LI. THE IMMUNITY OF THE WILD RAT IN INDIA.

It is natural to suppose that the relative susceptibility or immunity of the rat to plague infection is a matter of considerable importance in the epidemiology of this disease. We have referred to the immunity of the rat to plague on several occasions, among others, for example, when discussing the factors which possibly tend to bring an epidemic of this disease to a close. We were not, however, able to bring forward any experimental evidence to show that the immunity of the rat was a factor of importance in regulating the course of an epidemic. We made several attempts to prove that rats possess a high degree of immunity at the close of an epizootic. In particular we may refer to an attempt to test this point which is mentioned in our first report on our Poona observations (vol. x. p. 523), and also to the results obtained when we tested the immunity of the survivors of the epizootics we produced in our godowns (vol. x. p. 332; this volume, p. 298).

In the Poona experiments we were confronted with great technical We found that the varying climatic conditions at different difficulties. times of the year influenced greatly the mortality among the rats under experiment; a cold night was sufficient to cause a high mortality, sick rats apparently dying from the effects of cold. Indeed we found as the result of this experiment that, in place of the immunity of Poona rats increasing as the epizootic progressed, their immunity to plague, as tested by our method of subcutaneous injection of small doses of plague bacilli, varied rather with the temperature, so that the colder the weather the greater was the mortality. Again, during the monsoon months, when the cages in which the rats were kept were liable to remain damp for days, many deaths among the rats occurred either from plague or from some other cause; it was impossible to say that plague had not been the cause of death for all the rats had been injected with living plague bacilli and we could generally isolate that organism from their tissues and organs. In short we learned that the circumstances and surroundings in which the rats were kept had a considerable influence in increasing or lowering the death rate among them. Again it was a matter of no small difficulty to find some means of regulating the dose of plague bacilli injected so as to maintain an even dose in a long series

of experiments; two variable factors had to be regulated—the virulence of the organism and the number used in each dose. We soon learned that broth cultures were of little use for our purpose, and after a prolonged series of trials of different methods we adopted the method of spleen emulsions to be described presently. We also learned that in order to obtain more or less consistent results it was necessary to inoculate an equal number of rats of constant and standard resistance at the same time as the rats whose immunity to plague we proposed to measure. These experiments therefore, dealing as they did with many hundreds of rats, although they failed to demonstrate any increase in immunity among the Poona rats at the close of an epizootic, served a most useful purpose, for the experience gained was of great use to us in the experiments presently to be described.

In the godown experiments referred to above, in which we tested the immunity of the survivors of epizootics and compared their immunity with that of the rats which survived in the control godowns, we were forced to the conclusion that it was probable that the apparently high degree of immunity of the rats which survived the epizootics as compared with those of the control godowns was due to the death of susceptible individuals during the epizootic rather than to any immunity acquired by the rats in having suffered and recovered from the disease. This observation, together with the fact that we had found the rats caught in Belgaum very resistant to doses of plague which we knew killed a fair proportion of Bombay rats (see vol. x. p. 458), raised the question, whether the rats in places which had suffered from plague were more resistant to the disease than those caught in places which had not been invaded by it. We were confronted with the problem, were the rats in plague-infected places immune to plague because they had suffered from the disease or was this immunity a racial immunity or due to some other cause?

About this time we were making an inquiry as to the reasons why the Madras Presidency had suffered less from plague than other parts of India and for this purpose we were collecting and examining rats caught in Madras City¹, a place which had practically escaped the ravages of this disease. The occasion therefore afforded us an excellent opportunity to secure, as a standard of resistance, rats which we knew had not been exposed to infection. Arrangements were therefore made at our headquarters in Bombay to receive rats caught in Madras and Poona and to compare their immunity with that of rats caught in Bombay.

¹ See above, p. 209.

We decided to carry out the experiment in two ways :—(1) by inoculating a large number, if possible one hundred, rats at a time from each place with the same dose of plague bacilli subcutaneously, and (2) by subjecting equal numbers of rats from the three places to infection by fleas which had fed on rats infected by plague.

The technique adopted in the first experiment was as follows. One hundred rats from Madras and Bombay and seventy-six rats from Poona were placed in separate cages, two rats in each cage. The spleen of a rat which had died of acute plague having been removed aseptically was weighed. It was then placed in a sterile mortar and ground up with a known quantity of saline solution. The larger particles of this emulsion were allowed to settle and the supernatant fluid was decanted off; to this emulsion of bacilli fresh saline was added as necessary so that one cubic centimeter of the ultimate solution contained what was regarded as the equivalent of one one-hundredth part of a milligramme of the infected spleen¹. This we found to be the most convenient dose to use in our experiments, but occasionally we used larger doses and this was effected by decreasing the amount of saline added to the The cages containing the rats were kept in special godowns emulsion. so that they were all subjected to the same conditions. The events which occurred in this experiment are shown below. In all, while 83 $^{\circ}/_{0}$ of Madras rats died of plague (the remainder of the hundred having died of other causes than plague), only 44 % of Bombay rats and 30 % of Poona rats succumbed to the disease. Madras rats therefore were highly susceptible to the disease; Bombay and Poona rats comparatively immune.

In the second experiment we attempted to find out whether the above conclusion held true when the disease was propagated among the rats by infected fleas. For this purpose 25 Bombay rats were placed in each of two godowns, in two other godowns 25 Madras rats were placed in each, and in a third pair of godowns 25 Poona rats were placed in each. Into each of the six godowns containing the rats mentioned above five inoculated rats were introduced to infect the fleas which were present in the godown. In order to estimate the number of fleas in the godowns a weekly flea count was made; this was accomplished by counting the number of fleas on a certain number of the rats in each godown and finding the average number of fleas per rat. During the course of the experiment, as inoculated rats died off, others were added

¹ In later experiments the actual number of bacilli inoculated was ascertained by plating.

to the godowns so that five were added to each godown on the 28th January when the experiment started, five on the 12th February and three to each on the 26th February. Experiment II details the daily events occurring in the six godowns. Godowns 1 and 2 contained Bombay rats which showed an average weekly flea count of 4.2 and 2.2 respectively. Only three uninoculated rats died of plague in these godowns. Godowns 3 and 4 contained Poona rats. They showed an average weekly flea count of 4.4 and 4.7 fleas per rat respectively. Only one rat died in these godowns. Godowns 5 and 6 contained Madras rats. The flea count in these godowns was 4.3 and 5.0 respectively, and in them as many as thirty-six rats died of plague. This experiment showed, as the first had shown, that Poona and Bombay rats are, relatively to Madras rats, highly immune to infection.

In the first experiment a considerable mortality is recorded under the heading "deaths not due to plague." In judging whether a rat should be regarded as having died from plague or from other causes, no attempt was made to secure cultures, since all the animals alike had been inoculated, and we relied wholly on the naked-eye discovery of the typical post-mortem signs of plague with which we were now very familiar. The high mortality during the first few days was due partly to the rats having been recently trapped and so being unaccustomed to live in captivity and partly to the difficulty of handling wild rats for inoculation without causing them some injury. In other experiments the excess of "deaths not plague" occurred later on and was evidently not directly due to either of these factors. In our later experiments most of the early mortality was avoided by keeping the rats for a little while before inoculation and by greater technical experience; in the majority of experiments more than 100 rats were inoculated and the excess over a hundred surviving on the third day were killed. In stating the results of the experiments in numerical form it is difficult to make any very satisfactory correction for an excess of not-plague deaths. While it is evident that in experiment I, for example, the eleven rats which died on the two days following the day of inoculation, and to a less extent the four rats which died on the next day, had very little chance of dying of plague, and might reasonably be deducted from the number exposed to death; it is equally clear that, in experiment X, the eighteen rats which died from causes other than plague between the fourteenth and twenty-second days are in quite a different position, since the last plague death occurred on the twelfth day and all the rats which subsequently died of other causes had had just as good a chance of dying of plague as any of the others. The chief plague mortality has usually been on the third and fourth days after inoculation, and we have endeavoured to obtain a more accurate statement of the mortality by deducting the rats dying of other causes on the day of inoculation and the two days following. There are, however, comparatively few experiments (I, V, VI, VII) in which the alteration makes a material difference in the percentage mortality. Working along these lines we have completed twenty-three experiments, the details of which follow.

