PLAGUE IN SOUTH AFRICA: A STUDY OF THE EPIZOOTIC CYCLE IN GERBILS (*TATERA BRANTSI*) IN THE NORTHERN ORANGE FREE STATE

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(With Plates 10 and 11 and 3 Figures in the Text)

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INTRODUCTION

In this paper an account is given of the effect on the numbers of gerbils, *Tatera brantsi* (Smith), of a major epizootic of plague in a well-established enzootic area in the Orange Free State during 1940. The study area, comprising some 120 square miles of country, lay to the east and west of Rooiwal Station, six miles south-west of the small country town of Koppies. Plague reached here about 1922 from the south and south-west as a result of natural spread amongst gerbils and other wild and domestic rodents. Apart from the finding of a plague-infected rat, *Rattus rattus* (Linn.), on the farm Cyferfontein 17 miles south of Rooiwal (Union of South Africa, 1924), the first intimation of the presence of plague in the area was a series of human outbreaks in the summer months (January to April) of 1924. A few years earlier, in the Bothaville district, 100 miles to the west, Mitchell in 1922 obtained the first proof that wild rodents had become a reservoir of plague: thus were explained the sporadic human outbreaks on farms which had occurred since 1914 in the eastern Cape Province, north-western Orange Free State and southern Transvaal.

The northern Orange Free State was chosen in 1938 for detailed study of the ecology of gerbil populations (Davis, 1939) with the object of following up the pioneer researches of Mitchell, Pirie & Ingram (1927) and of Fourie (1936, 1938). When, in January 1940, it was discovered that an epizootic was impending in the vicinity of Rooiwal, the opportunity was taken of carrying the initial studies a stage further. Field studies of gerbils during the previous year had been conducted during an inter-epizootic period in an area about 50 miles to the south at Holfontein in the Kroonstad district (Davis, 1939). Conditions were closely similar in both areas.

The object of the field work was to follow the course of the epizootic in every gerbil colony that could be found within about 10 miles of Rooiwal. To this end, a census method was devised, based upon counts of the number of burrows reopened overnight after blocking. During the first few months sample counts were made on the larger warrens of each gerbil colony as it was found, and at regular intervals thereafter. Later, when the area had been surveyed, a more ambitious census was put into operation which involved counts, every 4 weeks, of all burrows occupied by each colony. The complete census was in operation by mid-June, at a time when most of the colonies still surviving were declining steadily. There were still some survivors in October, but their fate was not followed in such detail owing to work elsewhere. In January 1941, however, a careful search of the warrens that had been under observation failed to reveal any survivors, although a few occupied warrens were found at other sites. By then, therefore, the gerbil population of the area as a whole had been reduced to a minimum.

For the next 18 months the process of reoccupation was followed at 3-monthly intervals (until mid-1942). A general survey was carried out by a plague inspector of the Department of Health during 1943. From 1945 onwards, fairly large-scale control measures have somewhat confused the picture of normal recovery.

PRELIMINARY INVESTIGATIONS

The account of the preliminary investigations which follows is designed to introduce the species of rodents and fleas and the part they play in the spread of plague in the northern Orange Free State and to set the stage, as it were, for the main part of the paper on the course of the 1940 epizootic.

Investigation of two active foci

The events leading up to the situation found in January 1940 showed that plague had been occurring sporadically amongst wild and domestic rodents and in man during the previous 2 years. Two human outbreaks had occurred in February 1938, one on the farm Tweeling, 2 miles east of Rooiwal Station and the other on the farm Voorwaarts, 3 miles to the south. A further outbreak occurred again on the farm Tweeling, in November 1939, after a lapse of nearly 2 years. At this time plague-infected house rats (*R. rattus*) were found in farm buildings 10 miles west of Rooiwal Station and in a grain shed near the station itself.

Mortality amongst house rats and gerbils had been observed in other parts of the area.

The Tweeling focus

A survey of the Tweeling focus was made towards the end of January. The buildings and one small gerbil warren had been treated with cyanogas as a routine after the November outbreak. A search of the premises revealed the dried-up carcasses of house rats and multimammate mice, *Rattus* (*Mastomys*) *natalensis* (Smith),* under some bags, which may have been gassed, but a live rat was discovered harbouring under the sail of a windmill lying against an outer wall. It had on it the wild rodent flea, *Dinopsyllus ellobius ellobius* (Roths.), and the house-rat flea, *Xenopsylla brasiliensis* (Baker). The gerbil warren situated about 50 yards from the building showed little sign of activity, yet two gerbils and one *Mastomys* were trapped. A long runway, made by vlei rats, *Otomys irroratus* (Brants), in a strip of coarse grass along the edge of a dam, yielded two young live *Otomys*, the remains of carcasses of *Mastomys* and *Otomys* and a number of *Otomys* nests heavily infested with fleas (*D. e. ellobius*). The nests were either in grass tussocks or in shallow excavations just below the surface of the soil. The fleas were preserved in 2 % saline and dispatched to the South African Institute for Medical Research where they were ground up and inoculated into guinea-pigs. *Pasteurella pestis* was isolated from one batch.

The above findings illustrate the manner in which *P. pestis* circulates in an enzootic area. The primary reservoir in the gerbils was the source of infection to the semi-domestic *Mastomys* and the domestic *R. rattus* living in and around the farm buildings. The domestic rodent fleas, *X. brasiliensis*, were doubtless responsible for the human infections. *Mastomys*, in its role of intermediary between the wild rodents in the open veld and the domestic rodents in the farm buildings appears to have been responsible, first, for transferring *P. pestis* from the gerbils to *R. rattus* and man in the buildings, and also to an accessory reservoir in *Otomys*.

With the Tweeling focus as a starting-point, a survey of the surrounding country was begun. Judging by the degree of activity in the warrens, some colonies appeared to be healthy, but others were evidently decreasing, as shown by a high proportion of deserted burrows and absence of signs of active feeding. Before much progress was made, a human case of plague was traced to the farm Mooiwater, 8 miles west of Rooiwal Station. Activities were accordingly diverted to investigate its origin.

The Mooiwater focus

The patient, an African farm labourer, had been living in a hut near the farm outbuildings. He was taken ill during the last week in January. A dead rat (*R. rattus*) found in a kraal near the hut yielded a strain of *P. pestis*. The carcass was heavily infested with fleas (*X. brasiliensis*). From the floor of the plague hut, sixty *X. brasiliensis* were recovered from sweepings. Two groups of gerbil

* The name *natalensis* antedates *coucha* for the multimammate mouse (see Ellerman & Morrison-Scott, *Check-list of Palaearctic and Indian Mammals*, 1951, p. 601).

warrens, one in a small paddock and the other in a threshing floor about 50 yards away, were excavated. Plague-infected gerbil fleas, *X. philoxera* Hopkins,* were found in one warren. Three gerbils in various stages of decomposition were recovered from another: one of them was dried up and unfit for examination, the second was putrid and full of fly larvae, but *P. pestis* was recovered from bone marrow by animal inoculation; the third gerbil had just died and yielded a further strain. The fleas from the burrows (a mixed pool of *X. philoxera* and *D. e. ellobius*) were also proved infected.

SURVEY AND CENSUS METHODS

There are two species of gerbils in the northern Orange Free State: *Tatera brantsi* and *T. schinzi* (Noack). *T. schinzi* was not encountered in the Rooiwal area and was only once met with at Holfontein (the scene of previous studies already mentioned), but becomes progressively more common in the western districts (Davis, 1949). *T. brantsi* colonies inhabit open grassveld or fallow or cultivated lands and their warrens are usually grouped together. In some parts of the country—notably in the highveld of the eastern Transvaal—their warrens may extend for miles without a break, but in the northern Orange Free State, such wide occupation rarely occurs and colonies are separated by a mile or more. This made it possible to study the colonies as separate units.

