \cdot 00007459.$$

We are greatly indebted to Dr J. O. Irwin for showing us how to arrive at the error of N_0. Write the equation for the straight line in the form of $z = \bar{z} - k'(y - \bar{y})$, where $\bar{z}$ and $\bar{y}$ are the means of the observed values of z and y respectively. Since $k'N_0$ is the value of z when $y = 0$

$$k'N_0 = \bar{z} + k'\bar{y},$$

$$N_0 = \frac{\bar{z}}{k'} + \bar{y}.$$

Whence
$$V(N_0) = V\left(\frac{\bar{z}}{k'}\right) = \frac{V(\bar{z})}{k'^2} + \frac{\bar{z}^2 V(k')}{k'^4}$$

or
$$V(N_0) = \frac{\sigma^2}{k'^2}\left\{\frac{1}{n} + \frac{\bar{z}^2}{k'^2 S(y - \bar{y})^2}\right\},$$

where σ^2 is given by equation (9) above and n is the number of observations (18). Calculating this quantity and taking the square root, we have

$$N_0 = 485 \pm 37.$$

Now we might wish to test whether this estimated number of *rattus* is significantly different from some hypothetical number N'. The hypothesis to be tested is that the deviation $485 - N'$ is distributed normally about zero with a standard deviation of 37, which estimate is based on 16 degrees of freedom. Using "Student's" t test (Fisher, 1935)

$$t = \frac{485 - N'}{37}.$$

From the tables of the distribution of t, for 16 degrees of freedom t has a 5 % chance of lying outside the limits $\pm 2\cdot12$. Inserting this value of t in the equation

$$N' = 485 \pm 78.$$

Thus we can say that, assuming the validity of this theory of trapping, the fiducial probability is 95 % that there were between 407 and 563 *R. rattus* on the area at the time when the experiment was started.

6. DISCUSSION

It is an interesting speculation to carry this elementary theory a step further. In the constant $s = cV2r$, the fraction c and the quantity $2r$ refer to the properties of the traps and provided that the type of trap and the method of baiting are unchanged, they can be taken as constant in all such experiments. The quantity V is, however, more complex. We have tended to assume that it is dictated by the food-requirements of the animal. But it is clear that it refers to all the causes of activity on the surface and thus may vary from experiment to experiment, not only with regard to the difficulty of obtaining food at different seasons or on different areas, but also on account of other factors, such as, for instance, the particular species having an increased activity during the mating season. But it is possible to imagine certain conditions, for example a contemporary series of experiments, in which we might feel justified in assuming that V for some particular species could be taken as being approximately of the same relative magnitude on all the areas trapped. Then using the same type of trap and the same unit of trapping time—the latter is a convenience rather than a necessity—and having an estimate of

the value of $cV2r$ from a series of trappings on some unit area, it is theoretically possible to calculate the probable population on another area which has only been trapped once—an immense saving of labour. Any difference in the size of the areas requires an adjustment in the value of $cV2r$, since its essential constituent $V2r$, or the mean area traversed during a unit of time by an individual, is expressed in terms of the unit area. If a_1 be the size of the latter, a_2 the size of any other area and T the number of traps set, then $cV2r\,Ta_1/a_2 = k$: since we have an estimate of the error of $cV2r$, it is therefore possible to find the value of $k' \pm$ s.e. which will apply to the second area. From the proportion of unoccupied traps z is calculated together with its sampling error and z/k' is then the probable population on the area. The error of this estimate, where σ_2 and $\sigma_{k'}$ are the errors of z and k' respectively, is given by

$$\sigma_N = \pm \frac{1}{k'} \sqrt{\left\{ \left(\frac{z\sigma_{k'}}{k'}\right)^2 + \sigma_z{}^2 \right\}}.$$