10 10 7	100 Madras rats 100 Bombay rats 76 Poona rats						50 Madras mice 50 Bombay mice r					received 1/100,000 gramme plague rat's spleen on 7 January, 1910.					
	М	adras	rats	Bombay rats				Poona rats			Madras mice			Bomb ay mice			
Date 1910	Not plague.	Plague	Remaining /	Not plague)	Plague	Remaining	Not plague	Plague	Remaining	Not plague)	Plague	Remaining)	Not plague)	Plague	Remaining		
Jan. 7	-		100			100		—	76	—		50		—	50		
,, 8	5	—	95			100	_		76	7		43	_		50		
,, 9	6	1	88	. 3	1	9 6		1	75	2	_	41	7	1	42		
,, 10	4	47	37	5	20	71	3	4	6 8		13	28	1	19	22		
,, 11	1	24	12	6	14	51		4	64		9	19		2	20		
,, 12		8	4		2	49	—	3	61	1	6	12		2	18		
,, 13		1	3		3	46	—	2	59		1	11			18		
,, 14	—	2	1		1	45		3	56		—	11	—	-	18		
,, 15	—		_		1	44	_	1	55			11		2	16		
,, 16	1	—	0			44	1	1	53	_		11	_	1	15		
,, 17	—			6		38		—	53		—	11	1		14		
,, 18	—			1	1	36		1	52	—		11			14		
,, 19				1	—	35	1	2	49		—	11	—	—	14		
,, 20				1	—	34	_	—	49	—		11		_	14		
,, 21				2	1	31	1	1	47			11	—	_	14		
,, 22						31	1		46			11			14		
,, 23				_	—	31			46			11			14		
,, 24	-	—	_	2		29			46			11		—	14		
Totals	17	83	0	27	44	29	7	23	46	10	29	11	9	27	14		

Experiment I.

Percentages dead of plague :

Madras rats	•••	83 ⁰ / ₀ (93 ⁰ / ₀ *)
Bombay rats	•••	44 °/ ₀ (45 °/ ₀ *)
Poona rats		30 %
Madras mice		58 % (71 % *)
Bombay mice	•••	54 ⁰ / ₀ (63 ⁰ / ₀ *)

* Corrected for excessive not-plague mortality.

Experiment II.

50 Madras rats, 50 Bombay rats and 50 Poona rats put into godowns on 28 January, 1910. Into each godown were placed 5 rats inoculated with plague on 28 January, 5 more on 12 February and 3 more on 26 February. The deaths from plague were as follows:

	Bomba	y rats	Poona rats			Madras rats		
Date, 1910	Godown 1	Godown 2	0	down 3	Godown 4	Godown 5	Godown 6	
28th Jan3rd Feb.	0	0		0	0	0	0	
4th Feb10th	0	0		0	0	4	1	
11th17th	0	1		0	0	3	3	
18th24th	0	1		0	1	3	11	
25th — 3rd March	0	0		0	0	2	4	
4th March—14th "	0	1		0	0	3	2	
Totals	0	3		0	1	15	21	
Pcrcentages	dead of pla	gue :						
	Bombay	rats		6 º/o				
	Poona r	ats		2 %				
	Madras	rats	•••	72 º/ ₀				
Avera	ge flea prev	alence :						
	Godo	wn 1		4.2				
		2	•••	$2 \cdot 2$				
		3		4.4				
		4		4.7				
		5		4.3				
	,,	6	• • • •	5.0				

Experiment III.

 12 Madras rats
 ...
 ...
 ...
 ...
 were each inoculated with 1/20,000 gramme

 48 wild Bombay rats
 ...
 ...
 ...
 ...
 of plague rat's spleen on 5 May, 1910.

 48 rats bred from Bombay rats in captivity
 Image: spleen on 5 May, 1910.
 Image: spleen on 5 May, 1910.

The wild Bombay rats and the bred rats were matched in pairs as regards size and weight.

			1	Madras ra	ats	Wil	d Bomba	y rats	God	Godown bred rats			
	Date	e	Dead not plague	Dead of plague	Re- maining	Dead not plague	Dead of plague	Re- maining	Dead not plague	Dead of plague	Re- maining		
Mav	5.	1910	_		12	—		48			48		
nauj	6			_	12	2	—	46			48		
"	7	,,		1	11	2		44	—		48		
"	8	,,		8	3		5	39			48		
,,	ğ	,,		3	0		8	31		4	44		
,,	10	,,					2	29	-	1	43		
,,	11	,,		·			1	28		3	40		
,,	12	,,	· · · ·	_			1	27		3	37		
,,	13	"						27		2	35		
"	14	,,			_			27		2	33		
,,	15	,,						27	_	1	32		
,,	16	,,		_				27		2	30		
,,	17	,, ,,	_					27			30		
	Tot	als	0	12	0	4	17	27	0	18	30		
			Percenta	ges dead	l of plagi	ue :							
				Madra Wild Bred	as rats Bombay 1 rats	rats .	10 8 8	0 °/ ₀ 55 °/ ₀ (39 ° 37·5 °/ ₀	/0)				

Experiment IV.

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....

		10 10 10 10	00 Bhaga 00 Poona 00 Madra 00 Bomb	alpur a as oay	rats ,, ,, ,,	were ea of 19	were each inoculated with 1/20,000 gramme of plague rat's spleen on 2 June, 1910.								
·			В	hagalı	our	1	Poona			Madras			Bombay		
.]	Date		Dead of plague	Dead not plague	Remaining	Dead of plague	Dead not plague	Remaining	Dead of plague	Dead not plague	Remaining	Dead of plague	Dead not plague	Remaining	
June	2,	1910	_	_	100		—	100			100			100	
,,	3	"		_	100	—		100			100			100	
"	4	,,	_		100	_	—	100	1	—	99	_		100	
,,	5	,,	5	_	95	1		99	22	_	77			100	
,,	6	,,	14		81	1	—	98	39		38	5		95	
,,	7	,,	14		67	2		96	14		24	6		89	
,,	8	,,	11		56	2		94	10		14	6	-	83	
,,	9	,,	6		50	0		94	5		9	2	—	81	
. ,,	10	,,	1		49	1		93	2	-	7	2		79	
,,	11	,,	5	—	44	0		93	1	—	6	0	-	79	
,,	12	,,	1	_	43	2		91	0		6	1		78	
,,	13	,,	0	—	43	1	—	90	0		6	1	_	77	
,,,	14	,,	0		43	0		90	0	-	6	1	—	76	
,,	15	,,	0		43	0	-	90	0	—	6	1	2	73	
• • • •	16	,,	0	_	43	0	—	90	0		6	0	1	72	
,,	17	39	0		43	0		90	0		6	1	0	71	
Pe	T	otals	57 dead of	0 plage	43 1e ·	10	0	90	94	0	6	26	3	71	
10	MB	adras ombay	rats 7 rats		94 º 26 º	/o (95 º/o) /o)		Bhagalr Poona r	ur ra ats		57 10	°/0		

Experiment V.

100 Madras rats...100 Poona rats...100 Bombay rats...27 Madras bandicoots

were each inoculated with 1/20,000 gramme of plague rat's spleen on 8 July, 1910.

