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# THE RATE OF RECOVERY OF DECIMATED POPULATIONS OF BROWN RATS IN NATURE [1]

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The nature of population growth from a single pair of individuals to "population maturity" has been studied with various lower animals in stable laboratory environments. Very little is known, however, concerning the growth of populations in natural environments.

The breeding season gain of seasonal breeders has been measured in a number of wild species by comparing spring and fall densities. This gain, however, represents the rising phase of a normal annual cycle in a mature population rather than the growth or recovery of an undeveloped or suppressed population. Information is also available on the rate of increase of cyclic species, such as the snow-shoe rabbit, during the recovery phase of a ten-year cycle. This may possibly represent uncomplicated growth of a suppressed population; but at present we are unable to state whether it is growth toward a fixed asymptote, or a changing response to a cyclically shifting asymptote. Unpredictable and unmeasurable factors of the environment present difficulties to any study of population growth in nature except as the growing populations can be compared directly with mature populations exposed to the same environment, serving as controls.

The Brown Rat (*Rattus norvegicus*) appears to be a particularly favorable subject for studies of population growth. Unlike most species in the temperate zones, this animal breeds during every month and thus maintains a fairly stable population level throughout the year. Urban rats, furthermore, may segregate themselves into distinct population units coinciding with city blocks (Davis et al., Ms.). Such units permit the use of an experimental procedure, some units being used for experimental manipulation (reduction) while others are held undisturbed as controls. Interblock movements are of rare occurrence and hence immigration, a serious complicating factor in most population studies with wild animals, has no appreciable significance.

The aim of the present study was to determine the rate of recovery of decimated rat populations under natural conditions. For this purpose, block populations of Brown Rats were artificially reduced to fractions of their initial levels and then permitted to recover undisturbed, except for the usual repressive activities exerted by local residents. Repeated censuses were made of these experimental populations and of a number of undisturbed populations which served as controls. This work was done in Baltimore, Maryland, between July, 1944

[1] The work reported in this paper was conducted under a grant to The Johns Hopkins University by the Rockefeller Foundation, International Health Division, for research on rodent ecology. Parts of the field work were done under a contract, recommended by the Committee on Medical Research, between the Office of Scientific Research and Development and The Johns Hopkins University Medical School.

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and July, 1946. The intensive studies in residential blocks, which furnish most of the material, were done during the fall, winter, and spring of 1945–1946.

## Study Areas

Baltimore, located between the thirty-ninth and fortieth parallels of latitude, has a mild climate. Winter temperatures average 36° F. and fall below zero less than one day a year. Summer temperatures average 75° F. and exceed 90° an average of 22 days per year. Rainfall is rather evenly distributed throughout the year and averages 43 inches. Downtown sections of the city are characterized by row houses. Sanitary conditions and rat infestations are believed to be similar to those in other cities along the eastern seaboard of the United States.

Studies on population recovery were conducted in two types of rat habitat in Baltimore: public markets and residential communities.

*Public markets.* Four public markets in the central part of Baltimore were kept under observation for two years. Each market consisted of one or two low-roofed wooden sheds, 300 to 400 feet long and 55 to 75 feet wide (about ½ acre), surrounded on all four sides by paved streets, which on market days (three days a week) were cluttered with produce stands and tables.

Rat populations ranged from moderate to heavy (60 to 340 per shed) and were concentrated principally around poultry stalls and lunch counters. Food supplies were abundant though somewhat variable as a result of fluctuating market activity and semi-weekly washings. Rat harborage facilities were generally good but varied with the construction of stalls, drains and wall partitions. Cats were numerous but were generally ignored by the rats. Human activity kept rats under cover during the daytime but scarcely affected their activity at night, although

Fig. 1. Typical downtown residential area in Baltimore, showing alleys and row houses.

FIG. 2. Alley and back yards in typical downtown residential area of Baltimore, showing board fences, garages, junk piles and privies (near side of alley). Houses are of brick; extensions on the rear of houses are generally of wood.

the sheds were wide open and lighted at all hours.

*Residential communities.* The 34 residential blocks selected for study were grouped in a rather thickly inhabited part of the city, one mile northwest of the main business district. The houses, generally 2- or 3-story structures of brick, were arranged in solid rows facing the streets, with narrow back yards opening onto alleys in the rear (figs. 1 and 2). Blocks with shopping streets and industrial establishments were avoided in an attempt to make the area roughly homogeneous, but a number of corner stores and shops were inevitably included.

Rat populations in these residential blocks ranged from light to heavy (7 to 220 per block) and were unevenly distributed through yards, garages, and houses. Most of the rats (about 73 per cent) lived outdoors in burrows or trash piles.

Food materials, primarily garbage and food for pets, were generally abundant but often irregularly and sporadically available. From 10 to 45 per cent of the houses of a block had improper garbage disposal and thus provided reliable or occasional supplies of food for rats. Most blocks had from 1 to 3 untended trash piles with scattered garbage in the back yards. Harborage facilities provided by wooden fences, sheds, stairways, privies, junk piles, and broken concrete paving, and burrowing sites afforded by suitable protected soil were present in excess of usage in nearly all parts of the area. Dogs and cats were numerous in some blocks but seemed to affect the rat population only locally.

