XXXI. ON THE SEASONAL PREVALENCE OF PLAGUE IN INDIA.

Introduction.

ONE of the most striking feature of plague epidemics is their seasonal prevalence. This feature has been well marked in India since the disease was introduced into Bombay in the autumn of 1896. In places where plague has once become established, the epidemic period, lasting as a rule about 3 months, tends to recur always at the same season of the year. This yearly outbreak, however, does not coincide in point of time in different places in India, but, as we shall see, varies considerably in this respect. Further, it is to be noted that the first epidemic may be at a different season of the year from that which obtains in all subsequent outbreaks.

We propose in this communication to enquire whether the facts of seasonal prevalence are consistent with the view that, as far as epidemicsare concerned, the prevalence of plague depends upon the transmission of the plague bacillus from rat to rat and from rat to man by the rat flea. We propose to approach the problem, first by stating briefly the facts of seasonal prevalence as observed in six places in India. These places were specially chosen for the reasons, that they are more or less widely separated from one another, that they differ markedly from one another as regards their climatic conditions, that plague has annually recurred in them for the last 4 to 10 years, and that the yearly outbreak occurs at different seasons in the different places. Secondly, we shall proceed to state what possible factors, having regard to the part played by the rat and the rat flea in the epidemiology of the disease, might influence the rise and fall of the epidemic. Finally we shall discuss in detail each of these factors, bringing forward any experimental evidence which bears on each hypothesis. We do not propose to consider at this time the further problem of how the intervals between the acute epidemics are filled in, as the investigations on this question are not complete.

I. FACTS OF SEASONAL PREVALENCE OF PLAGUE IN SIX PLACES IN INDIA.

1. Bombay City.

Bombay City, with a population of about 1,000,000 inhabitants, is built on an island on the west coast of the peninsula. The climate on the whole is hot and damp. The daily mean temperature, considered over the whole year, is between 70° and 80° F., the mean diurnal range being only 12.5° F. It is subject to the south-west monsoon which blows from May to October, and during which period, especially in June, July and August, there is a heavy precipitation of rain. During the rest of the year the north-east monsoon prevails, there being at this season little or no rain.

Plague was recognised in Bombay in the latter half of September 1896. Up to the end of 1896 it did not assume any formidable proportions, the first real epidemic being in the spring of 1897. Since then the seasonal prevalence of plague in Bombay has been well marked and has shown little or no variation (Chart I). A study of the curve¹ will show that each year the epidemic begins in January, gradually rises until it reaches its maximum in March, then rapidly declines until by the middle of May the plague mortality has returned to what it was before the epidemic. Different years show a slight variation from this general scheme. For example, in 1900 the epidemic began a little earlier than usual, that is to say in December 1899, and lasted perhaps a little longer, while in 1906 it did not begin till February and was a little later in subsiding, namely the end of May. This latter phenomenon was also observed in 1905. Further, a study of the curve will show that in several years, especially in 1898 and 1901, there was a slight recrudescence in the months of August and September, which recrudescence, however, never reached the same proportions as the epidemics in the spring. We can, therefore, state that the seasonal prevalence of plague in Bombay is from January to April and that the factors which determine the epidemic must be most in evidence at this time. While this is so, as there is often a tendency to recrudescence during August to December,

¹ The method on which this and all subsequent curves are constructed was as follows. The bimonthly plague mortality for the period over which the curve extends was taken, and a mean of these figures calculated. Then the percentage above or below this mean for each bimonthly figure was determined and the curve constructed on these percentages. In this way the relative severity of the different epidemics in the same place can be seen at a glance.

the conditions at this season must be more favourable than in the latter half of May, June and July, when the plague mortality is always at its lowest.

2. Poona, City and Cantonments.

Poona is only 80 miles distant from Bombay. It has however different climatic conditions and a different seasonal prevalence of Poona is situated on the plateau of the Deccan about 40 miles inland from the summit of the Western Ghauts, and about The daily mean temperature for the 2000 feet above sea level. year is 70° to 80° F., while the diurnal range is on an average 22.5° F. Poona is subject to the south-west monsoon during the months of May to October. As, however, it lies some distance inland the rainfall is much less than on the coast, the greatest precipitation taking place on the Ghauts. During the months of March, April, May and June, Poona is hot but dry, the daily mean temperature being between In July owing to the cool south-west breezes there 83° F. and 90° F. is a marked fall which is sustained during the autumn months, the mean daily temperature during this season being between 75° and 80° F. the winter months Poona enjoys a delightful climate, the mean daily temperature being about 70° F. and the diurnal range about 30° F. A study of the curve (Chart II) will show that plague was first introduced year there was a distinct but comparatively slight epidemic which reached its height at the end of March and rapidly subsided during April. This is the only outbreak which Poona has had at this season of the year. The other epidemics all occurred between August and March and can be divided roughly into two groups, namely:

- (a) A group, in which the plague mortality begins to rise in August or September, reaches its height about the beginning of October and then comes down rapidly afterwards. We may call this group, into which fall the epidemics of 1897, 1900 and 1906, 'early epidemics.' We can also include in this category the epidemic of 1899, which however, as reference to the curve will show, began as early as March, but remained latent during the hot weather, rising during August to an abnormal height.
- (b) A second group, in which the epidemic does not begin till October or even December, as in 1902—1903, reaches its maximum in December or January and then falls till the mortality becomes normal in February or March. This group we may call 'late epidemics.' The

epidemics of 1901—1902, 1902—1903, 1903—1904, and 1904—1905 were of this description.

It does not appear that there is any great difference between the early and late epidemics as regards their severity, although, if anything, with the exception of the late epidemic of 1902—1903, the early ones have been more severe. It is noteworthy that there was no epidemic in 1898, nor again in the autumn or winter of 1905. On the whole, therefore, a study of the Poona epidemics leads us to conclude that while the most favourable time seems to be the autumn, namely, August to November, nevertheless the conditions must still be favourable during December to March. Further, it appears that from March to the beginning of July plague cannot exist in epidemic form.

3. Nagpur City.

Nagpur is a fairly large city situated in the centre of the Central Provinces, of which it is the capital. The climate is not unlike that of Poona, except that the mean temperature is higher both in the hot weather and in the rainy season. The hot weather begins in March, and lasts into June, the mean temperature being then between 85° and 95°F. In July, August and September, the mean temperature is a little over 80°F.; while in the cold weather during November, December, January and February it falls to between 70° and 75°F. The rainfall is almost all confined to the months of June to September and during this period there is an average fall of about 40 to 60 inches.

The curve (Chart III) shows that plague was first introduced in the cold weather of 1902—1903. During January and February of 1903 there was a rapid rise, the mortality reaching its highest point in the beginning of March. From this date it rapidly fell till by the end of April the plague mortality was practically nil. The next epidemic in Nagpur began in October 1903, reached its height in December and January and then rapidly fell till by the middle of March it had practically subsided. The remaining part of 1904 and practically the whole of 1905 were free from plague. The last epidemic began in December 1905, rose rapidly during January and February 1906, and reached its summit in the beginning of March. From this time it rapidly declined till it had practically subsided by the middle of April.

It will therefore be seen that Nagpur has suffered from three epidemics, two during the months of January—March, and the third

between October and February. Finally we may take it that in Nagpur the conditions on which seasonal prevalence depends are most favourable during the months from November to March. Epidemic plague has been unknown between April and September inclusive.

4. Belgaum City.

Belgaum is a city situated in the southern Maratha country, that is to say, in the southern extremity of the Bombay Presidency. It lies on a plateau about 2500 feet above sea level and 75 miles inland from the west coast of India. The climate of Belgaum is one of the most equable in India. During the greater part of the year, namely, from June to February the mean daily temperature is between 70° and 75° F., the average diurnal range being about 20° F. During the hot season, March to May, the mean daily temperature never rises very high, ranging about 80° F. The average annual rainfall is about 40 inches, most of which falls between June and October. At this season the humidity is at its maximum.