۰,

			Madras			Poona			Bombay				Bandicoots			
	Date		Dead of plague	Dead not plague	Remaining	Dead of plague	Dead not plague	Remaining	Dead of plague	Dead not plague	Remaining		Dead of plague	Dead not plague	Remaining	
Jul	y 8,	1910	_		100		_	100			100		_		27	
,,	9	,,	_		100	_		100		8	92				27	
,,	10	,,	5		95		_	100	5	4	83			_	27	
,,	11	,,	77		18	13	3	84	17		66				27	
,,	12	,,	13	_	5	12		72	22		44		8		19	
,,	13	,,	2		3	4	_	68	8		36		10	_	9	
,,	14	,,	_		3	3		65	5		31		5		4	
,,	15	••		_	3	4		61	1		30		3		1	
,,	16	,,		_	3	2	1	58	3		27				1	
,,	17	,,			3	2		56			27				1	
,,	18	,,	-		3	1	_	55			27				1	
,,	19	,,			3	<u> </u>		55	_	_	27				1	
,,	20	,,			3	1		54			27			_	1	
,,	21	,,	—		3		_	54	1		26		_		1	
,,	22	,,			3	_		54			26				1	
,,	23	,,			3		1	53	1		25				1	
,,	24	,,			3			53	_	_	25			1	0	
,,	25	,,		_	3	1		52	1	1	23		_		0	
,,	26	,,		—	3	-	—	52	—	—	23			·	0	
	Tota	ls	97	0	3	43	5	52	 64	13	23		26	1	0	

Percentages dead of plague :

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Madras rats	•••	97 %
Poona rats	•••	43 %/0

Bombay rats... ... 64 % (73 %) Madras bandicoots ... 96 %

Experiment VI.

100 Madras rats)	were each inoculated with 1/50,000 gramme
100 young Poona rats	of plague rat's spleen on 9 August,
100 young Bombay rats	1910.

Average weights:

Madras 120 grammes ... ••• Young Poona ... 30 Young Bombay ... 30

,,

,,

	Madras rats					You	ng Poona	a rats	Young Bombay rats			
	Date	B	Dead not plague	Dead of plague	Re- maining	Dead not plague	Dead of plague	Re- maining	Dead not plague	Dead of plague	Re- maining	
Aug.	9,	1910	_		100	_	_	100		_	100	
,,	10	,,		—	100	11		89			100	
,,	11	,,		2	98	1	4	84	1	6	93	
,,	12	,,		4	94		5	79		9	84	
,,	13	•,	. —	33	61		6	73	—	6	78	
,,	14	,,	—	29	32	—	11	62	. —	3	75	
,,	15	,,		11	21		2	60		5	70	
,,	16	,,		6	15		5	55		5	65	
,,	17	,,		5	10		3	52		2	63	
,,	18	,,	-	3	7		1	51	_	6	57	
,,	19	,,		1	6	_	1	50		0	57	
,,	20	,,	_	2	4		0	50		3	54	
,,	21	,,	_	0	4	_	1	49		2	52	
,,	22	,,		1	3		0	49		0	52	
,,	23	,,		1	2	—	0	49	1	0	51	
	Т	otals	0	98	2	12	39	49	2	47	51	

Percentages dead of plague :

Madras rats	 98 º/o
Young Poona rats	 39 % (44 %)
Young Bombay rats	 47 º/o

Experiment VII.

100 Madras rats...100 young Poona rats...100 young Bombay ratswere each inoculated with 1/20,000 gramme of
plague rat's spleen on 30 September, 1910.

1	Average	e weigh	ts:							
			Madi Your Your	ras ng Poona ng Bombay	 	94 gra 23 23	,, ,,			
		You	ng Poona	rats	You	ng Bombay	' rats	Madras rats		
Da 191	te 10	Not plague	Plague	Remaining	Not plague	Plague	Remaining	Not plague	Plague	Remaining
Septem	ber 30			100			100		_	100
October	1	28		72	4		96		_	100
,,	2	2	. 1	69	4	9	83	_	1	99
,,	3		1	68		5	78		43	56
,,	4	_	1	67	2	7	69		38	18
,,	5	2	5	60	3	16	50	<u> </u>	9	9
,,	6	1	6	53		6	44	_	6	3
,,	7	2	' 3	48		4	40	_		3
,,	8	-	1	47		6	34	_	—	3
,,	9			47	—	2	32			3
,,	11	2	1	44	—	2	30		_	3
,,	12		·	44			30	_	·	3
,,	13	1	1	42	—	—	30		—	3
,,	14			42		6864-ca	30	_		3
,,	15		_ .	42	—	-	30	-		3
,,	16		-	42	_	_	30			3
,,	17	_	—	42			30			3
,,	18			42		—	30	—	-	3
,,	19	_		42	-	<u> </u>	30	-		3
,,	20			42	_		30		_	3
То	tals	38	20	42	13	57	30	0	97	3

Percentages dead of plague:

Madras rats	97 %
Young Poona rats	20 % (29 %)
Young Bombay rats	57 % (62 %)

Experiment VIII.

100 Poona rats100 Kirkee rats100 Bombay rats
were each inoculated with 1/5,000 gramme of plague rat's spleen on 7 November, 1910

and

100 Madras rats received one-half the dose of the same emulsion.

	Poona			F	Lirkee		1	ladras	5	Bombay			
Date	Dead not plague)	Dead of plague	Remaining	Dead not plague)	Dead of plague	Remaining	Dead not plague)	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	
Nov. 7, 1910			100			100	_		100			100	
,, 8 ,,		—	100		—	100		· <u> </u>	100			100	
,, 9 ,,		2	98		1	99		12	88		4	96	
,, 10 ,,	—	28	70		50	49		86	2	1	27	68	
,, 11 ,,	—	25	45		22	27		1	1		19	49	
,, 12 ,,		9	36		11	16			1		8	41	
,, 13 ,,		7	29		7	9	—	—	1	_	9	32	
,, 14 ,,		3	26	—	2	7			1	_	3	29	
,, 15 ,,		1	25		1	6			1			29	
,, 16 ,,		1	24		1	5	—	1	0	_	—	29	
,, 17 ,,	_	0	24	_	-	5		—	0			29	
,, 18 ,,		1	23			5			0	—	2	27	
,, 19 ,,			23			5	—	—	0			27	
,, 20 ,,			23			5			0	_		27	
,, 21 ,,			23		—	5		-	0		1	26	
Totals	0	77	23	0	95	5	0	100	0	1	73	26	
	Percer	ntage	s dead	of plage	ie :								

Madras rats		100 %
Kirkee rats		95 %
Poona rats	•••	77 %
Bombay rats		73 º/o

Journ. of Hyg.

Experiment IX.

100 Madras rats100 Poona rats100 Bombay rats

were each inoculated with 1/5,000 gramme of plague rat's spleen on 5 January, 1911.

	N	ladras ra	ts		Poona ra	ts	Bombay rats			
Date	Dead not plague	Dead of plague	Re- maining	Dead not plague	Dead of plague	Re- maining	Dead not plague	Dead of plague	Re- maining	
Jan. 5, 191	1 —		100		_	100			100	
,, 6 ,,			100			100			100	
,, 7 ,,		8	92		3	97		_	100	
,, 8 ,,	-	79	13	1	13	83	2	38	60	
,, 9 ,,		10	3		31	52		23	37	
,, 10 ,,		3	0		14	38		5	32	
,, 11 ,,		_			11	27	_	5	27	
,, 12 ,,				_	4	23		3	24	
,, 13 ,,		—			1	22		1	23	
,, 14 ,,						22		2	21	
,, 15 ,,					1	21	_	1	20	
,, 16 ,,	—					21	_		20	
,, 17 ,,		—	—		_	21		2	18	
,, 18 ,,		—				21		_	18	
,, 19 ,,						21		1	17	
,, 20 ,,			_		—	21	_	1	16	
Totals	0	100	0	1	78	21	2	82	16	

Percentages dead of plague:

Madras rats	•••	100 º/o
Poona rats	•••	78 º/o
Bombay rats		82 º/ ₀

Experiment X.