## METHODS

The procedure followed in all study areas consisted of the following steps: (1) a preliminary census or series of censuses, (2) reduction of the population through a poisoning or trapping campaign and (3) periodic post-campaign censuses.

*Public markets.* In the markets censuses were based on counts of live rats seen during standard observation periods at night. Long aisles, 4–8 feet wide, ran the entire length of the market sheds and were lighted at all times. These were intersected at 15–20 foot intervals by narrower cross aisles. The standard survey used throughout the study consisted of 15 minute periods of observation from points at the ends of each of the two outer aisles. Counts varied considerably from night to night and from hour to hour on any given night and are obviously measures of population activity rather than of population size. Efforts accordingly were made to standardize the day of observation with respect to market activity, and the hour of observation with respect to sunset.

Unknown factors, many of them doubtless associated with obscure variations in local food supply, continued to produce a high variability. These reduce the value of the records considerably, but general information on population trends may be obtained by comparing successive counts from month to month. Counts of live rats harboring in drains were used to supplement aisle counts in the later surveys.

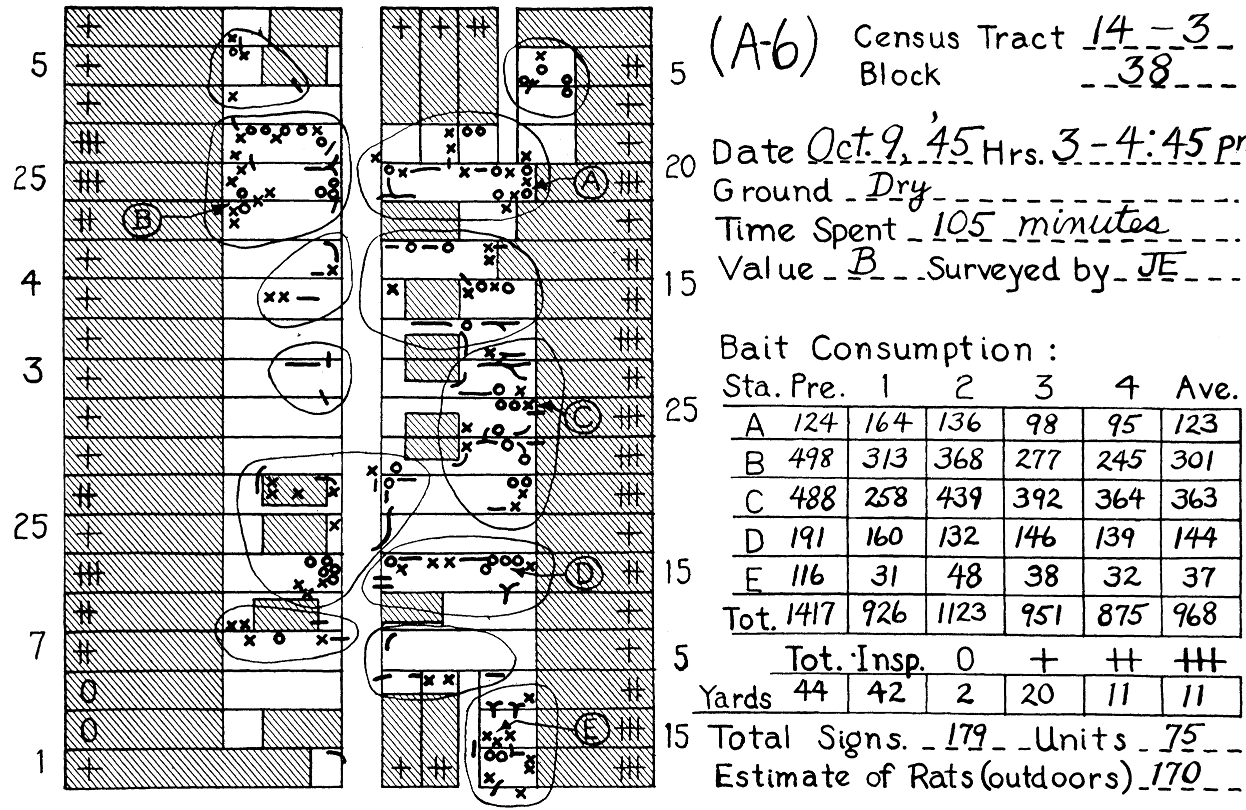
Reductions in the markets were made in overnight poisoning campaigns using ANTU rat poison in various baits. Fairly complete collections of dead rats following poison campaigns give data on the kills obtained.

*Residential areas.* In the residential area, square city blocks were adopted as the areal units in accordance with observations that city streets form effective natural barriers to random movement and thus segregate the rats into distinct and semi-isolated populations (Davis et al., Ms.). Several methods were employed to get a reasonably reliable and complete estimate of the size of populations in these blocks. These methods included:

(*a*) counting and mapping all signs of rat activity such as active burrows, fresh droppings, trails, slicks, foot prints, etc.
(*b*) measuring the consumption of bait at key points
(*c*) questioning residents
(*d*) comparing these observations with those made in conjunction with trapping campaigns in other areas.