The burrow census

Burrowing habits of gerbils

Gerbils stay underground during the hours of daylight but their nightly activities can be reconstructed from the appearance of the burrows and their vicinity. The field officers of the Health Department have become adept at interpreting gerbil signs (see Fourie, 1938), and can determine the stage of an epizootic by noting the degree and nature of gerbil activity. Normally, warrens occupied by healthy gerbils show clear evidence of abundant digging and feeding. The small mounds of soil at the entrances of the burrows have a fresh layer of soil scraped out during the night; there are usually food scraps nearby, and fresh spoors may be seen on the soft earth. The tracks on the surface leading from one warren to another show clear signs of use, and small pits round about the burrows point to the spots where succulent bulbs or grass bases have been dug out and eaten. When plague is active amongst them there is a gradual cessation of activity, cobwebs form over the entrances of some burrows, the tracks between burrows become less well-defined and scraps of fur and bones or even carcasses may be found at some of the entrances or just within. Furthermore, the scavenging activities of small carnivores, such as the polecat, *Ictonyx striatus* (Perry), and the yellow mongoose, *Cynictis penicillata* (G. Cuvier), are revealed by their spoors, by the enlargement of some burrows in the search for carcasses and by the presence of gerbil remains in the dung (see Fourie, 1936, 1938).

In an attempt to devise a way of measuring nightly activity, records had been kept during the previous year's work at Holfontein, of the number of 'active'

* Syn. *X. eridos* of authors.

and 'deserted' burrows found at weekly intervals (Davis, 1939). In the Rooiwal area this method was abandoned in favour of lightly blocking the burrow entrances and counting the number reopened by the following day.

Sample burrow counts

For the first 5 months sample counts were made of the burrows in the main warrens of a colony. The warrens were marked out with pegs and labelled, and a record was kept of the number of holes blocked and reopened. The counts were repeated at approximately monthly intervals. Comparison of the counts showed whether the colony was increasing, decreasing or stationary, but gave no index of population density either for each colony or for the area as a whole. Sample counts were abandoned in favour of complete counts over the occupied area of every colony that could be found in the study area.

Complete burrow counts

On marking out a colony for the first time the procedure was to flag the limits of burrows—deserted or active—to select a key point such as a certain fence post, gate or tree for future reference, in case the marks were obliterated, and from it to set out a line of stakes 50 yards apart running through the warrens, and from this base-line to peg off the whole occupied area in 50 × 50 yard squares. A line of men then advanced through the squares, lightly closing up all the burrows with spades. On the following morning the same procedure was repeated, all burrows opened overnight being closed again and counted. A record was kept of the number of burrows blocked and reopened. The number blocked gave a measure of activity over the 4-week period between counts, and the number reopened a measure of one night's activity. A reopened burrow was designated as 'active' and was adopted as the unit of measurement of population changes.

Census routine

The endeavour was to complete the counts in the first 2 weeks of a 4-week census period and to count each colony in the same order so that the census figures recorded 4-weekly changes in numbers. The second 2 weeks were devoted to further surveys, and to collecting material for plague test. Four-week census periods were numbered I–XIV and cover the period between 1 January 1940 and 26 January 1941.

Plague detection

In the preliminary investigations (pp. 428–430 above) two new sources of *P. pestis* were tapped. For the first time in South Africa, *P. pestis* was isolated from fleas from the bodies, burrows and nests of small rodents and from the bone marrow of a putrid carcass.

The inoculation of ground-up fleas as a routine technique in plague surveys was developed by the Sylvatic Plague Committee, appointed by the Western Branch of the American Public Health Association in 1935 (Meyer, 1936). Fleas are collected in saline from animals found dead or captured in the field. In most instances fleas from a number of animals from one locality are pooled. At the laboratory a suspension, made by grinding up the fleas, is inoculated into test animals.

Pons (1926) appears to have been the first to recommend bone marrow as a more reliable source of pure cultures of *P. pestis* in animal and human plague cadavers than the spleen, liver or lymph nodes, especially if putrefection has set in. Uriarte, Morales Villazon & Anchezar (1935) provided further evidence in favour of bone marrow, and stressed its value in the examination of animals that had been several days in transit to the laboratory. Devignat (1936), in the Belgian Congo, was similarly impressed with the method, and later (Devignat, 1940) developed a technique of plague detection based on the collection of bone marrow samples from batches of rodents caught in the field.

In the Rooiwal investigations, some plague material was inoculated in the field and the rest sent or taken to Johannesburg where it was examined either at the South African Institute for Medical Research or at the headquarters field station at Rietfontein Hospital. All isolations of *P. pestis* at the latter station were checked by the Institute. Laboratory-bred *Mastomys* were used by both laboratories as biological test animals when stocks permitted. The earlier tests were done on guinea-pigs.

During the routine of the census a lookout was always kept for signs of mortality. Dead gerbils were commonly picked up during counting operations. If gerbil remains were seen at the entrance to a burrow, this and others in the vicinity were excavated and fleas collected for test.

The collection of fleas for plague test

In the course of the work at Holfontein methods of recovering fleas from gerbil warrens had been worked out (Davis, 1939). Either whole warrens were excavated foot by foot to determine the distribution and numbers of fleas throughout a warren, or samples were scraped out of the first foot or two of a series of burrow entrances. The equipment for doing this consisted of a scraper with a semicircular plate, about the size of the burrow, riveted at right angles to an 18 in. hoop-iron handle; a small pan into which the loose soil containing the fleas was scraped; a mosquito-gauze sieve for sifting the material and holding back larger particles of soil and debris to facilitate the collection of the fleas; a large white enamel or tin basin into which the material was sifted; and an aspirator collecting tube with suction bulb.

The fleas were killed in the collecting tube by drawing in cyanogas fumes and transferred to a sterile Wasserman tube, which was filled with 2 % saline. After being identified at the laboratory the fleas were washed in normal saline and ground up in an agate mortar; the suspension so obtained was inoculated subcutaneously into test animals. A safer procedure, now in routine use, is to grind the fleas in the glass tube. The saline is removed with a pipette and a very small quantity of 'Aloxite' optical smoothing powder is added. The fleas are then quickly disintegrated by light grinding with a glass rod.

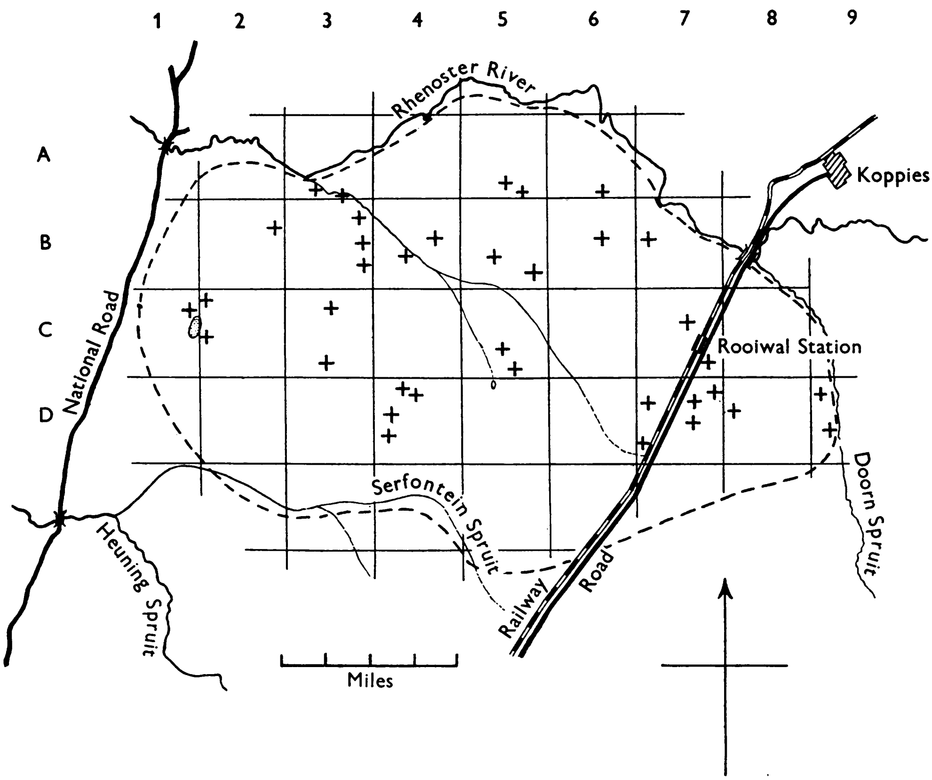
A provisional diagnosis of plague in a rodent can sometimes be made from post-mortem appearance, bone marrow, spleen and heart blood smears and cultures.