100 Madras rats 100 Bombay rats

100 Bombay rats 100 Kirkee rats 100 Poona rats •••

•••

•••

were each inoculated with 1/20,000 gramme of plague rat's spleen on 16 January, 1911.

100 Poona rats ... 23 Madras bandicoots.

		Ма	dras r	ats	Bon	ibay i	rats	Ро	on a ra	its	Ki	kee r	ats	ba	Madra andicoo	s ots
Da: 191	te	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining
Jan.	16		_	100		_	100			100	-		100			23
,,	17			100			100	_		100	-		100			23
,,	18	—	3	97	—		100	—		100	_	_	100			23
,,	19	_	27	70		1	99		7	93		3	97		1	22
,,	20	—	38	32	_	5	94		3	90		9	88		1	21
,,	21		15	17		8	86		4	86		10	78	_	5	16
,,	22	_	6	11		5	81		5	81		10	68		9	7
,,	23	—	5	6		3	78		1	80	—	4	64		5	2
,,	24		0	6	—	3	75		2	78	—	2	62	—	1	1
,,	25		2	4	1	0	74		1	77		1	61		0	1
,,	26		0	4			74		1	76	_	_	61			1
,,	27		0	4		_	74			76	—		61			1
,,	28		1	3		1	73		_	76			61			1
,,	29	_		3	_		73			76	—	_	61			1
,,	30			3	3		70		1	75	—		61			1
,,	31	_		3	7		63	1		74			61		—	1
Feb.	1	_		3			63		_	74	—	1	60			1
,,	2	—	1	2	1	_	62	1		73	—		60	_	-	1
,,	3	—		2	3		59	4	—	69	1	_	59	_		1
,,	4	_		2	2	—	57	_	—	69	—		59			1
,,	5	—		2			57			69	1		58		_	1
,,	6			2			57	2		67	2		56	_		1
,,	7	—	_	2	2	—	55	2		65			56			1
	Totals	0	98	2	19	26	55	10	25	65	4	40	56	0	22	1

Percentages dead of plague:

Madras rats	•••	98 %
Bombay rats		26 %
Poona rats		25 ⁰ / ₀
Kirkee rats	•••	40 %
Madras bandicoots		96 º/ ₀

16-2

Experiment XI.

100 young Poona rats 100 young Bombay rats 100 Madras rats

were each inoculated with 1/50,000 gramme of plague rat's spleen on 14 February, 1911.

Average weights:

			M Ya	adras oung Po	 ona	 	•	110 gra 40	mmes			
			Yc	oung Bo	mbay	 	•	40	,,			
			1	Young Po	ona	Young Bombay				Madras		
:	Date		Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining		Dead not plague	Dead of plague	Remaining
Feb.	14,	1911			100			100				100
,,	15	,,	—		100			100		_		100
,,	16	,,	—	2	98	4		96				100
,,	17	,,		6	92		10	86		—	71	29
,,	18	,,		3	89		10	76			22	7
••	19	,,		5	84		13	63			5	2
.,	20	,,		4	80		4	59			1	1
	21			5	75		6	53			1	0
	22	••		2	73		3	50		_		
	23		—	2	71		2	48		_		
	24		1		70			48				_
	25				70	_		48				
,,	26		1		69	1		47				
,,	27				69		_	47		_		_
,, ,,	28	,,			69	 1	_	46		_	—	
	Tot	als	2	29	69	6	48	46		0	100	0

Percentages dead of plague:

Madras rats		100 º/o
Young Poona rats		29 º/ ₀
Young Bombay rats	•••	48 º/o (50 º/o)

Experiment XII.

100 Madras rats 100 Dacca ,, 100 Poona ,, 100 Bombay ,,

,, were each inoculated with 1/100,000 gramme of plague ,, rat's spleen on 24 February, 1911.

	:	Madras rats		D	acca rat	ts	В	ombay i	ats	Poona rats			
Date 1911	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	
Feb. 24			100	_	_	100	_		100	_		100	
,, 25			100			100			100	_		100	
,, 26		_	100		4	96			100		1	99	
,, 27	3	85	12		45	51		16	84	—	14	85	
,, 28		6	6		29	22		18	66		14	71	
March 1	—	5	1		4	18		10	56		10	61	
,, 2		1	0		6	12	2	1	53	3	5	53	
,, 3			0	—		12		1	52	1	_	52	
,, 4			0			12		1	51		1	51	
,, 5	—		0		2	10	1	—	50		1	50	
,, 6	—		0	-	-	10		1	49	. 2		48	
,, 7			0	—	-	10	1	—	48		_	48	
,, 8	—		0		2	8			48			4 8	
,, 9	—		0			8	1	2	45	—		48	
,, 10			0		-	8		1	44		—	48	
,, 11	—		0		1	7			44			48	
,, 12	—		0	_		7	2		42	·		48	
,, 13			0		—	7	1		41	—	1	47	
,, 14	—		0			7		—	41			47	
,, 15			0	_		7	1	2	38			47	
,, 16		—	0	_		7		—	38	1	1	45	
Totals	3	97	0	0	93	7	9	53	38	7	48	45	

Percentages dead of plague:

Madras :	rats .	•••	•••	97 º/o
Dacca	,,	•••	•••	93 º/o
Bombay	,,			53 º/o
Poona	,,	•••	•••	48 %

•

Experiment XIII.

100 Madras rats 100 Dacca ,, 100 Poona ,, 100 Yeotgaon rats 100 Bombay ,,

were each inoculated with 1/50,000 gramme of plague rat's spleen on 10 March, 1911.

	М	adras	rats	Da	icca ra	ts	Po	ona r	ats	Yeo	tgaon	rats	Bo	mbay	rats
Date 1911	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining	Dead not plague	Dead of plague	Remaining
March 10			100	_		100	_		100			100	_		100
,, 11			100			100			100		_	100	_		100
,, 12	—	4	96			100	—		100	_	1	99	_	—	100
,, 13		65	31		46	54		5	95		15	84		6	94
,, 14	_	25	6		36	18		5	90		21	63	_	9	85
,, 15			6		5	13		5	85		9	54		6	79
,, 16		—	6	—	3	10	_	8	77		9	45		6	73
,, 17	—		6		3	7			77	—	2	43		2	71
,, 18		2	4			7	3	2	72		1	42		1	70
,, 19	—	1	3			7		2	70		3	39	_		70
,, 20			3		1	6	2	1	67	_	2	37		4	66
,, 21	_	_	3			6	5		62	—	1	36		_	66
,, 22		_	3		3	3	2	2	58		3	33		1	65
,, 23	—		3	_		3	3	_	55		2	31		1	64
,, 24		—	3			3		1	54	1		30	1	—	63
,, 25	—		3	—		3	2	_	52			30	1	—	62
,, 27	—	1	2	_	_	3	2		50		1	29	2		60
,, 29	-	_	2			3	2		48	_		29			60
April-1		_	2		—	3			48		—	29	2		58
Totals	0	98	2	0	97	3	21	31	48	1	70	29	6	36	58

Percentages of rats dead of plague:

Madras rats	•••			98 %
Dacca ,,				97 %
Poona ,,			•••	31 %
Yeotgaon rats	•••	•••		70 %
Bombay "	•••			36 %

Experiment XIV.