As regards the plague epidemics which have visited this city, a study of the curve (Chart IV) will show that the disease was first introduced in October 1897. This epidemic, a comparatively slight one, lasted throughout nearly the whole of the winter months, reaching its maximum in January 1898, and disappearing in the spring of that year. subsequent epidemics which have appeared in Belgaum have, with the exception of that of 1899, commenced in July or August, reached their maximum in October and disappeared towards the beginning of the new year. The epidemic of 1899 began in May, reached its height in August and subsided by October. It was, in short, two months earlier than usual. It is evident, therefore, that the epidemic season of plague in Belgaum is August-December, but that an epidemic may start earlier and come to an end before the time of year at which the usual outbreaks cease. Another interesting observation which is obtained from a study of the curve is, that since the epidemic of 1898, which was very severe, all subsequent epidemics, with the exception of that of 1902, have decreased in severity year by year until 1906, in which year there was practically no plague at all. It will be interesting to watch and see if there is any recrudescence in 1907.

5. Lahore City.

Lahore, the largest city and capital of the Punjab, is situated nearly in the centre of the plains of this Northern Province. It is about 700 feet above the sea level. Owing to its geographical situation Lahore is removed from the tract of the south-west monsoon and in fact receives comparatively little rain during the year. The climate of Lahore shows marked differences at different seasons of the year. From November to March the mean temperature is below 70° F., falling in January to about 54° F. During the rest of the year the mean temperature is above 70° F., in May, June, July and August ranging between 85° and 95° F. The heat during these months is intense. The diurnal range of temperature is extensive, being on an average 27.5° F., while in April and May it is 32.5° F., and in October and November as much as 35° F. The rainfall during the year is small, between 20 and 25 inches, the chief fall taking place in the months of July, August and September. There are also winter rains during January and February, much less in amount however than the autumn fall.

A study of the plague curve (Chart V) will show that the disease was first introduced into Lahore in the early part of 1902. There was no well-marked epidemic during the following spring, a slight outburst coming to an end with the advent of the hot weather in May. During the winter of 1902-1903 there was a slight recrudescence; but the first serious epidemic took place in the spring of 1903. This outbreak, beginning in March, reached its height early in May, after which date there was a rapid decline, until by the end of June the mortality was normal. The second epidemic, the most severe from which Lahore has suffered, began in March 1904, reached its maximum early in May, and then fell rapidly, until it had practically disappeared by the end of The third and fourth epidemics, namely those of 1905 and 1906, occurred at the same season of the year as the first and second. Further, during the cold weather of 1904—1905 and of 1905—1906 there were slight recrudescences, which, however, never reached the proportion of epidemics. Finally, we have to note that in October-November 1906 there was a marked increase in the plague mortality, which by the end of December was still on the upward tendency. Here evidently the winter recrudescence was assuming the proportions of a spring epidemic.

Viewing the epidemics in Lahore as a whole we conclude that March—May are the three months in which plague shows its most marked seasonal increase, that there is a tendency to recrudescence during the winter months and that during the hottest months of June—September the disease is never present in epidemic form.

6. Rawalpindi City and Cantonments.

Rawalpindi, a large native city with an extensive military cantonment adjoining, is situated in the north of the Punjab at the base of the Himalayas. The climate is not unlike that of Lahore but, as Rawalpindi is considerably further north and lies 1700 feet above sea level, the hot weather is not so severe nor so prolonged as in the former place. Further, situated as it is at the base of the Himalayas it receives more The daily range of temperature is considerable, rain than Lahore. namely, between 20° and 30° F. In the hot weather, namely, May, June, July and August, the mean temperature ranges between 80° and 92° F. The cold weather has an earlier onset and is more severe than at Lahore, the mean temperature at the coldest period falling to below The rainfall averages 30 to 40 inches per annum and while the principal fall is in July, August and September, the winter rains during January to April are not inconsiderable, namely, about 8 inches.

Plague first appeared in Rawalpindi (vide Chart VI) in the hot weather, namely June of 1903. It did not, however, assume epidemic magnitude till two months later. By September it had grown into a severe outbreak. This epidemic reached its maximum at the beginning of October, from which date it fell rapidly, until by the end of November it had disappeared. During the next 18 months, while there was no serious epidemic, there were several small recrudescences, the most marked in June 1905. This latter outbreak remained latent during the hot weather, bursting out into a small epidemic in the autumn. It reached its height early in November and by the end of the year had entirely disappeared. The plague mortality began to rise again in May 1906; did not increase during the hot weather, but rose to become a serious epidemic in the autumn. This outbreak reached its height towards the end of October and by the end of December had practically disappeared.

A study of the Rawalpindi curve (Chart VI) as a whole shows us that evidently the most suitable season for plague epidemics is the autumn, September to November, but that slight recrudescences may occur practically at any season of the year. It is especially noteworthy that in every year the disease has been present in the city in the spring, but on the three occasions on which an epidemic followed, this did not occur till the autumn.

II. Possible factors which influence the seasonal prevalence of plague.

We have now to pass on to a statement of the factors, which on the basis of the rat-flea-man theory might influence this seasonal prevalence. We can classify these factors as follows:—

A. Climatic conditions, especially temperature, rainfall and humidity.

When we came to consider in what way temperature might act it appeared to us that it might be by a direct influence on the transmission of the bacillus from animal to animal by the flea, that is to say, on the conditions to which the bacillus is subjected in the stomach of the flea, or by a direct influence on the disease in the rat, especially as regards the degree of septicaemia. Further, it is readily conceivable that climatic conditions might affect the seasonal prevalence of plague in so far as they influenced the life history and habits of the rat or of the flea, or the habits of man.

B. Variations in the virulence of the bacillus.

It has been suggested by some observers that the virulence of the plague bacillus is diminished by passage through the rat. If such a diminution occurred in nature or if there was any variation in virulence due to other causes, it is possible that such variation might influence the seasonal prevalence of plague, inasmuch as a bacillus of diminished virulence would tend to cause a localised, rather than a general infection, which latter condition is essential to enable the flea to become infected.

C. Variation in the total number of rats and variation in the proportion of immune to susceptible rats.

It is conceivable that the seasonal prevalence of plague might be dependent upon a variation in the total rat population or upon a variation in the proportion of immune to susceptible rats. The effect of a plague epizootic on the rat population must be to diminish, for the time being, the total number of rats and to leave a greater number of rats which as a result of recovery from mild attacks of plague are more or less immune to the disease. It is possible that an epizootic might be influenced in the direction of being brought to an end by these causes. Further, if there was a definite breeding season of rats, as a result of

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which the rat population was at one season of the year increased by a large number of young non-immune animals, we would have the conditions, as far as the rat population is concerned, suitable for the recrudescence of the epizootic. It is evident, therefore, that we shall have to consider the above as possible factors influencing the seasonal prevalence of the disease.

D. Variation in the number of fleas.

If we accept the flea as the only material means of transmission of the plague bacillus from animal to animal, there are a priori grounds for concluding that the severity of an epidemic would be directly influenced by the numbers of fleas present. With a small number of fleas the chances of infection would be less, few cases would occur and the rate of progress of the disease would be decreased. A great flea prevalence would have the opposite effect, namely, a large number of cases in a short interval of time, in other words an epidemic outbreak of the disease. We shall, therefore, have to enquire into what evidence we possess as to there being a marked seasonal prevalence of the rat flea.

III. Analysis of the influence of temperature in six plague infected localities.

We have already considered in a general way the relation of plague epidemics to different seasons of the year as observed in six widely separated districts in India. We have seen that outbreaks may occur at practically any season. As, however, the climatic conditions, especially temperature, show marked variations in these six places at any one season we have added to the plague mortality curves a curve of the daily mean temperature and a curve representing the degree of humidity. The temperature curve was constructed as follows: from the daily maximum and minimum temperatures, the daily mean temperature was calculated. In the case of Bombay, however, the mean temperature was determined from hourly records. The average daily mean temperature for each half month was then calculated, and the curves plotted out from these figures. The humidity curves were made in the same way, saturation being 100°.

A study of the plague mortality and temperature curve shows the following facts.

Bombay. (Chart I.)