The crucial test, however, is the isolation of a culture of *P. pestis* from the test animal. Bone marrow, for inoculation by scarification or subcutaneous injection, was obtained by cutting through the femur and withdrawing a small amount on a platinum needle or into a syringe containing a little normal saline. When it was desired to use one animal to test a batch of specimens, marrow samples from each were accumulated in one syringe.

THE STUDY AREA AND DISTRIBUTION OF GERBIL COLONIES

The study area

The block of farms which finally comprised the study area (Text-fig. 1) was bounded on the north by the Rhenoster River (flow perennial except in severe drought) on the west by the National road (N 1) and on the south and east by Serfontein Spruit and Doorn Spruit respectively (flow seasonal). Its extent was



Text-fig. 1. The study area, enclosed by the broken line, is 120 square miles in extent. The grid units are 2 miles square. Colonies may be located by the grid references given in the text and tables.

approximately 120 square miles. The country is slightly undulating, with little topographical relief. The soils are classified as highveld prairie soils by van der Merwe (1941) and fall into two main types: a sandy loam on the higher lying portions and a heavier more clayey soil in the lower-lying portions, especially on the fringes of the river and spruits. Gerbils do not excavate warrens in the clayey soils, unless they are overlain by a foot or so of lighter soil. They were therefore largely confined to the sandy loams. The harder soil along the river and spruits bounding the area on the north, east and south formed, in effect, a partial barrier to gerbil occupation; and to this extent the study area was a more or less isolated block, not influenced to any marked extent by infiltration of gerbils from outside. The sandy loams are devoted largely to the production of maize which is the chief agricultural industry of the area.

The climate is warm, with a dry winter and an annual rainfall of about 23 in. Most of the rain falls between November and March. Temperature in the summer may reach 85–90° F. during the day, but falls to 45–50° F. at night. In the winter the temperature may reach 65–70° F. in the daytime and fall to below freezing-point at night. The relative humidity is normally low during the day, rising at night with the sharp fall in temperature (see, for example, Union of South Africa, 1938).

The gerbil colonies

The particulars of thirty-four colonies are given in Table 1. They are listed in the order in which they were surveyed and brought into the census programme. Each is designated by a serial number and code letter (an abbreviation of the name of the farm), and a map reference is given for identification in Text-fig. 1.

By period VII (17 June–14 July) the survey was complete. By then there was reason to believe that most of the colonies in the study area had been discovered and that to all intents and purposes the whole gerbil population was under observation. There was a colony on the farm Die Pan, near Rooiwal Station, the history of which was followed for a short while and in which plague was proved, but which was dispersed by ploughing operations. A very large colony on the farm Uithoek was similarly dispersed by ploughing so that its fate could not be followed.

In the last column of Table 1 the period during which each colony became extinct is given. A colony was considered to be extinct when less than five 'active' burrows were recorded at the census.

Text-fig. 2 has been constructed to portray the general course of the epizootic during 1940, and of the post-epizootic attempts to recolonize old sites during 1941–2.

Distribution of colonies

The map references in Table 1 enable each colony to be located on the sketch-map (Text-fig. 1). The cells of the superimposed grid are 2 miles square. If more colonies than one fall within a cell, they are numbered from north to south. For example, there are four colonies in cell D4. Colony MS19, the most northerly of these, has map reference D4–1; next, colony MS20 is D4–2, GP16 is D4–3, and SS23, the most southerly, is D4–4.

The sketch-map shows that few of the colonies were more than 2 or 3 miles apart. The average distance apart, estimated by measuring the distance from one colony to another on the sketch-map, was $1{\cdot}3 \pm 0{\cdot}06$ miles.

The sites of warrens are described in column 5 of Table 1. They fall into three main groups: (1) 'Natural' habitats in undisturbed grassveld on sandy loam soils,

Table 1. *Particulars of gerbil colonies listed in order of survey*

Brought under observation during period	Colony code no.	Map ref.	Maximum occupied area (no. of census squares)	Site of warrens	Died out during period
I (1–28 Jan.)	LK 1	D 7–2	4	Maize threshing floor	XI (7 Oct.–3 Nov.)
	TK 2	C 5–2	24	Fallow maize lands	IX (12 Aug.–8 Sept.)
II (29 Jan.–25 Feb.)	DF 3	C 3–2	2	Maize floor near farmhouse	V (12 Apr.–19 May)
	GH 4	B 2–1	7	Maize floor and grassveld nearby	XII–XIV (4 Nov.–26 Jan. 1941)
	GK 5	A 3–1	3	Maize floor	VI (20 May–16 June)
	GK 6	A 3–2	3	Grassveld near huts	VI (20 May–16 June)
	MW 7	B 3–3	2	Maize floor and grassveld near outbuildings	II (29 Jan.–25 Feb.)
	MW 8	B 3–2	2	Grassveld between maize lands	III (26 Feb.–24 Mar.)
	NG 9	D 7–5	4	Grassveld bordering on maize lands	II (29 Jan.–25 Feb.)
	VL 10	B 4–2	3	Maize floor and grassveld near outbuildings	V (22 Apr.–19 May)
	VL 11	B 4–1	12	Grassveld alongside group of huts	III (26 Feb.–24 Mar.)
III (26 Feb.–24 Mar.)	DK 12	B 5–2	44	Grassveld	X (9 Sept.–6 Oct.)
	DT 13	A 6–1	9	Grassveld near farmhouse	XII–XIV (4 Nov.–26 Jan. 1941)
	DV 14	A 5–2	2	Around teff-grass stacks	XII–XIV (4 Nov.–26 Jan. 1941)
	DV 15	A 5–1	3	Maize floor	XI (7 Oct.–3 Nov.)
	GP 16	D 4–3	3	Grassveld around farmhouse and huts	IV (25 Mar.–21 Apr.)
	MD 17	D 7–3	2	Grassveld and fallow lands	VI (20 May–16 June)
	MM 18	B 5–1	42	Grassveld	X (9 Sept.–6 Oct.)
	MS 19	D 4–1	3	Maize floor and grassveld around farmstead	IV (25 Mar.–21 Apr.)
	MS 20	D 4–2	3	Maize threshing floor	V (22 Apr.–19 May)
	MW 21	B 3–1	66	Grassveld	IX (12 Aug.–8 Sept.)
	OD 22	D 7–4	11	Fallow maize lands	IX (12 Aug.–8 Sept.)
	SS 23	D 4–4	2	Maize floor and grassveld around homestead	IV (25 Mar.–21 Apr.)
	UV 24	C 7–2	4	Fallow maize lands	XII–XIV (4 Nov.–26 Jan. 1941)
IV (25 Mar.–21 Apr.)	TK 25	C 5–1	5	Grassveld and orchard near farmhouse	X (9 Sept.–6 Oct.)
V (22 Apr.–19 May)	GS 26	C 1–1	5	Grassveld	XI (7 Oct.–3 Nov.)
	GS 27	C 2–2	2	Grassveld	VIII (15 July–11 Aug.)
	GS 28	C 2–1	3	Grassveld	VIII (15 July–11 Aug.)
VI (20 May–16 June)	LK 29	D 7–1	6	Grassveld	X (9 Sept.–6 Oct.)
	MR 30	D 9–1	11	Grassveld	IX (12 Aug.–8 Sept.)
	UH 31	B 7–1	6	Maize floor near outbuildings	XII–XIV (4 Nov.–26 Jan. 1941)
	VS 32	D 9–2	6	Grassveld	XII–XIV (4 Nov.–26 Jan. 1941)
VII (17 June–14 July)	AS 33	C 3–1	11	Maize floor and grassveld nearby	XII–XIV (4 Nov.–26 Jan. 1941)
	DR 34	B 6–1	22	Grassveld	XII–XIV (4 Nov.–26 Jan. 1941)

where the main food supply was provided by the stem bases, roots and seeds of grasses and more particularly by the corms and stem bases of certain sedges (*Cyperus* spp.). (2) 'Semi-natural' habitats in fallow maize lands where annual weeds and grasses, and the corm-bearing sedge or watergrass (*C. esculentus*) formed the chief food supply. This habitat was subject to periodic partial or complete destruction during ploughing, sowing and cultivation. Surviving gerbils congregated in warrens at the edge of the lands bearing a crop of maize until the reaping season, when they reinvaded the lands and remained established there while these lay fallow. (3) Sites near farm buildings and native huts, where the normal food plants were supplemented by farm waste, usually of maize from the threshing floors. The thirty-four colonies were distributed among these three major habitats as follows (summarized from Table 1):

Maize threshing floors, and around farmsteads	18
Grassveld	12
Old lands	4

Thus more than half of the colonies inhabited sites around the farmstead, more than a quarter were in grassveld and the remainder in old lands. From the point of view of plague epidemiology, the nearness of many of the colonies to farm buildings—many of which were rat-infested—was of particular significance, as it allowed the free passage of *P. pestis* from wild to domestic rodents and vice versa.