100 Madras rats ... were each inoculated with 1/100,000 gramme of 50 Chit Baragaon rats ... plague rat's spleen on 22 April, 1911. 100 Bombay rats ... Chit Baragaon rats Madras rats Bombay rats Dead not plague Dead not plague Dead not plague Dead of plague Dead of plague Dead of plague Remaining Remaining Remaining Date ----50 100 100 April 23, 1911 ____ 1 $\mathbf{24}$ 100 ----50 99 --------,, ,, 25____ 19 81 -----50 99 ,, ,, 50 $\mathbf{26}$ 44 37 8 91 ,, ,, $\mathbf{27}$ 19 $\mathbf{18}$ 1 49 _____ _____ _____ 2 4 87 ,, ,, $\mathbf{2}$ 153 47 6 $\mathbf{28}$ 81 ,, ,, ____ $\mathbf{2}$ 29 1 $\mathbf{2}$ 45 1 80 ,, ,, 30 1 1 3 422 78 ,, ,, 4 38 2 1 1 76 May ,, 2 1 3 35 76 -----,, ,, 0 2 33 3 ____ 76 ,, ,, ____ 33 4 -----76 -----,, ,, 1 5 ____ 33 76 ,, ,, 1 31 6 74 ,, ,, 1 $\mathbf{2}$ 30 7 $\mathbf{72}$,, ,, 1 _____ 30 71 8 ,, ,, 9 30 1 70 ,, ,, 30 1 10 69 ,, ,, 30 69 11 ,, ,, 30 69 12,, ,, 30 69 13 ____ ,, ,, 30 69 14 _ ,, ,, _ -----30 69 15____ _____ ,, ,, 23 Totals 1 99 0 1 19 30 8 69

Percentages dead of plague :

 Madras
 ...
 99 %

 Chit Baragaon
 ...
 38 %

 Bombay
 ...
 23 %

Immunity of Wild Rats

gramme 1911.	Property and the second state of th	1 1 1 55 1 1 1 1 55 1 2 3 3 5 3 3 5 3 3 5 3	12 35 53 25 % 35 %
ed with 1/100,000 (spleen on 18 May,	P Pool <	11123	4 25 71 Adult Poona Young Poona
te each inoculate of plague rat's	об кра кра кра кра кра кра кра кра	1 2 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	$10 \ 34 \ 56$ $19 \ 9/_0$ $34 \ 9/_0$
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dult Madras rats oung Madras rats ucknow rats	Madata Markov M		0 95 5 • dead of plague : Madras 95 • Madras 100
100 a 50 y 100 L	Date 1911 May 1911 7, , , , , , , , , , , , , , , , , , ,		Totals Percentages Adult Young

Experiment XV.

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Immunity of Wild Rats



Experiment XVII.

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Experiment XVIII.

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Experiment XIX.

100 Lucknow rats80 Cawnpore rats60 Banda rats

90 Poona P.C. rats 100 Poona N.P.C. rats

100 Bombay rats

each received 1/100,000 gramme plague
rat's spleen (=20,000 plague bacilli)
on 28 October, 1911.

		uckn	ow	Ca	wnpo	ore	Banda			Ē	omb	ay	Po	ona F	P.C.	Poona N.P.C.			
Date 1911	Not plague	Plague	Remaining	Not plague	Plague	Remaining	Not plague	Plague	Remaining	Not plague	Plague	Remaining	Not plague	Plague	Remaining	Not plague	Plague	Remaining	
Oct. 28			100			80			60			100		_	90	_		100	
,, 29			100			80			60			100			90		_	100	
,, 30	—	1	99	—		80	<u></u> .	1	59		3	97	_	1	89		1	99	
,, 31		7	92		4	76		21	38		6	91		5	84		6	93	
Nov. 1		14	78	_	7	69		23	15		12	79	_	7	77	_	5	88	
,, 2		5	73		2	67	_	6	9		1	78		2	75		7	81	
,, 3		2	71		3	64	_	4	5		4	74	_	6	69		3	78	
,, 4		1	70	_		64		2	3		1	73		1	68		1	77	
,, 5		1	69			64		1	2	—	1	72		4	64		1	76	
,, 6	_	1	68	2		62		1	1	2	1	69		1	63	_		76	
,, 7		—	68			62		_	1		1	68	_	2	61			76	
,, 8	1		67	_	—	62		_	1	2		66		1	60	2		74	
,, 9	2		65		_	62			1		. 	66	_		60			74	
,, 10			65	·		62			1	1		65			60	1		73	
,, 11	—		65			62			1			65		_	60	1	_	72	
,, 12			65	—		62			1	—		65			60	1		71	
,, 13			65			62			1			65			60			71	
,, 14	2		63			62			1	2		63	1		59	2		69	
,, 15			63			62			1			63			59			69	
,, 16	—		63			62		—	1			63			59			69	
,, 17			63	_	—	62			1			63			59			69	
,, 18		—	63			62			1		—	63			59			69	
,, 19			63	_		62			1			63			59			69	
Totals	5	32	63	2	16	62	0	59	1	7	30	63	1	30	5 9	7	24	69	

Percentages dead of plague :

Lucknow	 $32 \ 0/_0$
Cawnpore	 20 $^{0}/_{0}$
Banda	 98 ⁰ / ₀

	✓ 10
Poona P.C 3 Poona N.P.C 24	$\left\{\begin{array}{c} 3 & 0/0 \\ 4 & 0/0 \end{array}\right\} \ 28 \ 0/0 \ 0 \ 1 \ 0/0 \ 0$

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 $Experiment \ XX.$

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Experiment XXI.

100 Madras rats...100 Bombay rats...80 Poona rats...75 Muzaffarnagar rats80 Delhi Shahdara rats

each received 1/100,000 gramme plague rat's spleen (=16,000 plague bacilli) on 31 January, 1912.

	Madras	Muzaffarnagar	Delhi Shahdara	Poona	Bombay
Date 1912	Not plague Plague Balance				
Jan. 31	— — 10 0	— — 75	80	<u> </u>	100
Feb. 1	<u> </u>	<u> </u>	80	80	<u> </u>
,, 2	— — 100	1 74	— — 80	80	100
,, 3	-12 88	74	80	— 377	- 4 96
,, 4	- 30 58	- 4 70	- 377	- 2 75	<u> </u>
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Percen	tages dead of p	elague :			

Madras	Muzaffarnagar	Delhi Shahdara	Poona	Bombay
98 º/o	27 °/0	29 °/ ₀	17 %	24 º/o

Godown bred Bombay rats 45 $0'_{6}$ 13 10300 9u3sIA 1 1 1 1 i 53 3 ən%eld to $_{\mathbf{N}}$ ÷ ł each received 1/100,000 gramme of a plague rat's spleen (=14,000 plague bacilli) on 27 April, 1912 Bombay (bred) Godown bred Madras rats 6 18 Balance 400 0 18 8 <mark>1</mark>2 8 3 9n2sIA 0 ən%sıd 40N 1 28 Survivors 0 Plague 1 1 1 ${{{{{\rm{nil}}}}_{0}}_{0}}^{0/0}$ 01 ən%s[d 40N 1 1 1 I 68 : : Bombay Plague 3 8 10 67 3 3 1 1 27 1 Ì 1 Madras (bred) ŝ ougalq to N Survivors 1 $\frac{71}{23}$ 00000 Podanur 87 9n3sIA 83 35 I 1 ən%sıd 10N 1 $\begin{array}{c} 92 & 0/_0 \\ 27 & 0/_0 \end{array}$ 1 11 1 1 Coimbatore 50 54 88 Balance 33 Experiment XXII. 47 12 Madras rats bred in Bombay Bombay rats bred in Bombay Survivors from experimental epizootics (see below, p. 292) : : 47 **5** 8 3 0 ļ 1 1 1 9n%sIA Podanur Bombay 0 ənselq toN 1 1 l 15 $225 \\ 222 \\ 222 \\ 222 \\ 222 \\ 222 \\ 225$ 2 5 $15 \\ 15$ 18 2 15 Balance 5 Bellary 0 **-** 0 10 ŝ 1 1 1 1 1 angala $\frac{40}{60}\frac{0}{0}$ 0 ən%s[d 40N 1 1 1 T 1 1 1 1 Bellary ... Coimbatore ... 61 14 14 14 26 2 4 5 5 6 6 Balance 6 2 2 14 14 14 21 20 4 14 5 Yeotgaon 30 18 30 18 521 1 Plague 1 0 anseld to N I 1 1 I 1 1 25 Bellary rats 100 Madura rats 95 Podanur rats 100 Bombay rats 80 84 668 92 668 88 78 78 Balance 66 Poona 3 13 1 1 1 Plague $\frac{13}{79} \frac{0}{0}$ anzelq to^N 1 1 1 1 : : 19 17 17 17 $^{22}_{21}$ 18 SS Balance **96** 73 34 2522 Yeotgaon Madura 100 Madras rats80 Coimbatore rats100 Poona rats66 Yeotgaon rats Poona 83 89 <u>6</u> 13 6 3 70 --3 ł 32 Plague 0 ənSslq toV 1 1 1 ŝ SS Balance $\begin{array}{c}
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Experiment XXIII.