The plague epidemic begins each year when the mean temperature is at its lowest point, namely, between 72° and 75° F.; it rises gradually as the temperature rises and assumes its maximum proportion when the mean temperature is about 78°--80° F.; very soon, however, after the mean temperature rises above this latter figure, the plague mortality begins to decline, the decline, as the temperature rises, being very rapid. While in the non-epidemic season, namely, May to October, the mean temperature is always above 80° F., there is observed to be a slight fall of temperature in August and September, when a recrudescence is liable to occur. It is noteworthy that the epidemics of 1897 and 1900, which began earlier and which, having reached their height, began to decline before the mean temperature passed 80° F. were of longer duration and declined more gradually than was the case with the other epidemics. These data, therefore, would seem to point to the conclusion that, while a high mean temperature, namely 80°-85° F., may have an influence in limiting plague epidemics, the factor of temperature is not the only factor which is concerned in the seasonal prevalence of the disease.

Poona. (Chart II.)

It will be remembered that plague was introduced into Poona early in 1897 and that the first epidemic was a slight one, coming to an abrupt end during April. A reference to the temperature curve will show that the mean temperature was gradually rising during the rise of the epidemic and stood at 81° F. when the epidemic was at its height. As the temperature rose above this figure the plague mortality rapidly became less. A possible explanation, therefore, of the cutting short of this outbreak is that the mean temperature became too high before the epidemic had gathered its full strength.

We have also seen that the usual epidemics in Poona may be divided roughly into two groups:

(a) a group in which the outbreak occurs between August and November and (b) a group in which the epidemic season is roughly November—February.

The period from the middle of March to June inclusive has been always free from epidemic plague. Now, when we co-relate these data with the temperature curve, we find that the daily mean temperature during the period July to middle of March is never above 80° F. and that during the period middle of March to June the mean temperature

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is always above 80° F. reaching nearly 90° F. in April and May. While the epidemics of both groups occur when the mean temperature is below 80° F., ranging between 66° and 78° F., they, however, decline and come to an end while the temperature still remains low, in fact, as we shall see, when the temperature would appear to be most suitable. Another factor, or factors, therefore, must be in operation in determining the decline of these epidemics, a conclusion which we have already reached from the study of the Bombay curves.

The epidemic of 1899 in Poona deserves especial notice. A reference to the chart will show that the plague mortality in this year began to rise in February, when the daily mean temperature was about 75° F.; that with a rising mean temperature it went on increasing till March, when it seemed to receive a check, the mean temperature being now above 80° F. In April, May and June, when the mean temperature remained high, the plague mortality remained low. The epidemic, however, burst out again in July with excessive severity, when the mean daily temperature fell to about 76° F. It would appear, therefore, that this epidemic, beginning when the temperature was suitable, was held in check during the hot months, when the mean daily temperature was above 80° F., until in July, when the temperature fell on the advent of the south-west monsoon, it burst out in full force.

Nagpur. (Chart III.)

As we have already seen, there have been three plague outbreaks in Nagpur, two during the months of January to March and the third between October and February, that is to say, the period from October to March is a season when the conditions are favourable for epidemic A reference to the temperature curve shows that during this period the daily mean temperature is below 80° F., while during the non-plague season, April to September, the mean temperature is above 80° F., reaching as high as 90° F. or above during April, May and June. While this is so, a study of the chart will show that a high mean temperature could not have been the factor which brought to an end the epidemic of the winter 1903-1904. The plague mortality in this outbreak came down rapidly in February, when the mean temperature was between 70° and 76° F. On the other hand, in the case of the other two epidemics the factor of temperature might have been instrumental in causing their rapid decline. Both of these outbreaks began in January, when the daily mean temperature was but a little above 70° F., increased during February, when the daily mean temperature was below 80° F.,

reached their height early in March and fell rapidly during the latter part of March and April, after the daily mean temperature had passed above 80° F. and was still rising. It is noteworthy that these two outbreaks, which seemed to be thus cut short by the temperature, while severe were of shorter duration and declined more rapidly than the third outbreak, which, as we have seen, came to an end irrespective of any rise in temperature.

Belgaum. (Chart IV.)

We have already seen that Belgaum enjoys a most equable climate, the daily mean temperature for the year being between 70° and 80° F. A study of the temperature curve will show that only during two months of the year, April and May, does the mean temperature rise above 80° F. and even then it is never above 83° F. It is evident, therefore, that we could not expect to find the influence of very high temperatures on the seasonal prevalence of plague in Belgaum and such an expectation is borne out by a study of the chart.

The plague season in Belgaum is August to December, when the daily mean temperature is between 70° F. and 75° F. and, as a study of the chart will show, all the epidemics have declined when the temperature was still about this level. While there is the general relationship between the plague epidemics and the mean temperature, namely, that the epidemics occur when the temperature is lowest, the influence of the higher mean temperature is not apparent.

Lahore. (Chart V.)

The epidemic season of plague in Lahore is during the spring, namely, March to May, the four severe outbreaks which have occurred having been at this time of year. When we come to co-relate the daily mean temperature with the plague mortality we find that in March the mean temperature, when the epidemic begins, is about 70° F.; that during April, when the plague mortality is increasing, the mean temperature is rapidly rising and that in May when the epidemic reaches its maximum the daily mean temperature is between 85° and 90° F. The fall of the epidemic takes place abruptly as the mean temperature is still rising. At first sight it would appear that the mean temperature, namely 80° to 85° F., which seemed in Bombay and Nagpur to influence the epidemics in the direction of bringing them to a close, had failed to act in the case of Lahore, and

that it was only when the mean temperature had reached above 90° F. that the plague mortality began to decline. We have, however, to draw attention to two facts which have a bearing on this question. First, a study of the temperature curve will show that the rise of temperature during the spring and early summer in Lahore is much more rapid than in the places we have already considered. As we can imagine that temperature would take some time to act, its influence in Lahore would not be felt until the mean had risen higher than in those places where the onset of the hot weather was more gradual. Secondly, in Lahore, as we have already pointed out, the diurnal range of temperature is very much greater than in Bombay, Poona or Nagpur, this range being in April and May as much as 30° to 35° F., so that there would be a considerable number of hours during which the temperature would be Whether or not the high temperature in May is far below the mean. the cause of bringing the epidemics in Lahore to an end, a study of the chart shows us, that in the hot months of the year which follow May, namely, June to September, when the daily mean temperature is well above 80° F., plague is never epidemic. Lastly, during the winter months, November to February, when the daily mean temperature is low, namely, between 50° and 70° there have been several recrudescences which, with the exception of the one in the end of 1906, did not reach epidemic magnitude. It is to be noted, however, that the onset of the cold weather was delayed on this occasion. This observation raises the question as to whether or not a low mean temperature, such as 50° F., has any influence on plague epidemics.

Rawalpindi. (Chart VI.)

We have already seen that the epidemic season of plague in Rawal-pindi is September to November. In September, that is to say towards the end of the hot weather, the daily mean temperature is declining, being then about 80° F. During October and November, when the epidemics are at their height, the mean temperature is still falling, being now below 80° F. The outbreaks have always come to an end in December when the mean temperature is low, namely, between 50° and 60° F.

When we study the chart more carefully we find that each year plague has been present in Rawalpindi in the spring or early summer, but has not assumed epidemic magnitude until the autumn, when the mean temperature had fallen nearly to or below 80° F. There has

never been a severe outbreak during May to August, when the mean temperature is highest. Further, it is also seen from the chart that plague has never been epidemic in Rawalpindi during the coldest months, namely, December—February, when the daily mean temperature falls to about 50° F.

Before passing on to consider the experimental data bearing on the temperature problem, we may sum up the results of our analysis of the relationship between the seasonal prevalence of plague and the daily mean temperature as studied in these six places in India as follows.

- 1. It appears that plague cannot exist in epidemic form in any of these places when the daily mean temperature is as high as 85° F.
- 2. If the outbreak is increasing in magnitude while the daily mean temperature is also rising, as soon as or very shortly after this latter has reached 85° F. or a little less, the plague epidemic receives a check and rapidly declines.
- 3. While this is so, it would appear that epidemics may come to an end when the temperature is most suitable. Another factor or factors must, therefore, be in operation in these instances.
- 4. A low daily mean temperature, such as 50° F., may be a factor in limiting plague outbreaks.

IV. EXPERIMENTAL DATA AS TO THE INFLUENCE OF TEMPERATURE ON THE TRANSMISSION OF PLAGUE BY FLEAS,

The experimental data were got from observations made in the course of the godown experiments and from several series of observations made in the laboratory at different seasons of the year at room temperature and in specially constructed chambers in which the temperature could be regulated.