The occupied area

The maximum occupied area of a colony was determined at the first census by the number of census squares (50 × 50 yards) containing burrows, whether occupied or not (see column 4, Table 1). In subsequent censuses the occupied area was determined by the number of census squares containing one or more 'active' burrows. In some cases, the occupied area increased during the census period: further squares were then set out to encompass the expansion.

POPULATION DYNAMICS

Before passing to the census results and the course of the epizootic, the meaning of the counts in terms of numbers of gerbils will be considered.

The burrow/gerbil ratio

Three colonies were trapped after census to provide a figure for the conversion of numbers of 'active' burrows (as defined on p. 431) into numbers of gerbils. The procedure was to count the burrows and then, a few days later, to set break-back traps across the mouths of every third burrow for one or two nights; then to block the burrows and do further trapping at each reopened burrow; and finally to repeat the burrow census. The results showed that about eight 'active' burrows were the equivalent of one gerbil. In trapping experiments in the Transvaal closely similar results have since been obtained. In the eastern Transvaal the ratio was 2882 'active' burrows/133 gerbils (8·7 burrows per gerbil). In the southern Transvaal the ratio was 565 'active' burrows/70 gerbils (8·1 burrows per gerbil).

The results of the three trapping experiments in the Rooiwal area were as follows:

(i) *Nooitgedacht* (*NG*9: *D*7–5), *February* 1940

The colony occupied four census squares. The census results were 673 burrows blocked of which 415 were reopened. The one night's trapping yielded thirty-nine gerbils, four *Mastomys* and one striped mouse, *Rhabdomys pumilio* (Sparrman). The last two species are left out of account in the calculations. The burrows were blocked after trapping, but the number reopened the following day was not recorded as news of the Mooiwater outbreak was received (see p. 429). Three weeks later a second census was taken giving a result of 80/291 burrows reopened. In 3 weeks, therefore, the survivors had reopened a total of 291 burrows yet the overnight reopening was on a relatively small scale (80 burrows). A gerbil, picked up a week before the second census was reported as plague-infected; the discrepancy between the numbers of blocked and 'active' burrows was thus explained. Further evidence of plague was obtained from burrow fleas (*X. philoxera*) which also proved to be plague-infected. *P. pestis* was evidently in circulation in the colony at the first census, and it is probable that the reduction in gerbil density and the relative increase in flea density on the gerbils that had escaped the first trapping, had hastened the spread of the epizootic. No further trapping was done as the survivors at the second census disappeared in a few days. If the figures are accepted at their face value, disregarding the fact that some gerbils died of plague between the first and second census, we get a ratio of 8·6 'active' burrows per gerbil, calculated by subtracting the 80 'active' burrows of the second census from the 415 'active' burrows of the first census and dividing by the thirty-nine gerbils trapped. If we assume that half the gerbils that survived the trapping had died of plague by the second census, then the figure would be $415 - 160/39 = 6{\cdot}1$.

(ii) *Uithoek* (*UH* 31: *B*7–1), *September–October* 1940

The colony occupied six census squares, the warrens being concentrated round a maize threshing floor which provided the main source of food.

Census and trapping results were as follows:

Date	Census results: Burrows blocked	Census results: Burrows 'active'	Trapping results: gerbils trapped
Period VII	604	315	—
Period VIII	571	314	—
Period IX	635	376	—
Period X:			
19–20 Sept.	627	428	—
3–5 Oct.	—	—	55
10–11 Oct.	—	—	8
Period XI:			
16–17 Oct.	223	30	—

'Active' burrow/gerbil ratio $= 428 - 30/63 = 6{\cdot}3$.

The marrows and fleas from the trapped gerbils were pooled separately and inoculated into *Mastomys* with negative results. However, during the trapping experiment on 10 October a dead *Mastomys* was found which, upon examination, was shown to have died of plague. Several months earlier plague had been proved in house rats, and in *Mastomys* and their fleas (all *X. brasiliensis*) from a shed adjoining the threshing floor. Plague was thus on the point of spreading from this domestic rodent focus, via *Mastomys*, to the gerbil colony. The negative result of the inoculation of the body fleas and bone marrows of the trapped gerbils suggests, however, that the census counts and trapping results were uninfluenced by plague mortality.

(iii) *Doreen* (*DR* 34: *B* 6–1), *September–October* 1940

This colony, in contrast to the others, was dispersed in scattered warrens and, at the time of trapping, occupied twenty census squares. The census history, as in the case of the Uithoek colony, showed no signs of decrease. The results of the census and trapping were as follows:

Date	Census results: Burrows blocked	Census results: Burrows 'active'	Trapping results: gerbils trapped
Period VII	637	363	—
Period VIII	720	430	—
Period IX	708	443	—
Period X:			
19–20 Sept.	728	434	—
25–26 Sept.	—	—	27*
4 and 10–11 Oct.	—	—	4
Period XI:			
16–17 Oct.	192	103	—

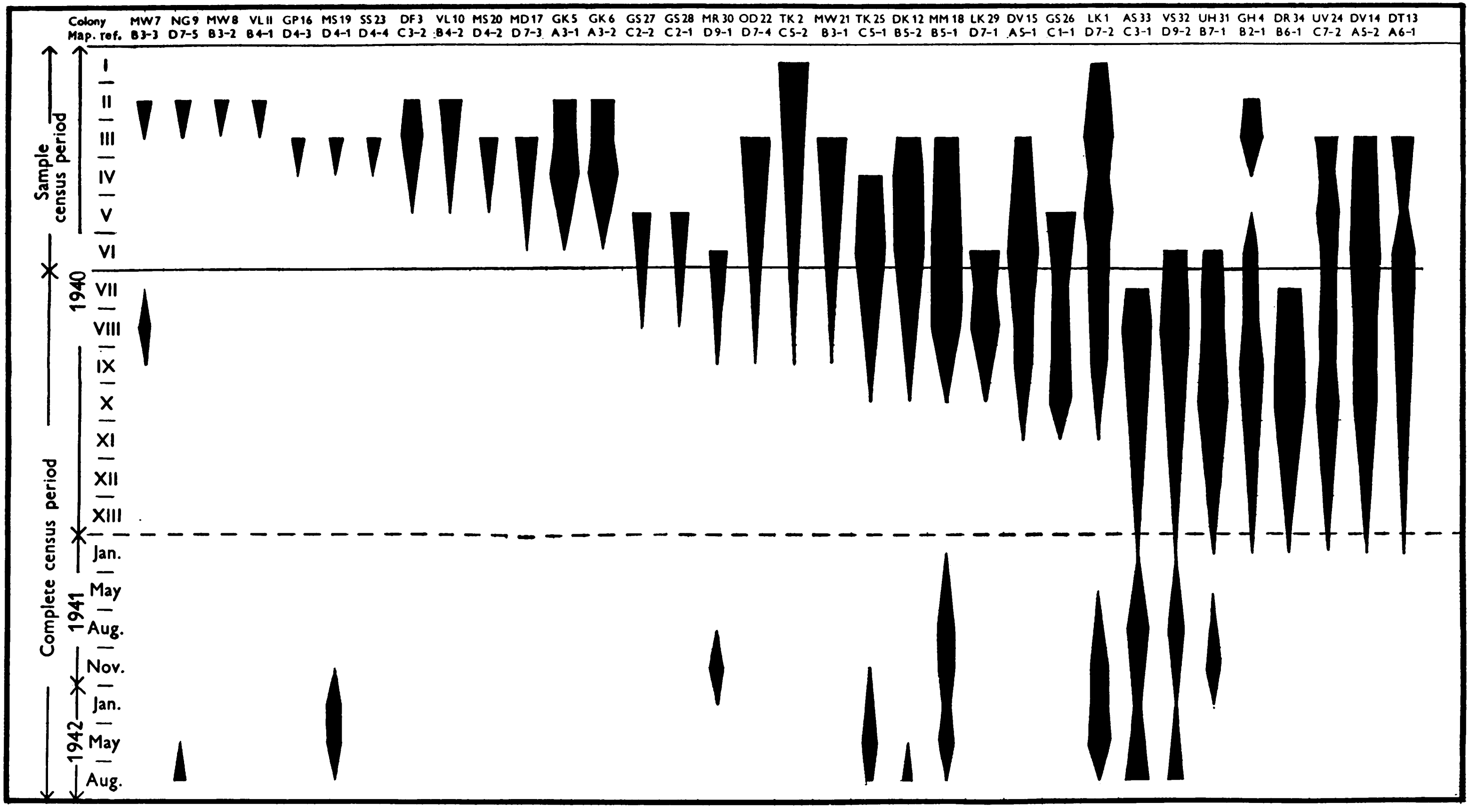
'Active' burrow/gerbil ratio = 434 – 103/31 = 10·7.