Surveys of fresh signs as recorded on maps provided the main basis for estimating populations. Each premise in a block was entered and a careful search made through the yard and outbuildings for any and all traces of rat activity. Holes were closed in advance so that only active ones would be recorded; droppings were stamped out at the time of each successive survey for the same purpose. Tracking dust was laid or smoothed in appropriate places, and flour was used as a tracking medium at a few sites. Large scale maps were carried by the survey maker and all signs recorded with appropriate symbols in red pencil (fig. 3).

Sign surveys were supplemented with measurements of bait consumption after the manner of Chitty ('42). Bait stations were set up at selected points in each block as an aid in estimating rat numbers in the larger colonies and at places where the evaluation of signs was particularly difficult. Finely ground wheat was put out in open topped boxes for 3 successive days to establish a station, then measured for 3–4 days to determine the nightly consumption. Trapping experiments indicated that, if propperly placed, the bait taken at these stations approximated 50 per cent of the local population's total diet (Stokes, Ms.). The measurements thus give a rough basis for estimating rat numbers as well as an index for comparing populations from one survey period to the next.




Census Tract 14 – 3
Block 38

Date Oct. 9, '45 Hrs. 3 – 4:45 pm.
Ground Dry
Time Spent 105 minutes
Value B Surveyed by JE

Bait Consumption:

| Sta. | Pre. | 1 | 2 | 3 | 4 | Ave. |
|---|---|---|---|---|---|---|
| A | 124 | 164 | 136 | 98 | 95 | 123 |
| B | 498 | 313 | 368 | 277 | 245 | 301 |
| C | 488 | 258 | 439 | 392 | 364 | 363 |
| D | 191 | 160 | 132 | 146 | 139 | 144 |
| E | 116 | 31 | 48 | 38 | 32 | 37 |
| Tot. | 1417 | 926 | 1123 | 951 | 875 | 968 |

| | Tot. Insp. | 0 | + | ++ | +++ |
|---|---|---|---|---|---|
| Yards | 44 | 42 | 2 | 20 | 11 | 11 |

Total Signs. 179 Units 75
Estimate of Rats (outdoors) 170

FIG. 3. Sample of the 5″ × 8″ form card used in making surveys of the rat populations in residential blocks. All visible signs of rat activity are entered on the map with appropriate symbols (o = active rat burrow; x = fresh rat droppings; heavy lines = active rat trails; T = fresh rat tracks in dust or mud. Letters in circles refer to bait measurement stations; plus signs give an evaluation of the infestation of each yard; figures along the outer margins give a balanced estimate of the number of rats in each of the groupings outlined on the map). Explanatory data, measurements of bait consumption and a summary of observations are entered to the right of the map. Verbal reports on rat conditions from residents are entered on a form on the reverse of the card (not shown).

Residents were questioned systematically in the initial and first post-campaign surveys and as opportunity afforded in others. Reports were obtained on current rat conditions in the house, cellar, yard, and the neighborhood, and on recent trends in rat numbers. Pertinent facts from these reports were recorded, with the address and an evaluation of the reporter on a special form printed on the back of the map card.

Evaluations of rat infestations and estimates of numbers were made immediately after completeing a survey and while still at the site. Each yard was reviewed on the basis of all available evidence and a symbol entered on the map to indicate the estimated degree of infestation, whether heavy (+++), moderate (++), light (+), or rat free (0). A summation of plus signs for all yards gives a record of the overall infestation of the block in terms of infestation units. Infestation signs, as they appear on the map, were reviewed, and the tendency for them to be aggregated in certain areas was utilized in outlining local rat groupings or "colonies." An attempt was then made to estimate the actual number of rats in each of these colonies on the basis of all available evidence. Experience gained in an extensive program of census-trapping in 1943, 1944, and 1945 (Emlen, Ms.) formed the basis for estimating numbers and showed that careful estimates should rarely be in error by more than 20 per cent. Such errors are of relatively minor importance for the present study where the main function of the survey data is comparative and not absolute.

In order to standardize the procedure for individual blocks, all surveys were made by two of the authors (Stokes and Emlen) in person, and successive surveys in any given block were made by the same man. As a check on variability due to personal factors, duplicate surveys were made in several blocks by both men working independently within a few days of each other. These gave reasonably similar results in terms of infestation units and estimates of numbers (table I).

TABLE I. *Comparison of results of sign surveys conducted independently by two of the authors in 3 blocks*

| Blocks | Infestation Units | | Estimate of Rats | |
|---|---|---|---|---|
| | Stokes | Emlen | Stokes | Emlen |
| 1 | 10 | 7 | 23 | 17 |
| 2 | 40 | 38 | 127 | 122 |
| 3 | 23 | 21 | 51 | 44 |

The reliability of the estimates for comparative studies may be statistically evaluated by measuring the deviations from the base level in the undisturbed (control) populations and from the smoothed recovery curve in experimental populations. These data indicate a coefficient of variation of 20 to 25 per cent. The values are, of course, based on the assumption that there were no irregular fluctuations in the populations during the study period. Since minor fluctuations undoubtedly occurred, it is probable that the variability of estimates is actually less than these computations indicate.