(a) Observations in the go-downs.

In previous papers (vol. vi. p. 450; vol. vii. p. 421) we have detailed a large number of experiments which were carried out in specially constructed cabins or godowns. We shall now refer only to the points which bear on the present problem. It is to be remembered that we have already proved that the rat flea alone was the transmitting agent of the infection in the epizootics which occurred in these godowns.

Table I contains a summary of the experiments which have been carried out in godowns 1 and 2 (i.e. non-flea proof) from June 1905 to

March 1907. These experiments may be divided into three groups according to the season of the year at which they were made.

- 1. Group 1 is made up of experiments 8, 9 and 10. The experiments of this group were carried out in June and July, the off-plague season in Bombay. A reference to the table will show that no marked epizootic developed in any of these experiments. In one instance no guinea-pigs, in another 2 guinea-pigs, and in the third four out of 50 guinea-pigs contracted the disease.
- 2. Group 2 is made up of experiments 5, 6 and 7, which were carried out during the season between August and November. In this season plague is not epidemic in Bombay but slight recrudescences have been observed on several occasions. It will be seen from the table, that in each of the experiments of this group an epizootic broke out, but that it came to an end before all the animals were infected. Further, a considerable number of days elapsed between the death of the first and last animal, i.e. the epizootic was slow in progress.
- 3. Group 3 is made up of experiments 1, 2, 3 and 4. These observations took place in the plague epidemic season in Bombay. In these experiments all the guinea-pigs died of plague with the exception of one which developed the disease but recovered. Further, in experiments 3, 9 and 10 the epizootic was extremely rapid, killing off 25 animals in from 3 to 9 days.

As we were unable to discover any variation in the virulence of the bacillus obtained from rats in Bombay at different times of the year, the two factors which suggest themselves as determining the differences between the results of the experiments in these three groups are prevalence of fleas and climatic conditions, such as temperature. is impossible accurately to appraise the relative importance of these two factors. In the experiments of group 1, all of which failed, fleas were not present in very large numbers, but the mean temperature was well above 80° F. In the experiments of group 2, fleas were abundant and the temperature was still above 80° F., although somewhat lower than during the experiments of group 1. group the epizootics were of slow progress and came to an end before all the animals had died. It would appear then that the most probable explanation of the limiting of these epizootics is the high temperature which then obtained. In the experiments of group 3, specially 3, 9 and 10, fleas were abundant and the temperature was well below 80° F., between 70° and 75° F. The epizootics in these instances were severe and ran a rapid course.

TABLE I.

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Remarks	Plague epizootic rising.	Plague epizootic in Bombay gaining strength.	Plague epizootic in Bombay beginning.	Plague epizootic height.	Plague epizootic a begin.	Season when plagu- tendency to recrud	Ditto.	Plague epizootic in at its lowest.	Ditto.	Ditto.	guinea-pig which did not die was noticed to be ill at the same time as the others. It, however, gradually got bet s after the death of the last animal it was killed with chloroform and was proved to be plague infected on bacteriolog on. It would evidently have recovered from the disease.
Interval between death of first and last guinea-pig	9 days	7 ,,	17 ,,	3 ", 16 on 1 day	18 days	21 ,,	16 "	1 day	11 days	I	others. It, howeved to be plague in
No. of guines- pigs which died of plague	25	26	49	24*	23	24	23	63	4	0	time as the and was prov
No. of guinea- pigs exposed to infection	25	26	49	25	25	25	25	25	50	w 25	at the same h chloroform ease.
Daily average mean temperature	72·8° F.	75° F.	78° F.	78° F.	80·6° F.	81·1° F.	81.8° F.	82·3° F.	82.5° F.	Minimum never below 80.5° F. and often above 82° F.	guinea-pig which did not die was noticed to be ill at the safter the death of the last animal it was killed with chon. It would evidently have recovered from the disease.
Flea census	107 on 3 guinea-pigs	115 on last 5 guinea-pigs	400 on last 2 guinea-pigs	1246 on 2 guinea-pigs	546 on 4 guinea-pigs	126 on 25 guinea-pigs	101on the last 2 guinea-pigs	50 on 25 guinea-pigs	49 on 3 guinea-pigs	, 39 on 5 guinea-pigs	which did not die w leath of the last ani d evidently have re
Season of year	January 1907	December 1905	Nov.—Dec. 1905	March 1907	ct.—Nov. 1906	August 1906	ept.—Oct. 1906	July 1906	une—July 1905	June 1906	guinea-pig vs after the don. It woul
No. of periment	=	63	ന	4	20	9	7	œ	6	10	Thr

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(b) Experimental observations in cages in the laboratory.

We have made several series of experiments which had as their object the transmission of plague from animal to animal by means of fleas, and in which all the conditions, except the temperature, were kept constant. The same number of fleas, which were always taken from plague infected rats which had numerous plague bacilli in their blood, was used for each experiment. For the general technique of these observations we would refer our readers to the first report (vol. v. p. 446).

These observations may be divided into four groups as follows:

1. Experiments made at different seasons of the year at room temperature.

Table II contains the details of these observations. From this table it is seen that both in the case of wild Bombay rats and in the case of guinea-pigs very many more successful transmissions were got in the plague season than in the off-season. It is to be remembered that the same number of fleas were used for each experiment and that only those fleas which had fed on rats, the blood of which contained abundant

TABLE II.

	Animals	Season of year	Mean daily temperature	No. of experiments completed	No. of successful trans- missions	P.c. of successful trans- missions	
1.	Bombay wild rats	Jan.—March 1906	73—78° F.	29	16	55	
		May—June 1906	82·5—85° F.	20	3	15	-
2.	Guinea-pigs	March—April 1906	75—80° F.	14	13	93	
		May—June	82·5—85° F.	22	3	13	

plague bacilli, were used. It would appear, therefore, that the most likely explanation of the diminution in the number of successful transmissions which was observed in May and June is the high mean temperature which then obtained. In the case of the Bombay rats this diminution might be partially accounted for by the presence of a greater number of immune rats at the end of the plague season, but this cannot apply to the experiments in which guinea-pigs were used. The guineapigs were all young animals which had never been used before for experimental purposes.

2. Experiments made in the hot weather, i.e. in the non-plague season, simultaneously at room temperature and in a specially constructed cool chamber in which the temperature could be regulated.

These experiments were carried out during the months of July and August, 1906. At this season of the year plague in both rats and men occurs in Bombay, but not in epidemic proportions, though in several years there has been observed a slight recrudescence beginning in August. The experiments were made simultaneously at room temperature (daily mean between 80°-83° F.) and in a cool room. This room was cooled by a carbon dioxide refrigerating apparatus, and was kept at a constant temperature of about 70° F. As the room had to be kept tightly closed the carbonic acid expired by the animals was absorbed by a layer of lime spread on the floor, which also served the purpose of keeping the room comparatively dry. Exactly the same technique was used in the experiments in which the animals were kept in the cool room, as in those in which they were kept at room temperature. The only occasion on which the fleas were removed from the cool room was at the time when they were being transferred from the inoculated animal which had died of plague to the healthy animal. This operation only lasted for about Working in this way we have completed three series of experiments, using (1) Bombay rats, (2) ship rats and (3) guinea-pigs, as the healthy animals to which the fleas were transferred. The results of these three series are detailed in Table III.

TABLE III.
July—August, 1906.

Animals	Conditions of experiment	Daily mean temperature	No. of experiments completed	No. of successful transmissions	P.c. of successful transmissions
1. Bombay rats	Room temp.	80—83° F.	29	5	17
	Cool room	70° F.	46	13	28
2. Ship rats	Room temp.	80—83° F.	25	8	32
	Cool room	70° F.	27	18	66
3. Guinea-pigs	Room temp.	80—83° F.	8	4	50
	Cool room	70° F.	15	15	100

From this table it is seen that the same result was got in each series, namely, the proportion of successful transmissions at 70° F. was about twice that at 81.5° F. The only factor which could be responsible for this difference appears to us to be the higher temperature at which the experiments outside the cool room were carried out.