These errors are relatively very great: as an example suppose another area, which will be taken as being of the same size as our unit area for the sake of simplicity, had 210 traps set of which 50 were found to have caught *rattus* and $n = 0$. Then

$$N = \frac{57\cdot1061 \pm 8\cdot1009}{0\cdot105642 \pm 0\cdot014009}$$

$$= 541 \pm 105.$$

The percentage error is 19·4 compared with 7·6 which was obtained for the probable population on the unit area: the reason being that the latter is an average figure to the accuracy of which each of the 18 trappings has contributed its quotum of information. In the case of the single trapping, even if k' were known exactly, we would have $N = 541 \pm 77$; that is to say, more than two-thirds of the total error is due to the sampling errors involved in an estimate made from the proportion of unoccupied traps. The degree of accuracy which is obtained at any particular level of proportionality, depends on the number of traps set. Suppose that 50 traps had been set on another area and that $a_1/a_2 = 4\cdot2$, $n = 0$; then k' still has the same value. If 12 *rattus* were trapped—approximately the same proportion of unoccupied traps as in the previous example and also for the first trapping on our unit area—$z = 13\cdot7218 \pm 3\cdot9736$, $N = 130 \pm 41$ and the percentage error has risen to 31·5. With increasing proportions of unoccupied traps it rises still higher; for example with 88 % of traps unoccupied and 50 traps set, $z = 6\cdot3917 \pm 2\cdot6112$ and $N = 61 \pm 26$ or a 42·6 % error. These considerations affect not only this somewhat speculative application of an estimated value of $cV2r$ to the results from a single trapping, but also the analysis of any experiment designed on the same lines as that in Freetown. If this latter had been carried out on the scale of 50 traps to approximately 5 acres, it is very doubtful whether we

would have been able to establish any agreement between the observed results and those expected from theory.

There is, however, an improvement in the design of such experiments which follows logically from the argument and which would appear well worth the trouble of investigating. In discussing the employment of the single trap we have already touched upon the limitations which this imposes on the values of $k'N/T$. It is true that the latter can always be adjusted to the requisite magnitude either by increasing the number of traps or by leaving them in contact with the population for a shorter period of time. But if, instead of there being one trap at a certain point on the area, a group of three or four traps be set together at the same point, thus forming a trap-unit, many of the difficulties disappear. Theoretically this would permit of a wider range of values for $k'N/T$ giving consistent results, since up to three or four collisions with a trap-unit can now result in capture. Moreover, if the values of $k'N/T$ be such that the probability of there being more collisions than there are traps in the unit is very small indeed, then the conditions symbolized in equation (5) are realised and it follows that the number of animals trapped during a unit of time is proportional to the population or $R = k'N$. The estimate of $k'N$ is now based on a count of a definite number of individuals: a more satisfactory estimate than the less precise one derived from the proportion of unoccupied traps.

Finally it may be suggested that, if the purpose of a trapping experiment be to determine the density of a species at some particular time, it is somewhat unsatisfactory to adopt a method which involves the destruction of a greater part of the population. A system of live-trapping and marking is ecologically much sounder. It is to be hoped that the technique of this type of experiment can be developed along the lines suggested in the preceding paragraph, so that all the effective collisions with a live-trap unit result in capture. Then to take the simplest example of a constant population over the time of the experiment, if every animal captured be marked and released, the total number marked (m) up to the time of any particular trapping is known. Assuming that no deaths occur among the marked individuals and that both marked and unmarked are trapped with equal ease, the number unmarked is $N_0 - m$; then if u be the number of the latter caught at any trapping, $u = k'N_0 - k'm$; and the results are thus susceptible to the same type of arithmetical analysis as used in the present instance. But it is useless entering into details in the absence of any data and this is only a rough sketch of the type of experiment we have in mind. Moreover, further work on this trap-animal reaction may well show that the theory requires a more complicated mathematical treatment than the one employed here as a first approximation.

7. SUMMARY

The results from a series of trappings, all done on the same area in Freetown, Sierra Leone, have been analysed in the light of a theory of trapping, which is merely an adaptation of the elementary kinetic theory of gases. The development of this theory is given in full and the arithmetical analysis of the results has revealed nothing which is inconsistent with the fundamental hypothesis. The probable number of *R. rattus* on this area has been calculated and the errors involved in this type of estimate are discussed, leading to certain suggestions for the design of such experiments in the future.

8. ACKNOWLEDGEMENTS

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