## PROCEDURE

Surveys were conducted in the 34 residential blocks in October, 1945, just prior to the campaigns of reduction. The populations in 27 of these had not been seriously disturbed for over 18 months and were considered to be at capacity. Populations in the remaining 7 (marked with an asterisk in figure 5) were incompletely recovered from previous campaigns; the figures for the capacity level are therefore based on earlier surveys and trapping records.

The pre-treatment and first post-treatment surveys included houses and cellars as well as yards; subsequent surveys covered only the outdoor populations. The omission of indoor inspections was considered advisable because of the lower accuracy of indoor surveys and the consequent reduction in value of overall census figures. It was considered per-

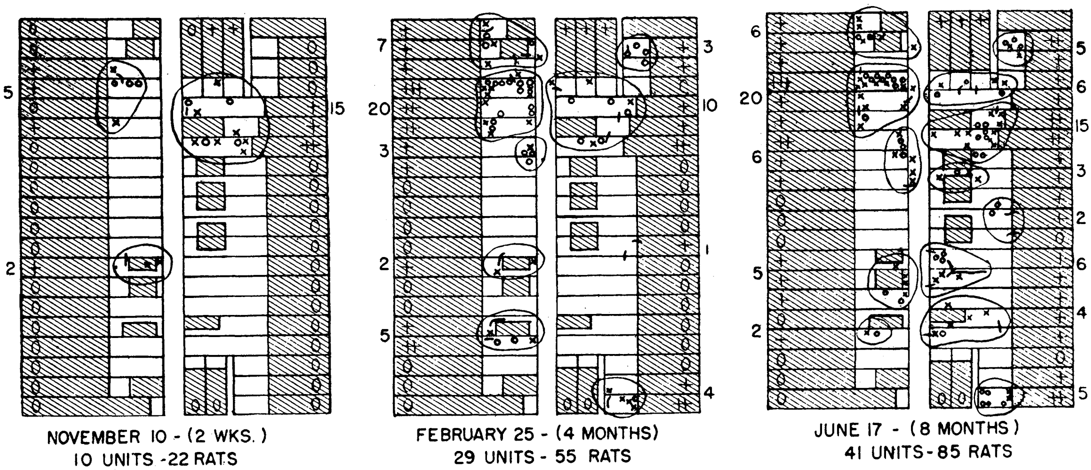



FIG. 4. Series of survey maps of block A6 made at intervals of ½, 4, and 8 months after the experimental reduction. The original (pre-treatment) condition in this block is shown in figure 3.

missible after it was discovered that indoor populations usually comprised less than one quarter of the total and were generally quite distinct from outdoor populations. The figures used in all the recovery measurements are therefore for rats living entirely outdoors plus a few that move in and out of buildings and leave signs outdoors.

The presence of a large indoor population in a block sometimes led to confusion in interpreting signs and was also considered as a potential factor in the recovery rate of the outdoor population. Six blocks in which the initial survey indicated an indoor population of 30 per cent or more of the total were therefore tabulated in a separate series.

Five blocks which had less than 25 rats in the initial survey, and one which received an irregular treatment in the poisoning campaign, could not be considered comparable with the rest and were accordingly omitted from the tabulations.

Reduction campaigns utilized a variety of poisoning and trapping techniques and, according to comparisons of pre- and post-campaign sign surveys, resulted in reductions of from 0 to nearly 100 per cent. Details of the eradication procedures used are described elsewhere (Emlen, '47; Emlen and Stokes, '47). Two blocks in which the poisoning campaigns were completely ineffective, as evidenced by lack of population response, were grouped with untreated blocks as controls.

The first post-campaign survey for each block was made in November, 1945, from 8 to 20 days after the treatment; subsequent surveys were made at approximately two-month intervals through June, 1946. A sample series of survey maps is shown in figure 4.

## RESULTS

The data presented in table IIa show that rats multiply more rapidly at heavily reduced than at mildly reduced population levels. This is in accord with the observations of Errington ('45) that the rate of population increase in quail and other wild species is inversely related to the population level. With our rats, furthermore, this rate of increase retarded as the population rose. This may be interpreted as indicating a dampening effect on population growth exerted as the population approached capacity levels.