3. Experiments made in the cool weather, i.e. in the plague season, simultaneously at room temperature and in a specially constructed hot chamber, in which the temperature could be regulated.

This series of experiments was the reverse of the last series. It was carried out during the months of January and February 1907, at a time when both the epizootic and epidemic were steadily rising in Bombay. The experiments were made simultaneously at room temperature, the daily mean temperature being about 75° F., and in a hot chamber which was kept between 85° and 90° F. The same technique was used as was employed in the previous series.

TABLE IV.
January—February, 1907.

Animals	Conditions of experiment	Daily mean temperature	No. of experiments completed	No. of successful transmissions	P.c. of successful transmissions
Guinea-pigs	Room temp.	75° F.	25	21	84
	Hot room	85—90° F.	25	8	32

The results of this series, in which guinea-pigs alone were used, are detailed in Table IV. From this table it is seen that while at room temperature 84 p.c. of the experiments were successful, at the higher temperature of 85° to 90° F. only 32 p.c. gave a successful result. In this series, also, it would appear that the higher mean temperature had hindered the transmission of the disease by the flea.

When we consider the results of these three series of experiments we feel justified in coming to the conclusion that a high mean temperature, namely, above 90° F., has a direct hindering influence on the transmission of plague from animal to animal by means of fleas. The higher this mean temperature the greater is the influence felt. The experimental evidence, both in the godowns and in the laboratory, is therefore in harmony with the facts which were observed concerning the seasonal prevalence of plague in six different places in India.

When we come to consider in what way the higher temperature exerts its influence, we cannot offer an altogether adequate explanation in the present state of our knowledge. There is no doubt that the action must be in the direction of influencing the conditions under which the bacilli are living in the stomach of the flea.

In a previous paper (vol. vii. p. 402) we have compared the fate of the plague bacillus in the stomach of the flea in two series of experiments, one of which was carried out in the cool weather of the plague epidemic season and the other in the hot weather of the non-epidemic season.

TABLE V.

Season when experiment was carried out	P.c. of fleas with plague bacilli in stomach between 2nd and 6th day after they had imbibed septicaemic blood	No. of days from time of imbibing septic- aemic blood during which plague bacilli were found in stomach of fleas	No. of days from time of imbibing septicaemic blood during which fleas remained infective for guinea-pigs
Cold weather: plague epidemic season	31.2	20	15
Hot weather: non-)	5.2	7	7

Table V contains a summary of these two series of observations. A study of this table shows us that during the hot weather fewer fleas were found infected, and that they lost their power of infecting animals much sooner than in the cold weather. In the hot weather the bacilli disappeared from the stomach of the flea much more quickly than in the cold weather.

Further two series of experiments were done in January and February 1907, one at room temperature, namely 75° F., and the other in the hot room at about 90° F. In these series we tested the duration of the infectivity of the faeces of the fleas. A large number of fleas, caught on the animals when they were removed from the cage each day, were placed in two or three test tubes and left there for about 2 hours. They were then removed and returned to the cage. The tubes were now washed out with a small quantity of sterile normal salt solution, which was forthwith injected subcutaneously into a guinea-pig. This operation was performed each day.

We found that in the case of the fleas kept at room temperature (75° F.) the faeces infected up to the 21st day, and in the case of the experiment done at 90° F. only for 3 days. It would appear, therefore, that the higher temperature acts in the direction of clearing the bacilli out of the stomach of the flea. On what this clearing action depends is a problem which is dealt with in a separate paper (this vol., p. 260).

4. Experiments made at low temperature.

From a study of epidemic plague in relation to temperature in Lahore and in Rawalpindi it appeared that a low mean temperature such as 50° F. might be a factor in limiting plague outbreaks. We have investigated this point experimentally. Three series of flea transmission experiments were carried out with guinea-pigs in a cool chamber at

40° F., 50° F. and at 60° F. respectively. The technique of these experiments was the same as has already been described.

The results were as follows:-

At 40° F. 10 experiments were carried out: three of the guineapigs soon died of cold, the other seven all succumbed to plague.

At 50° F. 10 experiments were done: the 10 guinea-pigs all died of plague.

At 60° F. 10 experiments were done: all 10 guinea-pigs died of plague.

It would appear, then, that low temperatures, under the circumstances of these experiments, do not hinder the transmission of the disease by fleas. It is to be remembered, however, that only those fleas which were taken from rats which had died with abundant plague bacilli in their blood, were used.

				TABLE	VI.			
			Mean temp. at which rais were kept	No. of rats which died of plague	Average no. of days between inoculation and death of rat	P.c. of rats in which plague bacilli were found in blood	P.c. of rats in which abundant plague bacilli were found in blood	P.c. of rats in which no plague bacilli were found in blood
1.	Series 1	(a)	82.5° F. Room temp.	81	3.0	69	33	31
		(b)	40° F. Cold room	72	2.1	10	3	90
2.	Series 2	(a)	80.6° F. Room temp.	60	3.1	70	33	30
		(b)	50° F. Cold room	107	2.4	19.5	7.5	80.5
3.	Series 3	(a)	76.8° F. Room temp.	19	3.2	7 9	58	21
		(b)	60° F. Cold room	36	2.7	41	25	59
4.	Series 4	(a)	75° F. Room temp.	65	3.0	84	49	16
		(b)	90° F. Hot room	57	2.6	72	33	28

In the course of these experiments it was early noticed that only a small proportion of the rats, which had been inoculated with a virulent plague culture and then placed along with the fleas in the cold room, developed septicaemia. We, therefore, in a series of four experiments further investigated the influence of temperature on the disease in the rat with special reference to the development of septicaemia. The technique was as follows. In each series a number of rats caught in

Bombay city were inoculated, each with the same amount of the same culture of plague bacilli. Some were kept at room temperature, while others were kept, in the case of three of the experiments in the cool room at varying temperatures, and in the case of the fourth experiment in the hot room about 90° E. As soon after death as possible the rate were examined. In the case of those which had died from plague a careful microscopical examination of the blood was made and the presence or absence of plague bacilli was noted. If present it was recorded whether they were abundant or only few in number.

The data of these series of experiments are given in Table VI.

A study of this table shows us that low temperatures affect plague infected rats in such a manner that they die more quickly, and do not develop septicaemia to such an extent as rats kept at higher temperatures. It is also seen that the lower the temperature at which the rats are kept the more marked is this action. Further, from series 4 of these experiments it would appear that a high temperature such as 90° F. has little or no influence on the disease in the rat.

We have, therefore, obtained experimental evidence which goes to show that a low mean temperature, such as 50° F., would have a limiting influence on a plague epidemic, inasmuch as fewer rats would develop a good septicaemia and in consequence fewer fleas would have an opportunity of taking plague bacilli into their stomachs.

Conclusions as to the direct influence of temperature on the seasonal prevalence of plague.

- 1. A plague epidemic is checked when the mean daily temperature passes above 80° F. and especially when it reaches to 85° F. or 90° F.
- 2. A mean temperature above 80° F. affects the conditions to which the plague bacillus is subjected in the stomach of the flea. At high temperatures about 90° F, the plague bacilli disappear from the stomach of the flea much more quickly than at lower temperatures, namely, between 70° and 80° F. Fleas remain infective for a much longer time at the lower temperature.
- 3. A plague epidemic may, however, come to an end when the temperature is most suitable. Other factors must, therefore, be present in these cases.
- ¹ It must be remembered in this connection that the absence of a well-marked septicaemia *post mortem* may be the result of the low temperature inhibiting multiplication of bacilli in the blood of the rat after death.

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4. A mean temperature about 50° F. may have a direct influence on the seasonal prevalence of plague. At such a temperature the number of plague infected rats which develop septicaemia is very much less than at high temperatures. The lower the temperature the fewer rats become septicaemic. A very high mean temperature seems to have little or no influence in the reverse direction.

V. SEASONAL VARIATIONS IN THE LIFE HISTORY AND HABITS OF THE RAT.

(a) Breeding of rats.

It is possible that climatic conditions might affect the breeding season of these rodents and in this way indirectly influence outbreaks of plague. We have made observations on this point both in the Punjab and in Bombay.

(1) Punjab.