* Also one *Mastomys*.

The ratio for the three colonies was 1064/133 = 8·0. For conversion of 'active' burrows into number of gerbils the value 8 may henceforth be used, on the assumption that the number of 'active' burrows bears a reasonably constant relation to the number of gerbils in occupation at all seasons and in all circumstances.

Population decline in 1940

The sporadic occurrences of human and rodent plague in the Rooiwal area during 1938–9 have already been described (see pp. 428–9). At the start of these investigations, in January 1940, there were scattered foci of infection throughout the area; these brought about the general collapse of the gerbil population by the end of the year. It is impossible, on the data available, to determine the time when the population as a whole reached its peak level. A glance at Text-fig. 2 shows that colonies were extinguished at the rate of 2–4 every 4 weeks. From period VII, when the complete census was begun, few colonies held their own for long. The turning point seems to have been reached for about half of the colonies some

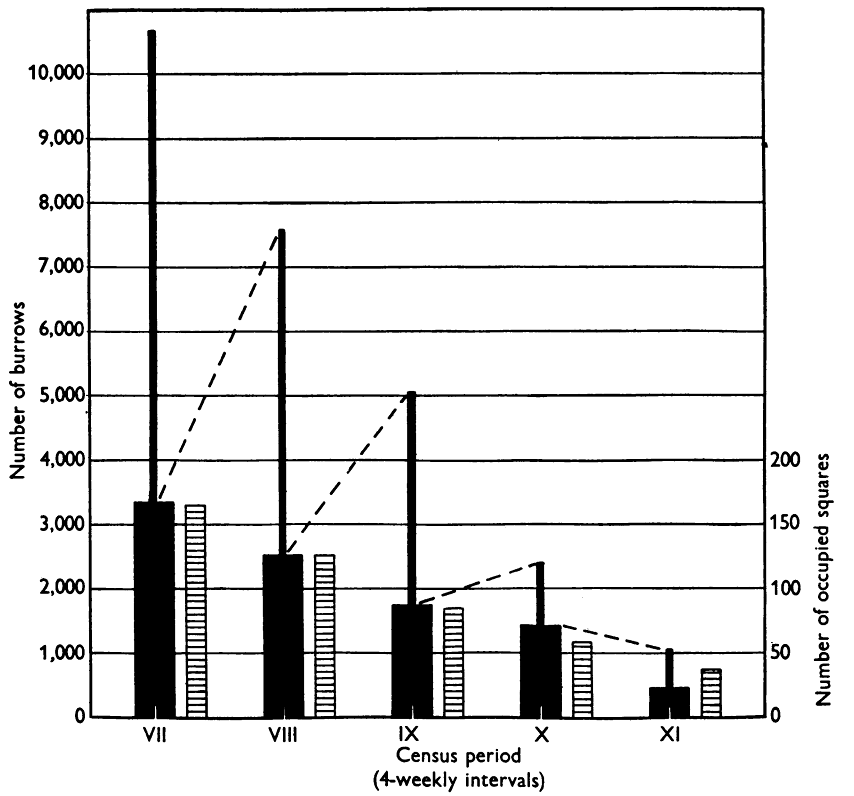


Text-fig. 2. The population trends for each colony are represented by vertical diagrams. Increase, no change and decrease in numbers are represented by widening, parallel and contracting sides respectively. The width of each diagram bears no relation to the actual size of the population or to absolute changes in numbers. Events in colony DK 12, for example, are interpreted as follows: first sample census in period III, increase during III–IV, no change IV–VI, decrease from VI to extinction in X. The location of each colony in Text-fig. 1 (map) may be found from the grid references. To economize space, events in the post-epizootic period, 1941–2, are represented on a smaller scale (about one-quarter), in the lower portion of the diagram.

4–8 weeks before the first exact census of the population was made. In other words, the complete census was in operation only in the final phase of the epizootic.

Census results

The census results during this final phase are shown in Table 2. The course of the epizootic may be followed by three measures of population size: (1) the number of 'blocked' burrows, (2) the number of 'active' burrows, and (3) the number of



Text-fig. 3. The narrow column represents the number of blocked burrows, the broad base the number of active burrows and the hatched column to the right the number of occupied census squares (50 x 50 yards = approx. half an acre). The broken line connecting the number of active burrows at one census to the number blocked at the next census represents the capacity of the surviving gerbils to reoccupy burrows over the 4-week inter-census period. The census results in period XI were lowered by trapping (see pp. 437–8).

'occupied squares' (see p. 431 for definitions). It has been shown (pp. 436–8) that measure (2) is the nearest we can get to an estimate of the actual numbers of gerbils. It will be noticed, however, from Table 2, that the three measures taken at successive censuses all reflect a consistent, steady decline. This is brought out clearly in Text-fig. 3. The successive values of 'blocked' and 'active' burrows and of occupied squares suggest an exponential decline, but as the figures refer only to one phase of the epizootic cycle no attempt is made to use them to devise a formula for the course of the epizootic wave.

Table 2. *Complete census results*

Colony code no.	Map ref.	Max. occupied area (no. of census squares)	VII (17 June–14 July) No. burrows blocked	No. burrows reopened	No. occupied squares	VIII (15 July–11 Aug.) No. burrows blocked	No. burrows reopened	No. occupied squares	IX (12 Aug.–8 Sept.) No. burrows blocked	No. burrows reopened	No. occupied squares	X (9 Sept.–3 Nov.) No. burrows blocked	No. burrows reopened	No. occupied squares	XI (7 Oct.–3 Nov.) No. burrows blocked	No. burrows reopened	No. occupied squares
GS 27	C 2–2	2	222	14	1	—	—	—	—	—	—	—	—	—	—	—	—
GS 28	C 2–1	3	175	23	2	—	—	—	—	—	—	—	—	—	—	—	—
MR 30	D 9–1	11	371	164	10	304	10	2	—	—	—	—	—	—	—	—	—
OD 22	D 7–4	11	507	172	8	303	68	6	—	—	—	—	—	—	—	—	—
TK 2	C 5–2	24	823	146	11	335	36	9	—	—	—	—	—	—	—	—	—
MW 21	B 3–1	66	1,915	324	18	503	27	5	—	—	—	—	—	—	—	—	—
TK 25	C 5–1	5	360	98	5	306	69	5	146	18	2	—	—	—	—	—	—
DK 12	B 5–2	44	1,007	232	17	862	216	8	516	25	1	—	—	—	—	—	—
MM 18	B 5–1	42	1,878	493	24	1,906	510	30	1,485	243	23	—	—	—	—	—	—
LK 29	D 7–4	6	418	222	6	410	240	6	326	13	3	—	—	—	—	—	—
DV 15	A 5–1	3	155	118	3	113	84	3	130	91	3	103	64	3	—	—	—
GS 26	C 7–1	5	269	33	4	180	38	4	116	43	4	82	20	3	—	—	—
LK 1	D 7–2	4	83	55	3	71	53	3	74	46	2	57	42	3	—	—	—
AS 33	C 3–1	11	263	99	8	167	45	3	143	69	3	85	18	4	23	12	2
VS 32	D 9–2	6	145	38	3	95	28	3	73	35	2	96	53	3	96	61	5
UH 31	B 7–1	6	604	315	6	571	314	6	635	376	6	627	428	6	223	30*	4
GH 4	B 2–1	7	123	28	3	56	23	3	73	23	3	91	50	3	62	21	2
DR 34	B 6–1	22	637	363	21	720	430	20	708	443	20	728	434	20	192	103*	10
UV 24	C 7–2	4	168	68	2	174	94	2	198	84	2	207	115	4	146	58	3
DV 14	A 5–2	2	281	222	2	239	161	2	209	157	2	198	154	2	166	89	2
DT 13	A 6–1	9	270	127	7	264	105	6	213	93	9	132	58	7	148	81	9
	Total	293	10,674	3,354	164	7,579	2,551	126	5,045	1,759	85	2,406	1,436	58	1,056	455	37

* Post-trapping counts (see p. 436).