If we adopt our pre-campaign estimate as the capacity level of each block, we

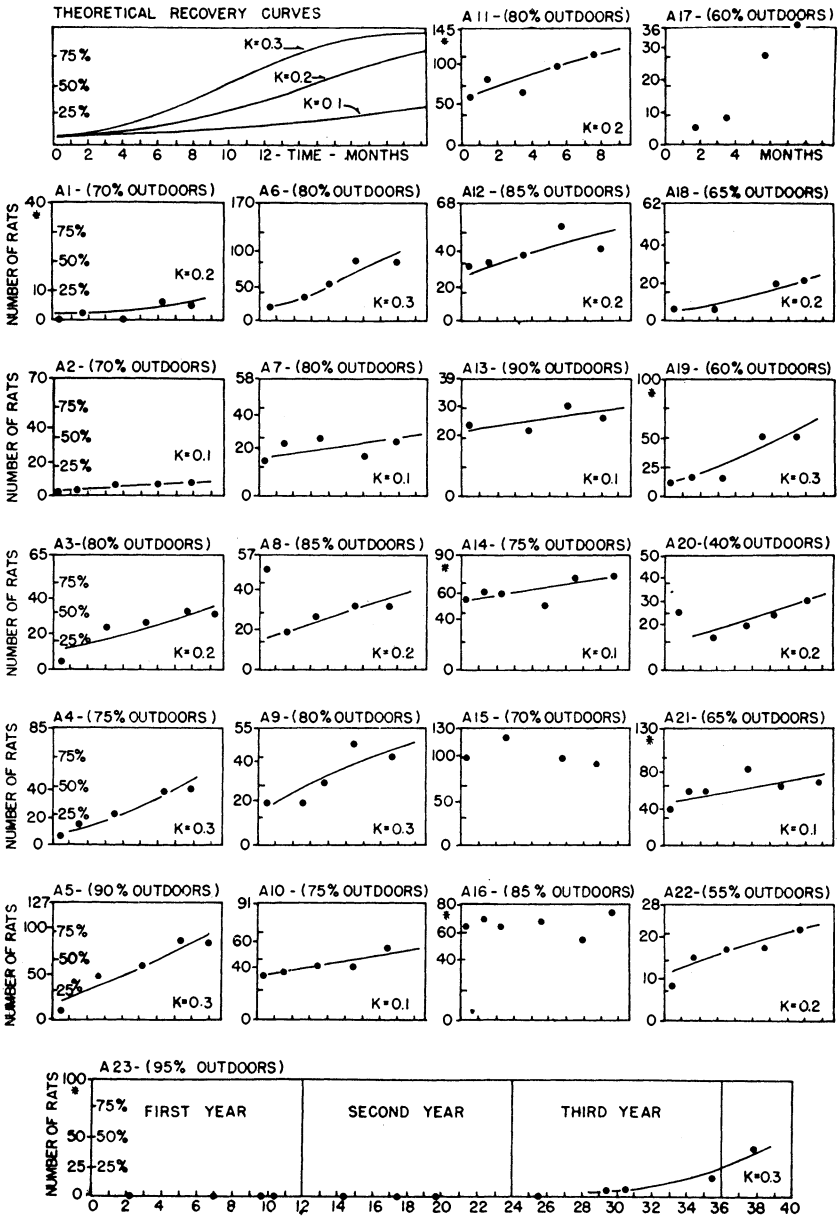



FIG. 5. Recovery curves of decimated rat populations in 23 residential blocks over an 8–10 month period. The scale of the ordinate values for each graph is in terms of per cent of the threshold (pre-treatment) population level as determined in initial surveys; a scale of the absolute rat numbers is given on the outer left margin of each graph. Units of time are months. Each dot represents a census estimate. Curved lines represent segments of logistics, the rate constants (*k* values) of which are designated in the lower right corner of each graph. The graph in the upper left corner of the page shows portions of the smooth curves derived from the logistic equation for three pertinent values of *k*. Graphs A1 to A16 represent a series arranged in order of the degree of reduction obtaining at the start of recovery. Graphs A17 to A22 are arranged as a separate series because of their larger indoor populations (more than 30 per cent of the total). Graph A23 traces the history of a block which was completely cleared of rats in 1943.

can conveniently plot all measurements of the recovering population in relation to it, and thereby trace the progress toward that level. Figure 5 shows such recovery curves for each of the 23 experimentally reduced block populations.

It can here be seen that where populations were moderately reduced (between 50 and 90 per cent) the rats showed early signs of recovery and increased at rates of about 4 per cent (2 to 6 per cent) of the capacity level each month. As they approached capacity they slowed down to a rate of about 2 per cent per month or less. Populations reduced more than 90 per cent (blocks A1, A2, and A18) recovered at a slower rate of between 1 and 3 per cent per month until they had advanced above the 10 per cent level. In the one case where complete extirpation was obtained (A23) no recovery occurred for over 2 years; progress then followed the usual course, slow at the start and gradually accelerating as the population gained a foothold.

Undisturbed populations in the control blocks (fig. 6 and table IIb) showed irregular fluctuations but no consistent trends during the period of observation.

Counts in the markets varied considerably from week to week, but after accumulating a considerable number of records it became clear that population growth between reduction campaigns followed a more or less regular course (fig. 7). Initial surveys were lacking or were inadequate to determine the original levels in these markets, so population growth cannot be measured in terms of per cent of capacity. The general trends, however, resemble those observed in the block populations. Where reductions were moderate, the recovery rates were fairly rapid; where reductions were great, recoveries were slow and sometimes delayed for considerable periods of time (fig. 7—first recovery period in A, second period in B, first and second periods in C).

*Supplementary observations.* Various observations made in conjunction with other phases of the rat population study supplement the data from the planned experiments described above.