The detailed figures have been already published (vol. vii. p. 906 and chart). The main result is that the rats breed all the year round but with more vigour at some seasons than at others. In the winter months, November to February, the months just preceding the plague epizootic season, breeding is at its lowest. While during the rest of the year the percentage of pregnant females to total females is always about or above the mean, there seem to be three months, namely April, September and October, in which breeding is most vigorous. In this connection it may be remarked that the mean temperature of April does not differ much from that of September and October, namely about 80° F. The plague season in this part of India falls between February—June. It is evident, therefore, that any loss in the rat population caused by an epizootic during this season would be amply made up by the addition of a large number of young susceptible animals before the next outbreak took place.

(2) Bombay.

In Bombay we have investigated this question of the breeding of rats both in the case of M. decumanus and in the case of M. rattus. The results have been given already (vol. vii. pp. 748-9 and charts). The main facts are that M. decumanus breeds all the year round. In

the months of December, January and February, that is to say at the beginning of the epizootic, the percentage of pregnant females to adult females is lower than at any other time. During the rest of the year there seem to be three seasons at which breeding is most vigorous, namely, March, July—August and October. The curve showing the percentage of young to adult rats follows the 'pregnant curve' very closely. The plague epizootic amongst *M. decumanus* begins in January, is raging during February and March and rapidly declines in April. While, therefore, there is no direct relationship between the breeding season of this species and the plague epizootic, there is no question that between the end of one epizootic and the beginning of the next one there would be a large number of young susceptible individuals added to the rat population.

M. rattus in Bombay, as in the Punjab, breeds all the year. During the months December to March the percentage of pregnant females to adult females is lowest, and reaches its maximum during the months July to September. The curve showing the percentage of young rats to adult rats follows the 'pregnant curve' very closely. When we come to the epizootic curve we find that plague begins in January, increases during February, is at its maximum in March and April and declines during May. The chief breeding season in Bombay for M. rattus is, therefore, during the non-epizootic season. It is also seen that before the epizootic there is a large addition of young animals to the population.

(b) Habits of rats. It is further possible that the habits of the rat might be so affected by varying climatic conditions, as to influence the seasonal prevalence of the disease. We have made observations on this point, both in Bombay and in the Punjab over a period of 18 months, with negative results.

In Bombay city we have closely observed the habits of these rodents and at no time of the year have we noticed any change in them. Further, both in the four villages in the neighbourhood of Bombay and in the villages of Kasel and Dhand in the Punjab, in all of which villages rats were systematically trapped by us for over a year, we have never observed any migration from the houses to the fields nor any other seasonal change of habit. In the case of the Punjab villages it has been suggested that the decline of a plague epidemic may be due to the migration of the rats to the fields at a time when the crops are being cut. Now in Kasel at the height of the epidemic, when rats were dying in large numbers in the village, the crops had just recently been cut. There had evidently been no migration of the rats to the fields,

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and no migration was noticed. We can, therefore, only conclude that, as far as we have investigated the subject, climatic conditions appear to have no influence on the habits of rats in any way that might influence the seasonal prevalence of plague.

(c) Seasonal variations in the total rat population. Apart from breeding, plague epizootics would appear to be the chief factor which might produce considerable variations in the total rat population. In a city like Bombay where the rat population is enormous it would be impossible to appraise with any accuracy the effect of the plague epizootic on its numbers. The general result however must be that there is some diminution in the total number of rats.

However, in the two villages of Dhand and Kasel in the Punjab some observations in the above directions were made, which observations, although by no means conclusive, seem to support this conclusion.

The result of the systematic trapping month by month in Dhand is shown in Table VII. During the two months before the plague epizootic began over 1500 rats were caught and killed. Plague amongst the rats appeared in February and lasted till about the middle of April. As far as could be judged from the number of dead rats found, 46 in all, the outbreak was not very severe, possibly due to the

TABLE VII. Dhand.

Month	No. of traps set	Total no. of rats taken	Average no. of rats per 100 traps	Remarks
December	943	742	80	
January	2393	801	34	
February	1699	258	15	Epizootic began.
March	1492	141	10	Epizootic continued.
April	436	21	5	Epizootic stopped.
May	$\bf 534$	17	3	
June	936	28	3	
July	_			No traps set.
August			_	No traps set.
September	233	78	34	
October	301	149	50	
November	875	283	32	

diminution in the rat population brought about by the previous trapping. During the epizootic trapping still went on but very few rats were taken. After the outbreak had come to an end, catching continued but with very poor results, only 45 animals being taken during May and June. No traps were set during July and August. Operations were begun again in September, when, as will be seen from

the table, the number of rats had evidently increased considerably, as the takes during the next three months were about equal to what they were when the operations were first begun. There is no doubt that even before the epizootic began the rats in Dhand had been considerably diminished in number on account of the trapping. We cannot, therefore, attribute the great diminution at the end of the plague outbreak, which was readily acknowledged by the people themselves, to the epizootic alone. The important part, however, of the observations is that between the time when the epizootic ended in April and October the rat population had evidently again increased to a number as great, if not greater, than what it was when the epizootic began.

TABLE VIII. Kasel.

Month	No. of traps set	Total no. of rats taken	Average no. of rats per 100 traps	Remarks
December	782	1086	138	
January	Nil	Nil	Nil	Trapping stopped.
February	448	398	89	Trapping began again on
March	1260	870	69	20. ii. 06.
April	586	316	54	Epizootic began.
May	927	315	34	Epizootic continued.
June	1048	202	19	Epizootic stopped.
July	772	132	17	
August	774	232	30	
September	619	292	47	
October	531	215	40	
November	854	587	69	

In Kasel very similar observations were made. It will be seen from Table VIII, that during the first month of trapping a large number of rats were taken, over 1000 being removed from the village. After the village had been once trapped systematically, house by house, the operations were suspended for about six weeks, being begun again on the 20th February. In March, the month before plague began, an average of 69 rats per 100 traps was obtained. During the epizootic which lasted from April to June, and which was evidently fairly severe, as over 300 dead plague infected rats were found, this average gradually diminished, until in July, the month after the epizootic had ceased, only 17 rats per 100 traps were caught. That the removal of some rats by trapping was not altogether responsible for this diminution is shown by the observation that, although breeding was no more vigorous than during the epizootic, the number of takes began to rise in August, and went on increasing, until by December as many rats were caught as at the time when plague started.

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It appears to us, therefore, that we have here evidence supporting the hypothesis that a plague epizootic may greatly diminish the number of rats for the time being, but that after the epizootic has stopped, the population may soon assume its usual proportions.

(d) Seasonal variations in the proportion of immune to susceptible individuals amongst the rat population.

It is a priori justifiable to infer that during a plague epizootic a number of rats suffer from a mild attack of the disease and, recovering therefrom, are more or less immune to a second attack.

This hypothesis receives a certain amount of support from a comparison of the flea transmission experiments done with Bombay rats at room temperature in the plague season with similar experiments done at the beginning of the non-plague season in the cool room at 70° F. That the conditions of experiment in the latter series were otherwise suitable for successful results is borne out by the fact that a series of guinea-pig experiments carried out under exactly the same conditions yielded 100 p.c. of successes.

Table IX contains the details of these observations, the experiments with guinea-pigs being put in for the sake of comparison. From this

TABLE .	IX.
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Animals	Season of year	Temperature at which kept	No. of experiments completed	No. of successful transmissions	P.c. of successful transmissions
Bombay rats	Jan.—March 1906	Room temp. 73—78° F.	29	16	55
	July—August 1906	Cool room 70° F.	46	13	28
Guinea-pigs	March—April 1906	Room temp. $75-78^{\circ}$ F.	14	13	93
	July—August 1906	$\begin{array}{c} \text{Cool room} \\ \textbf{70}^{\circ} \text{ F.} \end{array}$	15	15	100

table it is seen that in the plague season 55 p.c. of the rats exposed to infection contracted the disease, while after the epizootic had come to an end only 28 p.c. became infected. It is to be remembered that the rats were in each instance got in the city of Bombay, no distinction being made between *M. decumanus* and *M. rattus*. Further, we have stated that the conditions were as far as possible the same in both series of experiments and were certainly, as shown by the guinea-pig results, not less favourable in the series made at the end of the epizootic.