In Text-fig. 3 the slope of the broken line joining the 'active' burrows of one census to the 'blocked' burrows of the next becomes less and less, indicating a decreasing ability on the part of the survivors to reopen their normal quota of burrows. The census in period XI was lower than it would have been had not the two supposedly plague-free colonies VH 31 and DR 34 been trapped heavily to obtain the active burrow/gerbil ratio.

At the first complete census twenty-one colonies occupied 164 census squares (85 acres) with an estimated population of about 420 animals or about five per acre of the occupied area. The population fell from 420 to 180 in 12 weeks (periods VII to X). Ninety-four gerbils were trapped between periods X and XI. The population in period XI would otherwise have numbered about 150. Between the end of October (period XI) and the end of January 1941, when no censuses were taken, the survivors of this last census disappeared.

The contraction in the occupied area tallied closely with the decline in active burrows, showing that population density (number of animals per occupied unit area) remained much the same. This could be interpreted as indicating a certain amount of regrouping into family units during the epizootic—a phenomenon that has been observed during the post-epizootic recovery by Fourie (1938).

Post-epizootic recolonization, 1941–2, *and subsequent plague history*

At intervals of approximately 3 months, the sites of the thirty-four colonies were visited until August 1942 in order to follow the process of recolonization. Censuses were taken of those that were found occupied. The results are shown in Table 3 and in the lower part of Text-fig. 2. In the space of 20 months (January 1941–August 1942) ten old sites were recolonized, mostly with little success. In the course of the surveys a lookout for any new colonies was kept: a few isolated warrens were found from time to time, but they have not been taken into account.

From Table 3 and Text-fig. 2 it can be seen that the gerbils had a tenuous hold in the area, and that 20 months after the end of the epizootic, only four colonies were increasing. These were occupied by possibly twenty animals in all. The highest level reached during the 20-month period was in August 1941, when a total of approximately eighty-six gerbils were distributed among five colonies. Specimens of fleas from deserted warrens were taken at intervals, but *P. pestis* was not detected.

The explanation of the fluctuations in numbers is probably connected with the failure to maintain numbers through breeding. *Tatera brantsi* in the northern Orange Free State has a biannual breeding rhythm, although pregnant animals are found throughout the year. The period of greatest production of young is normally in the spring (September–October) and autumn (April–May). Breeding slackens in midwinter and midsummer.

The history of the gerbils in the area from 1942 to 1951, as recorded during routine surveys by officers of the Anti-Plague staff of the Union Health Department, indicates that the population never regained its former strength. All reports refer to relatively short periods of increase in different colonies, followed by

Table 3. *Census results in post-epizootic period*, 1941–2

Colony code no.	Map ref.	May 1941			Aug. 1941			Nov. 1941			Jan. 1942			May 1942			Aug. 1942		
		No. burrows blocked	No. burrows reopened	No. occupied squares	No. burrows blocked	No. burrows reopened	No. occupied squares	No. burrows blocked	No. burrows reopened	No. occupied squares	No. burrows blocked	No. burrows reopened	No. occupied squares	No. burrows blocked	No. burrows reopened	No. occupied squares	No. burrows blocked	No. burrows reopened	No. occupied squares
LK 1	D 7–2	—	—	—	12	4	1	50	19	3	44	20	2	84	35	1	34	—	—
NG 9	D 7–5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	8	1
DK 12	B 5–2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	5	1
MM 18	B 5–1	130	60	4	750	345	18	683	344	21	598	126	17	494	217	17	476	—	—
MS 19	D 4–1	—	—	—	—	—	—	—	—	—	12	7	1	23	8	1	—	—	—
TK 25	C 5–1	—	—	—	—	—	—	—	—	—	59	14	1	115	108	1	148	69	1
MR 30	D 9–1	—	—	—	—	—	—	57	8	3	—	—	—	—	—	—	—	—	—
UH 31	B 7–1	—	—	—	29	16	3	140	81	6	58	—	—	—	—	—	—	—	—
VS 32	D 9–2	53	25	3	302	170	7	213	55	6	117	—	—	9	5	1	31	8	3
AS 33	C 3–1	95	50	2	237	149	7	200	98	7	101	18	4	108	35	8	147	51	8
	Total	278	135	9	1,330	684	36	1,343	605	46	989	185	25	833	408	29	894	141	14

decrease, on much the same pattern as was observed during 1941–2. During the years 1942–51, six cases of human plague were contracted (farms Mooiwater (1943), Die Pan (1946), Uithoek (1948) and Rooiwal (1949)) and ten strains of *P. pestis* were isolated from rodents and their fleas at the time of the outbreaks.

The circulation of P. pestis *during the* 1940 *epizootic*

The circumstances in which *P. pestis* was isolated, taken in conjunction with the census results, throw some light on the mode of spread and persistence of plague in the area, and illustrate the routes by which *P. pestis* was carried from the gerbil reservoir to other rodent species and man.

History of plague in individual colonies

The progress of the epizootic in individual gerbil colonies is represented in the upper portion of Text-fig. 2 which depicts the relative changes in numbers of surviving gerbils during the sample and complete census period. The decline in numbers in many of the colonies became sharper 3–4 months before extinction; this indicates the point when the reproductive capacity of the colony failed to keep pace with losses due to plague, and was the first sign of mortality to be brought out by the census results. In a few colonies *P. pestis* was isolated before numbers began to fall. Consideration will now be given to the history of plague in different colonies and to its persistence in burrow fleas after the gerbils had died out.

Early detection of P. pestis. *P. pestis* was recovered from colony DK 12, 6 months before the gerbils died out. Numbers remained steady, in fact they increased slightly during the 3 months of the sample census and then dropped to nil 3 months later (Text-fig. 2). The presence of plague was thus not reflected by a downward trend in the census counts for about 3 months. In four other colonies, namely OD 22, TK 2, MW 21 and UV 24, 4–5 months elapsed between the first proof of plague and extinction. In all but the last, a decline in numbers was already detectable and continued until the extinction of the colony. Colony UV 24, however, showed a drop at the time when plague was proved, but the numbers recovered to their earlier level and remained there until the last census, when they dropped again.

Colony GH 4 fell to nil during periods IV and V. Plague was not proved amongst the gerbils, but a house rat was found dead of plague at the time in a shed 50 yards from the warrens. In period VI the warrens were re-invaded by a few individuals, which were still surviving in period XI. These last two colonies were small, and it is possible that their normal movements did not bring them into contact with the infected foci in their midst.

A similar case to GH 4 occurred with colony DT 13; its numbers fell almost to nil between periods III and IV and then rose again from periods VI to VII, and were maintained with some fluctuations until period XI.

LK 1 is an example of a colony, of which the natural rate of increase was balanced against plague mortality for 3–5 months. The sample census in this case covered the whole occupied area, as it was a small compact colony around a maize threshing floor. In period I there were sixty-four active burrows. No census was taken in period II. From periods III to XI the numbers of active burrows were 74, 63, 102, 50, 55, 53, 46, 42, 0. A plague-infected gerbil was found in the course of each census in periods VII, IX and X when the counts were 53, 46 and 42 respectively. This mortality is reflected in the census figures, but not so markedly as would be expected. It appears either that numbers were being reinforced from nearby, for which there was no direct evidence, or that the breeding rate kept pace with the mortality rate for a time.

These observations suggest that during the pre-epizootic phase, plague gradually spreads from warren to warren within a colony, causing an odd death here and there until there are sufficient infected fleas to raise the infection rate and so precipitate the downward trend to extinction.

Persistence of P. pestis. It was part of the routine of the census to block all burrows on both census days to facilitate accurate counting. When a colony died out, therefore, the burrows remained blocked; this ensured that the burrow fleas were deprived of a blood meal from any casual visiting rodent.