The opinion of residents of treated areas was sampled in a group of 9 blocks one year after the completion of a local campaign. Reports from housewives and others suggested that, in most cases, rats had not returned to their former abundance at this time:

Conditions still much better than before campaign, 35.

Conditions better than before campaign, 103.

Conditions as bad as before campaign, 44.

Conditions worse than before campaign, 6.

Surveys made at irregular intervals in a number of residential blocks outside of the experimental area show in a crude way the same general picture of variable reductions and gradual increase (tables III and IV).

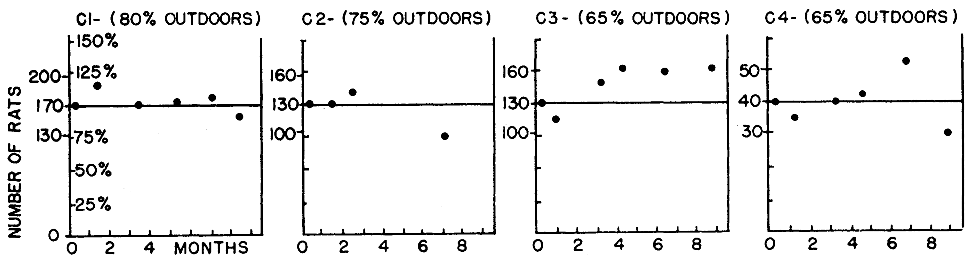



FIG. 6. Fluctuations of undisturbed populations in 4 city blocks used as controls (drawn to the same scale as the recovery curves in figure 5). Each dot represents a census estimate.

TABLE IIa. *Census data obtained before and at intervals after reduction in 23 experimental blocks*

| Initial survey (threshold level) | | | | Recovery period surveys 1945–1946 | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Outdoor rats only | | | | | |
| Block | Date | Per cent outdoors | Outdoor rats | Oct. | Nov. | Dec.–Jan. | Feb.–March | Apr.–May | June |
| A–1* | Aug. '43 | 70% | 40 | | 0 | 2 | 0 | 6 | 5 |
| A–2 | Oct. '45 | 70% | 70 | | 3 | 4 | 6 | 7 | 7 |
| A–3 | Aug. '45 | 80% | 65 | 5 | | 24 | 27 | 33 | 32 |
| A–4 | Oct. '45 | 75% | 85 | | 7 | 15 | 23 | 39 | 41 |
| A–5 | Aug. '45 | 90% | 127 | 10 | | 47 | 59 | 88 | 84 |
| A–6 | Oct. '45 | 80% | 170 | | 20 | 35 | 49 | 87 | 80 |
| A–7 | Oct. '45 | 80% | 58 | | 17 | 26 | 28 | 20 | 28 |
| A–8 | Oct. '45 | 85% | 57 | | 50 | 18 | 27 | 32 | 32 |
| A–9 | Oct. '45 | 80% | 55 | | 20 | 20 | 29 | 48 | 41 |
| A–10 | Oct. '45 | 75% | 91 | | 35 | 37 | 42 | 41 | 56 |
| A–11* | Mar. '43 | 80% | 145 | | 60 | 81 | 66 | 98 | 115 |
| A–12 | Oct. '45 | 85% | 68 | | 32 | 34 | 38 | 55 | 43 |
| A–13 | Oct. '45 | 90% | 39 | | 24 | | 22 | 30 | 26 |
| A–14** | Jun. '44 | 75% | 90 | 55 | 60 | 60 | 50 | 72 | 73 |
| A–15 | Oct. '45 | 70% | 130 | | 99 | 124 | | 98 | 91 |
| A–16** | Aug. '43 | 85% | 80 | 65 | 70 | 65 | 67 | 56 | 74 |
| A–17 | Oct. '45 | 60% | 36 | | 0 | 5 | 8 | 27 | 37 |
| A–18 | Oct. '45 | 65% | 62 | | 7 | 7 | | 20 | 22 |
| A–19* | Jul. '43 | 60% | 100 | | 14 | 16 | 16 | 51 | 51 |
| A–20 | Oct. '45 | 40% | 50 | | 25 | 14 | 19 | 24 | 30 |
| A–21** | Mar. '44 | 65% | 130 | 40 | 60 | 60 | 84 | 66 | 69 |
| A–22 | Oct. '45 | 55% | 28 | | 8 | 15 | 17 | 18 | 22 |
| A–23** | Apr. '43 | 95% | 100 | 7 | 7 | | 5 | 16 | 42 |

* Blocks in which the population was below capacity at the start of the experiment. Figures for the capacity population in these blocks are based on earlier surveys.

** Blocks with subcapacity populations in which no reduction campaign was staged in the fall of 1945.

TABLE IIb. *Census data for 4 untreated "control" blocks*

| Block | Per cent out-doors | Periodic surveys (1945–1946) | | | | | |
|---|---|---|---|---|---|---|---|
| | | Oct. | Nov. | Dec.–Jan. | Feb.–March | Apr.–May | June |
| C–1 | 80% | 170 | 195 | 170 | 172 | 179 | 155 |
| C–2 | 75% | 130 | 130 | 140 | | 96 | |
| C–3 | 65% | 130 | 110 | 150 | 165 | 160 | 165 |
| C–4 | 65% | 40 | 35 | 40 | 42 | 53 | 30 |

## DISCUSSION

The data here presented on the recovery rates of decimated rat populations suggest adherence to the characteristics of the Verhulst-Pearl-Reed logistic widely applicable to growth curves of human populations and of laboratory populations of lower animals. For the present purposes this logistic equation may be written:

$$y = \frac{100}{1 + e^{-kt}}$$

in which $y$ = population, $k$ = rate constant, $t$ = time measured from the point at which $y$ reaches the midpoint of its growth.