The hypothesis gains further support from the results of an analysis of the post-mortem findings in rats which died of plague during the epizootic and in rats which died in the non-plague season. In Table X are set forth the results of the microscopic examination of the blood, as

TABLE X.

Season of year	P.c. of rats whose blood contained no plague bacilli	P.c. of rats whose blood contained only a few plague bacilli	P.c. of rats whose blood contained abundant plague bacilli
Plague epizootic season	13.5	53.4	33.1
Non-epizootic season	56.7	32.0	11.3

regards the degree of septicaemia present, in two series of rats which had been found dead of plague in Bombay city, namely,

- (a) a series of 1000 rats found during the plague epizootic, and
- (b) a series of 900 rats found during the non-epizootic season, namely, from 30th May to 30th October 1906. From this table it is seen that in the non-epizootic season a much larger number of rats died from plague without any bacilli appearing in the blood than during the epizootic, and vice versa the number which developed a good septicaemia was much greater in the epizootic season than in the non-epizootic season. We take it that this pathological difference points to a greater number of rats possessing a certain amount of resistance to the disease after the epizootic than during the epizootic season.

As far as they go, therefore, these observations seem to show that there is a greater proportion of immune to susceptible rats in Bombay at the end than at the beginning of the plague epizootic.

VI. INFLUENCE OF CLIMATIC CONDITIONS ON THE HABITS OF MAN.

It is now generally accepted that the infection of plague is in the buildings, and that huts, rooms or houses in which plague has occurred amongst rats are during an epidemic highly infectious. Further, the infection clings to these localities even after they have been evacuated, so that individuals returning to them have promptly contracted the disease. This infectivity of houses is at once explained on the basis of the rat-flea-man theory. The infection will be kept up as long as the plague mortality amongst the rats continues. Rats dying in the open outside the houses would be less dangerous inasmuch as the fleas on leaving them would soon be destroyed or dispersed by sunlight. Accepting, therefore, that the infection of plague is wholly within the

houses, we can imagine that, if owing to climatic conditions the inhabitants were accustomed to evacuate their buildings and live in the open at any particular season, this habit would influence the seasonal prevalence of the disease. We can conceive that a plague epidemic might be brought to an end by such a migration. There is no doubt that in many of the villages of the Punjab, as happened at Kasel while it was under our observation, the plague epidemic, occurring as it does at the beginning of the hot weather when the people are cutting the

Further, in Bombay no general seasonal evacuation of houses can be said to occur. There is no doubt that more people sleep out of doors in the hot weather than in the cold, but the difference is so insignificant as to be negligible.

crops, may be limited by partial evacuation. This evacuation, however, is not at all general and cannot be said to have any influence otherwise

than in limiting somewhat the number of attacks.

In Poona we have seen that the plague epidemic season is as a rule in the autumn, coming to an end about December. At this time, when the mean temperature is comparatively low, there can be no suggestion of the people living in the open. The same holds good for Rawalpindi, in which place, as we have seen, the epidemics decline at the beginning of the cold weather, at a time when the inhabitants are living indoors.

A survey of the whole subject, therefore, leads us to the conclusion that those habits of the people, which are dependent upon varying climatic conditions, have no influence on the seasonal prevalence of plague.

VII. VARIATION IN THE VIRULENCE OF THE BACILLUS.

We have shown (vol. vi. pp. 496, 502) that, contrary to the results got by some other observers, the plague bacillus does not become diminished in virulence by passage through rats. In one series of experiments, in which the subcutaneous method of injection was used, twenty-six passages from rat to rat were effected without recourse to cultivation on artificial media. No alteration in the virulence of the bacillus was brought about by these passages. In another series of experiments, in which the cutaneous or rubbing-in method of inoculation was employed, again no alteration of virulence was observed after twenty-six passages.

We have also shown (vol. vii. p. 352), that the plague bacillus isolated from rats during the off plague season in Bombay is of full

virulence. There appears to be no difference in the virulence of the plague organism when isolated from naturally infected rats at any season of the year in Bombay.

These observations, therefore, appear to us to warrant the conclusion that variation in the virulence of the plague bacillus plays no part in determining the seasonal prevalence of the disease.

VIII. SEASONAL VARIATIONS IN THE LIFE HISTORY AND HABITS OF RAT FLEAS.

(a) Influence of temperature on breeding. We have already detailed experiments (see above, p. 243) which show that a high mean temperature affects the breeding of fleas to a considerable extent, in that it appears not only to restrain the imago from depositing eggs, but also to be deleterious to the development of the eggs into larvae. It is well known that quite cool weather materially extends the time required for the complete metamorphosis.

(b) Seasonal variation in the number of rat fleas.

While it is a priori certain that the number of rat fleas present must have an influence on a plague epizootic, it has been shown experimentally in the course of the godown experiments (vol. vii. p. 428) that, other conditions being the same the rate of progress of a plague epizootic amongst the guinea-pigs was much slower in those godowns in which the flea infestation was slight than in the godowns which were abundantly supplied with fleas. The questions, therefore, to be now answered are (a) is there in nature a seasonal variation in the number of rat fleas? and (b) if so, does it correspond to the rise and fall of the plague epidemic? Answers to these questions were sought for both in Bombay and in the Punjab villages.

1. Observations in Bombay.

In Bombay it is notorious that fleas are more common at one season of the year than at another. The season of greatest prevalence is generally stated to be during March, April and May. The observations on which these statements are based probably refer to *Pulex irritans* or to *Pulex felis* and they are not supported by any definite figures.

In order to obtain more accurate data regarding *P. cheopis*, two methods were adopted by us:

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(A) Thirty houses in different parts of Bombay city were selected. These houses had at one time when plague infected come under our observation and were therefore known to be rat infested. When the present observations were made they were free from plague. At intervals of about two months two guinea-pigs were placed in each house and left in over night. They were then chloroformed and searched for fleas, which were carefully enumerated. Between June 1906 and May 1907 seven countings were made in each house, and the data obtained are given in Table XI and chart. These seem to indicate that there is a distinct

TABLE XI.

Season when observations were made	P.c. of total houses which contained any fleas	Average number of fleas per house
End of June 1906	24	0.4
Beginning of October 1906	26.6	1.3
End of November 1906	43.3	1.7
Middle of January 1907	60	3.8
Beginning of March 1907	$72 \cdot 4$	4.9
Middle of April 1907	59	2.5
Beginning of May 1907	46	2.3

seasonal variation in the number of rat fleas, the largest number being found from January to April or May, with a maximum prevalence in March.

(B) In the description of the methods which were used for studying the epizootic we indicated (vol. vii. p. 738) the means which were adopted to obtain as accurate a census as possible of the fleas infesting the rats. Traps were set daily in different situations in the various districts of the city. Immediately after it was found the trap was enclosed in a stout canvas bag. When the traps arrived at the laboratory, each one was removed from the bag and both traps and bag were at once put into a tin box to which chloroform was added. Four of these boxes were in constant use. Each of them had a metal tray resting on the bottom. After the rats were killed by the chloroform the tray and its contents were removed 'en bloc.' The fleas on the tray were then counted, after those in the bag had been shaken out. At the same time each rat was separately searched and the fleas found on it added to the total.

From 1st November 1906 to 30th October 1907, on an average between 100 and 200 rats were daily dealt with in this manner so that the data, which we are now about to present, are founded on figures sufficiently large to minimise the error inseparable from the method.

A summary of the data month by month is given in Table XII and Chart VII. In the case of *M. rattus*, the number of fleas is above the mean during the months, February—May, reaching a maximum in March and April. The same may be said of the fleas infesting *M. decumanus* with the slight difference that the mean line is crossed in January. During the rest of the year, namely June to January, the number of fleas on both species is below the mean, being lowest during the months September—December. These results coincide remarkably with

TABLE XII. Flea prevalence in Bombay.