The four colonies GP16, MS19 and 20, and SS23 were small and near to one another. They were discovered when the epizootic was in its last stages amongst them and were only under observation for a few weeks before they died out. Just before, and at the time of extinction, seven strains of *P. pestis* were isolated from gerbils and fleas. Thereafter groups of blocked burrows were excavated from time to time and searched for fleas. Plague was proved in collections of *X. philoxera* 22, 44 and 120 days after the warrens had become untenanted. Plague-infected fleas were recovered by similar means from three colonies in other parts of the area. Colony VL10 yielded plague-infected *X. philoxera* that had been immured for 77 days, colony DF3 for 34 days; and colony MD17 yielded infected *D. e. ellobius* after 15 days.

The warrens around the homestead of the farm Mooiwater (MW7) which were associated with the human case of plague (see pp. 429–31) remained untenanted from periods II to IX. In period IX (on 4 September) it was noted that a few burrows at one of the old warren sites had been reopened (Text-fig. 2, MW7). A dead gerbil was found in a nest and both it and the fleas on it proved to be plague-infected. The strain from the gerbil was normally virulent and was used for some time as the stock test strain at the S.A. Institute for Medical Research. The strain from the fleas (*X. philoxera*) killed the test *Mastomys* in 4 days, but the culture was later found to be avirulent. Eight months had elapsed since this warren was deserted, and it is possible that this odd roving gerbil had been bitten by a flea that had survived in the nest for that time and that some of the plague bacilli in the flea's gut had lost their virulence. The other alternative, of course, is that the gerbil found its way to this warren either already infected or carrying infected fleas. Other old burrows in the vicinity were systematically searched for fleas but none was found. The odds were thus slightly in favour of the gerbil having brought the infection with it. This was the only instance of a suspected transfer of infection from one gerbil colony to another. The means by which plague spreads between colonies will probably remain obscure until an epizootic can be studied with marked animals.

Interchange of P. pestis *between gerbils and other rodents*

The circumstances in which rodents other than gerbils were found plague-infected illustrate the mode of spread of infection from the gerbil reservoir and give some indication of the frequency with which this occurred. No secondary spread of plague was observed from most of the gerbil colonies, the epizootic being, as far as could be determined, self-contained. In the remainder, particulars of which follow, varying degrees of secondary spread were observed or suspected, and in one instance the reversal of the normal sequence was all but proved.

(i) *From* Tatera *to* Mastomys. The combination of trapping and plague caused the disappearance of colony NG 9 by the end of February (see p. 437). On 18 March a *Mastomys* was found dead near a deserted gerbil burrow about 100 yards from this colony. Direct microscopic examination revealed *Pasteurella pestis*-like bacilli, but the biological test was negative. On 26 March house rats were reported to have disappeared from an outbuilding of a farmhouse nearby. No rats were caught in the traps set, but fleas (*X. brasiliensis*) collected from the floor of the store were tested for plague, with negative results. On 12 April another *Mastomys* was found dead near the same place. *P. pestis* was isolated from a test animal inoculated with bone marrow. Secondary spread to *Mastomys*, but not to *R. rattus*, was thus established.

(ii) *From* Tatera *to* Rattus. The colony GH 4 disappeared in mid-April. Sixteen *X. philoxera* from the deserted burrows were tested with negative results. On 27 April a dead *R. rattus*, plague-infected, was found in an outbuilding 50 yards from the warrens. In spite of the negative result from the gerbil fleas, it is likely that the rats in the outbuildings picked up infection from the gerbil burrows.

(iii) *From* Rattus *to* Mastomys *to* Tatera. At the end of May on the farm Uithoek, in a cowshed adjoining the maize threshing floor occupied by the gerbil colony UH 31, there was heavy mortality amongst the rats. *P. pestis* was recovered from *R. rattus*, its body fleas and fleas from floor sweepings (both *X. brasiliensis*). A week later a further batch of fleas (*X. brasiliensis*) from floor sweepings was proved infected and shortly afterwards, four plague-infected *R. rattus* and one *Mastomys* were found. On 20 September, nearly 4 months later, a plague-infected *Mastomys* was found in one of the gerbil warrens of the colony UH 31. No mortality had occurred amongst the gerbils and it seems reasonable to assume that, had matters been left to take their course, a focus would have been established, which would have precipitated an epizootic amongst the gerbils. However, the colony was heavily trapped (see p. 437). The fleas and bone marrows from the trapped animals were inoculated into test *Mastomys* with negative results, indicating that plague apparently had not gained a foothold amongst them. The final proof of this sequence of events is thus lacking.

Human infections in the study area

There were two outbreaks of human plague in the study area. The outbreak in January on the farm Mooiwater has already been described (p. 429). In this there was a clear-cut *Tatera-Mastomys-Rattus rattus* sequence. Early in October a native youth contracted plague on the farm Dumfermline on which colony DF 3 had died out during period V, 5 months before. As the gerbil colony was situated near the farm buildings it is probable that secondary infection of house rats had taken place. Investigation, however, failed to reveal any direct evidence of recent mortality.

DISCUSSION

The plague complex in the Rooiwal area and elsewhere in the northern Orange Free State has as its focus the gerbil population, which is the permanent natural reservoir of *P. pestis*. Plague among domestic rodents is of secondary importance in the maintenance of the reservoir, but it is the main source of human infections. It may, in special circumstances (see p. 446), expose healthy gerbil colonies to infection.

The factors which ensure the survival of *P. pestis* in the wild rodent reservoirs in different parts of the world are not fully known (Meyer, 1942). It seems certain, that so far as the *Tatera brantsi* reservoir in South Africa is concerned, the occurrence of the flea *X. philoxera*, is one of the crucial factors. *X. philoxera* is not only an efficient plague vector but also, it seems, more suited than other gerbil fleas (e.g. *D. e. ellobius* and *Chiastopsylla rossi*), to retain *P. pestis* for relatively long periods. This observation is based on our knowledge of the host and geographical distribution of *Tatera* fleas (De Meillon, 1942; Davis, 1948). Of the three species, the distribution of *X. philoxera* tallies very closely with the enzootic plague area, whereas the other two species are as frequent outside as in it. *X. philoxera* seems to be adapted to living in *Tatera* burrows in the semi-arid and arid regions of the highveld and Kalahari in the under 25 in. rainfall area. The combination of *T. brantsi* and *X. philoxera* evidently provides an ideal host-vector relationship for the survival of *P. pestis*.

The results of this study at Rooiwal reaffirm the conclusion come to by Pirie (1927) that gerbil fleas were more important agents in the carry-over of plague from one epizootic to another than the gerbils themselves. He considered that 'the mechanism of the persistence of plague in the wild rodent reservoir...is... not too difficult of explanation even when the population is scanty'. The results Pirie obtained in the experimental enclosures showed that infected fleas survived without a host for 3 and possibly 6 months and were capable of transmitting plague to 'clean' rodents put into the enclosures at the end of the experiments. These findings are paralleled in the present study by the recovery of *P. pestis* in fleas that had been immured in warrens without a host for varying lengths of time up to 4 months (p. 445).

The observations made on the course of the gerbil epizootic in 1940 support the view expressed by Fourie (1936, 1938) that the epizootics run their course irrespective of the time of year. In this study, the general impression was that a colony took about 6 months to die out after *P. pestis* first appeared in it. The general course of the epizootic in the area as a whole was strikingly uniform while the complete census was in operation, i.e. from June to October (midwinter to early summer). It was also observed that a small colony took about as long to die out as a larger one. This comparatively lengthy course of the epizootic can be put down in part to discontinuity in distribution of the gerbil colonies and to the consequent lack of regular contact between them.

The results of a flea-survey of gerbils at Holfontein (Davis, unpublished) showed that there was a considerable variation in the flea-index throughout the year (1938–9). Fleas began to increase towards midsummer (December), to remain numerous until the beginning of winter and then to decline sharply. It is reasonable to assume that in the Rooiwal area in 1940 there were similar seasonal changes. There appears to be no connexion between rate of mortality amongst gerbils and the abundance of fleas in their warrens and burrows and on their bodies.