The diagram at the top of figure 5 shows the form of this equation for several values of $k$.

The data available for the rat populations here described do not warrant any elaborate attempt at curve fitting. With standard errors of the order of 25 per cent, and with no more than 5–6 observations on each curve, a rough approximation is all that seems justified. Accordingly, each observation, expressed as a per cent of the pre-campaign estimate

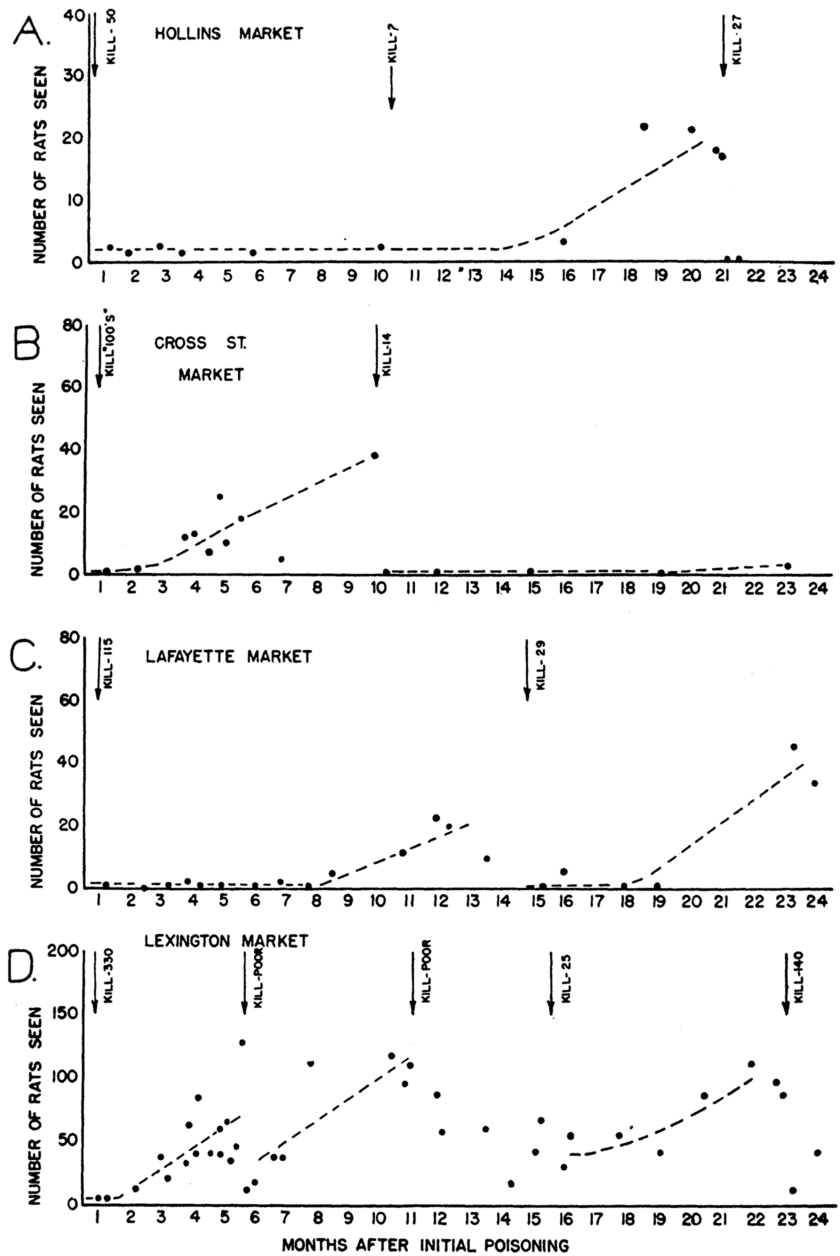



FIG. 7. Population fluctuations in 4 city market sheds subjected to periodic poison treatments during 24 consecutive months. Each dot represents a count of the number of rats seen in a half hour observation period over a standard course. The times of poisoning campaigns are indicated by vertical arrows at the top of each graph. The figures accompanying each arrow give the number of dead rats found or, when contained in quotation marks, reported. Dashed lines indicate the apparent trend of recovery during the intervals between poison treatments.