90 Madras rats 97 Belgaum rats 98 Banda rats 100 Bombay rats

each received 1/100,000 gramme of a plague rat's spleen (=20,000 plague bacilli) on 27 May, 1912.

		Madra	.8	1	Belgau	m		Band	la		Bomb	ay
Date 1912	Not plague	Plague	Balance	Not plague	Plague	Balance	Not plague]	Plague	Balance	Not plague	Plague	Balance
May 27	_		90	_		97			98			100
,, 28		_	90			97			98			100
,, 29	_		90	_		97			98		_	100
,, 30		8	82		2	95		· 10	88		2	98
,, 31	_	33	49	_	1	94		- 32	56	_	5	93
June 1		20	29		3	91		- 19	37		4	89
,, 2		11	18	_	1	90		- 16	21		2	87
,, 3	_	6	12		2	88		- 4	17		4	83
,, 4		2	10		1	87		- 4	13		1	82
,, 5		2	8			87		- 2	11		1	81
,, 6		1	7			87		- 2	9			81
,, 7		1	6	1	_	86		. 1	8	2		79
,, 8			6			86			8	1		78
,, 9		2	4	_		86			8			78
,, 10		,	4			86			8	1	—	77
,, 11		1	3	1		85		· 1	7	_	1	76
,, 12			3	_	—	85		·	7			76
,, 13	_	—	3			85		·	7		—	76
,, 14			3			85			7		1	75
,, 15	—		3	1		84		·	7			75
,, 16	_		3	_		84			7	_		75
,, 17		—	3			84		· —	7	. —	—	75
Totals	0	87	3	3	10	84	0	91	7	4	21	75

Percentages dead of plague:

Madras	Belgaum	Banda	Bombay
97 º/o	10 º/o	93 °/0	21 %

As regards adult wild rats, the results are summarised in table I and in table II is given shortly the plague history of the places from which the rats were derived. Their geographical relations are shown in the appended map.

Table I shows clearly that the susceptibility to fatal plague infection varies a great deal in rats from different places, and by comparison with table II it appears that the resistance of the rats varies in a general way with the local prevalence of plague in recent years. The places investigated fall into three main groups.

(1) Places which have suffered severely and almost continuously from plague for about ten years or more. Bombay rats have been compared with the standard susceptible Madras rats in 18 inoculation experiments with an average mortality of $38 \, 0_0'$ against $97 \, 0_0'$ in the Madras rats. Rats from Poona have in the same way been tested against Madras and Bombay rats on 14 occasions by inoculation : the total result is that of 1390 Madras rats 1347 died $(97 \, 0_0')$, of 1387 Bombay rats 533 $(38 \, 0_0')$ and of 1355 rats from Poona only 446 $(33 \, 0_0')$. Similarly the resistance of rats from the two other large plague-infected towns of Cawnpore and Lucknow was found to be of a high grade, the summed figures of comparative experiments being

> Madras, 485 out of $500 = 97 \, {}^{\circ}/_{\circ}$. Bombay, 173 out of $598 = 29 \, {}^{\circ}/_{\circ}$. Poona, 138 out of $587 = 24 \, {}^{\circ}/_{\circ}$. Cawnpore, 75 out of $414 = 18 \, {}^{\circ}/_{\circ}$. Lucknow, 117 out of $349 = 34 \, {}^{\circ}/_{\circ}$.

Other towns in this group were investigated less frequently. Belgaum, where plague has for many years been exceptionally severe, yielded rats only 10 % of which died¹. Surat (Bombay), Bellary (Madras), Bandsdeh (United Provinces) and Chit Baragaon (United Provinces) gave figures (37 to 42 % or mortality) rather higher than those for Bombay (29 %) in parallel experiments, as also did Kirkee. Two other places in the United Provinces were examined—Muzaffarnagar and Delhi Shahdara—and in both places the rats were found about as little susceptible as those of Bombay. Nagpur alone of the places with a long history of severe plague gave susceptible rats, 97 and 98 % dying in two experiments. Pending further enquiries this result must be regarded as exceptional. The rats, however, were not collected

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¹ In an experiment already published (vol. x. p. 458) Bombay, Poona and Belgaum rats were exposed to infected fleas: there died 18, 27 and 9 per cent. respectively.



Map showing the places from which rats were obtained for immunity experiments.

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noitaluqoT 1901	Bombay ¹	Cawnore 183,712 Lucknow 264,049 Bellary 58,247 Bagalpur ⁴ 75,760 Nagpur ⁵ 127,734 Belgaum ⁶ 26,237 Surat 119,306 Muzaffarnagar ⁷ —	Coimbatore 53,080 Calicut 76,981 Palghat 44,177 Podauur 6,568 Vaniyambadi 12,908	Madras ⁸	 Vol. vII. p. 726, vol. vi 4 Vol. xI. supplement, p. 7 Details for these villag vol. xI. supplement, This volume, p. 209.

TARLE II. Plague deaths per 10,000.

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under the immediate supervision of the Commission and it may be that they came from a part of the town which has been relatively free from plague.

(2) Places which have suffered relatively slightly from plague. Chief among these is Madras City which has been free from plague except for one small outbreak in the outskirts of the city in 1905. The susceptibility of the rats from here is sufficiently evident. Raipur (Central Provinces) also falls in this group and has very susceptible rats. All the other five places are in the Madras presidency: Vaniyambadi suffered from two very severe epidemics some time since but has been free from plague for eight years. Calicut, Palghat and Podanur have had several small outbreaks scattered over a number of years, and the rats from all four towns proved highly susceptible. They were rather more resistant from Coimbatore, where plague prevailed rather extensively during the three years preceding the time when the rats were obtained for experiment.

(3) Places which have been free from plague. The four places under this heading all yielded susceptible rats. It is of some importance to note that they are widely scattered about India. The rats from Banda (United Provinces), Madura (Madras) and Dacca (Assam) were as little immune as those from Madras City. A figure was obtained indicating a rather greater resistance, though much less than in Bombay, Poona and other places in group 1, for Yeotgaon, a village in the immediate neighbourhood of Poona in which on careful enquiry we could obtain no evidence that plague had ever been present.