		Mus rattus 1		Mus decumanus 2			All rats 3			
	Month	Total no. of rats	Total no. of fleas	Average no. of fleas per rat	Total no. of rats	Total no. of fleas	Average no. of fleas per rat	Total no. of rats	Total no. of fleas	Average no. of fleas per rat
1906	November	1,313	3,231	2.5	410	2,348	5.7	3,483	11,264	$3 \cdot 2$
	December	2,087	5,362	2.6	489	2,803	5.7	4,591	14,429	3.1
1907	January	1,927	6,150	$3 \cdot 2$	465	4,227	9.0	4,371	19,648	4.5
	February	1,693	7,689	4.5	309	3,666	11.9	3,283	18,362	5.6
	March	1,799	9,345	$5\cdot 2$	300	3,838	12.8	4,425	29,814	6.7
	April	1,911	9,981	5.2	306	4,250	13.9	4,032	27,478	6.8
	May	1,721	7,972	4.6	421	5,043	12.0	3,752	21,589	5.8
	June	1,426	4,893	3.4	331	2,718	$8 \cdot 2$	3,713	16,888	4.5
	July	1,118	4,291	3.8	305	2,139	7.0	3,746	16,083	4.3
	August	767	2,766	3.6	198	1,358	6.9	3,216	12,604	3.9
	September	1,116	3,722	3.3	326	1,361	4.2	4,018	12,782	$3 \cdot 2$
	October	1,555	4,232	2.7	327	1,607	4.9	5,183	15,041	2.9

the conclusions which have been tentatively drawn from the figures obtained by the other method. There can, therefore, be little doubt that there is a seasonal variation in the number of rat fleas in Bombay and that the months February to May are those in which these insects are most numerous, the maximum being reached in March and April. We have now to co-relate this seasonal variation of rat fleas with the seasonal prevalence of the plague epidemic. The epidemic season of plague in Bombay, as regards both the rat and man, is from January or February to April or May, the maximum prevalence being either in March or April. It is apparent, therefore, as far as Bombay is concerned,

¹ The traps contained only Mus rattus,

² The traps contained only Mus decumanus.

³ All traps containing M. rattus, M. decumanus, either alone or together with a few Nesokia and mice.

that the plague season is contemporaneous with the season of prevalence of rat fleas, and that during the off plague season the number of rat fleas is well below the mean.

(2) Observations in the Punjab.

During the year that the observations were in progress in the Punjab villages of Dhand and Kasel a census of the fleas infesting the rats was made. The method adopted was the same as has been already described for Bombay, only rats caught alive being used.

Two species of fleas were found on the rats, namely, Ceratophyllus fasciatus and P. cheopis.

(a) Ceratophyllus fasciatus.

Only about 2 % of all the fleas taken belonged to this species. This flea had a very definite seasonal prevalence in the villages investigated (see vol. vii. p. 917). When the observations were begun in December 1905 Ceratophyllus fusciatus was found to be present on the rats in both villages. It disappeared from Dhand about the end of March and from Kasel about the middle of April, except for an isolated specimen found in May. From this date no fleas of this species were found till the first week in November when they reappeared almost simultaneously in both villages. They remained present until trapping was stopped in the first week in December.

(b) P. cheopis.

P. cheopis is the common rat flea in the Punjab as it is in Bombay. The data obtained regarding the seasonal variation in its numbers have been already given (vol. vii. p. 916 and chart). They show that the number of P. cheopis is above the mean from November to May with a maximum probably in April. During the remaining months—June to September—the flea prevalence is below the mean, the absolute minimum being reached in August and September when the number per rat is six times less than in April.

Now the plague season in the Amritsar district of the Punjab in which the villages are situated is from February to May inclusive. It will also be remembered that in the year 1906, plague was present in Dhand from 27th January to 21st April and in Kasel from 2nd April to 17th July, reaching its maximum during the first half of May. By the beginning of June the epidemic was practically over, after that date

only a few scattered cases occurring. The seasonal prevalence of *P. cheopis* therefore corresponds fairly closely with the plague mortality. The connection may, perhaps, best be stated in saying that the non-plague season corresponds to the months when the average number of fleas per rat is below the mean, while the epidemic season corresponds to the period when the average number of fleas per rat is above the mean.

TABLE XIII. Flea prevalence in Dhand and Kasel (Punjab).

Month	Total no. of rats on which fleas were recorded	Total no. of fleas	Average no. of fleas per rat
December 1905	1631	12024	7.4
January 1906	809	9085	11.2
February ,,	647	$\boldsymbol{6258}$	9.7
March ,,	1020	8069	7.9
April ,,	350	4396	12.6
May ,,	341	2482	7.3
June ,,	232	1131	4.9
July ,,	136	514	3.8
August "	226	447	2
September ,,	374	853	$2\cdot 3$
October ,,	375	1955	$5\cdot 2$
November ,,	867	6780	7·8

The epizootic continued in Dhand from February to April, and in Kasel from April to June.

SUMMARY.

- 1. Both in Bombay city and in the Amritsar district of the Punjab there is a distinct seasonal variation in the number of rat fleas.
- 2. In these places this seasonal variation of rat fleas corresponds directly in a general way with the plague mortality. During the season when plague is epidemic the average number of fleas per rat is above the mean, while during the non-epidemic season it is below the mean. The height of the epidemic corresponds fairly closely with the season of maximum flea prevalence.

IX. GENERAL SUMMARY AND CONCLUSIONS.

I. The seasonal prevalence of plague has been studied in six different places in India. These places are widely separated from one another and are under the influence of quite different climatic conditions. It was found that plague, once it has become established tends to

recur every year at the same season. The plague season was found to vary in different places.

II. The possible factors which might influence the seasonal prevalence of plague were considered. Three factors have been indicated which influence the rise and fall of the epidemic as follows:

A. Temperature.

- 1. Epidemiological facts. From a study of the mean temperature in co-relation with the plague mortality in six widely separated places in India, it appears that plague cannot exist in epidemic form in any of these places when the daily mean temperature is as high as 85° F. and over. If an epidemic is in progress, as soon as or very shortly after the temperature has reached the above height or even less, the plague epidemic receives a check and rapidly declines. While this is so, it would also appear that epidemics may come to an end when the temperature is most suitable. Another factor or factors must, therefore, be in operation in these instances.
- 2. Experimental data. At all seasons of the year experiments were carried out in the godowns and in cages in the laboratory. Specially constructed hot and cold chambers were also used. These experiments showed (a) a mean temperature, of 85° F. and over, affects the fate of the plague bacillus in the stomach of the flea. At this temperature fewer successful transmissions from animal to animal are obtained and besides the flea does not retain its power of infecting nearly so long as it does at a lower temperature, i.e., 70° F. At the higher temperature the plague bacilli disappear from the stomach of the flea much more quickly than at the lower temperature.
- (b) While a mean temperature high in comparison with 70° F. has no effect on the number of plague infected rats which contain bacilli in the blood at death, at a low mean temperature, such as 50° F., the number of infected rats which die before bacilli appear in the blood is much greater than at the higher temperature, i.e. 70° F.

B. Variation in the total number and in the susceptibility of rats.

Evidence has been adduced to show that a plague epizootic considerably diminishes for the time being the total number of rats present in a place. There is also evidence to show that the effect of a plague epizootic is to increase the proportion of immune to susceptible rats. It is clear that these two factors would have an influence in limiting and in bringing to an end plague amongst the rats.

It was found both in Bombay and in the two Punjab villages that breeding of rats goes on all the year round, but that it is especially vigorous during the season between the end of one epizootic and the beginning of the next. During this interval there would therefore be added to the rat population a large number of young susceptible individuals, a factor which would evidently influence the rise of the epidemic.

C. Seasonal variation in the number of rat fleas.

It has been shown both in Bombay and in the Punjab that there is a seasonal variation in the number of rat fleas. And further it has been found that the plague epidemic season corresponds with the season of greatest flea prevalence, while during the months when plague is at its minimum fleas are fewest in number.

III. In conclusion we may state the following propositions:—

The rise of the rat epizootic and in consequence the human epidemic depends upon:

- (a) A suitable mean temperature, somewhat below 85° F. and in general over 50° F.
 - (b) A sufficient number of susceptible rats.
 - (c) A sufficient number of rat fleas.

The fall of the rat epizootic and in consequence of the epidemic, is determined by some or all of the following factors:

- (a) A high mean temperature, 85° F. and above.
- (b) A diminution in the total number of rats and an increase in the proportion of immune to susceptible animals.
 - (c) A diminution in the number of rat fleas.