TABLE III. *Supplementary data on population recovery in residential blocks obtained incidental to the planned recovery study*

(* Per cent recovery = population gain/population deficiency × 100, where population gain represents the numerical growth during the recovery period and where population deficiency represents the reduction suffered at the time of the campaign.)

| Block | Preliminary survey | | Post-campaign survey | | Subsequent survey | | Recovery interval (months) | % Recovery* |
|---|---|---|---|---|---|---|---|---|
| | Date | Rats | Date | Rats | Date | Rats | | |
| X-1 | July '43 | 70 | July '43 | 0 | Jan. '44 | 4 | 6 | 6% |
| X-2 | Jan. '44 | 145 | Mar. '44 | 39 | Sept. '44 | 135 | 6 | 90% |
| X-3 | Mar. '44 | 160 | Mar. '44 | 10 | Sept. '44 | 60 | 6 | 33% |
| X-4 | June '43 | 80 | June '43 | 5 | Jan. '44 | 19 | 7 | 19% |
| X-5 | Oct. '43 | 150 | Oct. '43 | 20(?) | Sept. '44 | 80 | 11 | 46% |
| X-6 | Oct. '43 | 300 | Oct. '43 | 22 | Sept. '44 | 105 | 11 | 30% |
| X-7 | Apr. '43 | 180(?) | Oct. '44 | 54 | Oct. '45 | 182 | 12 | complete |
| X-8 | Mar. '43 | 145 | Oct. '44 | 19 | Oct. '45 | 70 | 12 | 40% |
| X-9 | June '43 | 80 | Oct. '44 | 3 | Jan. '46 | 79 | 15 | complete |
| X-10 | Feb. '44 | 210 | Mar. '44 | 20 | Oct. '45 | 210 | 19 | complete |

TABLE IV. *Data showing the degree of recovery in 5 blocks exhaustively trapped in February–March of 1944 and again in July–August of 1945, 17–18 months later*

Differences in season must be considered in comparing the records. No other organized control activities were carried on prior or subsequent to the trapping programs.

| Block | February-March, 1944 | | | July-August, 1945 | | | Interval (months) | Degree of recovery |
|---|---|---|---|---|---|---|---|---|
| | Catch | Est. residue | Tot. | Catch | Est. residue | Tot. | | |
| Y1 | 165 | 15 | 180 | 210 | 5 | 215 | 17 | Complete+ |
| Y2 | 42 | 5 | 47 | 38 | 7 | 45 | 18 | Complete |
| Y3 | 70 | 10 | 80 | 84 | 5 | 89 | 18 | Complete+ |
| Y4 | 51 | 10 | 61 | 71 | 10 | 81 | 17 | Complete+ |
| Y5 | 108 | 15 | 123 | 122 | 16 | 138 | 18 | Complete+ |

of population, was plotted on tracing paper. The resulting pattern was then adjusted by eye to one or another of the logistics as shown at the top of figure 5. The sloping lines superimposed on each block record in figure 5 show the resulting fits; the figure in the lower right corner of each graph indicates the particular curve chosen in each case.

The progress of a population over the central range of this curve may, for practical purposes, be considered to be roughly linear. Slopes obtained by the process of curve fitting indicate that a population reduced to 10 per cent of its original level should climb to 90 per cent of complete recovery in about 15 months when the $k$ value of the selected curve is 0.3, 22 months when it is 0.2, and 44 months when it is 0.1.

Slow or delayed recovery of heavily decimated populations, such as here seen in block A23 and certain of the markets, has been noted by various observers of wild animal populations. Darwin ('59) commented on the lowered ability to recover and the danger of extermination when a species is reduced to extremely low levels. Allee ('31) summarizes evidence of the undesirable effects of sparse populations in laboratory colonies and the beneficial effects of "optimum populations." In the present study it is believed that irregularities in the sex and age composition of decimated colonies and the sedentary nature of these animals were at least in part responsible for the slow initial response of low populations.

A retardation of growth of populations as they approach the upper asymptote (here seen in blocks A13, A14, A15, A16 and others) has been noted and discussed by Pearl ('25) and others for a variety of species. The inverse relationship of basic rate of gain to stage of reduction is forcefully brought out in several of the present records of rat populations. For example, the 32 survivors in block A12 (reduced from 68) produced new rats at a rate of only 2.8 per month, while the same number in block A6 (reduced from 170) were producing 10.2 per month. Errington ('46) believes that the dampening effect on near-capacity populations is the result of increased vulnerability to predators and other controlling factors. We have at present little evidence as to the mortality factors involved in urban rat populations.

## Summary

The rate of increase of 23 free-living populations of Brown Rats in Baltimore, Maryland, was traced over periods of from 8 months to 2 years following reductions effected by intensive trapping campaigns or single applications of poison.

Population levels before the reduction and at intervals during the recovery period were determined by a combination of censusing techniques which included (1) counting live rats crossing standard courses during standard observation periods at night, (2) counting and mapping all fresh signs of rat activity, (3) measuring bait consumption at fixed stations, and (4) questioning the people.

The rate of recovery staged by a decimated population was found to be related to the original (pre-reduction) level as well as to the size of the surviving stock. Populations reduced between 50 and 90 per cent recovered at a rather constant rate of about 4 per cent (2–6 per cent) of their original levels each month. Populations only slightly reduced and those severely reduced recovered at slower rates. Undisturbed populations remained essentially constant during the period of study.

The typical curve of recovery suggests that of a logistic.

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