In comparing the figures in table I with one another it should be noted that the degrees of immunity indicated are relative to the dose, and that no very exact comparison can be made between the results of one experiment and those of another even if the dose is nominally the same since it cannot be assumed that the infectivity of the bacilli was The experiments (XVII to XXIII) in which the in all cases constant. bacilli were enumerated in a constant quantity of emulsions, made from spleens of acute plague rats showing approximately an equal number of bacilli on microscopical examination, show that $\frac{1}{100}$ mgm. contained from 12,000 to 26,000 bacilli. This is perhaps under the circumstances a very satisfactory degree of uniformity, but at the same time the range of variation shows that a dose of $\frac{1}{20}$ mgm. cannot be regarded as being necessarily greater than one of $\frac{1}{50}$ mgm. With wide differences in dosage, however, the difference in effect is plain enough: $\frac{1}{5}$ mgm. (experiments VIII and XI) killed 78 % of Bombay rats and 77 of

those from Poona, as against 42 and 26 $^{\circ}/_{\circ}$ with $\frac{1}{20}$ mgm., 31 and 24 $^{\circ}/_{\circ}$ with $\frac{1}{100}$ mgm., and 6 and 2 % with flea infection¹. It should also be understood that the dose which suitably brings out the difference between batches of rats of widely varying resistance is not necessarily an appropriate quantity for the examination of animals more nearly Thus a dose of $\frac{1}{100}$ mgm. killed on the average 97 % of Madras alike. rats, and this mortality could not be much increased under any circumstances: it rises to the limit with $\frac{1}{5}$ mgm. and falls to 72 % in the flea-infection experiment. All the rats from Vaniyambadi and Raipur were killed by the same dose of $\frac{1}{100}$ mgm. and more than 90 % from Nagpur, Calicut, Podanur, Banda, Madura and Dacca, but it does not follow that the resistance was in all cases approximately the same. Further experiments with smaller doses may show considerable variation in the rats from these different localities. In the case of Kirkee $\frac{1}{5}$ mgm. killed 95 % but a second trial with $\frac{1}{20}$ mgm. showed that the rats from this place possessed a pretty high degree of resistance. Similarly larger doses might show that the animals from Poona, Cawnpore and Belgaum really differ more widely than the present series indicates.

Taking the series of experiments as a whole it seems clear that the resistance of rats to plague is associated with the past prevalence of plague, and is not due to racial and local variations in susceptibility. There is of course no doubt that among a series of batches of rats all conforming to the type of Mus rattus it is possible to discover special and characteristic features in the specimens from certain places, not as a rule wholly confined to any one locality but being predominant in one place more than in another². Thus the fur of Madras City rats is exceptionally rufous, and a very large proportion of Palghat rats had white fur on the under surface of the body while this feature was extremely rare in Poona. Rats from the colder northern places had thicker fur than southern specimens, and Belgaum rats were always on the whole larger than those caught in Bombay or Poona. But no external differences could be detected in the rats from Poona, Kirkee and Yeotgaon, which are situated within a few miles from one another. Poona has suffered severely from plague, Kirkee less severely and Yeotgaon not at all, and we found that the immunity of the rats from each place was proportionate to the degree of plague prevalence. Similarly

¹ The difficulty of conveying infection by a single flea emphasises the importance of dosage in this means of infection (see vol. vn. p. 411).

² See "The Races of Indian Rats," by R. E. Lloyd, in *Records of the Indian Museum*, vol. 111. part 1, and especially p. 84.

with respect to Cawnpore, Lucknow and Banda in the United Provinces. It was not possible to distinguish the rats of Cawnpore or Lucknow from those of Banda by external appearances, but on testing them by inoculation Banda rats proved to be as susceptible as Madras rats, and Cawnpore and Lucknow rats both highly immune, the former markedly more than the latter. The plague histories of the three places have been widely different; the disease has been nearly twice as severe in Cawnpore as in Lucknow, and epidemics have recurred yearly in Cawnpore while in some recent years Lucknow has escaped. Banda has been entirely free from the disease. Any local or racial variations in resistance to plague which may be associated with morphological differences such as we have indicated seem therefore to be obscured in the present series of experiments, and, as will be seen from the map, there is no evidence of any geographical distribution of immunity. Highly susceptible rats were found in such widely separated parts of India as Madras, Dacca, Madura and Banda, and highly immune animals in Bombay, Belgaum and Cawnpore. It would also be an extraordinary coincidence if plague had visited just those places where the rats were naturally most immune to the disease and spared those with the most susceptible rat populations.

It will not have escaped notice that the rats of Vaniyambadi proved to be very susceptible in 1911 and that the place had suffered from exceptionally severe plague in 1901-1903. Evidently therefore any immunity resulting from these epidemics had disappeared in seven or eight years. On the other hand we have evidence that resistance may persist during a period free from plague. In Poona the last evidence of indigenous plague was obtained in March 1909 and though the place was kept under careful observation with continuous rat examination, it remained free from plague until September 1911, a period of some An epidemic of moderate severity then began, 630 deaths 30 months. being recorded up to the end of 1911 and a further 457 by April 1912, when the outbreak came to an end. The immunity experiments cover the period from January 1910 to April 1912 and there is nothing in the results which suggests that the resistance of the rats underwent any alteration during that period. We have no definite information as to the length of life of Mus rattus in nature, but if the data obtained in the breeding experiments (vol. IX. supplement, p. 205) indicate with only approximate accuracy the natural rate of growth the average rat used for experimental purposes could not be more than about 6 months Hence in January 1910 the great majority at any rate of the rats old.

tested may be presumed to have been born since the disappearance of plague from the rat population of Poona¹, and in the later experiments of 1911 there can be no doubt that this became more absolutely true in the sense that many of the animals would not only have never had a chance of experiencing epidemic plague themselves, but would be the grandchildren or great grandchildren rather than the sons and daughters of any rats which ever had. Hence we reach the conclusion that the resistance found is not due merely to the previous reception by the experimental rats of sublethal and immunising doses of plague bacilli during the prevalence of epidemic plague but to the generation of a relatively immune progeny by the survivors of epidemics.

This conclusion is supported by two further sets of experiments. In the first place we tested the resistance of quite young rats, from Madras, Bombay and Poona, which can have been only a few weeks old. The results show that the immunity of these baby rats is of the same

TABLE III. Showing the percentage mortality among young wild rats.

		Madras		Bombay		Poona	
Date	Dose	Adult	Young	Adult	Young	Adult	Young
Aug. 9, '10	1/50 mgm.	98			47	_	39 (44 *)
Sept. 30, '10	1/20 "	97			57 (62*)		20 (29*)
Feb. 14, '11	1/50 ,,	100			48 (50*)	—	29
May 18, '11	1/100 ,,	95	100	19	34	25	35
June 21, '11	1/100 ,,	100	—	45	48		28
	Date Aug. 9, '10 Sept. 30, '10 Feb. 14, '11 May 18, '11 June 21, '11	Date Dose Aug. 9, '10 1/50 mgm. Sept. 30, '10 1/20 ,, Feb. 14, '11 1/50 ,, May 18, '11 1/100 ,, June 21, '11 1/100 ,,	Ma Date Dose Adult Aug. 9, '10 1/50 mgm. 98 Sept. 30, '10 1/20 ,, 97 Feb. 14, '11 1/50 ,, 100 May 18, '11 1/100 ,, 95 June 21, '11 1/100 ,, 100	Madras Date Dose Adult Young Aug. 9, '10 1/50 mgm. 98 Sept. 30, '10 1/20 ,, 97 Feb. 14, '11 1/50 ,, 100 May 18, '11 1/100 ,, 95 100 June 21, '11 1/100 ,, 100	Madras Bo Date Dose Adult Young Adult Aug. 9, '10 1/50 mgm. 98 Sept. 30, '10 1/20 ,, 97 Feb. 14, '11 1/50 ,, 100 May 18, '11 1/100 ,, 95 100 19 June 21, '11 1/100 ,, 100 45	Madras Bombay Date Dose Adult Young Adult Young Aug. 9, '10 1/50 mgm. 98 47 Sept. 30, '10 1/20 ,, 97 -57 (62*) Feb. 14, '11 1/50 ,, 100 48 (50*) May 18, '11 1/100 ,, 95 100 19 34 June 21, '11 1/100 , 100 45 48	Madras Bombay Pec Date Dose Adult Young Adult Young Adult Aug. 9, '10 1/50 mgm. 98 — — 47 — Sept. 30, '10 1/20 ,, 97 — — 57 (62*) — Feb. 14, '11 1/50 ,, 100 — — 48 (50*) — May 18, '11 1/100 ,, 95 100 19 34 25 June 21, '11 1/100 , 100 — 45 48 —

* Corrected for non-plague mortality during first three days.

order as that of the average adult rat from the same place, whether that place is and has been free from plague (Madras), is and has been heavily infected with plague (Bombay) or is free from plague with a history of severe infection in the past (Poona). Absolutely the young rats seem to be definitely rather more susceptible than the corresponding adults receiving an equal dose: this is confirmed by other experiments detailed below (p. 265).