A factor that may influence the rate of spread of plague in gerbil populations is the normal range of movement of individuals in a colony between the warrens they inhabit and between one colony and another. A year's study of the movement of gerbils was done in 1942–3 (Union of South Africa, 1943) in the southern Transvaal. It was found that once a female had had her first litter, she remained closely tied to a single warren or group of adjoining warrens, that adult males usually roved from one warren to another, and that the young adults at or near sexual maturity sometimes moved widely. Such movements would lead to a gradual but steady dispersal of *P. pestis* throughout the warrens of a colony and might well, from time to time, carry the infection from one colony to another.

SUMMARY

1. The course of an epizootic of plague in thirty-four colonies of gerbils (*Tatera brantsi*) was observed by counting, at 4-weekly intervals, the number of burrows which, when they had been closed on one day, were found open on the next. One gerbil could open an average of eight burrows in one night.

2. Regular censuses on the twenty-one colonies which survived until the last phase of the epizootic showed that the gerbil population fell from about 420 at the end of June 1940 to none at the end of January 1941. From May 1941 to August 1942, 3-monthly counts revealed some recolonization, but field officers reported that between 1942 and 1951 the gerbils sometimes died from plague, and the population never regained its former level.

3. During 1940, two to four colonies died out every 4 weeks. The time of year seemed not to influence the course of the epizootic.

4. *Pasteurella pestis* was detected in some gerbil colonies 4–6 months before they died out.

5. Plague-infected gerbil fleas were found which had been immured in blocked deserted burrows for periods of up to 120 days.

6. The passage of infection was traced from the reservoir in gerbils to other wild rodents (*Otomys irroratus*, *Rattus* (*Mastomys*) *natalensis*), to house rats (*Rattus rattus*) and to man.

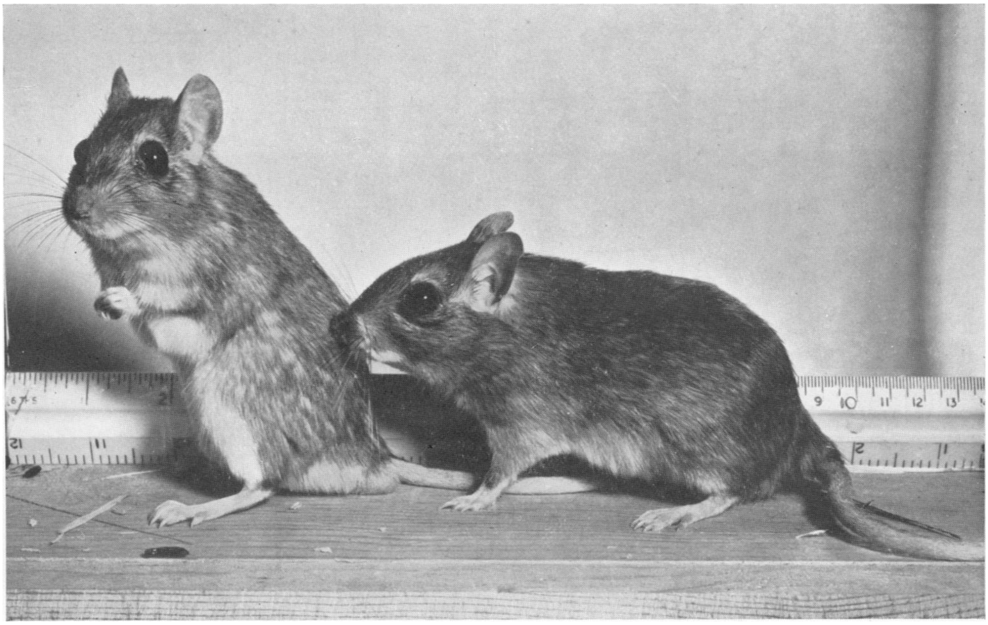


Fig. 1.

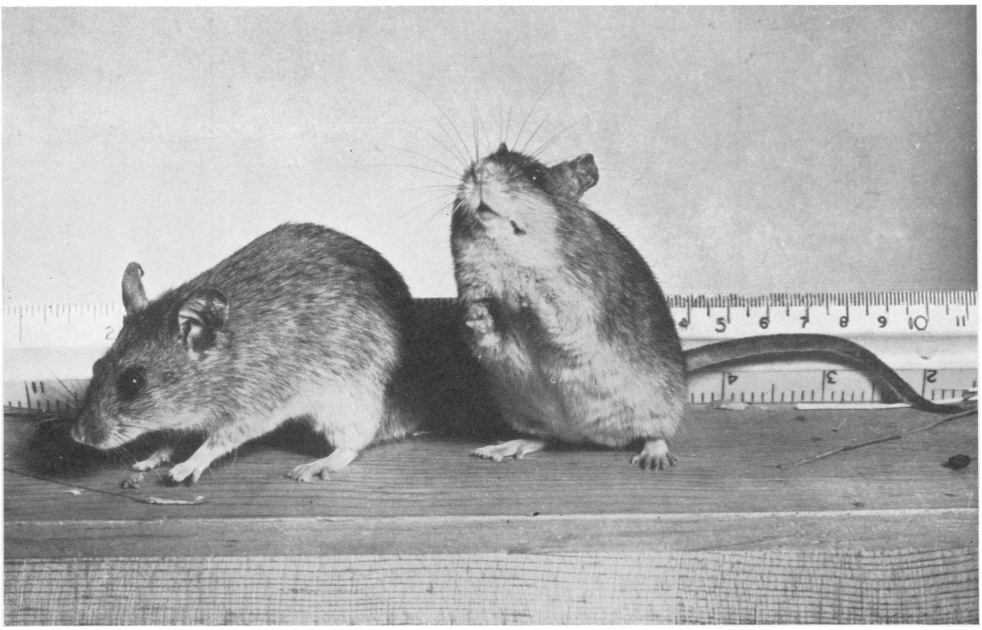


Photo: Film Division, Pretoria

Fig. 2.

Fig. 1.

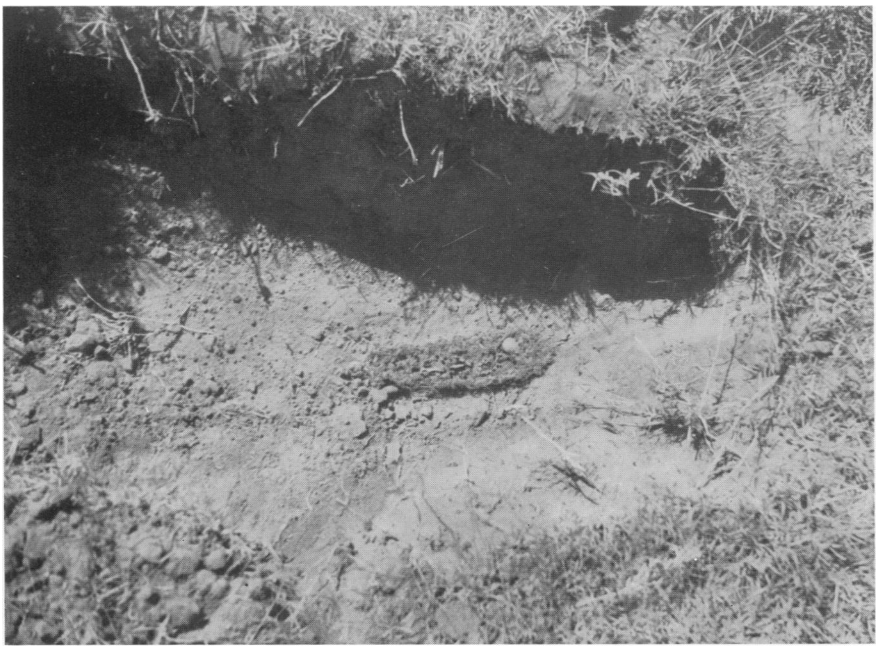


Photo: D.H.S.D.

Fig. 2.

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EXPLANATION OF PLATES 10 AND 11

Plate 10

Fig. 1. Gerbils, *Tatera brantsi*.
Fig. 2. Multimammate mice, *Rattus* (*Mastomys*) *natalensis*.

Plate 11

Fig. 1. Gerbil (*T. brantsi*) warrens in grassveld, maize lands in the distance. There are pegs at most of the burrow entrances. The warrens are about 50 yards apart.
Fig. 2. Dried-up remains of a gerbil (*T. brantsi*) found on the floor of a burrow during excavation of a deserted warren. Plague-infected fleas were recovered.

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