In the second place young rats were obtained by breeding from wild rats in flea-proof godowns at Parel (vol. XI. supplement, p. 193), and as far as the results go they show that the young reproduce the resistance of their parents with remarkable fidelity.

We do not think that there is any reason to suppose that this inherited resistance is due to rats becoming immunised during an epidemic and transmitting this immunity to their offspring. The facts

¹ For some further evidence on this point, see below, p. 279 and note.

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TABLE IV. Showing the percentage mortality among young rats bred in captivity.

			Ma	iras	Bombay	
Experiment	Date	Dose	Wild	Bred	Wild	Bred
ш.	May 5, '10	1/20 mgm.	100	_	35	37
XVII.	Aug. 2, '11	1/100 ,,	9 9		21	20
XXII.	April 27, '12	1/100 ,,	97	100	27	22

are more easily explained by supposing that the susceptible members of a rat population are destroyed during an epidemic and that subsequent generations continue, for a time at any rate, to exhibit the resistance of the survivors. The average immunity of the rats after an epidemic will therefore in a general way be proportional to its severity, dispersion and duration, a mild epidemic leaving many rats of moderate resistance alive and a severe outbreak destroying all but those of the highest immunity. The natural process appears to be the same as that which we have already investigated in connection with the experimental godown epizootics. Thus in one series (vol. x. p. 332) 74 of 143 wild Bombay rats survived flea-borne infection in the godowns and none of them died when they were subsequently inoculated with the same dose of spleen emulsion which killed 68 of 137 $(50 \, ^{\circ}/_{0})$ control rats. Similar results were obtained in subsequent experiments (this volume, p. 298), and the details are given above (p. 253, experiment XXII) of a test in which none of 30 survivors of experimental epidemics died with a dose which killed 97 % of Madras, 27 % of Bombay and 13 % of Poona rats. From other survivors 25 young rats were bred in captivity (p. 248, experiment XVII): of these one only died as against 99 %, 21 % and 21 % of Madras, Bombay and Poona rats respectively. If the same process went on in nature, it is easy to see how the 2 or $3 \circ/_{o}$, or with larger doses presumably the one per thousand or ten thousand, of the rat population of a place such as Madras which lived through a severe epidemic would quickly give rise to a highly resistant race¹.

Experiments on other animals.

Incidentally a few comparative experiments were also made with Madras bandicoots (experiments V and X) and with mice from Madras and Bombay (experiment I). The former show a susceptibility equal, with the doses used, to that of Madras rats (see also vol. VII. p. 760, vol. x. p. 459). Mice on the other hand proved relatively immune, whether they came from a plague-infected or a plague-free place.

¹ For the possible rate of reproduction of rats see vol. xI. supplement, p. 198.

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TABLE V. Showing the percentage mortality from plague of bandicoots and mice compared with rats.

Experi- ment	Dose	Madras rats	Bombay rats	Poona rats	Madras mice	Bombay mice	Madras bandicoots
v.	1/20,000	97	64 (73 *)	43		_	96
x.	1/20,000	9 8	26	25			96
I.	1/100,000	83 (93 *)	44	30	58 (71 *)	54 (63*)	

* Corrected for early mortality from causes other than plague: see p. 232, above.

SUMMARY.

1. Rats from different places show varying degrees of immunity to plague.

2. This immunity is relative to the infecting dose.

3. Immunity is greatest in places which have suffered most severely from plague, less marked in those places which have suffered to a moderate extent and least in those places in which epidemic plague has not occurred.

4. This immunity is not always acquired from an attack of plague, and is transmitted by the parents to their offspring which have not been exposed to infection.

APPENDIX.

On the influence of size and sex on the percentage mortality.

Experiments such as those detailed above have involved the use of rats varying somewhat in size; quite small animals were, however, never used except in the particular experiments designed to test the resistance of young rats. It is important therefore to know whether a moderate variation in size or any sexual differences in the various batches of rats would be likely to lead to any considerable variation in the results of inoculation, the same dose being used whatever the size of the animal. The pretty regular uniformity in the results for Madras and Bombay rats with which many experiments were made is evidence that these factors have not introduced any very material error. We give here, however, the analysis of another series of observations made in Poona in 1909 with the idea of testing for seasonal changes in resistance (see vol. x. p. 523). All the animals received as far as possible the same dose of spleen emulsion. Table VI gives the results for 2000 consecutive rats (77 of which died from causes other than plague) in groups of 500 classified by weight, and table VII deals with the same animals grouped also by sex.

Weight grammes	Jan. 22 to Feb. 28	March 2 to April 13	April 13 to May 18	May 19 to June 25	Total inocu- lated	Total died of plague	Per cent. died of plague
11-30	$15/45 = 33^{0}/_{0}$	$25/61 = 41 0/_0$	$43/84 = 51^{0}/_{0}$	$39/80 = 49^{0}/_{0}$	270	122	$45 \cdot 2$
3150	23/67=34	38/128 = 30	15/54 = 28	38/82 = 46	831	114	34.4
5170	11/58 = 19	12/48 = 25	28/78 = 36	28/83 = 34	267	79	29.6
71—90	32/65 = 49	15/53 = 28	22/70 = 31	17/67 = 25	255	86	33.7
91-110	43/112 = 38	19/88 = 22	25/92 = 27	23/65 = 35	357	110	30.8
111-130	23/57 = 40	11/49 = 22	10/52 = 19	18/59 = 31	217	62	28.6
131-150	15/41 = 37	6/38 = 16	11/42 = 26	13/41 = 32	162	45	27.8
151-170	5/15 = 33	7/13 = 54	1/9 = 11	3/11 = 27	48	16	3 3·3
171—210	2/4 = 50	0/4=0	0/4 = 0	2/4 = 50	16	4	25.0
Totals	$169/464 = 36^{0}/_{0}$	$133/482 = 28^{0}/_{0}$	$155/485 = 32^{0}/_{0}$	$181/492 = 37^{0}/_{0}$	1923	638	33·2º/0

TABLE VI.

It appears from this that young rats are definitely more susceptible than older individuals¹, the dose being the same for all weights. The difference is however in no way proportional to the weight and is small relatively to the differences dealt with above in rats from different

	Males			Females					
Weight grammes	Inoculated	Died = Pe		er cent.	Inoculated	Died = Pe		er cent.	
71— 90	109	38		35	146	48		33	
91	141	50		35	216	6 0		28	
111—130	89	29		32	128	33		26	
131-150	88	28		32	74	17		23	
151-170	30	12		40	18	4		22	
171210	13	3		23	3	1		33	
Totals	470	160	=	34.0%	585	163	=	27·9°/0	

TABLE VII.

places. Among grown-up rats there is no definite relation between weight and percentage mortality. As regards sex, table VII shows that females are apparently somewhat less resistant than males, but the difference is not sufficient to enable one to definitely exclude the errors of chance selection.

¹ At the time these experiments were made, some of the older animals had probably had experience of a plague epidemic.